Winter habitat and distribution of Arctic grayling in Upper Red Rock Lake, Red Rock Lakes National Wildlife Refuge, Montana

by Michael Matthew Gangloff

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in Biological Sciences

Montana State University

Abstract:
Observations on Upper Red Rock Lake during periods of ice cover in the winters of 1994-1995 and 1995-1996 indicate that the lake became severely deficient in dissolved oxygen during the first winter but not the second, and that the distributional behavior of Arctic grayling, Thymallus arcticus. differed markedly between the two winters. During the first winter, dissolved oxygen declined to very low concentrations, generally about 0.5 to 0.15 ppm, in midlake and other sampling locations by mid to late January. Dead invertebrates and fish (suckers, Catostomus sp.) were seen at two locations where holes were drilled through the ice for habitat measurements. Two radio-tagged Arctic grayling remained in two small areas with higher oxygen concentrations of about 2.6 to 10 ppm throughout the period of ice cover. These apparent oxygen refugia were located off the mouths of two major tributary inlets, Red Rock Creek and Grayling Creek. In contrast, oxygen concentrations remained relatively high, generally above 5 ppm, beneath ice cover through the winter of 1995-1996. Radio-tagged fish located by telemetry during this second winter—four Arctic grayling, seven cutthroat trout, and two burbot—remained widely distributed through the lake. Differences in oxygen concentrations beneath ice cover appeared related to conditions which favored greater growth of macrophyte vegetation during the preceding summer and fall, and effects of snow and ice cover on light penetration during winter. Results indicate that a combination of eutrophication, water depth, and snow cover over ice, can produce lethally low levels of dissolved oxygen during some winters, and that Arctic grayling then occupy small oxygen refugia near the mouths of inlet streams. The observations also suggest that any natural or anthropogenic factors that would increase plant production in the lake, contribute to further reduction in lake depths, or reduce flow or oxygen content of inlet streams, could have serious adverse effects on the unique Arctic grayling population of Upper Red Rock Lake.

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APPROVAL

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Michael Matthew Gangloff

This thesis has been read by each member of the thesis committee and has been found to be satisfactory regarding content, English usage, format, citations, bibliographic style, and consistency, and is ready for submission to the College of Graduate Studies.

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ABSTRACT

Observations on Upper Red Rock Lake during periods of ice cover in the winters of 1994-1995 and 1995-1996 indicate that the lake became severely deficient in dissolved oxygen during the first winter but not the second, and that the distributional behavior of Arctic grayling, Thymallus arcticus, differed markedly between the two winters. During the first winter, dissolved oxygen declined to very low concentrations, generally about 0.5 to 0.15 ppm, in midlake and other sampling locations by mid to late January. Dead invertebrates and fish (suckers, Catostomus sp.) were seen at two locations where holes were drilled through the ice for habitat measurements. Two radio-tagged Arctic grayling remained in two small areas with higher oxygen concentrations of about 2.6 to 10 ppm throughout the period of ice cover. These apparent oxygen refugia were located off the mouths of two major tributary inlets, Red Rock Creek and Grayling Creek. In contrast, oxygen concentrations remained relatively high, generally above 5 ppm, beneath ice cover through the winter of 1995-1996. Radio-tagged fish located by telemetry during this second winter--four Arctic grayling, seven cutthroat trout, and two burbot--remained widely distributed through the lake. Differences in oxygen concentrations beneath ice cover appeared related to conditions which favored greater growth of macrophyte vegetation during the preceding summer and fall, and effects of snow and ice cover on light penetration during winter. Results indicate that a combination of eutrophication, water depth, and snow cover over ice, can produce lethally low levels of dissolved oxygen during some winters, and that Arctic grayling then occupy small oxygen refugia near the mouths of inlet streams. The observations also suggest that any natural or anthropogenic factors that would increase plant production in the lake, contribute to further reduction in lake depths, or reduce flow or oxygen content of inlet streams, could have serious adverse effects on the unique Arctic grayling population of Upper Red Rock Lake.

INTRODUCTION

Arctic Grayling in Red Rock Lakes National Wildlife Refuge, Montana

Upper Red Rock Lake, located in the Red Rock Lakes National Wildlife Refuge in Montana, contains what is believed to be the only viable native lacustrine population of Arctic grayling (Thymallus arcticus) remaining in Montana and elsewhere south of Canada and Alaska (Kaya, 1992). The native range of Arctic grayling in Montana extended through the Missouri River and its tributaries upstream from the Great Falls (Kaya, 1992). Grayling in Montana were historically confined to riverine or fluvial systems, with the exception of those found within Upper and Lower Red Rock lakes and Elk Lake (near Red Rock Lakes). While Montana Arctic grayling no longer occur in most of their native fluvial range, they have been planted in numerous lakes in western states. Many naturally reproducing, lacustrine populations have become established where no Arctic grayling existed before (Kaya, 1992). In most cases, these fish were progeny of fish from the Red Rock Lake and the Ennis Reservoir-Madison River populations.

Lacustrine Arctic grayling populations in the Red Rock Lakes area have not fared as well as their transplanted progeny. The population in Elk Lake may have gone extinct earlier in the century and then re-established by stocking (Randall, 1978). The genetic relationship between Elk Lake and Red Rock lakes populations is not known. A potential historical migration corridor between the systems existed in the form of Elk Springs

Creek which once flowed from the southern tip of Elk Lake to the northeastern corner of Upper Red Rock Lake. This has since been altered so that movement of fish between the two systems is no longer possible. Lower Red Rock Lake is also thought to be currently devoid of Arctic grayling, with the exception of transient fish. Seven Arctic grayling were captured during fish trapping operations on Odell Creek, a tributary to the lower lake, during the spring of 1994 (Mogen 1996a). These may represent fish that had passed through the lower lake to spawn in Odell Creek.

Upper Red Rock Lake historically supported the most robust Arctic grayling population. Arctic grayling were observed to spawn in virtually every major tributary (Nelson, 1954). Refuge reports and "old-timer" accounts alike suggest that Arctic grayling were formerly abundant (Unthank, 1991). Unfortunately, quantifiable results concerning the size and timing of these runs are scarce. Recent observations suggest that grayling populations in Upper Red Rock Lake are declining (Unthank, 1991; Kaya, 1992; Mogen, 1996a; Mogen 1996b).

Possible Reasons for Decline

Numerous hypotheses have been proposed to explain the apparent decline in the Arctic grayling population of the Red Rock Lakes, including habitat loss or alteration, and competition or predation from other, native or introduced fishes. One of the most often cited involves increased sediment transport in Red Rock Creek as a result of upstream land use, leading to accelerated filling of the lake and subsequent habitat loss. This hypothesis is supported by an old report stating that the depth of the upper lake approached 7 m (Brower, 1897). Present maximum depth is only about 2 m. However, this hypothesis seems to have been refuted by recent paleolimnological data which suggest that sedimentation rates in Upper Red Rock Lake have not increased within the last century (Hamilton, 1996).

Another hypothesis is that dissolved oxygen (d.o.) may decline to very low concentrations in Upper Red Rock Lake during the winter months. The proliferation of aquatic macrophytes during the summer months represents biomass which eventually must decay, and the severity of local winters produces thick ice cover, often with substantial accumulations of overlying snow. This combination could produce serious oxygen depletions beneath winter ice cover in Upper Red Rock Lake. A shallow lake, by virtue of its limited volume, has relatively little capacity to accommodate high winter respiration. The phenomenon of winterkill is common in lakes of similar morphology and trophic status throughout the north temperate latitudes (Greenbank, 1945; Moorman, 1956; Barica and Mathias, 1979; Babin and Prepas, 1985; Magnuson et al., 1985).

The development of hypoxic conditions beneath winter ice cover is not a simple process. Many variables contribute to the extent and severity of oxygen depletion beneath ice cover. The amount of respirable material (usually in the form of decaying macrophytes or highly organic sediments), lake morphometry, lake water volume and oxygen content when it first freezes over, and the duration of ice cover are major contributing factors. Also important are ice thickness, ice transparency, snow cover (these three directly influence light transmission and subsequent photosynthetic activity), biological productivity, and water replacement rate (Greenbank, 1945; Casselman and Harvey, 1975; Welch, 1976; Barcia and Mathias, 1979; Stewart and Brockett, 1984; Babin and Prepas, 1985).

The most likely mechanism by which low dissolved oxygen affects aquatic organisms is asphyxiation from low oxygen pressures (Greenbank 1945; Petrosky and Magnuson,1973;.Davis, 1975; Dunn and Hochachka, 1986; Schurmann et al., 1991). However, other associated gasses may be involved. The formation of hydrogen sulfide and carbon dioxide is often associated with the decomposition of organic matter (Davis, 1975), and can accumulate to concentrations toxic to aquatic organisms. Early investigators of winterkills often speculated that such gases could be the primary cause of mortality (Greenbank, 1945; Cooper and Washburn, 1949; Sheppard, 1955; Moorman, 1956; Casselman and Harvey, 1975). However, subsequent studies have shown that, in general, oxygen declines are likely to become lethal long before toxic concentrations of these gases can accumulate (Magnuson and Karlen, 1970; Dunn and Hochachka, 1986; Shurmann et al., 1991; Nurnberg, 1995). Various authors have speculated on the extent to which winterkill events may limit fish numbers. Greenbank (1945) stated that only under the most unusual of circumstances will winterkills result in the complete extirpation of a population. He stated as evidence the observation that most populations seem eventually to recover without artificial augmentation. However, no quantitative evidence was offered. Later studies have supported this claim. Moorman (1956) observed that partial kills seem to be more widespread than total kills. Casselman and Harvey (1975) reported that despite frequent winterkill events, northern pike (Esox lucius) were able to persist at their study site.

A variety of behavioral mechanisms have been reported for fishes in winterkill lakes in Wisconsin. Magnuson et al. (1985) observed different responses including aggregation at tributary inlets, emigration from the lake, and aggregation at the ice-water interface by species of Cyprinidae, Gasterosteidae, and Percidae. Magnuson and Karlen (1970) reported that northern pike oriented themselves at the water-ice interface to better utilize the shallowest, more oxygen-rich water. Magnuson and Karlen (1970) also reported that concave domes were formed at the bottom of the ice surface by the ventilatory flow of water created by individual northern pike, and that the fish held positions in these domes. The domes were thought to concentrate water containing more oxygen.

Other investigations of behavioral responses of fishes to low d.o. have concluded that as d.o. progressively declines to very low concentrations, fish engage in increased, apparently random, movements to different parts of a lake (Sheppard, 1955; Magnuson and Karlen, 1970; Magnuson et al., 1985; Kramer, 1987). It has been proposed that an increase in random movements is a mechanism by which fish can locate areas with higher oxygen (Magnuson and Karlen, 1970; Magnuson et al., 1985; Kramer, 1987). It has also been reported that fish then conserve movements when they encounter an area with higher dissolved oxygen (Magnuson and Karlen, 1970).

Although the preceding observations suggest that fish find areas with higher oxygen largely by trial and error, there are other possible mechanisms for movement to such areas. Spoor (1989) reported that brook trout (Salvelinus fontinalis) in an experimental channel were able to detect and respond to oxygen gradients. However, other studies have reported fish to be unable to sense oxygen gradients (Javaid, 1967; Petrosky, 1973; Schurmann et al., 1991). The steep gradient in small experimental tanks, as well as the fact that d.o. gradients in lakes have more than one dimension, may account for this discrepancy. Additionally, different species have been reported to be able to sense temperature gradients (Javaid and Anderson, 1967; Bryan et al., 1984; Cech et al., 1990; Schurmann et al., 1991; Smale and Rabeni, 1995). It is possible that thermal orientation would enable a fish to find the mouth of an inlet stream and thereby place itself in area with oxygenated water.

Movements by fishes into wintering habitat have been reported for Arctic grayling and other species. Studies in Alaska and Montana have described movements into wintering habitat. Craig and Poulin (1975) reported that Arctic grayling move into refugia associated with spring seeps in Alaskan rivers. West et al. (1992) tracked radio-tagged Arctic grayling in Alaskan rivers and found that they undergo extensive (> 100 km) migrations in search of suitable winter habitat. Principal wintering areas identified included spring-fed regions of open water, deep pools, and lakes (West et al., 1992).

Similarly, Shepard and Oswald (1989) concluded, from recaptures of tagged fish, that Arctic grayling in the Big Hole River, Montana, spawn and may spend part of summer in upstream reaches but move downstream to winter in deeper pools and areas of groundwater recharge. Fish were observed to move as much as 80 km between areas. Wick and Hawkins (1989) found that squawfish (Ptychocheilus lucius), while maintaining a high degree of fidelity to particular river regions, made seasonal movements into wintering habitat. These movements were observed to be into very specific localities. It is possible that Arctic grayling in Upper Red Rock Lake may also undergo movements to wintering areas if habitat becomes unsuitable in large areas of the lake. Numerous tributary streams flow into the lake and refuge staff indicate that spring seeps are abundant.

The very few measurements taken thus far of dissolved oxygen concentrations beneath winter ice cover in Upper Red Rock Lake (summarized by Randall, 1978) suggest that hypoxic conditions do occur, at least during some years. Measurements at five sites in 1974 yielded relatively high d.o. of 7 to 13 ppm from top to bottom of the water column. However, measurements at seven sites in 1976 yielded d.o. of 1 to 2 ppm at two of the sites. The latter are lower than or similar to critical oxygen minima of about 1.3 to 1.7 ppm for Arctic grayling acclimated to about 6 to 8 C (Feldmeth and Eriksen, 1978).

Study Site

Upper and Lower Red Rock lakes occupy shallow depressions in the floodplain of the Upper Red Rock River (called Red Rock Creek upstream of Lima Reservoir) of the Upper Missouri River drainage. The lakes are located in Montana's Centennial Valley near the headwaters of Red Rock Creek, and probably represent remnants of a much larger postglacial lake that once covered much of the present valley floor (Brower, 1897).

The Centennial Valley has an approximately east-west orientation in the southeastern corner of Beaverhead County, between Red Rock Pass (elevation 2170 m) to the east and the vicinity of Interstate Highway 15 and the town of Lima (elevation 1965 m) to the west. The valley is bordered by the Snowcrest and Gravelly Mountain Ranges to the North, the Centennial Mountains, Idaho Border and Continental Divide to the East and South, and the Beaverhead River Valley to the West. The valley is approximately 70 km in length east to west, and averages a north-south distance of approximately 30 km.

Upper Red Rock Lake has a surface area of approximately 890 hectares and a maximum depth of 2 m (Unthank, 1991; Neithammer, 1992, unpublished data). It is approximately 6 km long (from the mouth of Tom Creek to the Lake Outlet) and 3.5 km across at its widest (north-south) point at the boat/access site at the campground. The lake typically freezes over in November and remains ice-covered until early May (Sue Linneman, Assistant Refuge Manager, pers. comm.). Lower Red Rock Lake, located downstream (west) from the upper lake, is very shallow with a maximum depth of 1 m, and is not known to be permanently inhabited by Arctic grayling.

The upper lake has five principle tributary streams. Red Rock Creek drains the eastern portion of the Centennial Valley (Alaska Basin) and enters the lake at its northeast corner. Red Rock Creek is the system's single largest source of surface water (Gangloff and Linneman, 1995, unpublished data). Red Rock Creek is also the principal stream used by Arctic grayling for reproduction (Mogen, 1996a). Tom Creek enters the upper lake slightly to the south of Red Rock Creek. Tom Creek drains the south face of Taylor Mountain and runs mostly through private land (Unthank, 1991). Elk Spring Creek contributes spring flow from three Refuge ponds (Culver, Widgeon, and MacDonald ponds) and Elk Lake into the north-central region of the Upper Lake. Grayling Creek and East Shambow Creek are spring-fed systems which enter the lake in its southwest corner. These three spring creeks display little variation in annual flow (Gangloff and Linneman, 1995, unpublished data) and remain ice-free for much of the winter. Additionally, numerous small creeks and groundwater seeps emerge directly within Upper Red Rock Lake and their contributions to the hydrologic regime of the system are unknown.

Upper Red Rock Lake appears to be a highly eutrophic system. Large rooted macrophyte species of the genus _Potamogeton_ dominate the aquatic flora of the system, and also present in lesser numbers are species of _Philotria_ and _Myriophyllum_ (Paullin, 1973). Because of the shallowness and productivity of the lake, macrophytes are extensively distributed throughout the lake basin (Paullin, 1973). This extensive distribution and luxuriant growth of macrophytes continues to be readily apparent at present (personal observations).

The aquatic invertebrate fauna of this system is quite interesting in that it represents a convergence zone between the ranges of prairie species, glacial relicts and a more cosmopolitan montane fauna (D.L. Gustafson, Montana State University, pers. comm.). Upper Red Rock Lake hosts an abundance of pelagic crustacea, dominated by Cladocera, Copepoda, and Amphipoda. Snails of the genera *Physella*, *Stagnicola*, *Lymnea*, and *Valvata* have been collected here. Several unusual aquatic insects have also been collected at this locality, the most notable of these being a species of Corixidae, *Dasycorixa johanseni*, of which the only other known occurrence on this continent comes from the western shore of Hudson Bay (D.L. Gustafson, pers. comm.). Oligochaete worms appear to comprise a large proportion of the benthic invertebrate biomass in the sediments.

The fish fauna of Upper Red Rock Lake includes the native mountain whitefish (*Prosopium williamsoni*), longnose sucker (*Catostomus catostomus*), mountain sucker (*Catostomus platyrhynchus*), white sucker (*Catostomus commersoni*), longnose dace (*Rhinichthys cataractae*), mottled sculpin (*Cottus bairdi*), and burbot (*Lota lota*). Introduced species include the Yellowstone cutthroat trout (*Onchorynchus clarki bouvieri*), rainbow trout (*Onchorynchus mykiss*) and the brook trout (*Salvelinus fontinalis*). Most of the Yellowstone cutthroat trout in the Red Rock system show evidence of intergression with rainbow trout (Pat Dwyer, U.S. Fish and Wildlife Service, pers. comm.). Westslope cutthroat trout (*O. clarki lewisi*) were native to Upper Red Rock Lake, but are presently only found in headwater streams in the Centennial Valley (T. Tiplady, U.S. Fish and Fish and Wildlife Service, pers. comm.).

Objectives

Because of concerns about the potential for development of hypoxic, winterkill conditions in Upper Red Rock Lake, and the decline of its unique, native lacustine population of Arctic grayling, the present study was proposed as an investigation of winter habitat and behavior of Arctic grayling beneath the ice cover of the lake. The purpose of the study was to test the following hypotheses.

1. During the period of seasonal ice cover, dissolved oxygen declines to levels lethal to Arctic grayling through most of Upper Red Rock Lake

2. Arctic grayling in Upper Red Rock Lake have behavioral responses or physiological adaptations to low dissolved oxygen that enable them to survive otherwise lethal conditions.

Behavioral responses to low dissolved oxygen could include moving out of the lake into inlet streams, particularly Red Rock Creek, or moving to areas where oxygen levels are maintained at higher levels through the influence of inlet streams or springs. Physiological adaptation could include the ability to acclimate to very low dissolved oxygen , particularly at near-freezing temperatures . Alternatively (null hypothesis), the fish may not have behavioral responses or physiological adaptations, and may die when lake conditions become intolerable. Survivors may represent fish that happened to be in areas kept adequately oxygenated through the period of ice cover.

A corollary to hypothesis #2 would be that Arctic grayling may be indirectly harmed by low dissolved oxygen if they are forced into stressful or unsuitable habitats. For example, movement into inlet streams could subject them to greater stresses during winter. Or, aggregations in oxygen refugia may include other species, for example the cutthroat trout and burbot in the lake, and may subject Arctic grayling to increased interspecific or intraspecific competition, agonistic interactions, or predation.

To test these hypotheses, the specific objectives of this study were: (1) to determine the extent to which oxygen levels decline in Upper Red Rock Lake during winter ice cover; (2) to determine the acute tolerance of Arctic grayling to low dissolved oxygen levels; and (3) to monitor the movements of Arctic grayling in the lake during the winter months to determine their response to changing environmental conditions.

METHODS

1994-1995

Radio Telemetry

During the fall of 1994, we attempted to capture 10 to 12 Arctic grayling for telemetry studies through the use of gill nets and hoop nets. Six "experimental" gill nets, each 38 m in length and with (stretched) mesh sizes ranging from 40 mm to 100 mm, were set end to end, forming a long line, before dark on the evenings of 22, 23, and 24 September. The nets were constantly monitored so that any fish captured could be released with minimum harm. The first night's netting took place north of the campground on Upper Red Rock Lake, in the region of the lake indicated by Neithammer (1993) as having the greatest depth (Appendix A, Figure 1). This location yielded no Arctic grayling. On the following evenings, the line of gill nets was placed near the mouth of Red Rock Creek, extending outward from near the shoreline. Four large Arctic grayling were captured during the second night's efforts, one of which died in the net, and none the third night. In addition, approximately fifty large (>500 mm) cutthroat trout were captured in the nets during these two nights. All gill net sets yielded many burbot and white suckers.

On 13 October, six hoop nets were set in the upper lake. Two 1.2 m diameter hoop nets with 15.2 m leads were set near the mouth of Grayling Creek and four 0.9 m diameter hoop nets with 15.2 m leads were set end-to-end off the mouth of Red Rock Creek. The nets were left overnight and retrieved the following morning. No Arctic grayling were captured during this attempt. Several large cutthroat trout and many very large (>600 mm) burbot were captured (Appendix B, Table 1). A second intended gill netting on 27 October had to be abandoned because ice formed over the lake the previous night.

Advanced Telemetry Systems (ATS; Isanti, Minnesota) radio transmitters with external antennas were surgically implanted into the three large Arctic grayling captured alive during the night of 23 September (Table 1). The transmitters had an expected duration of six months, weighed 8-9 g, and had frequencies of 49.817 to 49.867 MHz. The implanted fish weighed 450 g or greater, and thus the transmitter was less than 2 % percent of the fish's body weight (Winter, 1983). Fish were anesthetized prior to surgery using a solution of Tricaine Methanesulfonate (MS-222). Incisions were made laterally in the body wall and were sutured with 2-0 Vicryl material with an FS-1 needle. Fish were then allowed to recover until full activity was regained before being released.

Radio-tagged fish were located using an ATS receiver with a "null type" antenna. Attempts to locate tagged fish were made on 14 October, 27 October, 2 December, 16 January, 27 January, 9 February, 25 February, and 31 March. The attempts on 14 and 27 October were limited to specific locations because efforts were focused on capturing fish (14 October) or thin ice cover prevented travel on the lake (27 October). From 2

Table 1. Lengths, weights, and transmitter frequencies for Arctic grayling implanted with radio tags on 23 September, 1994, near the mouth of Red Rock Creek.

Length (mm)	Weight (g)	Frequency (MHz)
378	580	49.817
362	501	49.833
352	500	49.867

December through 31 March all location attempts were made from atop ice cover. This was the principal field season for attempts to locate radio-tagged fish, and its duration was the period during which the ice cover on Upper Red Rock Lake was deemed by refuge staff to be safe for vehicular and personnel traffic. Other intended attempts to locate fish during this first field season were canceled or postponed due to highly adverse weather.

When the signal from a radio-tagged fish was detected, its approximate location was determined by triangulating the signal strength using two separate receiving units. During winter ice cover, the exact location was determined by walking toward the signal source until the null point appeared directly beneath the antenna. The latitude/longitude coordinates were recorded with a portable global positioning satellite (GPS) receiver (Eagle Accunav Sport Unit).

Habitat Monitoring

Water depth, d.o., water temperature, and ice thickness were measured at the location of radio-tagged fish. A hole was drilled in the ice (if present) and the total water depth was measured, with a circular metal plate suspended on a marked line, as the distance from the top of the water column or ice cover to the bottom of the lake. Thickness of the ice cover was similarly measured, and the water depth beneath the ice was determined by subtraction. Temperature and d.o. were measured using a YSI Model 57 electronic oxygen meter. D.O. measurements were also taken on 27 January with a Hach Portable Water Quality Test Kit. Water samples were taken from various locations around the lake with a Kemmerer bottle and d.o. estimated by titration (Winkler procedure) to compare with the electronic measurements (Koenings et al., 1987). Linear regression was used to compare d.o. measured through titration and with the meter.

Several stations were monitored on a regular basis in an effort to standardize our observations. One of these was the lake outlet, where the outflowing water could provide an index to the average conditions present in the upper lake. In addition, we monitored the conditions near the mouth of Red Rock Creek, the major source of water for Upper Red Rock Lake, and at the mouth of Grayling Creek, a spring-fed tributary. Midlake sites were sampled as time and weather conditions permitted.

Habitat parameters measured during 1994-1995 were analyzed with a Studentized Neuman-Keuls Multiple Comparison Test and the microcomputer program SAS. Comparisons were made between mean d.o., temperature, water depth beneath ice cover, and ice thickness at the locations of each radio-tagged Arctic grayling, midlake, and lake outlet sites. Comparisons were made for the time period of 16 January through 25 February. Differences were considered significant when $P < 0.05$.

1995-1996

Radio Telemetry

In order to alleviate the problems associated with capture efficiency experienced during the fall of 1994, we obtained a portion of our grayling earlier in the year, as they descended Red Rock Creek in the spring and early summer of 1995. A fish trap maintained on the creek upstream from the Elk Lake Road crossing (Mogen, 1996a), about 6 stream km from the lake, provided Arctic grayling and cutthroat trout. To provide long tag life that would extend through the following winter, we acquired 9-month (250-day) duration tags from Advanced Telemetry Systems. These tags were heavier (10-11 g) than the 6-month tags used during the previous winter. The increased weight of these tags necessitated that we capture fish of at least 550 g in order to be within 2 % of subject bodyweight (Winter, 1983). Data from the 1994 fish trapping in Red Rock Creek (Mogen, 1996a) indicated that Arctic grayling of this size class should be readily available from the trap at this time of year. It was decided to also radio-tag cutthroat trout and burbot for the second field season. Additional funding became available to purchase more radio tags. It was hoped that these tags would allow concurrent observations of distributional behavior of these species.

Implantation procedures were identical to those employed during 1994. Fish were removed from the downstream trap, anesthetized with MS-222 and implanted with radio transmitters. Fish were allowed to recover in a netted holding pen. When the fish regained equilibrium, they were released downstream from the weir.

Six Arctic grayling and four cutthroat trout captured at the weir were implanted with radio tags during the spring and summer of 1995 (Table 2). Four cutthroat trout were tagged on 24 May and the fifth on 23 June. Cutthroat trout ranged from 650 g to 870 g. Three Arctic grayling were tagged on 1 June, two others on 23 June and a sixth on 6 July. A seventh Arctic grayling was captured by electrofishing in Red Rock Creek on 1 September. Arctic grayling ranged from 500 g to 650 g in weight and 369 mm to 425 mm in length. Fish sizes and radio-tagging data are presented in Table 2.

The remainder of the 9-month tags (n = 15) were intended for implantation into fish captured directly within Upper Red Rock Lake. Most were captured in hoop nets set by Laura Katzman, starting in early June (Katzman, 1995, unpublished progress report). All fish captured were transported in holding pens to the work station at the mouth of Red Rock Creek, where they were anesthetized and implanted with radio tags. Fish were allowed to recover in a large holding pen. Recovery time ranged from 0.5 to several

Table 2. Lengths, weights, transmitter frequencies, and symbol for figures (18-28) of fish implanted with radio tags in 1995.

Date	Species	Length (mm)	Weight (g)	Frequency (MHz)	Figure Symbol
24 May	O. clarkii	432	700	49.312	
24 May	O. clarkii	415	650	49.030	
24 May	O. clarkii	410	670	49.272	
1 June	T. arcticus	425	650	49.072	
1 June	T. arcticus	402	555	49.521	
1 June	T. arcticus	391	535	49.110	
22 June	T. arcticus	369	535	49.172	
23 June	T. arcticus	384	553	49.210	
23 June	O. clarkii			49.010	
6 July	T. arcticus	374	500	49.192	
19 July	O. clarkii	495	1494	49.292	
9 August	O. clarkii	405	734	49.491	
9 August	L. lota	560	1418	49.413	
1 September	T. arcticus	366	590	49.251	
21 September	T. arcticus	341	851	49.091	
21 September	O. clarkii	446	1333	49.430	
22 September	L. lota	665	3799	49.470	

Table 2-Continued

Date	Species	Length (mm)	Weight (g)	Frequency (MHz)	Figure Symbol
22 September	L. lota	690	2863	49.332	
29 September	L. lota	553	1333	49.510	
29 September	L. lota	683	2240	49.350	
29 September	L. lota	683	2466	49.370	
12 October	S. fontinalis	369	765	49.773	
20 October	O. clarkii	496	> 1000	49.803	
20 October	O. clarkii	499	> 1000	49.452	
21 October	T. arcticus	424	770	49.232	
21 October	T. arcticus	361	490	49.893	
21 October	T. arcticus	371	510	49.757	
21 October	T. arcticus	372	475	49.787	

hours and varied considerably within and between species. Once fish regained equilibrium and appeared to be well recovered, they were released into the lake at the mouth of Red Rock Creek.

Four cutthroat trout were captured in hoop nets set in the lake, on 19 July (Katzman), 9 August (Gangloff), and 20 October (Katzman, two fish), and another was captured by angling in the lower end of Red Rock Creek, approximately 1.6 km upstream from Upper Red Rock Lake. The ten cutthroat trout implanted during the summer and fall 1995 operations (five from the weir, four from the lake, and one from the lower creek near the lake) ranged from 449 mm to 499 mm in length and from 650 g to 1495 g in weight. Four 9-month radio tags and one 6-month radio tag were implanted into cutthroat trout.

Six burbot were captured by hoop net and implanted with radio tags, on 9 August (Gangloff), 22 September (Gangloff and Barndt, two fish), and 29 September (Gangloff and Barndt, three fish). Burbot ranged from 553 mm to 690 mm in length and from 1332 g to 3799 g in weight (Table 2). Burbot all received 9-month tags.

One large brook trout (765 g, 369 mm) was captured by electrofishing near the mouth of East Shambow Creek in Upper Red Rock Lake on 12 October. The fish was implanted with a 6-month radio tag.

Four Arctic grayling were captured in the lake or the lower portion of Red Rock Creek and implanted with radio tags. A single Arctic grayling (weight 840 g, length 341 mm) was captured by angling in the lower portion of Red Rock Creek on 21 September and implanted with a 9-month radio tag. Four were captured in hoop nets set on 21 October by Laura Katzman. Three of these fish came from nets set off the mouth of Grayling Creek in the southwest corner of Upper Red Rock Lake and a fourth from a hoop net set off the mouth of Red Rock Creek. Fish were transported from the capture sites to the campground boat launch and surgically implanted later that evening. These fish ranged in weight from 475 g to 770 g and from 361 mm to 424 mm in length (Table 2). Three fish received 6-month duration radio tags and the fourth fish received a nine-month tag. Fish were released at the boat launch. Locations where Arctic grayling, cutthroat trout, and burbot were implanted with radio tags and released during 1995, dates of implantation, and the transmitter frequencies of each fish, are summarized in Figure 1.

Observations during the second year included determining locations of radio-tagged fish during summer and early fall. By knowing where fish were located during the preceding ice-free period, we could better determine how they responded to conditions associated with the onset and duration of ice cover.

Telemetry from a boat or canoe on the lake was conducted on the following dates: 14 July, 16 July, 18 July, 19 July, 4 August, 14 August, 15 August, 16 September, 17 September, 28 September, 19 October, and 20 October. Generally, searches were conducted at an automated scanning rate of four seconds per radio-tag frequency as the canoe was paddled across the lake. Red Rock Creek was surveyed on two occasions during the summer to determine whether fish tagged at the weir remained in the stream. Radio tags located during summer were generally noted with an approximate location and corresponding GPS coordinates. We attempted, where possible, to attain several corresponding locations and directional bearings. On the open water of the lake, it was not possible to follow signals directly to their source.

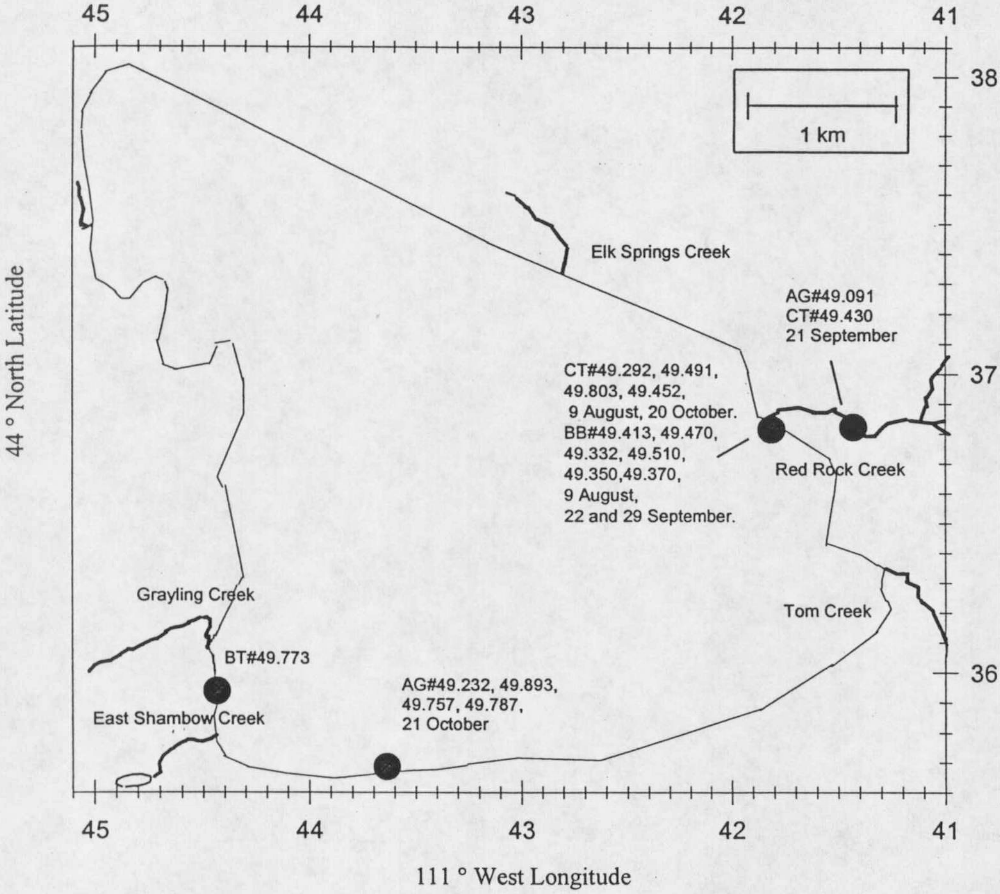

Figure 1. Locations and dates of radio implantation and release of Arctic grayling (AG), cutthroat trout (CT), burbot (BB) and brook trout (BT) in Upper Red Rock Lake in 1995, and radio frequencies of each fish. In addition, six Arctic grayling (frequencies 49.072, 49.251, 49.110, 49.172, 49.210, and 49.192) and four cutthroat trout (49.312, 49.030, 49.272, 49.010) were radio-implanted and released at the weir, located in Red Rock Creek about 6 stream km from the lake.

In the spring of 1995, refuge staff attempted to locate radio-tagged fish during two aircraft flights. Flights covered the Centennial Valley from the headwaters of Red Rock Creek downstream to Lima Reservoir, and included a pass up the Elk Lake Valley to Hidden Lake and a pass up Odell Creek to its headwaters. These flight paths took the aircraft over and beyond both upper and lower Red Rock lakes, and their major tributaries.

Formation of a thin layer of ice on Upper Red Rock Lake on 28 October ended boat-based field operations and initiated telemetry from shore and later, on the ice surface. Telemetry was attempted on the following dates in 1995-1996: 28 October, 30 November, 14 December, 9 January, 10 January, 16 January, 23 January, 6 February, 21 February, 22 February, and 19 March. Radio telemetry was conducted at each of the habitat sampling stations established for the 1995-1996 winter field season (Figure 2). Additionally, we attempted to coordinate search efforts in the following manner; starting from a point in the southwest corner of Upper Red Rock Lake (usually about 300 m east of the inlet of East Shambow Creek (Figure 2), and using landforms as a reference, we proceeded northward, pausing every 300 m to scan through the range of frequencies on the receiver unit. Upon reaching the opposite shoreline, we traveled perpendicular to our original course for a distance of approximately 300 m and began to track a course which was roughly parallel to our initial path. This process was repeated until the entire lake had been covered.

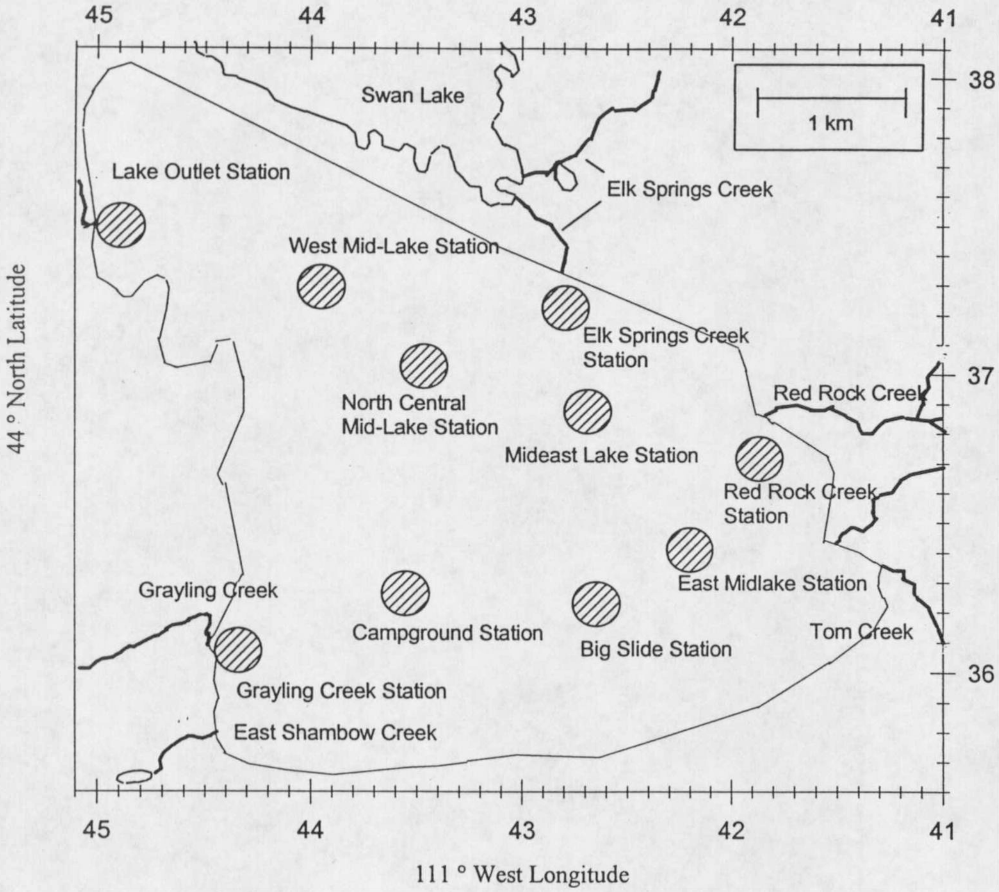

Figure 2. Habitat monitoring stations during winter of 1995-1996,
Upper Red Rock Lake.

For each relocation we attempted to get both a GPS location and a bearing on the tag signal at two or more locations. Because weather and time constraints occasionally limited our abilities to get valid GPS data, some approximations of fish locations are reported. Telemetry from shore and on the ice lasted until 19 March, 1996, when ice conditions were deemed unsafe to support travel. A subsequent visit to the lake on 2 April revealed rapidly melting lake ice.

We attempted to estimate the approximate distance over which radio transmitters in Upper Red Rock Lake could be detected through ice cover, and also the margin of error involved in determining specific transmitter locations. On 24 January we lowered a radio transmitter to the bottom of Upper Red Rock Lake in approximately 2.0 meters of water. Distance over which the signal could be heard was estimated by walking away from the location until the signal could not be detected by the receiver. The margin of error involved in identifying the specific location of the transmitter was estimated by approaching the transmitter site from different directions while simulating radio-tracking of the signal to its source.

Habitat Monitoring

Winter habitat monitoring for the 1995-1996 field season differed from that conducted the previous year in that fixed habitat observation sites were established. Habitat measurements were not taken at specific fish locations because, unlike during the previous winter of 1994-1995, radio-tagged fish were widely distributed over the lake.

We monitored a total of ten sites (Figure 2). Each site was marked by a 1.0 m fiberglass stake which was anchored into a hole chiseled into the ice. Three sites were associated with the inlets of larger tributaries. We hypothesized that these were most likely to contribute oxygenated water to the lake during the winter. Stations were located near the mouths of Grayling (GRC) and Elk Spring Creeks (ESC), both of which are spring-fed and remained open for much of the winter, and at the mouth of Red Rock Creek (RRC).

Six sites were distributed through the middle areas of the lake. These sites were established in a pattern which provided a broad profile of midlake conditions. The sites were assigned the following names, in a clockwise pattern from the lake outlet (Figure 2): west midlake (WML), north midlake (NML), mideast lake (MEL), east midlake (EML), big slide (BSS), and campground (CGS). Each of these sites was monitored every two weeks except for station BSS which was not monitored after 20 February because its marker melted through the ice during a thawing event.

The tenth site was located adjacent to the lake outlet (OUT). We had hoped to be able to monitor conditions at this location to determine whether the outflow would represent average d.o. concentrations in the lake. However, this site remained ice-free for the duration of the field season and the water was exposed to aeration from the atmosphere. On several occasions we measured habitat parameters adjacent to the outlet, but it should be noted that due to the presence of open water nearby, these values do not approximate the averages for the lake.

At each site, at approximately two week intervals, a hole was drilled in the ice and the following parameters measured: water depth, ice thickness, dissolved oxygen (at top and bottom of the water column if over one meter deep), and water temperature (also at top and bottom of water column). In addition, GPS coordinates were read at each location in order to approximate the variability involved with the use of the portable receiver. Oxygen probe readings were validated and calibrated by extracting water samples at these sites with a Kemmerer bottle on several occasions (Appendix B, Figure 2), and measuring d.o. with the standard Winkler procedure (Koenings et al., 1987). Samples were fixed in the field and transported back to the refuge headquarters where final titrations were performed.

For 1995-1996, habitat parameters were analyzed using SigmaPlot for Windows, an interpolative graphics package (Jandel Scientific, 1995). Data were plotted as z-coordinates in an x-y-z grid with x and y-coordinates corresponding to the latitude and longitude of Upper Red Rock Lake. The program was then used to construct the theoretical contour lines represented in figures 8 - 10 and 13 - 15. It should be emphasized that the generation of such figures was accomplished using a limited number (10-15) of data points. As such, the figures do not provide a rigorous topographical model of the contours of Upper Red Rock Lake, rather they are meant to provide an approximation of the existing conditions beneath the ice cover.

Habitat parameters at sites where radio-tagged fish were located during the ice-covered period of 1995-1996 were estimated by using the measurements obtained at the habitat sampling site closest to the fish's location. At sites deeper than 1.0 m, where temperature and d.o. were measured at the top and bottom of the water column, the higher values for temperature and d.o. were used. The higher value would provide the maximum temperature and d.o. that would be potentially available to a fish in the area.

Habitat parameters measured during 1995-1996 were analyzed using the Studentized Neuman-Keuls Multiple Comparison Test and the microcomputer program SAS. Mean d.o., water temperature, water depth beneath ice cover, and ice thickness were compared for the time period extending from 10 January to 31 March. Comparisons were made between parameters measured at locations of cutthroat trout, Arctic grayling, stations associated with tributary mouths (stations GRC, RRC, and ESC), and midlake stations. Habitat parameters at fish locations were assumed to be those at the habitat monitoring station nearest the fish location. Parameters at these locations were not included in the determination of midlake and tributary habitat attributes.

T-tests were performed to compare differences in habitat parameters at locations of Arctic grayling and midlake sites between the two winters. Differences were considered significant when $P < 0.05$. T-tests were performed using QuatroPro Version 5.0 for Windows, a spreadsheet and graphics package (Borland International, 1993).

Attempt to Estimate Acute Low Oxygen Tolerance of Arctic Grayling

We attempted to estimate the acute tolerance of Arctic grayling to low d.o. at winter-like temperatures of 0 to 4 ° C with a specialized test apparatus available at the Bozeman Fish Technology Center. Several efforts were made, after fish were acclimated to 0 to 4 ° C. However, the apparatus could not maintain d.o. concentrations below 1mg/l at low temperatures of 0 to 4 ° C, and we were unable to produce valid results.

RESULTS

Radiotracking Accuracy

The accuracy with which the position of a fish could be estimated and plotted on a map was affected by both the variability of GPS readings taken with the portable receiver, and the margin of error involved in tracking the signal to its location beneath the ice. GPS readings taken on separate dates at given sampling sites produced coordinates that were generally within a radius of approximately 75 m. For example, Figure 3 illustrates the range in 17 GPS readings taken at sampling site CMP during the winter of 1995-1996. Occasional, more distant coordinates appeared related to GPS receiver malfunction from weak battery strength, and adverse weather conditions, especially very cold air temperatures.

The signal from a transmitter placed at a known location beneath the ice cover could be detected from a distance of approximately 700 m, and could be followed to within about 50 m of the source. Within a radius of about 50 m, however, it often became more difficult to precisely localize the direction of the signal source. Signal strength became sufficiently strong to make it more difficult to accurately and consistently identify the null point of signal direction. Other variables such as reflections of signals by the under surface of the ice, or movement of the fish being radio-tracked, also could have contributed toward this uncertainty when close to the transmitter.

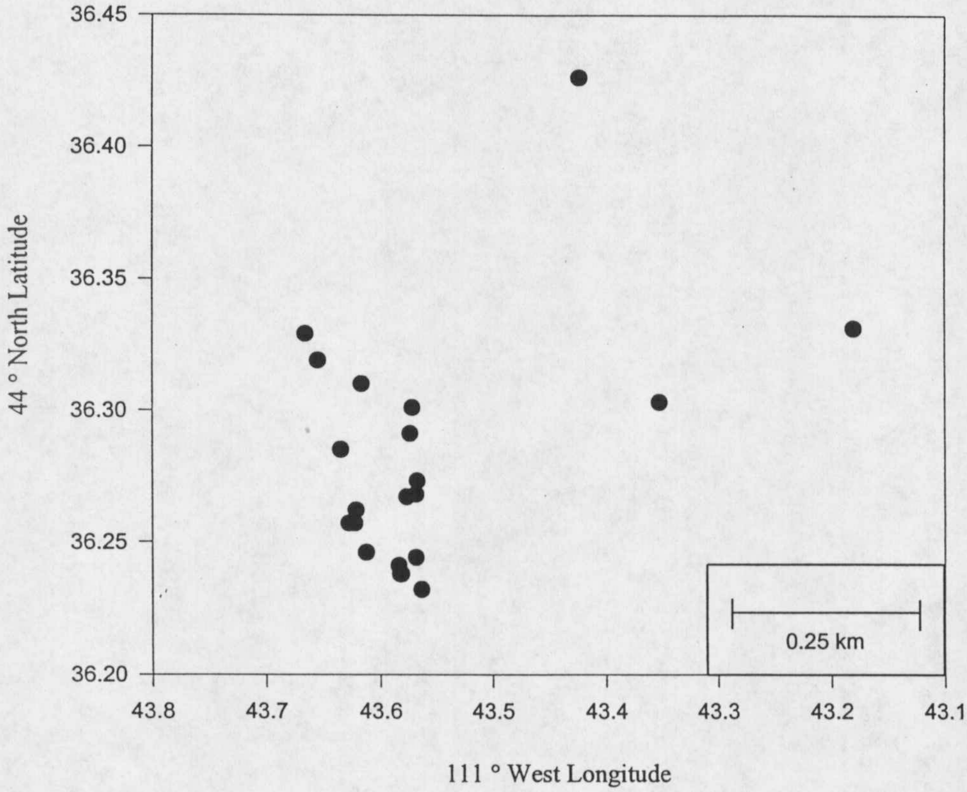

Figure 3. Variation of locations for a known, fixed site as indicated by portable GPS receiver outputs. Axis units are minutes north latitude and west longitude.

The margin of error for transmitter locations plotted on a map was estimated to be an area with a radius of about 125-150 m. This margin of error represents the combined estimated radii for variability of GPS coordinates for a fixed site (about 75 m), and for uncertainty of transmitter location within close range (about 50 m). This potential margin of error is represented by the diameters, drawn to approximate scale, of the circles used to identify locations of habitat sampling sites (Figure 2) and radio-tagged fish (Figures 4, 5, and 18-28).

Fall and Winter 1994-1995

Initial, preliminary attempts to locate the radio-tagged Arctic grayling prior to formation of ice cover were hampered by mechanical and physical problems, and yielded only approximate indications of fish presence. On 14 October, during the course of hoop netting operations, faint signals from radio-tagged fish were detected in the locality of Grayling and Red Rock Creeks. Malfunctioning of the outboard motor prevented more definite transmitter locations. On 27 October, an intended attempt to locate the radio-tagged fish was impeded by the formation of a thin ice cover over the lake the previous night. Radio tracking was attempted on foot from the southwest lake shoreline. One fish, which carried a radio tag with a frequency of 49.837 Mhz (hereafter, all radio-tagged fish will be referred to by a number corresponding to the tag's frequency, e.g., #49.837), was contacted northeast of the mouth of Grayling Creek. We were unable to get a more precise location from shore. We were unable to reach the shore near the mouth of Red Rock Creek to determine whether any radio-tagged fish were near that location. The signal from the third Arctic grayling which had been radio-tagged in September was not heard again after the date of implantation.

Telemetry of radio-tagged fish from over the ice surface and measurement of habitat parameters at sites where fish were located began on 2 December, about a month after the formation of seasonally permanent ice cover, and continued until 31 March. Arctic grayling #49.837 and #49.867 were consistently located within relatively small areas on the six telemetry dates of 2 December, 16 January, 27 January, 9 February, 25 February, and 31 March. Arctic grayling #49.837 remained in the southwest part of the lake near the mouth of Grayling Creek (Figure 4). Sites at locations of this fish had d.o. ranging from 2.7 to 8.5 mg/l; temperature of 0.1 to 3.0 °C, and water depths beneath the ice of 0.20 to 0.78 m (Table 3). Arctic grayling #49.867 remained in the eastern part of the lake near the mouth of Red Rock Creek (Figure 5). Sites at locations of this fish had d.o. ranging from 2.5 to 8.4 mg/l, temperature of 0.1 to 2.5 °C, and water depths of 0.54 to 1.69 m (Table 3).

Other midlake and lake outlet sites where holes were drilled through the ice to measure habitat parameters are indicated on Figures 6 and 7. Measurements for each site and date are presented in Appendix B, Table 2. A summary of habitat measurements for these midlake and lake outlet sites (Table 4) indicates that d.o. declined to low

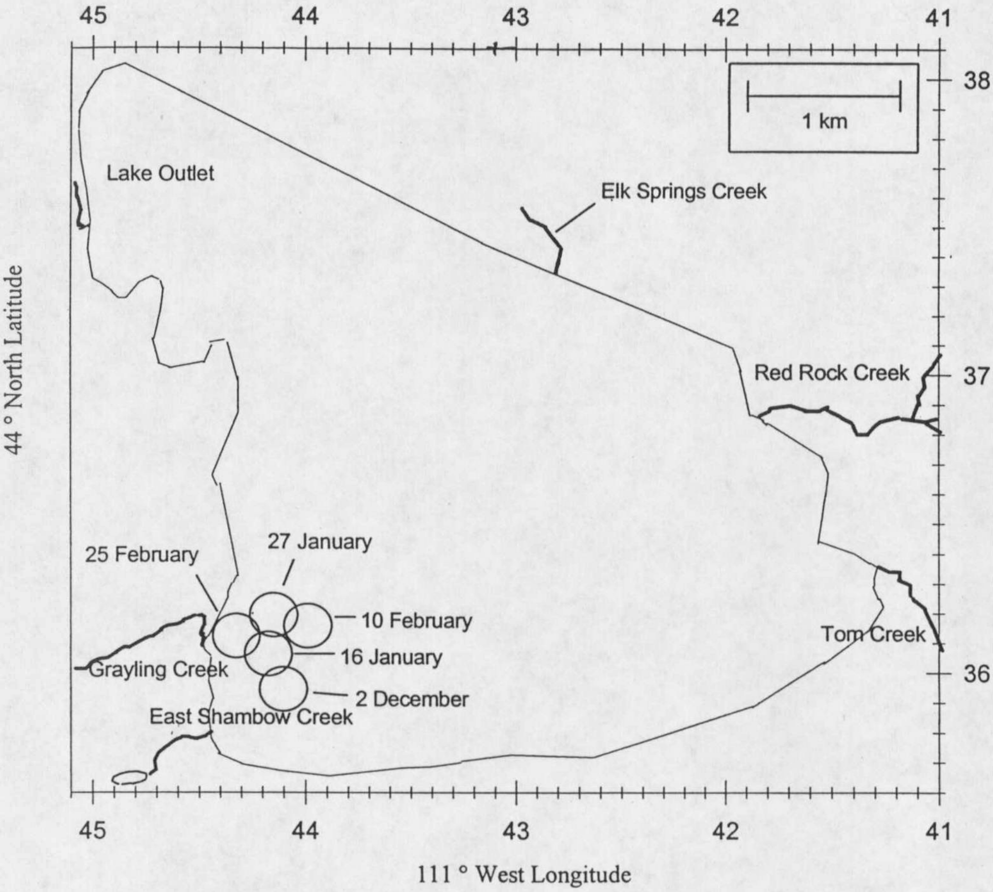

Figure 4. Locations of radio-tagged Arctic grayling #49.837 in Upper Red Rock Lake during the 1994-1995 winter field season.

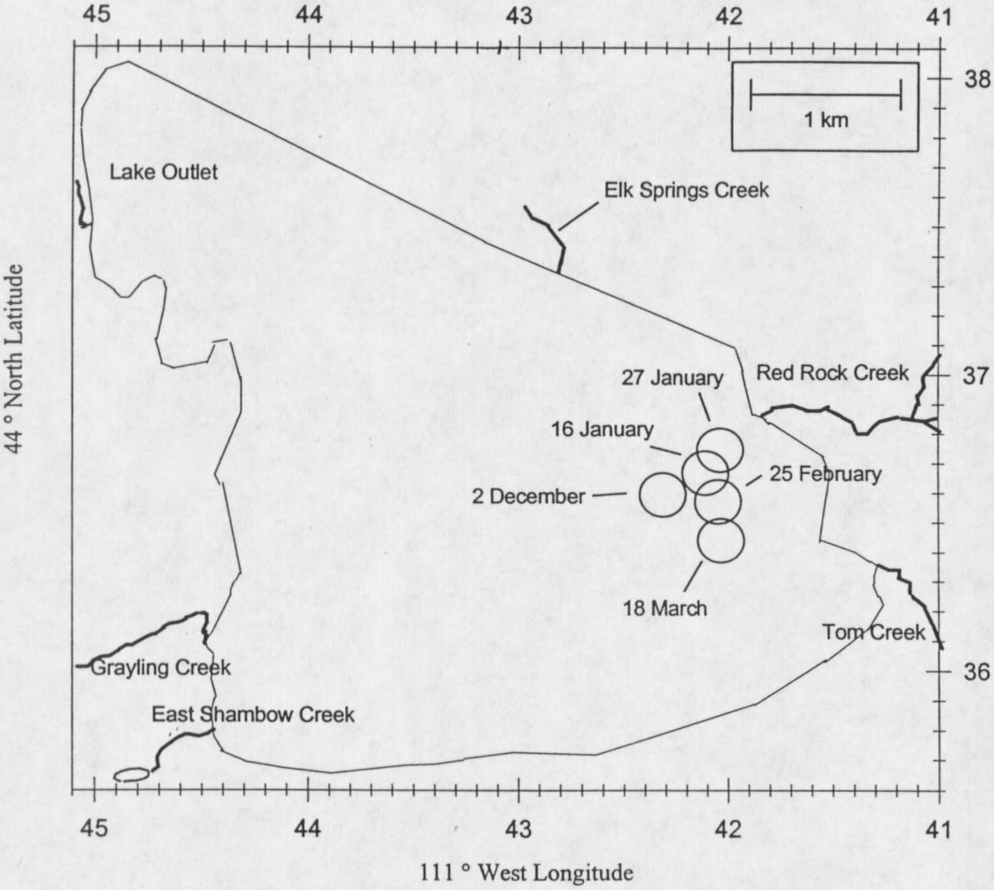

Figure 5. Locations of radio-tagged Arctic grayling #49.867 in Upper Red Rock Lake during the 1994-1995 winter field season.

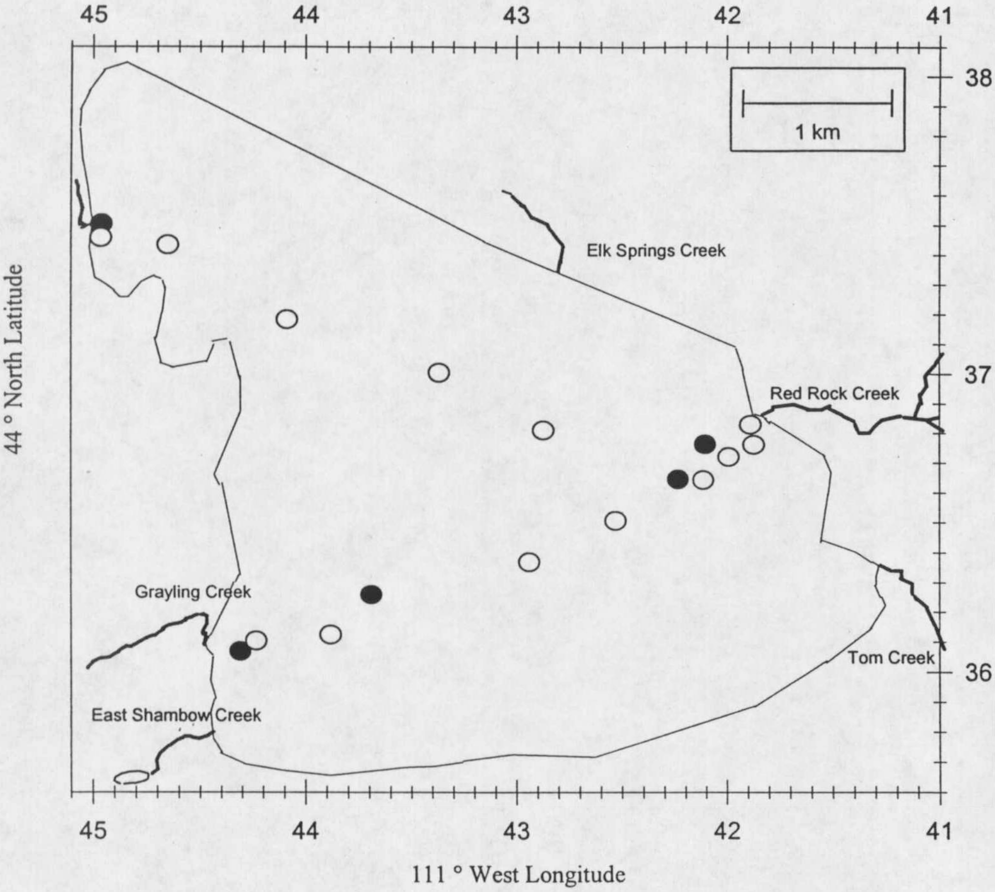

Figure 6. Sites of habitat measurements, Upper Red Rock Lake
16 January (●) and 27 January (O) 1995.

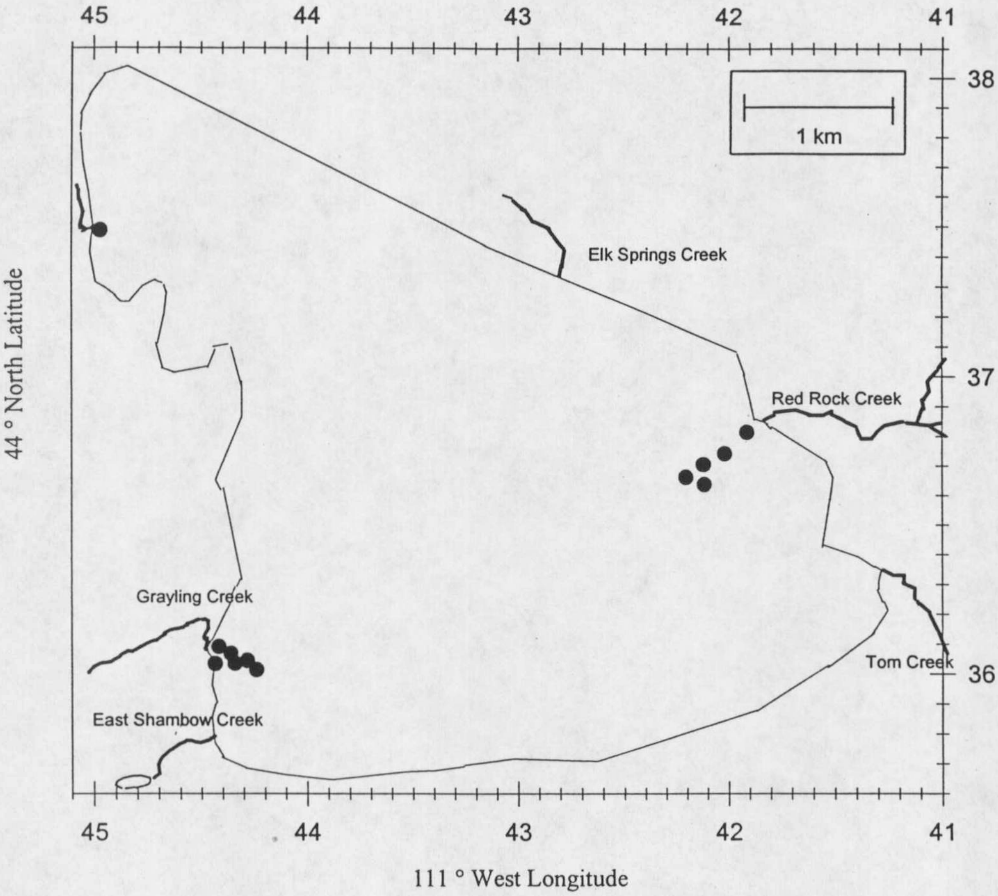

Figure 7. Sites of habitat measurements, Upper Red Rock Lake
25 February 1995.

Table 3. Dissolved oxygen (D.O.), temperature, water depth beneath ice, and ice thickness at locations of two radio-tagged Arctic grayling (#49.837 and #49.867) beneath ice cover over Upper Red Rock Lake, 2 December 1994 to 31 March, 1995.

Fish #	Date	D.O. (mg/l)	Temperature (°C)	Water Depth (m)	Ice (m)
49.837	2 December	4.1	1.5	0.45	0.30
	16 January	2.8	0.1	0.55	0.45
	27 January	3.7	n/a	0.78	0.42
	10 February	8.50	3.0	0.30	0.00
	25 February	7.8	2.3	0.20	0.40
49.867	2 December	6.1	1.0	0.85	0.30
	16 January	2.5	1.4	0.93	0.45
	27 January	7.5	0.1	0.59	0.58
	10 February	8.4	0.0	0.50	0.70
	25 February	7.8	0.5	0.54	0.68
	31 March	5.6	0.8	1.26	0.43

concentrations of about 0.5 mg/l or less by mid January and remained low until at least the end of February. On two dates, 16 and 27 January, holes drilled at lake outlet sites

(Figure 6) had d.o. of 0.15-0.50 mg/l (Table 4), accompanied by the smell of hydrogen sulfide and the presence of dead invertebrates (Dytiscidae spp. and Corixidae spp.) and dead fish (juvenile white suckers). By 31 March, when ice cover was deteriorating and large openings had developed in the ice cover, d.o. in midlake and lake outlet sites had increased to 3.2 to 5.0 mg/l (Table 4).

To affirm the validity of the very low d.o. readings with the YSI meter, Winkler titrations were conducted with a Hach portable water quality kit on water samples taken on 27 January. D.O. measured by Winkler titrations and YSI meter are compared in Appendix B, Figure 1. Of the eight samples taken for comparison, only two deviated from the meter readings by more than 0.25 mg/l (+0.37 and +0.47).

From mid-January to late February, when d.o. concentrations were very low in mid-lake and lake outlet sampling sites, the two radio-tracked Arctic grayling remained at locations with significantly higher ($P < 0.05$) mean d.o. than at mid-lake and lake outlet sites (Table 5). The two radio-tracked Arctic grayling were located in areas of the lake which had significantly lower water depths below ice cover than midlake sites, but which were not significantly different from water depths measured at the lake outlet (Table 5).

Mean water temperature at the locations of Arctic grayling #49.837 and #49.867 differed significantly from one another, but mean temperature at the location of Arctic grayling #49.867 did not differ significantly from those measured at the lake outlet and mean temperature at the location of Arctic grayling #49.837 did not differ significantly

Table 4. Means and (range) of dissolved oxygen (D.O.), temperature, water depth beneath ice, and ice thickness at midlake and lake outlet sites in Upper Red Rock Lake, 2 December 1994 to 31 March, 1995. At sites where water depth was greater than 1 m, D.O. and temperature were measured at the top and bottom (Appendix B, Table 2); values presented here are the greater of the two. N = number of sites measured on that date.

Date	N	D.O. (mg/l)	Temperature (°C)	Water Depth (m)	Ice (m)
			Midlake		
2 December	1	2.20	1.60	1.25	0.35
16 January	1	0.50	3.00	1.43	0.40
27 January	7	0.24	1.48	1.00	0.53
		(0.15-0.35)	(1.00-2.50)	(0.30-1.50)	(0.49-0.60)
31 March	4	4.25	3.40	1.33	0.61
		(3.20-5.00)	(3.20-4.50)	(1.15-1.48)	(0.40-0.72)
			Lake Outlet		
2 December	1	2.90	1.60	0.80	0.20
16 January	2	0.45	0.40	0.45	0.55
		(0.40-0.50)	(0.30-0.50)	(0.40-0.50)	(0.50-0.60)
27 January	4	0.14	0.47	0.49	0.41
		(0.15-0.25)	(0.3-1.0)	(0.27-0.69)	(0.38-0.49)
10 February	1	0.30	0.50	0.70	0.20
25 February	7	0.69	0.48	0.55	0.39
		(0.60-1.20)	(0.00-1.50)	(0.13-0.75)	(0.30-0.60)
31 March	2	3.2	3.0	0.70	0.40
		(3.30-3.10)	(3.00)	(0.66-0.73)	(0.28-0.53)

Table 5. Comparisons of dissolved oxygen (D.O.), temperature, water depth beneath ice, and ice thickness at locations of radio-tagged Arctic grayling #49.837 and #49.867 and at midlake and lake outlet sites for January and February 1995. Means and (standard deviations) are given for fish location and lake measurement sites. Within a column, means sharing a common letter (a, b, c) are not significantly different ($p > 0.05$, studentized Neuman-Keuls multiple comparisons test).

Fish or Lake Sites	N	D.O. (mg/l)	Temp (°C)	Water Depth (m)	Ice (m)
49.837	4	5.73 a (2.90)	1.80 a (1.51)	0.46 b (0.26)	0.32 c (0.21)
49.867	4	6.56 a (2.73)	0.50 b (0.32)	0.64 b (0.20)	0.60 a (0.11)
Midlake	8	0.29 b (0.11)	1.71 a (0.88)	1.03 a (0.32)	0.52 ab (0.06)
Outlet	14	0.47 b (0.35)	0.47 b (0.41)	0.53 b (0.22)	0.40 cb (0.11)

from those measured at midlake sites (Table 5). Mean ice thickness at the location of Arctic grayling #49.867 was significantly greater than that at the location of Arctic grayling #49.837. Mean ice thickness did not differ significantly between the location of Arctic grayling #49.867 and midlake sites. Ice thickness did not differ significantly between the location of Arctic grayling #49.837 and lake outlet sites (Table 5).

Summer and Fall 1995

Summer and fall habitat variables were recorded only occasionally, on Upper Red Rock Lake, because considerable effort was devoted towards capturing Arctic grayling large enough to be radio-tagged. D.O. measured during the open water period were at or near saturation with the atmosphere (Appendix B, Table 3). This is likely due to a combination of photosynthetic oxygen production by the abundant vegetation and the water circulation produced by frequent afternoon winds.

Winter 1995-1996

Freezing over of the lake during the late fall of 1995 was interrupted on several occasions by thawing events. In mid-October, ice often formed at the lake margins after dark and melted the following morning. By the morning of 28 October a thin film (about 2 cm) was observed to have covered the entire surface of the lake. This ice melted by late afternoon. Refuge staff reported that Upper Red Rock Lake was completely frozen on 7 December, partially open several days later, and completely frozen once again on 14 December. After 14 December only localized thawing was observed. Ice thickness on 14 December was sufficient to permit foot travel on the eastern edge of the lake.

Ice cover on 14 December and for much of the following four months remained clear and with little or no snow. On 9 and 10 January, ice thickness on Upper Red Rock Lake ranged from 15 to 35 cm (Figure 8). Most stations had ice in excess of 20 cm at this

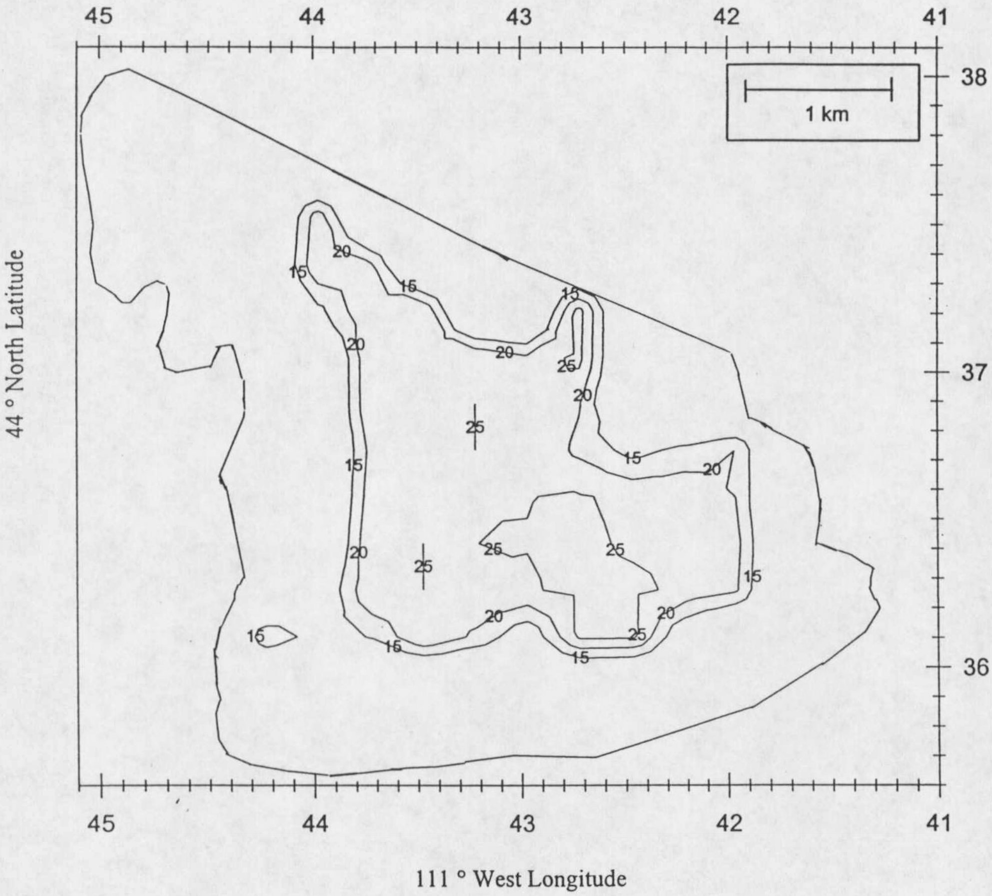

Figure 8. Ice thickness (cm) on Upper Red Rock Lake, 10 January, 1996.
Contour interval = 10cm.

time (Appendix B, Table 2). By 23 January ice thickness had increased to greater than 30 cm for a large portion of the Upper Lake (Figure 9). By 6 February the majority of the lake ice was in excess of 40 cm (Appendix B, Table 2). Lake ice continued to thicken until about 4 March, when we measured ice thickness in excess of 60 cm at several locations (Figure 10; Appendix B, Table 2). At approximately this time during the ice-covered period, ice growth ceased and melting began. Observations on 18 March demonstrated that most stations experienced a net decrease in ice thickness (Appendix B, Table 4).

Water temperatures measured at the tributary stations remained considerably lower than at the midlake sites. Mean water temperature during the period of seasonal ice cover at station RRC was 0.48 °C (Figure 11; Table 6). At station GRC water temperatures averaged 1.06 °C (Figure 12; Table 6). Mean water temperatures for all midlake sites averaged above 3.0 °C during the period of seasonal ice cover with the exception of station NMC which had an average water temperature of 2.4 °C (Table 6).

Temperatures at the midlake sites increased as the season progressed (Appendix B, Table 2). Bottom temperatures were, in all instances, greater than near surface temperatures (Appendix B, Table 2). Bottom temperatures exhibited the most noticeable change, and in some instances, a differential of nearly 3.0 °C from January to March was observed (Figure 13, 14)

D.O. concentrations measured in Upper Red Rock Lake during the winter of 1995-1996 differed substantially from those measured during the winter of 1994-1995.

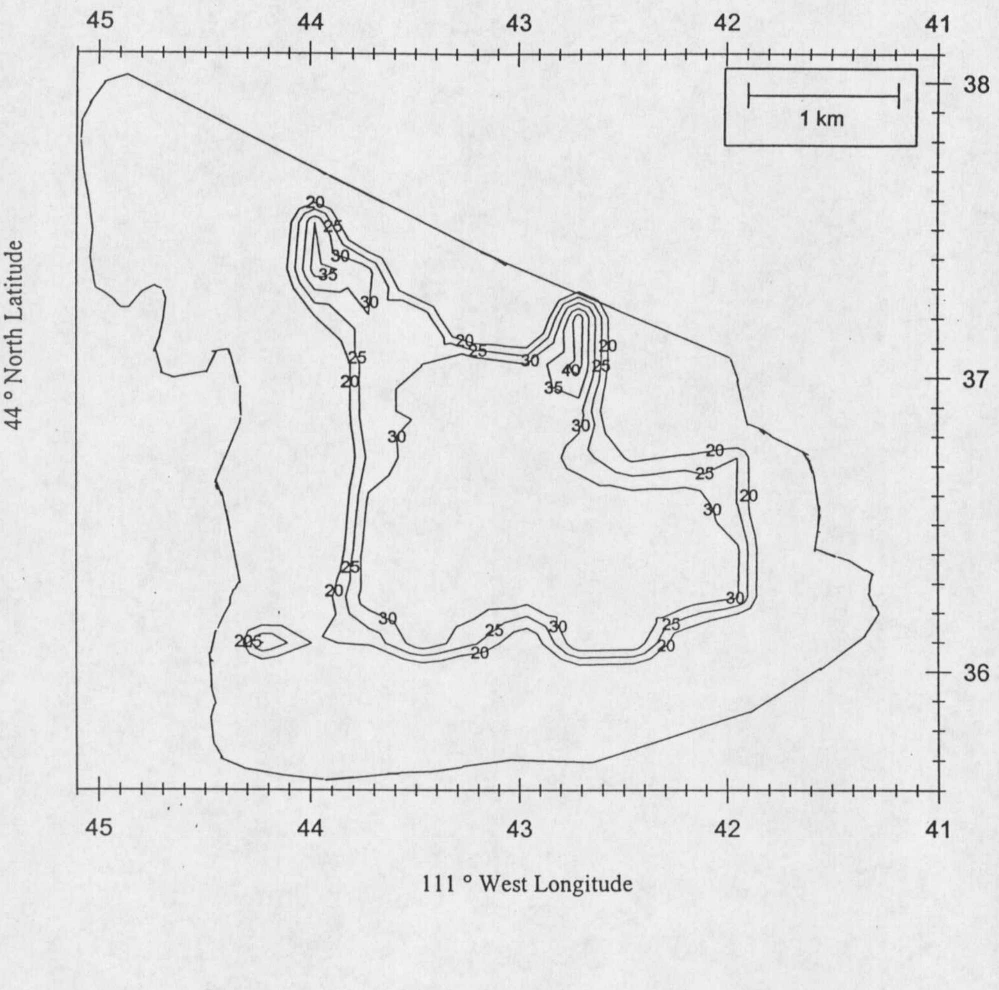

Figure 9. Ice thickness (cm) on Upper Red Rock Lake, 23 January, 1996.
Contour interval = 10 cm.

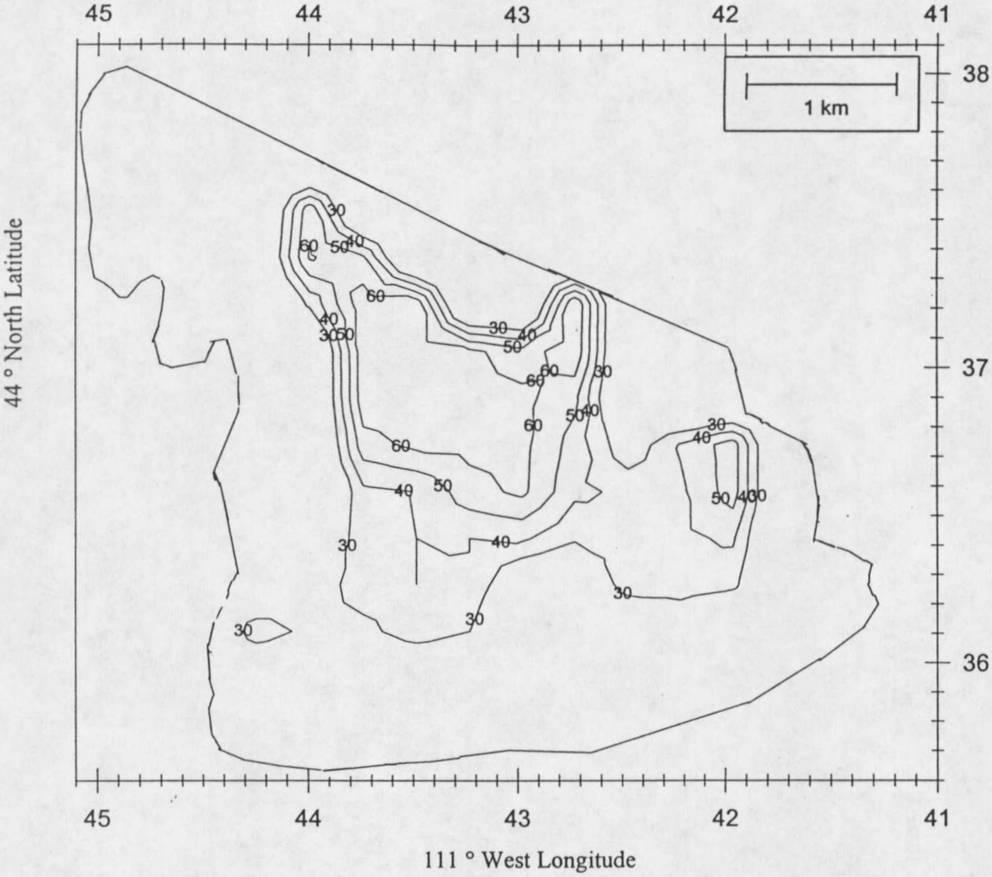

Figure 10. Ice thickness (cm) on Upper Red Rock Lake, 4 March, 1996. Contour interval = 10 cm.

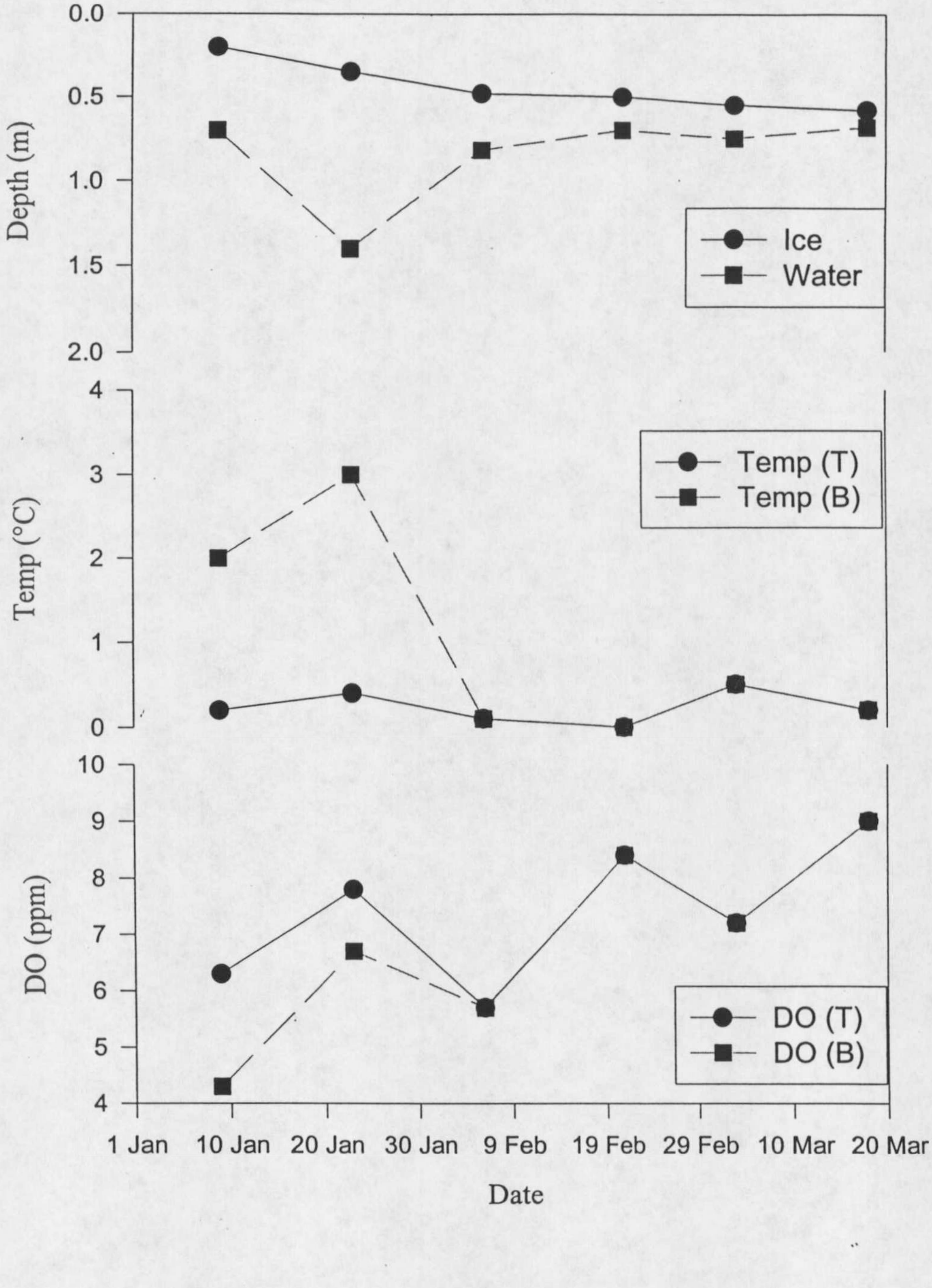

Figure 11. Habitat parameters at Red Rock Creek station, Upper Red Rock Lake, Winter 1996. For d.o. and temperature, measurements are given for the top (T) and bottom (B) of the water column.

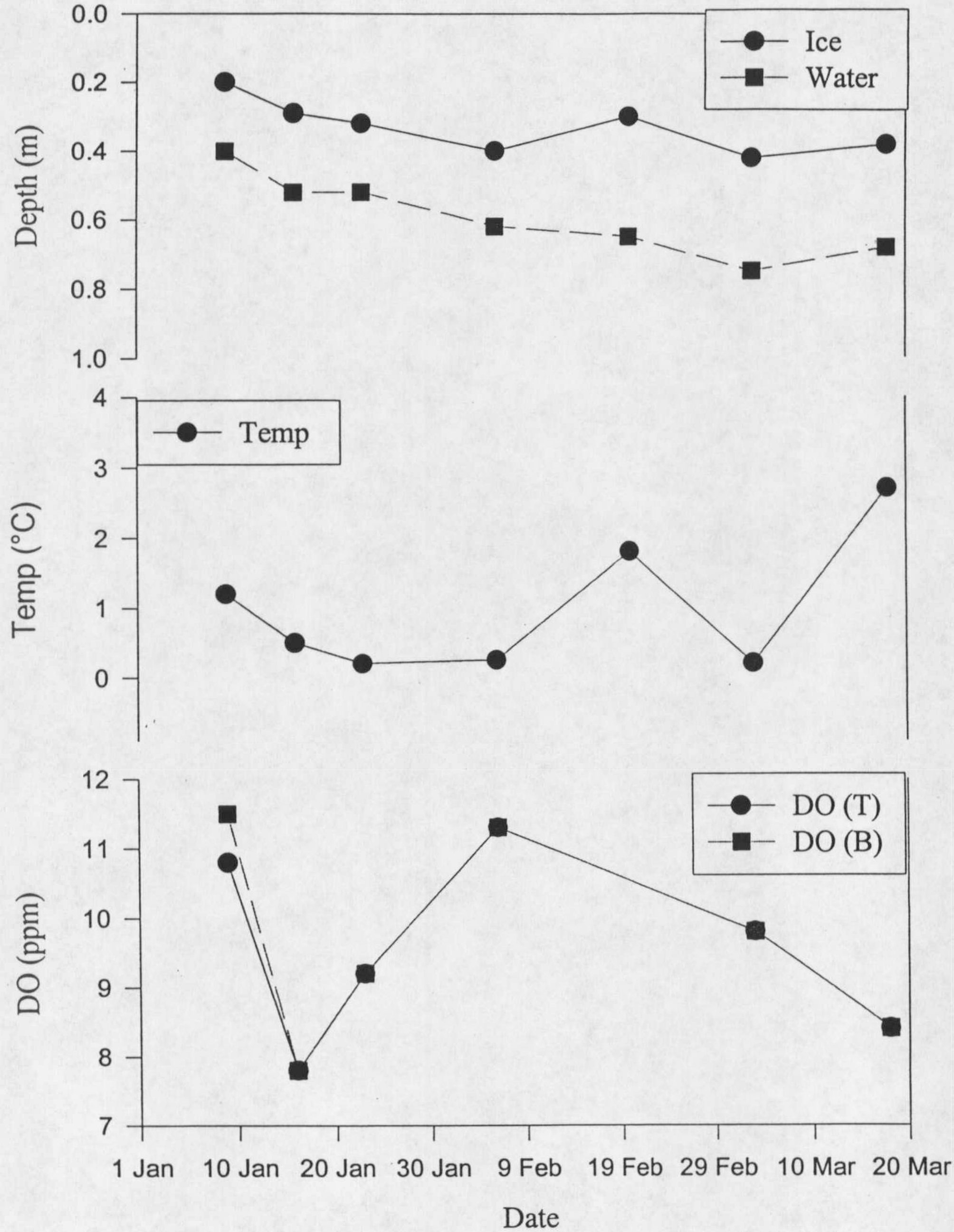

Figure 12. Habitat parameters at Grayling Creek station; Upper Red Rock Lake, Winter 1996. For d.o. and temperature, measurements are given for the top (T) and bottom (B) of the water column.

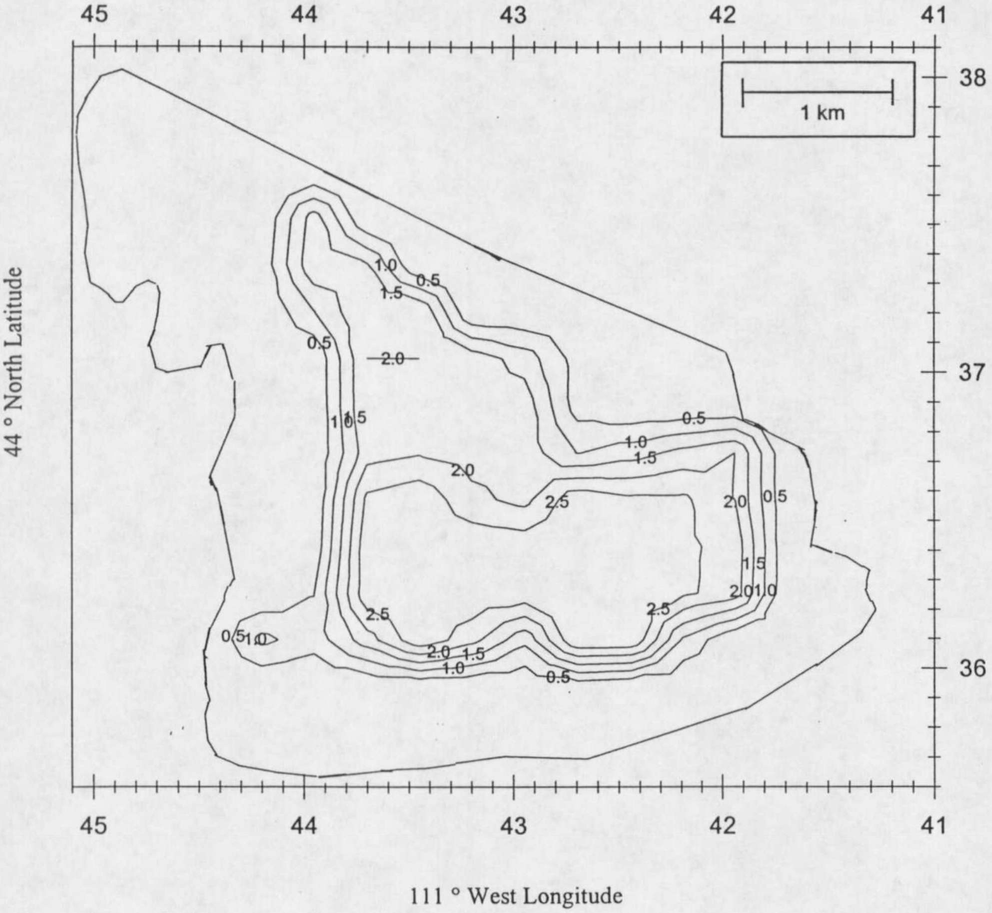

Figure 13. Bottom temperatures (°C) of Upper Red Rock Lake, 10 January, 1996.

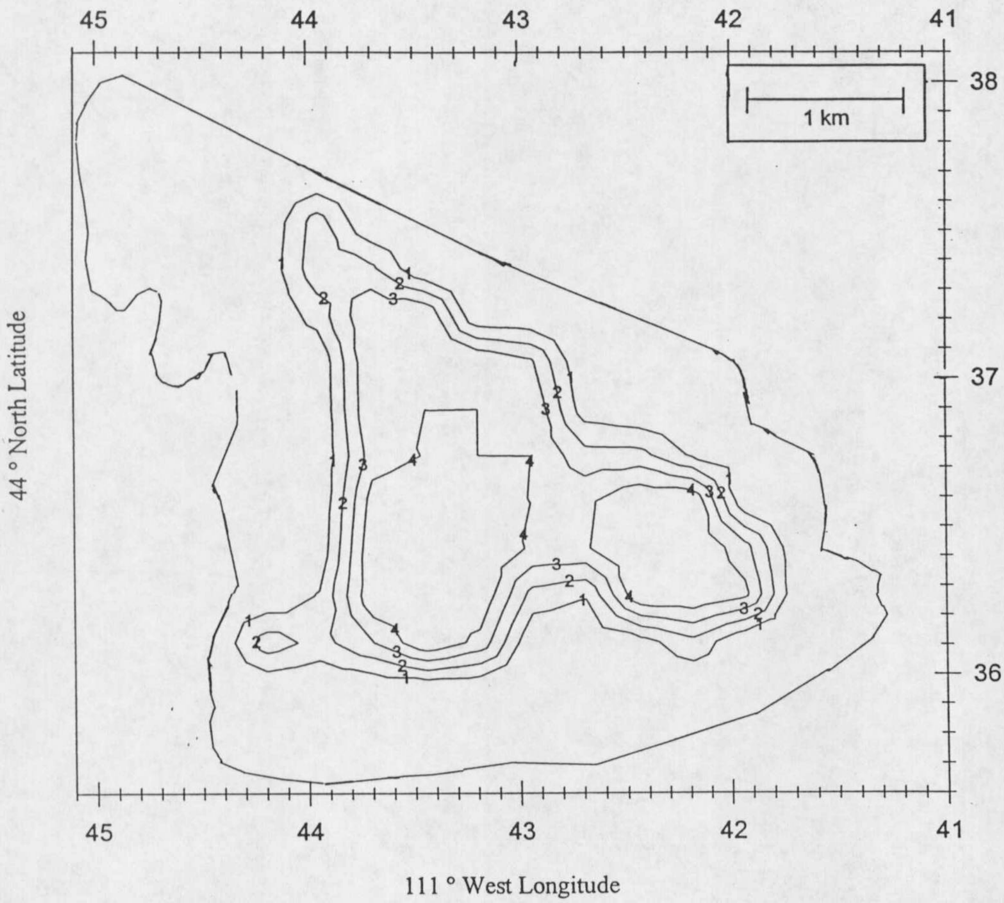

Figure 14. Bottom temperatures (°C) of Upper Red Rock Lake, 18 March, 1996.

Table 6. Mean and (standard deviation) of dissolved oxygen (D.O.), water temperature, water depth beneath ice, and ice thickness at sampling stations during winter 1995-1996 on Upper Red Rock Lake.

Station	D.O. (mg/l)	Temp (°C)	Water Depth (m)	Ice (m)
GRC	10.04 (1.34)	1.06 (1.04)	0.27 (0.07)	0.37 (0.08)
RRC	7.38 (1.25)	0.48 (0.76)	0.33 (0.12)	0.39 (0.14)
ESC	5.15 (1.02)	0.33 (0.26)	0.38 (0.05)	0.53 (0.12)
NML	9.12 (2.32)	3.08 (0.64)	1.17 (0.07)	0.47 (0.16)
CGS	9.78 (3.21)	4.01 (0.75)	1.54 (0.06)	0.37 (0.07)
BSS	8.1 (1.53)	3.63 (0.43)	1.41 (0.10)	0.34 (0.07)
MEL	9.07 (1.96)	3.28 (0.86)	1.26 (0.07)	0.45 (0.14)
EML	8.24 (4.83)	3.53 (1.18)	1.27 (0.05)	0.37 (0.07)
WML	7.04 (1.32)	2.4 (0.41)	1.03 (0.05)	0.44 (0.13)

D.O. was high when the lake froze over and remained so throughout the winter. At no time during our investigations of 1995-1996 did we measure d.o. below 3.0 mg/l at the top of the water column, and in most cases d.o. was twice this level. An example of midwinter d.o. concentrations is presented in Figure 15 , for 23 February. Some localized incidents of hypoxia were observed in waters adjacent to the lake bottom (Appendix B, Table 4). Successive visits to these sites suggested that such events were spatial and temporal anomalies in the overall aquatic habitat.

Statistical comparison of water quality parameters between the two winters indicates that mean midlake d.o. was significantly lower ($P < 0.001$) in 1994-1995 than in 1995-1996 (Table 7). Additionally, mean midlake temperatures were significantly greater ($P = 0.013$) during the winter of 1995-1996. Mean ice thickness was significantly thinner ($P = 0.003$) during the winter of 1995-1996 (Table 7). Mean water depth beneath ice cover was not significantly different at midlake sites during the two winters (Table 7). Temporal progression of d.o. and ice thickness at midlake sites during the winters of 1994-1995 and 1995-1996 is illustrated in Figure 16.

In 1995-1996, the comparisons between dissolved oxygen measurements from Winkler titrations and from the YSI meter did not exhibit the close agreement observed in 1994-1995. The r^2 value for the regression was 0.995 for 1994-1995, but only 0.531 in 1995-1996 (Appendix B, Figure 1, Figure 2). Discrepancies in the second year were likely associated with the relatively high d.o. concentrations and the gradients in d.o.

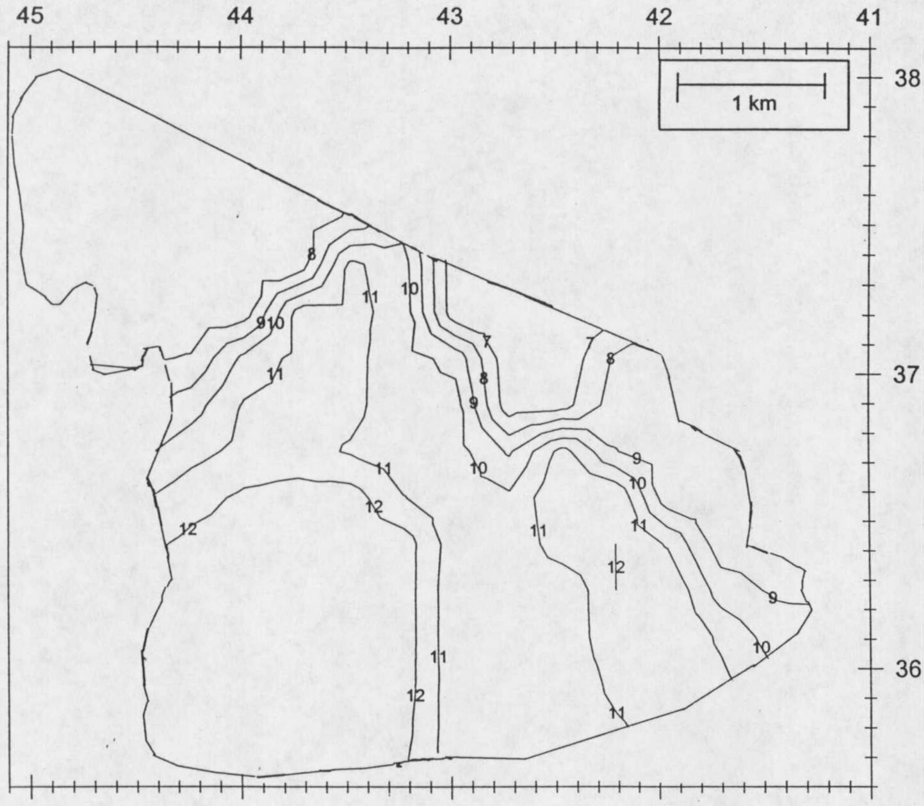

Figure 15. Dissolved oxygen (top of water column) in Upper Red Rock Lake, 23 February, 1996. Contour interval = 1 ppm.

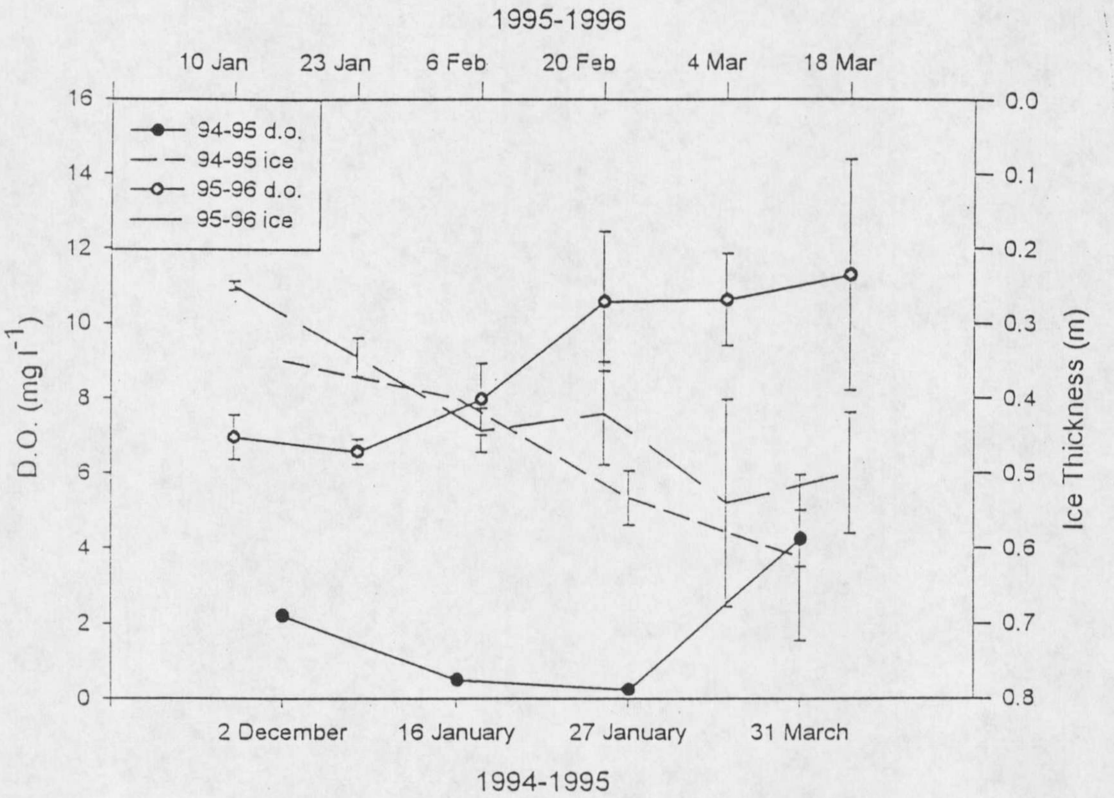

Figure 16. Mean dissolved oxygen (d.o.) and ice thickness at midlake sites on Upper Red Rock Lake during winter 1994-1995 and winter 1995-1996. Vertical bars indicate maximum and minimum measurements on a given sampling date.

Table 7. Comparisons of dissolved oxygen (D.O.), temperature, water depth beneath ice cover, and ice thickness at locations of radio-tagged Arctic grayling and midlake sites during winter 1994-1995 versus winter 1995-1996, Upper Red Rock Lake. Statistical comparisons represent t-test of mean measurements between years. For D.O. and temperature, the greatest concentration or temperature measured at each site is used. The parameters for winter 1994-1995 are for the period of time extending from 16 January 1995 to 31 March 1995, and for winter 1995-1996 are from 10 January 1996 to 18 March 1996.

Parameter	Locations	1994-1995 mean (SD)	1995-1996 mean (SD)	P-value
D.O. (mg/l)	grayling	6.08 (2.47)	11.12 2.71)	0.004
	midlake	1.60 (2.00)	8.53 (2.20)	< 0.001
Temp (°C)	grayling	1.03 (1.12)	3.28 (1.61)	0.013
	midlake	2.38 (1.24)	3.22 (0.81)	0.024
Water (m)	grayling	0.63 (0.32)	1.18 (0.56)	0.046
	midlake	1.13 (0.30)	1.25 (0.17)	0.113
Ice (m)	grayling	0.46 (0.21)	0.35 (0.09)	0.101
	midlake	0.55 (0.08)	0.42 (0.13)	< 0.003

beneath the ice. It was not unusual for d.o. to differ by 1-3 mg/l or more between the top and bottom of the water column, which was only about 1.6 m or less in depth (Appendix B, Table 4). The Kemmerer bottle used to extract water samples for the Winkler titration hangs vertically in the water when taking a sample, and is 42 cm long. Thus, the bottle samples water from a column 42 cm long, with a gradient in d.o. concentrations within the column, whereas the YSI meter measures d.o. at the specific depth of the probe's tip.

Of the 28 fish radio tagged during summer and fall of 1995 (12 Arctic grayling, 9 cutthroat trout, 6 burbot, and 1 brook trout), 12 were not detected following their release. These included 6 Arctic grayling, 3 cutthroat trout and 3 burbot. Aerial telemetry conducted by refuge staff in August 1995 located ten radio-tagged fish, but none of the missing fish despite extensive survey of the Centennial Valley. All fish located from aircraft were in Upper Red Rock Lake or the lower 1.0 km of Red Rock Creek. No fish were found in Lower Red Rock Lake or the Red Rock River downstream of Upper Red Rock Lake.

Radio-tagged Arctic grayling, cutthroat trout, and burbot were located at widely dispersed locations during July, August, September and October (Figure 17, 18, 19, 20). Four cutthroat trout were repeatedly located off the mouth of Red Rock Creek on 16, 18, and 20 July (Figure 17). Five cutthroat trout and one Arctic grayling (#49.192) were located on three telemetry dates in August (Figure 18). Five cutthroat trout, three Arctic grayling, and one burbot were located on two telemetry dates in September (Figure 19).

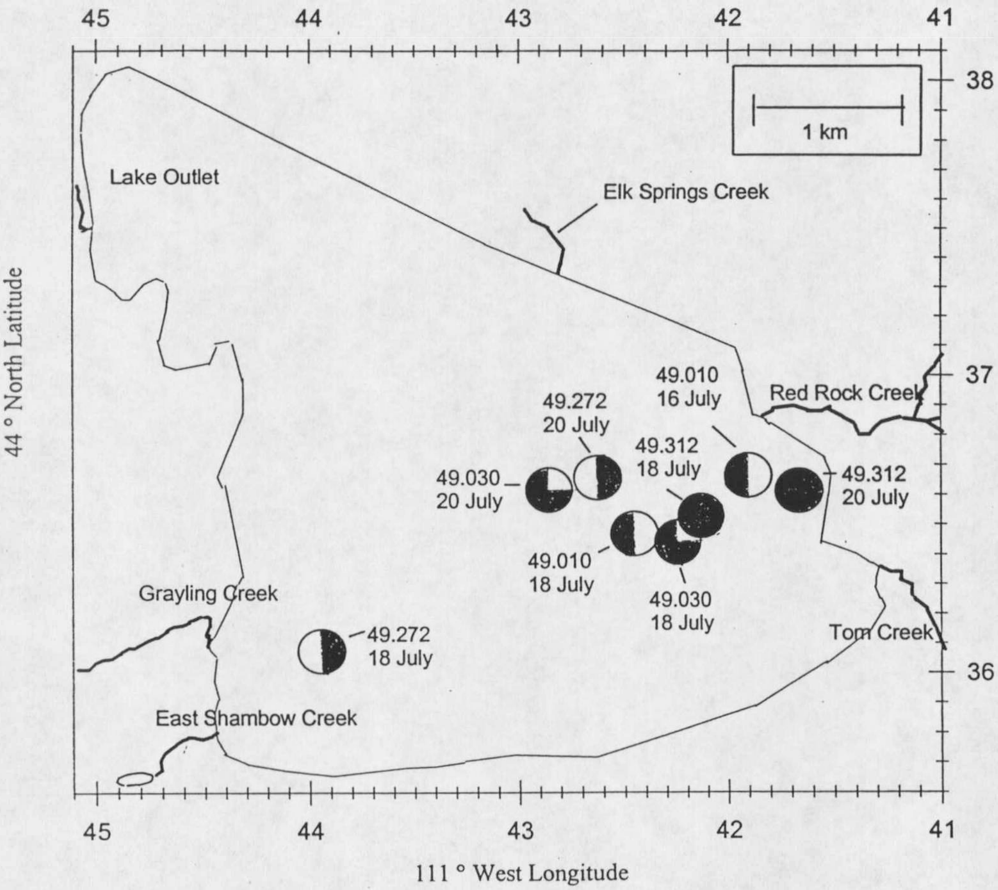

Figure 17. Locations of radio-tagged cutthroat trout (#49.010, 49.272, 49.030, and 49.312) in Upper Red Rock Lake, 16, 18, and 26 July, 1995.

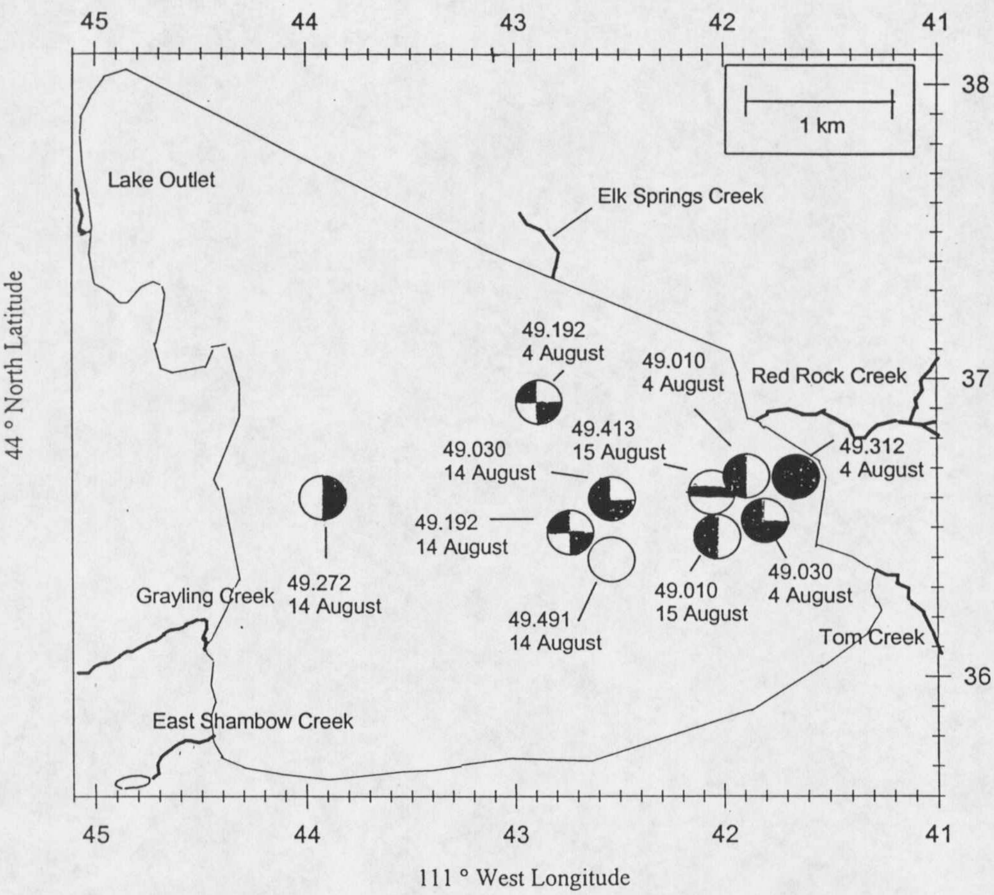

Figure 18. Locations of radio-tagged cutthroat trout (#49.010, 49.030, 49.312, 49.272, 49.491) and Arctic grayling #49.192 in Upper Red Rock Lake, 4, 14, and 15 August, 1995.

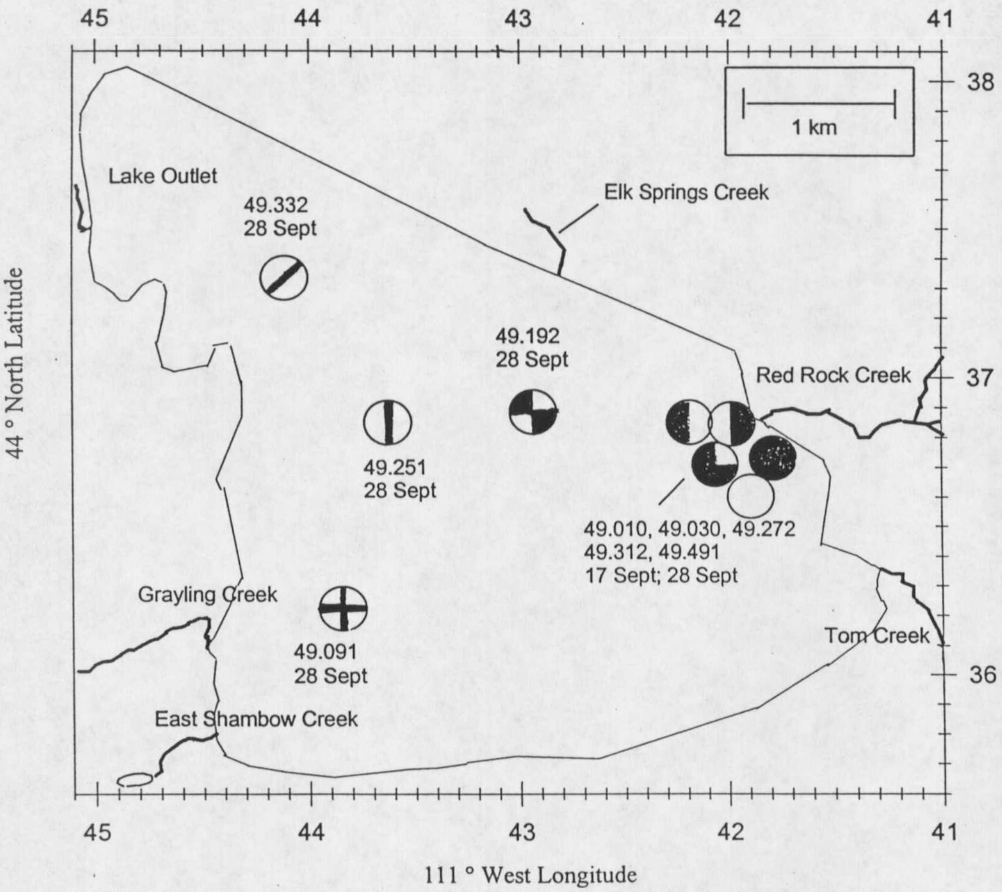

Figure 19. Locations of radio-tagged cutthroat trout (#49.010, 49.030, 49.272, 49.312, and 49.491), Arctic grayling (#49.091, 49.192, and 49.251), and burbot #49.332 in Upper Red Rock Lake, 17 and 18 September, 1995.

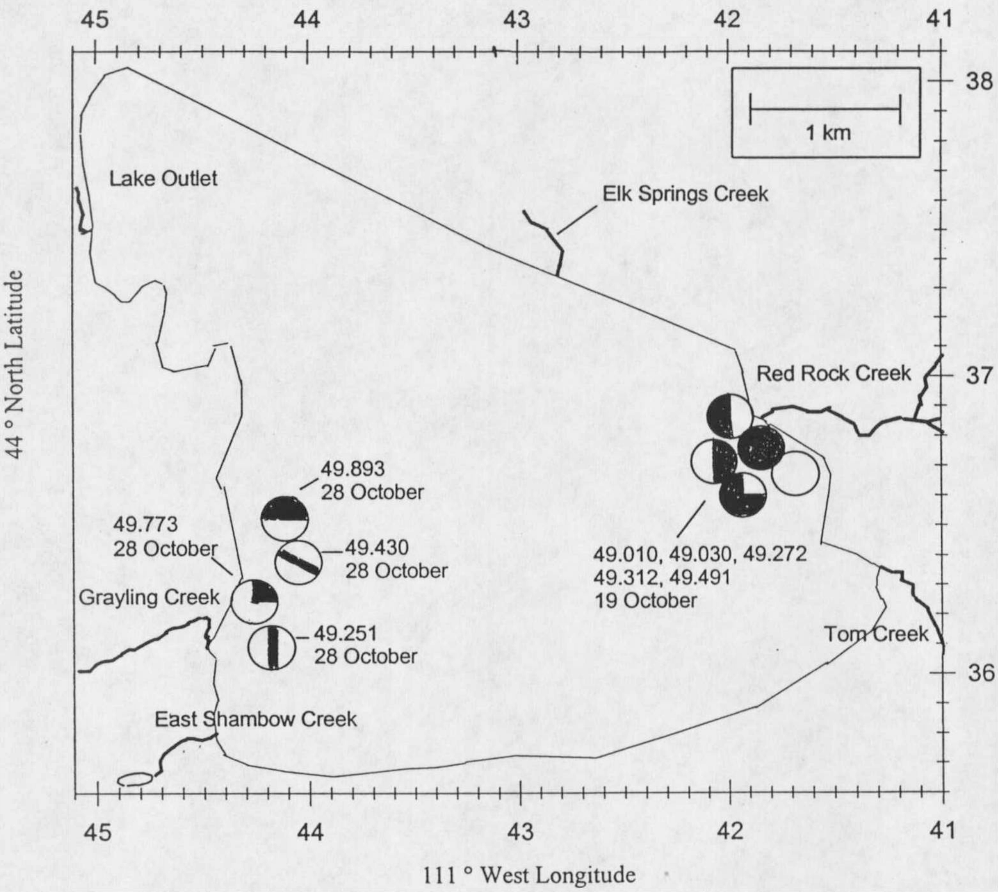

Figure 20. Locations of radio-tagged cutthroat trout (#49.010, 49.030, 49.312, 49.272, 49.430) and Arctic grayling (#49.251, 49.893) in Upper Red Rock Lake, 19 and 28 October, 1995. Telemetry was conducted only from the western shore on 28 October.

These included three previously undetected radio-tagged fish, Arctic grayling #49.091 and #49.251, and burbot #49.332. All three had been tagged and released within the preceding 30 d in the eastern portion of the lake or in Red Rock Creek. Five cutthroat trout were located on 19 October, all near Red Rock Creek (Figure 20). This was the last date of telemetry from a boat for the 1995-1996 field season, because of the subsequent formation of ice on the lake.

Because of the presence of thin ice that was not safe to travel on, limited telemetry from shore was conducted on 28 October and 14 December. On 28 October, thin ice had formed on the lake and telemetry was limited to walking along the western shore. Arctic grayling #49.251 was located along the shoreline north of Grayling Creek, brook trout #49.773 was located near the mouth of East Shambow Creek, and Arctic grayling #49.893 was located near Grayling Creek (Figure 20). On 14 December, two new contacts, Arctic grayling #49.757 and cutthroat trout #49.803 were located near the mouth of Red Rock Creek (Figure 21).

Radio telemetry from over the ice surface started on 10 January and continued to 18 March. Fish located during this second season of ice cover, their positions on dates when they were located , and the approximate distances from their last known locations are presented in Figures 21, 22, 23, 24 and Table 8. In contrast to the first season of 1994-1995, fish were widely dispersed through the lake during this second season of ice

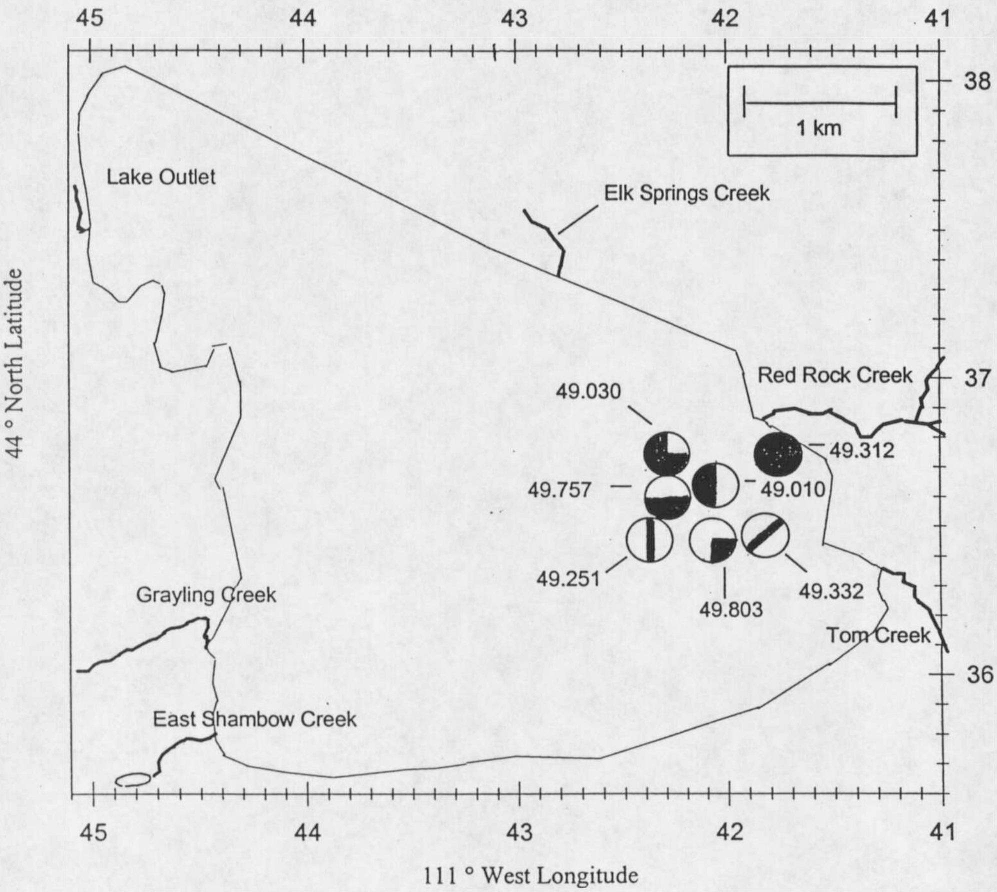

Figure 21. Locations of radio-tagged cutthroat trout (#49.010, 49.030, 49.312, 49.803) and Arctic grayling (#49.251, 49.757) and burbot #49.332 in Upper Red Rock Lake, 14 December, 1995. Only the eastern shore of the lake was searched on this date.

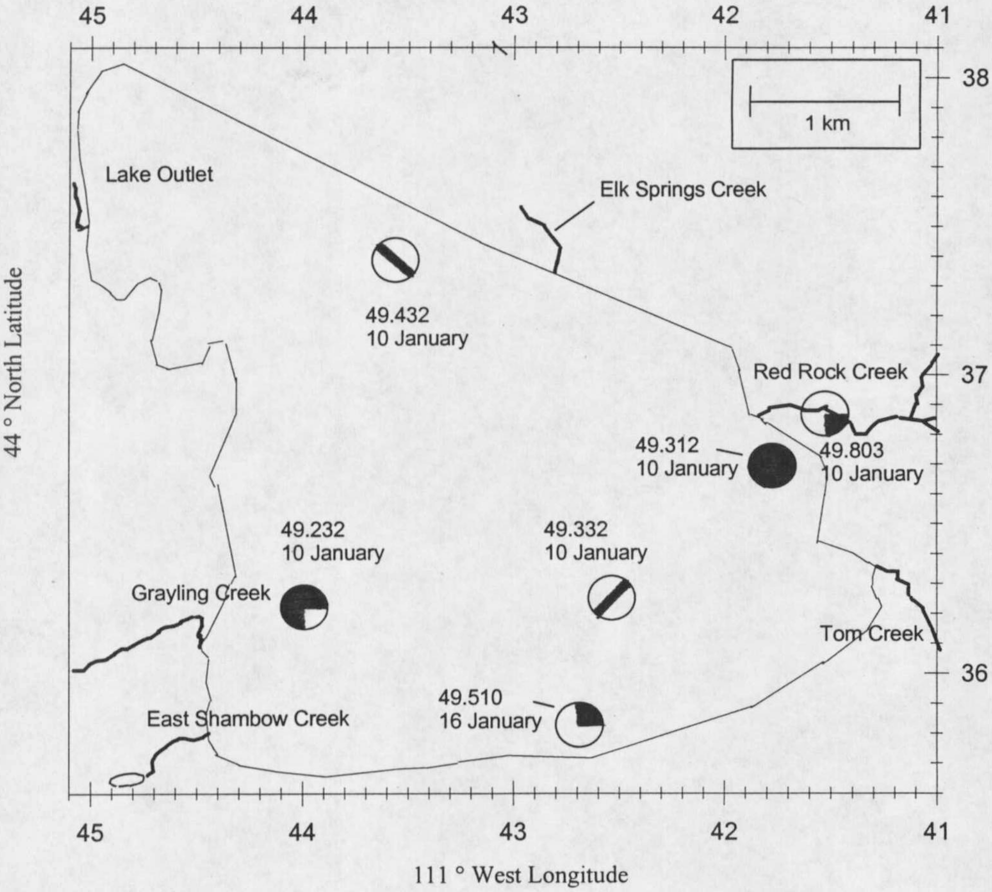

Figure 22. Locations of radio-tagged cutthroat trout (#49.032, 49.312, 49.432, 49.803), Arctic grayling #49.232 and burbot (#49.332, 49.510) in Upper Red Rock Lake, 9 and 16 January, 1996.

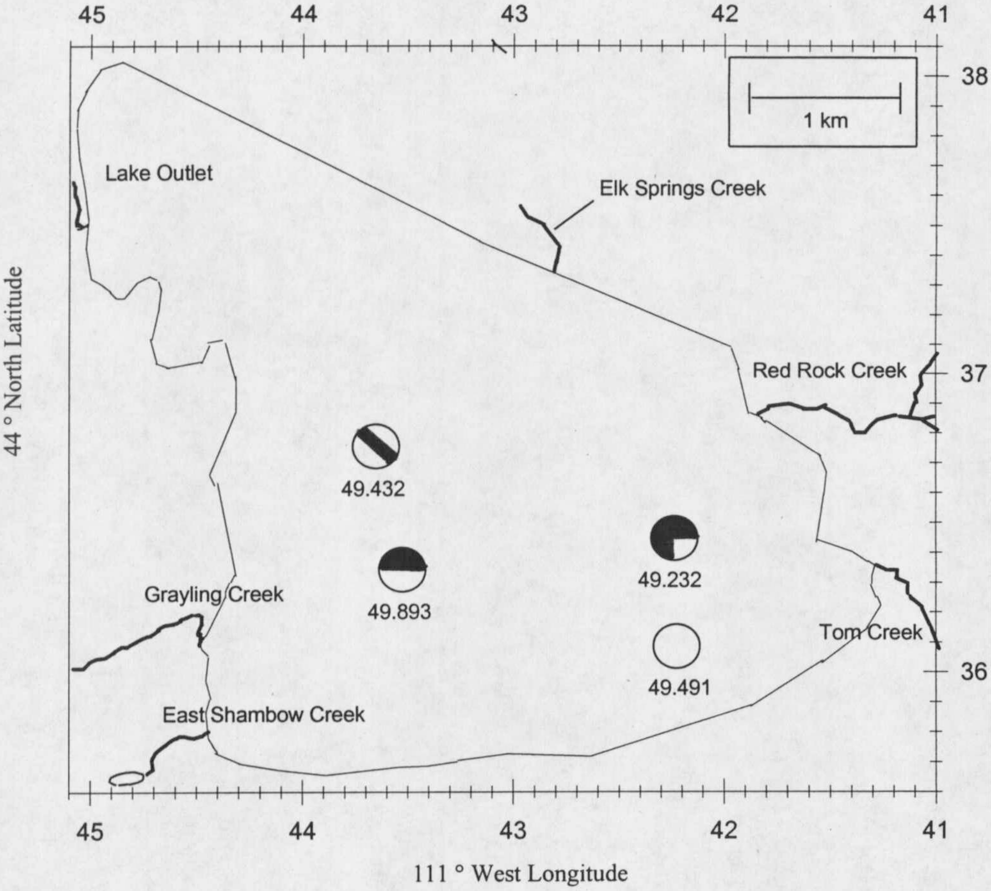

Figure 23. Locations of radio-tagged cutthroat trout (#49.432, 49.491) and Arctic grayling (#49.232, 49.893) in Upper Red Rock Lake, 21 February, 1996.

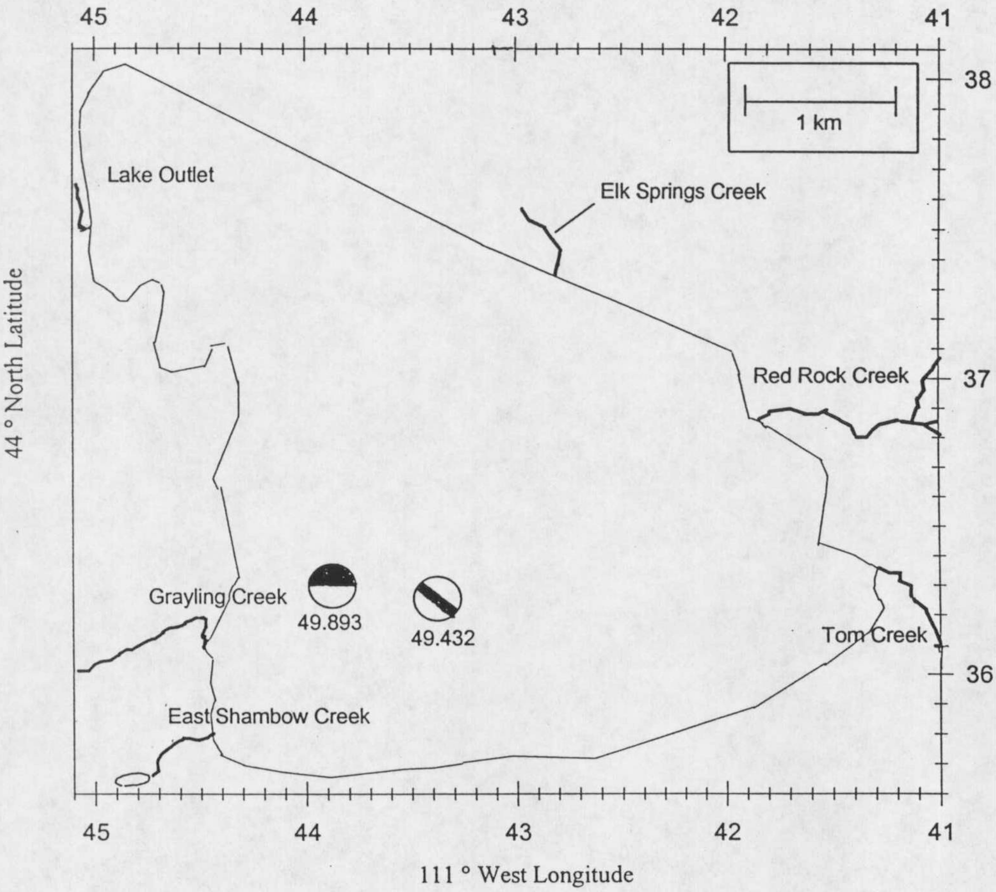

Figure 24. Locations of radio-tagged cutthroat trout #49.432 and Arctic grayling #49.893 in Upper Red Rock Lake, 18 March, 1996.

cover. Telemetry from over the ice surface ended on 18 March; an intended effort on 2 April had to be canceled because the ice was melting and had become unsafe to travel on.

Comparisons of habitat parameters at locations of radio-tagged fish, near the inlets of tributary streams, and at midlake stations over the winter 1995-1996 field season are presented in Table 9. Mean d.o. concentrations at locations of cutthroat trout, midlake sites, and near tributary inlets were not significantly different from one another (Table 9). However, d.o. concentrations at stations nearest the locations of Arctic grayling were significantly greater than those measured at the other sites (Table 9).

Water temperatures did not differ significantly between locations of Arctic grayling, cutthroat trout, and midlake stations. Water temperatures near tributary inlets were significantly lower than those measured elsewhere in Upper Red Rock Lake (Table9). Similarly water depth beneath ice cover did not differ significantly between cutthroat trout, Arctic grayling, and midlake sites, yet was significantly lower at stations associated with tributary mouths (Table 9). Significant differences in ice thickness were observed between cutthroat trout locations and sites associated with tributary inlets (Table 9).

Table 8. Dates, locations (latitude and longitude coordinates, and mapped figure references) and approximate distances from previous location of Arctic grayling (AG), cutthroat trout (CT), and burbot (BB) in Upper Red Rock Lake during winter of 1995-1996.

	Location Date	Latitude, Longitude	Text Figure	Approx. Distance (km)
AG#49.251	14 December	44.36.400 111.42.400	21	
AG#49.757	14 December	44.36.550 111.42.350	21	
AG#49.232	10 January	44.36.200 111.44.000	22	
	21 February	44.36.450 111.42.200	23	2.3
AG#49.893	21 February	44.36.300 111.43.550	23	
	18 March	44.36.300 111.43.850	24	0.5
CT#49.010	14 December	44.36.650 111.42.100	21	
CT#49.030	14 December	44.36.700 111.42.300	21	
CT#49.312	14 December	44.36.750 111.41.800	21	
	10 January	44.36.750 111.41.800	22	0

Table 8-Continued

	Location Date	Latitude, Longitude	Text Figure	Approx. Distance (km)
CT#49.432	10 January	44.37.400 111.43.550	22	
	21 February	44.36.750 111.43.600	23	1.3
	18 March	44.36.250 111.43.350		1.0
CT#49.803	14 December	44.36.450 111.42.100	21	
	10 January	44.36.900 111.41.500	22	1.2
CT#49.491	21 February	44.36.100 111.42.200	23	
BB#49.332	14 December	44.36.450 111.41.800	21	
	10 January	44.36.250 111.42.550	22	1.0
BB#49.510	16 January	44.35.850 111.42.700	22	

Table 9. Comparison of dissolved oxygen (D.O.), temperature, water depth beneath ice cover, and ice thickness at sites of radio-tagged cutthroat trout and Arctic grayling, versus at midlake sites and sites near tributary inlets (stations GRC, RRC, ESC) for 10 January to 18 March 1996. Fish relocations are pooled over entire period of seasonal ice cover by species. For each site mean and (standard deviations) are given. Within a column, means with the same letter (a, b) are not significantly different from one another ($P > 0.05$, studentized Neuman-Keuls multiple comparison test).

Station	N	D.O. (mg/l)	Temp (°C)	Water Depth (m)	Ice (m)
Cutthroat	9	8.23 a (2.63)	2.68 a (1.39)	1.04 a (0.44)	0.31 b (0.11)
Grayling	5	11.12 b (2.71)	3.28 a (1.61)	1.18 a (0.25)	0.35 ab (0.09)
Tributary	12	7.47 a (2.24)	0.45 b (0.73)	0.30 b (0.08)	0.46 a (0.01)
Midlake	25	8.53 a (2.20)	3.22 a (0.81)	1.25 a (0.17)	0.42 ab (0.13)

DISCUSSION

Observations on Upper Red Rock Lake during periods of ice cover in the winters of 1994-1995 and 1995-1996 indicated that the lake became severely depleted of dissolved oxygen during the first winter but not during the second, and that the distribution of Arctic grayling differed considerably between the two winters. During the period of 10 January to 25 February 1995, d.o. declined to very low concentrations, averaging 0.28 mg/l at midlake, and 0.47 mg/l at lake outlet sites (Table 4). Two radio-tagged Arctic grayling remained near the inlets of tributary streams. These areas had d.o. averaging 5.73 and 6.56 mg/l (Table 3, 5) and obviously served as oxygen refugia from hypoxic conditions prevalent in the main body of the lake. In contrast, d. o. remained significantly higher ($P < 0.001$) and averaged 8.53 mg/l at midlake sites through the winter of 1995-1996 and radio-tagged Arctic grayling, cutthroat trout, and burbot remained widely distributed throughout the lake beneath the ice cover (Table 7, 8; Figure 15, 21, 22, 23, 24).

Thus, results of observations during the first winter supported both hypotheses: (a) that during the period of seasonal ice cover, dissolved oxygen declines to lethal levels through most of the lake; and (b) that Arctic grayling in the lake have behavioral responses or physiological adaptations to low dissolved oxygen that enable them to survive otherwise lethal conditions. Behavioral responses were indicated by the confinement within oxygen refugia of the Arctic grayling radio tracked during the first winter. Because attempts to determine dissolved oxygen tolerance of Arctic grayling acclimated and tested at very low, winter-like temperatures were not successful, it is not known whether members of this population have also developed physiological tolerance to low oxygen concentrations.

Oxygen concentrations declined rapidly during the first winter of 1994-1995. By 2 December 1994, only about five weeks after the lake had frozen over permanently for the season, d.o. had declined to 2.2 mg/l at a midlake sampling site (Figure 16). Oxygen concentrations at sampling sites toward the middle of the lake and near the outlet declined to even lower levels of about 0.5 to 0.15 mg/l by January 16 and remained very low in late February (Table 4; Appendix B, Table 2). Not until open water started appearing along the lake edges in late March did oxygen concentrations recover to relatively high values of from about 3 to 5 mg/l.

In contrast, oxygen concentrations remained high beneath ice cover through the winter of 1995-1996 (Table 6, 9; Figure 16). Permanent seasonal ice cover formed on about 14 December 1995, about seven weeks later than in 1994. Until open water started appearing near the end of March, d.o. remained generally between about 5 and 10 mg/l near the top of the water column and generally between about 3.5 to 9 mg/l near the bottom, with occasional, apparently temporary, higher or lower concentrations (Table 4; Appendix B, Table 2).

Differences in oxygen concentrations beneath ice cover of the two winters appeared related to abundance of macrophyte vegetation produced during the preceding growing season of spring, summer and fall, and by snow cover over the ice. Although abundance of vegetation was not studied, it was apparent from incidental observations that macrophyte production was very high during the low water year of 1994. Vegetation was so thick and the water near shore so shallow, that using a boat on the lake required that it first be dragged for several hundred meters, through mats of macrophytes near the launching site at the campground. The thickness of vegetation made it difficult to use a conventional outboard motor, and we used a "Go-Devil" outboard motor with a slanted shaft, designed for use in shallow, weedy waters. In 1995, however, vegetation was not nearly as extensive. Beds of macrophytes appeared less dense than in 1994. It was much easier to launch a boat and we were able to use both conventional outboard motors and jet motors to travel on the lake.

Thickness of ice cover was significantly less ($P < 0.003$) during the winter of 1995-1996 (Table 7; Figure 8, 9, 10; Appendix B, Table 2, 4), and snow cover obviously differed. No actual data on snow depths is available because snow depths were not measured and varied substantially among different sampling dates, and among different sites on a given date. Wind blowing over the lake moved the snow around or off the lake, and on a given day there were often mosaic patterns of bare ice alternating with snow-covered areas. However, the contrasts between the two years were obvious, even though based on incidental observations and subjective comparisons. During the first winter, snow depths of about 0.5 m were common over the ice surface by 16 January, with drifts that appeared about 1 m deep. Such conditions prevailed for much of the first winter of

1994-1995. In contrast, during the second winter of 1995-1996, the ice remained generally more transparent and free of snow. The often strong winds blew snow off the lake, or snow would melt during temporary warm periods.

It is likely that the combination of dense macrophyte vegetation, ice thickness, duration of seasonal ice cover and depth of snow over the ice during the first winter of 1994-1995, created the serious depletions of d.o. measured in the lake. Oxygen could have been reduced because respiration by the plants exceeded their photosynthesis. There also seemed to be a high amount of decomposing plant material, as indicated by the smell of hydrogen sulfide at holes drilled through the ice near the lake outlet in January, relatively early in the ice-covered period. Decomposing organic matter could have originated both from dying vegetation and from the sediment. Reduction of d.o. through uptake by lake sediment has been demonstrated by Hargrove (1969), and is evident in the generally lower oxygen concentrations near the bottom of sampling sites on Upper Red Rock Lake (Appendix B, Table 2, 4) .

In contrast, during the second winter of 1995-1996, the combination of apparently lower amounts of macrophyte vegetation and typically clear, snow-free ice probably contributed to the maintenance of high oxygen concentrations through the period of ice cover. Again, incidental observations support this speculation. On 21 February, 18 March, and 19 March, Pat Dwyer of the Bozeman Fish Technology Center accompanied us to attempt photography of fish with an underwater video camera. Although attempts to photograph fish had only very limited success, the images obtained at sampling sites near Station CMP and the lake outlet suggest active photosynthesis, with macrophytes that appeared healthy, and with gas bubbles evident on stem and leaf surfaces.

The differences in oxygen concentrations between the two winters had a marked effect on the behavioral distribution of grayling during winter ice cover. During the first winter, the two radio-tagged grayling remained confined to small areas which retained oxygen concentrations of about 2.6 to 10 mg/l through the period of ice cover. These two locations were at opposite ends of the lake, one off the mouth of Red Rock Creek along the eastern shore, and the other off the mouth of Grayling Creek along the western shore (Figure 4, 5). In contrast, the radio-tagged fish which were successfully located during the second winter-- four Arctic grayling, seven cutthroat trout, and two burbot--were widely distributed through the lake during the period of ice cover (Figures 21, 22, 23, 24).

Locations of individual fish on different dates also demonstrate their movement through wide areas of the lake through the second winter (Table 8; Figure 21, 22, 23, 24). This is demonstrated by the locations on different dates of Arctic grayling #49.251 (Figure 25) and cutthroat trout #49.491 (Figure 26), individuals that were repeatedly located during winter by radio tracking. Their changing locations and use of midlake areas differ markedly from the confinement into small, nearshore areas of the two radio-tagged grayling of the first winter (Figure 4, 5).

During the winter of 1994-1995, observations of behavioral distribution of Arctic grayling under ice cover were limited by the small number of fish radio-tagged and tracked. Only three were captured alive and radio tagged during the fall before ice

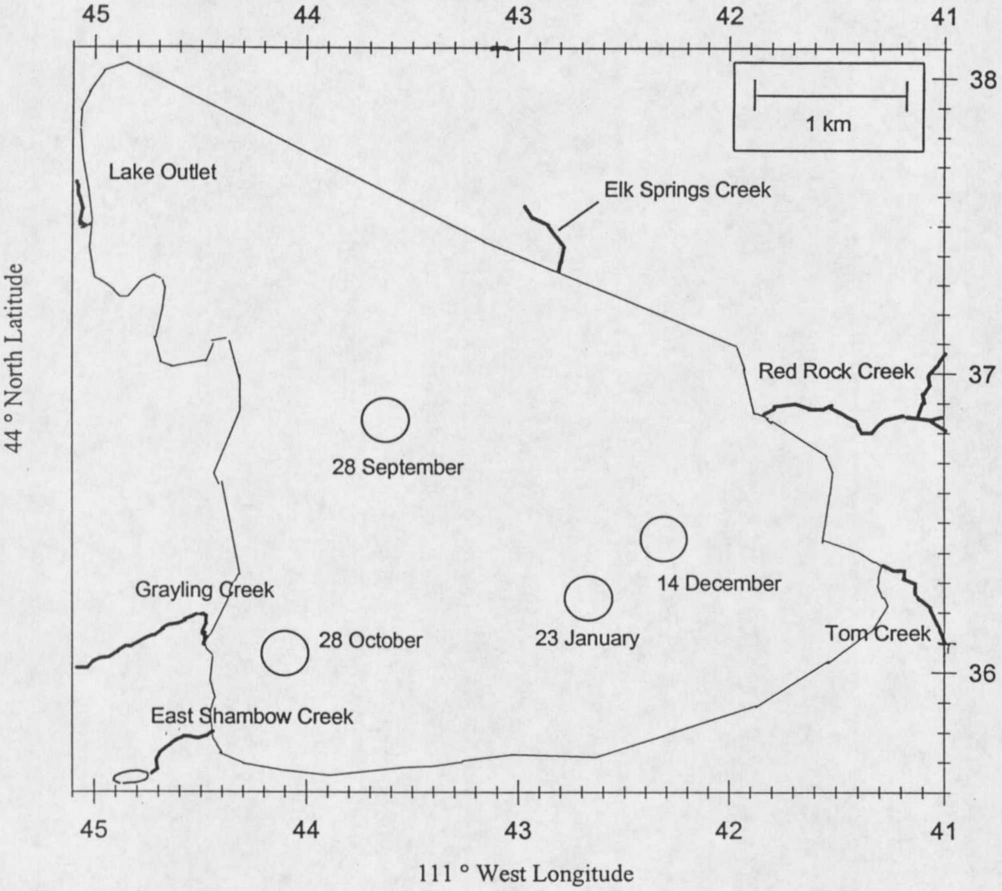

Figure 25. Locations of radio-tagged Arctic grayling #49.251 in 1995-1996 before (28 September, 28 October) and after (14 December, 23 January) formation of permanent seasonal ice cover over Upper Red Rock Lake.

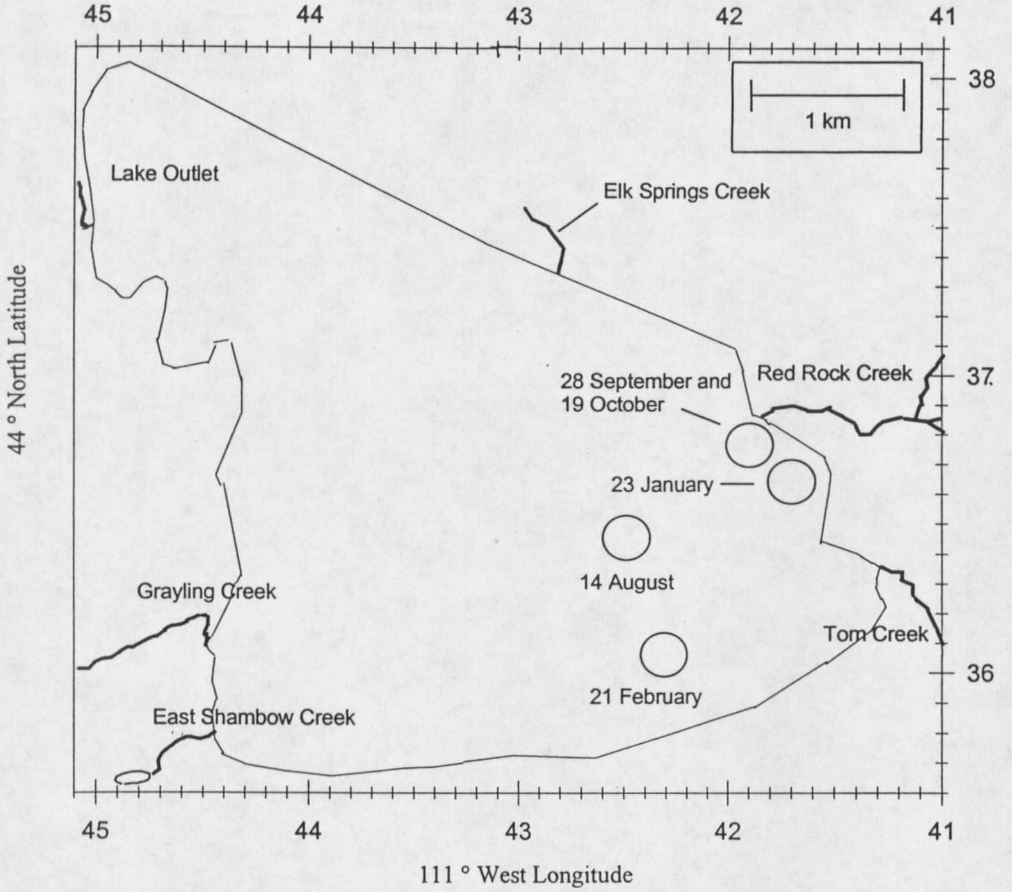

Figure 26. Locations of radio-tagged cutthroat trout #49.491 in 1995-1996 before (14 August, 17 and 28 September, and 19 October) and after (23 January and 21 February) formation of permanent seasonal ice cover over Upper Red Rock Lake.

started forming on the lake, and one of the three signals was never heard again after the fish was released. The small number of fish were related to the attempts to capture specimens during fall. To minimize size and weight of the internal tags, 6-month transmitters were used the first winter. Because it was important to have the tags continue transmitting through the period of ice cover, until approximately late March or early April, implantation and activation of the 6-month tags could not begin until early October. We were optimistic that gill netting and trapping of fish would yield the 10 to 12 specimens desired. These capture methods had been used successfully by others in the past to sample Arctic grayling and other species in the upper lake (Nelson, 1954; Unthank, 1989; Ron Skates, U.S. Fish and Wildlife Service, pers. comm.; unpublished data from files of the Red Rock Lakes National Wildlife Refuge). The relatively few grayling we captured, despite capturing many more cutthroat trout and burbot, may have been related to low numbers of adult grayling present in the lake. In a concurrent study, Mogen (1996a) captured only 116 spawning adults in 1994 at a weir across Red Rock Creek. This appears to be the only spawning tributary for this population at present, with the exception of a few fish that use Odell Creek.

The small areas occupied by the two radio-tagged grayling through the first winter were obviously oxygen refugia produced by inflowing water, from Red Rock Creek for the eastern refugium and from Grayling Creek and possibly East Shambow Creek for the western refugium. There are different mechanisms through which flowing water can enhance dissolved oxygen concentrations in a frozen lake. The most obvious is through the inflow of oxygenated water. Streams may not have as much respiring plants or bacteria, or decomposing organic matter to reduce oxygen concentrations. Also, streams often do not freeze over completely and may thereby remain well aerated through gas exchange with the atmosphere.

Another, less obvious mechanism involves the effect of turbulent, moving water on ice. Through continual movement past a given location, of water with temperature above freezing, turbulent water motion can create thinner ice or even open water. This effect may have been important in the western refugium during the first winter. Grayling Creek is spring-fed and often created open water in the lake around the mouth of the creek during both winters of the study. Aeration of this open water via exchange with the atmosphere probably helped maintain dissolved oxygen concentrations within an area near the creek, and this area was important as an oxygen refugium during the first winter.

Behavioral mechanisms for surviving episodes of hypoxia beneath lake ice cover include aggregation at tributary inlets, emigration from the lake, and aggregation at the ice-water interface (Magnuson and Karlen, 1970; Magnuson et al., 1985). Arctic grayling in Upper Red Rock Lake displayed one of these behavioral responses, aggregation at tributary inlets, during the winter of 1994-1995. Additionally, one radio-tagged cutthroat trout, #49.803, emigrated from the lake the second winter and was located in Red Rock Creek approximately 0.5 km from the lake (Figure 22). However, because oxygen remained high in the lake the second winter, this movement into the stream may have been related to some other, unknown factor.

Results of this study did not provide insights on how the two radio-tagged Arctic grayling found the oxygen refugia during the first winter, or the oxygen concentrations that were associated with their movement to these areas. Both Arctic grayling were already within the two oxygen refugia when their specific positions were first identified on 2 December, 1994, and d.o. was already very low in the lake by that date. The two radio-tagged Arctic grayling became confined to their respective, small, oxygen refugia areas as d.o. quickly declined to very low concentrations through the main body of the lake.

Fish movements in response to temperature gradients have been documented over a wide range of taxa, including salmonids (Javaid and Anderson, 1967; Bryan et al., 1984; Cech et al., 1990; Schurmann et al., 1991; Smale and Rabeni, 1995a). It is possible that thermal orientation may enable Arctic grayling to find the mouth of an inlet stream and thereby place itself in area with oxygenated water. Water temperatures at sites near tributary inlets during the winter of 1995-1996 were found to have significantly lower water temperatures than those at midlake sites (Table 9). Due to the limited number of data points associated with midlake sites, it was not possible to determine whether this pattern existed during 1994-1995.

Additionally, it is possible that these Arctic grayling were returning to wintering areas that they had used before. According to Mogen's (1996a) determination of sizes at different ages of Arctic grayling from Upper Red Rock Lake, Arctic graylings #49.837 and #49.867 were age III fish. Thus, each had experienced past winters and could have somehow learned the locations of these more oxygenated waters. Studies of Arctic grayling movements in coastal Alaskan streams have shown that Arctic grayling repeatedly return to the same wintering pools (those which do not freeze solid during seasonal ice cover) (West et al., 1992). Similarly, Wick and Hawkins found that individual Colorado squawfish used the same reaches of river during successive winters (1989).

Although this study was directed toward Arctic grayling, radio tags were also implanted in cutthroat trout and burbot for observations during the second winter. This was an attempt to determine whether the behavior of other species under winter oxygen stress would be similar to that of Arctic grayling, and whether these different species may also occupy the same small refuge areas. A corollary hypothesis of this study was that low dissolved oxygen may force Arctic grayling to occupy areas that would expose them to other stresses, including possible negative interspecific interactions with cutthroat trout or burbot, such as habitat competition or predation. However, the abundance of d.o. through the second winter, and the accompanying wide distribution and movements of all three species beneath ice cover, precluded comparisons of their wintering locations under conditions of oxygen stress. The severity of oxygen depletion and the behavioral distribution of Arctic grayling observed during the first winter, did suggest that other species would also occupy oxygen refugia in which Arctic grayling were also present.

Conditions observed during the second winter, of relatively high d.o. and wide distribution of fishes under ice cover, would seem less stressful to fish. High d.o. and availability of large areas for winter habitat could enhance over-winter survival, and contribute to such other aspects as reproductive success during the following spring. Such possible relationship is suggested by monitoring of adults ascending Red Rock Creek during their spawning runs of 1994, 1995, and 1996. The number of adults trapped in the creek was 116 in 1994, but declined to only 54 in 1995 (Mogen 1996a) after the severely hypoxic conditions observed in the lake in the winter of 1994-1995. After the apparently favorable wintering conditions of 1995-1996, the number of spawning adults trapped in the creek rose to 140 in 1996 (Mogen 1996b). However, other factors may be affecting these fluctuations in numbers of adults in the spawning run-- including interspecific interactions with cutthroat trout, burbot, or other species; and the potential, unknown effects of whirling disease (Myxobolus cerebralis) which was recently discovered in this population but probably has been present for a number of years (Jim Peterson, Montana Department of Fish, Wildlife and Parks, pers. comm.).

Results of this study also suggest that any factors or influences which result in increased abundance of macrophytes, including shallower water depths during summer, may contribute to more serious oxygen depletion under winter ice cover and thereby could seriously harm this unique, apparently greatly diminished, population of Arctic grayling. Reduction in depth could progress slowly, from natural processes of sedimentation or eutrophication, or could be accelerated by anthropogenic influences. Such influences could include increased sedimentation or nutrient input related to agricultural or logging practices in the drainage basin of the lake. Similar, natural or anthropogenic factors which had the effect of reducing the dissolved oxygen content of tributary inlets could reduce or eliminate oxygen refugia and, thereby, critical winter habitat for Arctic grayling and other species.

Conclusions

1. Dissolved oxygen concentrations declined rapidly under winter ice cover over Upper Red Rock Lake during the first winter of 1994-1995, and were reduced to 0.15 to 0.5 mg/l through the main body of the lake by mid to late January.
2. During this first winter, two radio-tagged Arctic grayling remained in two separate areas with higher dissolved oxygen, of generally about 2.6 to 5.0 mg/l, through the period of ice cover. These areas, which apparently provided oxygen refugia, were located around the mouths of two inlet tributaries at opposite ends of the lake, Red Rock Creek in the east and Grayling Creek in the west.
3. Dissolved oxygen concentrations remained relatively high under ice cover during the second winter, of 1995-1996, at concentrations generally greater than 5 mg/l.
4. During this second winter, radio-tagged Arctic grayling, cutthroat trout, and burbot remained widely distributed through the lake during the period of ice cover. Unlike the first winter, there was no evidence of fish being limited in distribution to small areas with higher dissolved oxygen.
5. The results thus indicate that during some winters, but not others, factors affecting Upper Red Rock Lake produce conditions that support both hypotheses: (a) that

during the period of seasonal ice cover, dissolved oxygen declines to lethal levels through most of the lake; and (b) that Arctic grayling in the lake have behavioral responses or physiological adaptations to low dissolved oxygen that enable them to survive otherwise lethal conditions. Behavioral responses were evident, but attempts to test for physiological adaptation (tolerance of low dissolved oxygen concentration) were not successful.

6. Although neither macrophyte abundance nor snow cover were measured, incidental observations suggest that differences in oxygen concentrations beneath ice cover during the two winters were related to growth and abundance of macrophyte vegetation during the preceding growing season, and to amount of snow cover over the ice.

Management Implications and Future Research

Comparison of results of this study and those by Mogen (1996a, 1996b) suggest that there could be a relation between severity of winter habitat and numbers of adult Arctic grayling ascending Red Rock Creek the following spring to spawn. Future management and study could include continued monitoring of the spawning runs into Red Rock Creek, as has now been conducted for three consecutive years, in conjunction with a program to monitor winter habitat conditions in upper Red Rock Lake. The latter could be accomplished by periodic measurements through winter of dissolved oxygen concentrations at one or more midlake sites. The results of oxygen measurements during two winters suggest that even one midlake site could provide an index of dissolved oxygen conditions through the main body of the lake. Longer-term comparisons between numbers of adult grayling in spawning runs and dissolved oxygen concentrations beneath ice cover, could provide a better indication of the extent to which severity of winter habitat affects the population of Arctic grayling.

Results of this study also suggest that any changes, natural or anthropogenic, that directly or indirectly increase abundance of macrophyte vegetation in Upper Red Rock Lake or decrease depths of the lake, could aggravate depletion of dissolved oxygen beneath ice cover and thereby detrimentally affect the welfare of the lake's unique Arctic grayling population. Increased nutrient input or shallower water depths could increase macrophyte production. Either could be produced by various factors, including deliberate manipulation of lake levels or nutrient availability to manage habitat for waterfowl; accelerated sediment input from increased grazing or logging within the drainage; or natural processes affecting sedimentation and eutrophication from within the lake and from its drainage. Future study could focus on the relationship of these and other variables on macrophyte productivity and abundance, and on the relationship between macrophyte production and abundance on dissolved oxygen levels beneath ice cover of the following winter. If causal relationships are demonstrated, then management practices could be designed, within the lake or in its drainage, to control macrophyte productivity or slow the rate of reduction in lake depth.

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APPENDICES

APPENDIX A

DEPTH CONTOURS OF UPPER RED ROCK LAKE
(FROM NEITHAMMER, 1993)

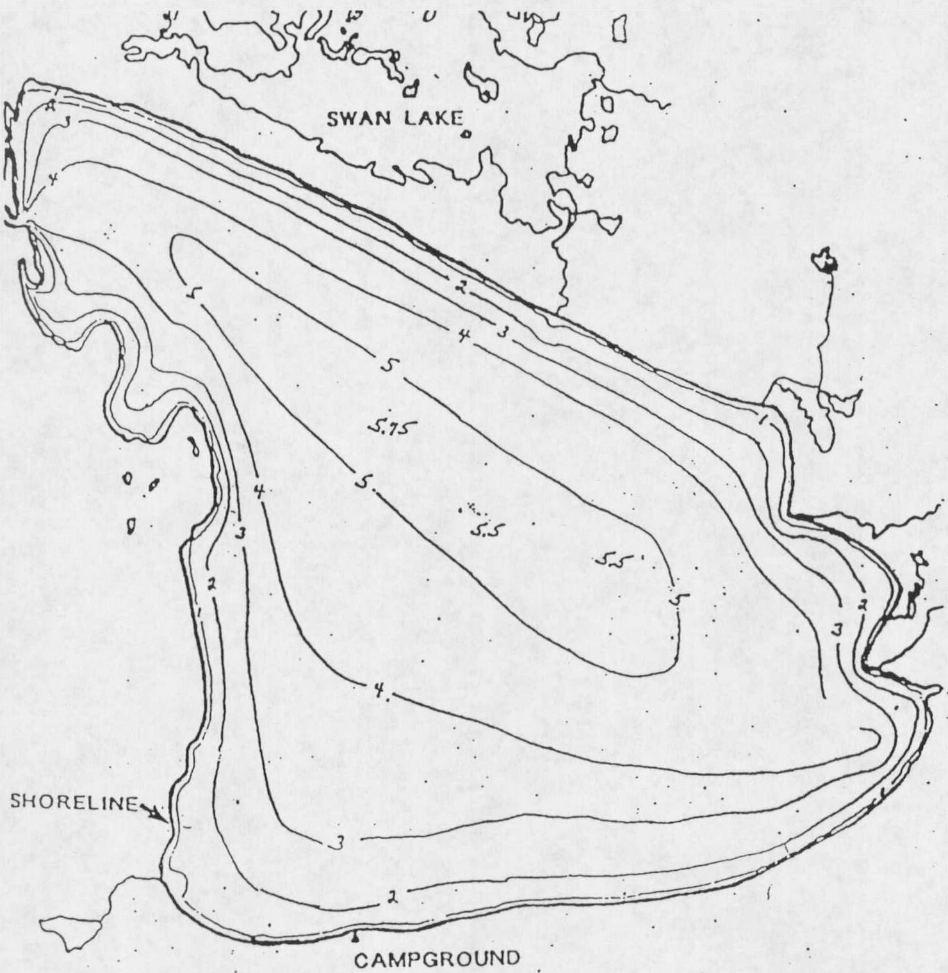

Figure 1. 1993 Depths in Upper Red Rock Lake. One foot contour interval. (Neithammer 1993)

APPENDIX B

HOOP NETTING RESULTS, AND WINTER HABITAT MEASUREMENTS AT SAMPLING SITES ON UPPER RED ROCK LAKE.

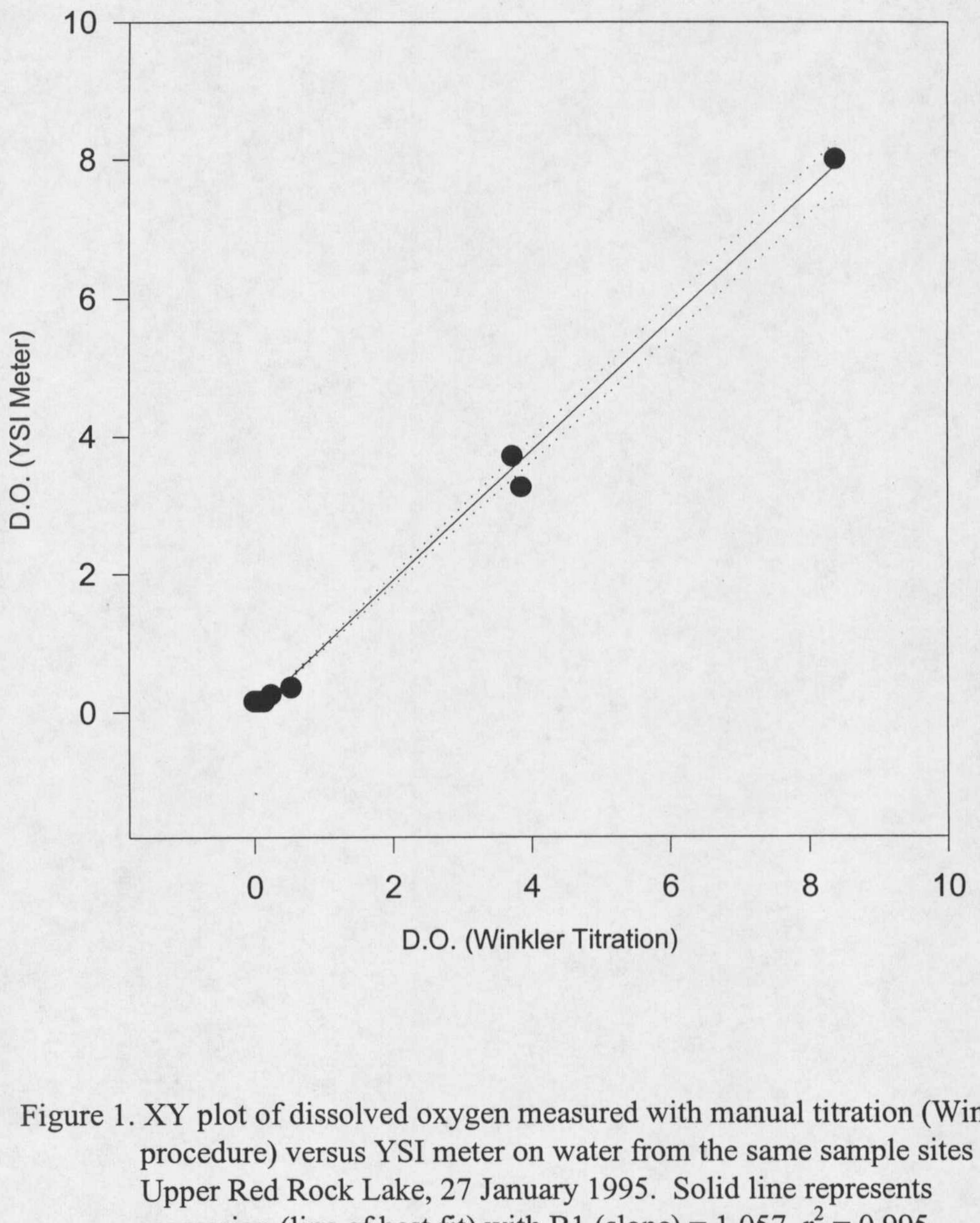

Figure 1. XY plot of dissolved oxygen measured with manual titration (Winkler procedure) versus YSI meter on water from the same sample sites on Upper Red Rock Lake, 27 January 1995. Solid line represents regression (line of best fit) with B1 (slope) = 1.057, $r^2 = 0.995$. Dashed lighter line represents 95% confidence interval. Units = mg/l.

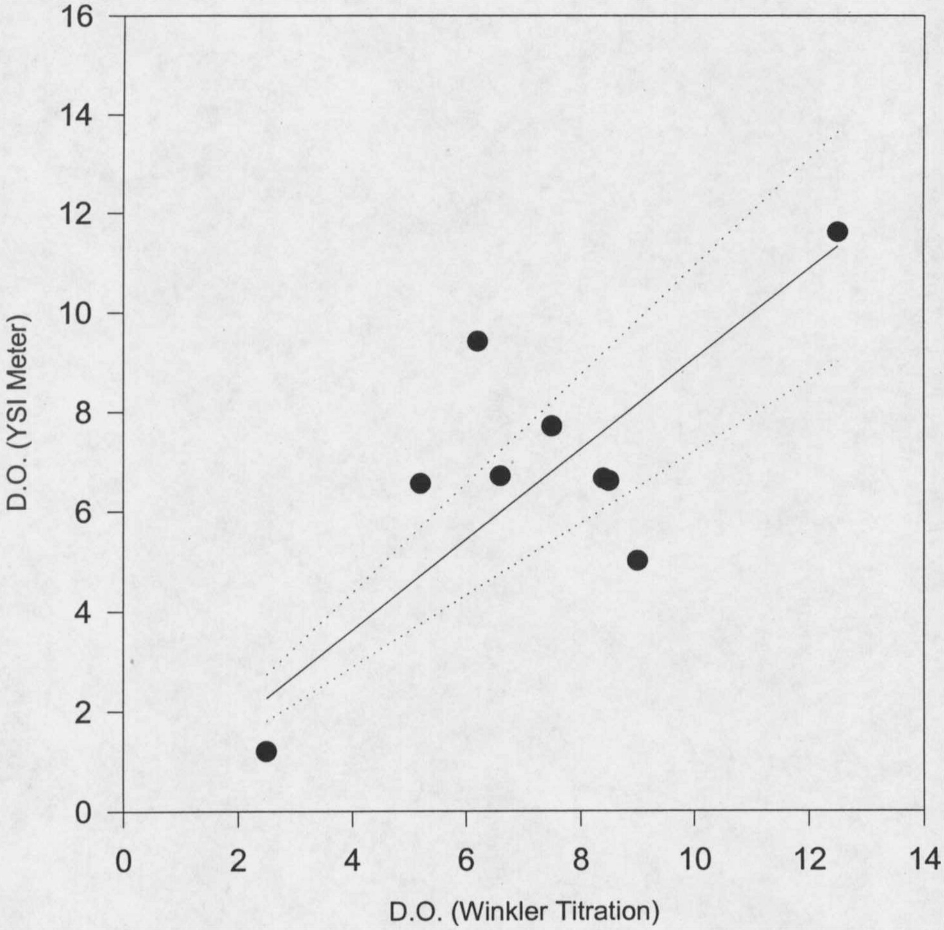

Figure 2. XY plot of dissolved oxygen measured with manual titration (Winkler procedure) versus YSI meter, on water from the same sample sites on Upper Red Rock Lake, winter 1995-1996. Solid line represents regression (line of best fit) with B1 (slope) = 0.910, r^2 = 0.531. Dashed lighter line represents 95 % confidence interval. Units = mg/l.

Table 1. Results of hoop netting on Upper Red Rock Lake, 13 October 1994 and 6 August-29 September 1995. Hoop nets were set end to end and left overnight. Total numbers of burbot and white suckers captured on 29 September were not recorded.

Date	Location	Species	Number
13 October, 1994	Grayling Creek	burbot	143
		white sucker	33
		cutthroat trout	1
	Red Rock Creek	burbot	36
		white sucker	56
		cutthroat trout	3
		mottled sculpin	1
6 August, 1995	Red Rock Creek	burbot	15
		white sucker	410
		cutthroat trout	2
		longnose sucker	1
9 August, 1995	midlake	burbot	15
		white sucker	139
		Arctic grayling	4
		cutthroat trout	2
13 August, 1995	Red Rock Creek	burbot	20
		white sucker	42
		Arctic grayling	2
		longnose sucker	1
14 August, 1995	Red Rock Creek	burbot	13
		white sucker	43
16 August, 1995	Tom Creek	burbot	53
		white sucker	5
		cutthroat trout	2
22 September, 1995	Red Rock Creek	burbot	6
		white sucker	54
		cutthroat trout	1
29 September, 1995	midlake	burbot	6
		white sucker	> 20
29 September, 1995	Elk Springs Creek	burbot	> 12
		white sucker	77
		cutthroat trout	2

Table 2. Dissolved oxygen (mg/l) at the top (T) and bottom (B) of the water column, water temperature (°C) at the top (T) and bottom (B) of the water column, total water depth (m), and ice thickness (m). Upper Red Rock Lake, winter 1994-995.

Date	Location	D.O. (T)	D.O. (B)	Temp (T)	Temp (B)	Water	Ice
2 Dec., 1994	Grayling Creek	4.1	---	1.5	---	0.7	0.3
	Red Rock Creek	6.1	---	1.0	---	1.25	0.3
	mid-lake	2.2	---	1.6	---	1.6	0.35
	lake outlet	2.9		1.6	---	1.0	0.2
16 Jan., 1995	lake outlet	0.4	---	0.3	---	1.0	0.6
	lake outlet	---	---	---	---	0.7	0.5
	lake outlet	0.51	---	0.5	---	1.0	0.5
	Red Rock Creek	7.6	---	0.2	---	0.62	0.55
	Red Rock Creek	0.3	2.5	0.7	2.0	1.38	0.45
	mid-lake	0.5	0.25	1.0	3.0	1.63	0.4
	Grayling Creek	2.75	2.6	0.1	---	1.0	0.45
27 Jan., 1995	Grayling Creek	3.7	3.3	---	---	1.20	0.42
	lake outlet	0.25	---	1.0	---	0.91	0.49
	lake outlet	0.15	---	0.3	---	1.0	0.40
	lake outlet	0.15	---	0.3	---	1.07	0.38
	lake outlet	0.15	---	0.3	---	0.65	0.38
	mid-lake	0.2	---	0.3	---	0.85	0.55
	mid-lake	0.35	0.25	0.95	1.1	1.58	0.53
	mid-lake	0.15	0.13	0.6	1.0	1.58	0.5
	mid-lake	0.2	---	0.5	1.6	1.54	0.54
	Red Rock Creek	7.5	---	0.1	---	0.71	0.60
	Red Rock Creek	8.0	---	0.1	---	0.93	0.62
	Red Rock Creek	7.2	---	0.1	---	0.5	0.45
	Red Rock Creek	7.5	7.0	0.1	---	1.17	0.58
	Red Rock Creek	3.25	1.4	0.1	---	1.42	0.50
	mid-lake	0.3	---	0.9	2.1	1.65	0.60
	mid-lake	0.25	0.20	0.5	2.5	1.72	0.52
	mid-lake	0.25	---	0.45	2.1	1.84	0.49

Table 2-Continued

Date	Location	D.O. (T)	D.O. (B)	Temp (T)	Temp (B)	Water	Ice
10 Feb., 1995	Grayling Creek	8.5	8.5	3.0	---	0.3	0
	Grayling Creek	6.2	6.2	1.0	---	0.88	0.4
	Grayling Creek	1.3	0.45	0.1	2.0	1.42	0.7
	lake outlet	0.25	0.30	0.5	---	0.9	0.2
	Red Rock Creek	8.4	7.5	0.0	---	1.2	0.7
25 Feb., 1995	lake outlet	1.2	---	1.5	---	0.8	0.60
	lake outlet	0.6	---	0.2	---	1.05	0.35
	lake outlet	0.35	0.50	0.3	---	1.05	0.30
	lake outlet	0.3	---	0.3	---	1.07	0.32
	lake outlet	0.45	---	0.1	---	1.1	0.35
	lake outlet	1.2	---	0	---	0.55	0.42
	lake outlet	0.6	---	1.0	---	0.95	0.37
	Grayling Creek	10.2	---	2.4	---	---	---
	Grayling Creek	9.8	---	2.8	---	---	---
	Grayling Creek	10.1	---	2.8	---	---	---
	Red Rock Creek	7.7	---	0.1	---	0.82	0.6
	Red Rock Creek	6.9	---	0.7	---	1.04	0.75
	Red Rock Creek	7.8	---	0.5	---	1.22	0.68
	Red Rock Creek	7.2	3.1	0.9	---	1.29	0.45
	Red Rock Creek	3.6	0.3	0.9	---	1.5	0.32
	Grayling Creek	7.9	---	2.3	---	0.6	0.40
	Grayling Creek	7.75	---	---	---	0.72	0.37
	Grayling Creek	7.3	---	1.2	---	0.79	0.02
	Grayling Creek	7.4	7.7	1.9	---	0.85	0.52
	Grayling Creek	6.2	7.9	0.8	1.5	1.04	0.49
31 Mar., 1995	lake outlet	3.3	0.95	1.2	3.0	1.01	0.28
	lake outlet	3.1	1.8	0.95	3.0	1.19	0.53
	Red Rock Creek	8.3	---	1.3	---	0.82	0.77
	Red Rock Creek	5.6	1.3	0.8	2.0	1.69	0.43
	mid-lake	4.4	0.7	1.0	3.2	1.87	0.72
	mid-lake	4.4	0.8	0.9	3.5	2.03	0.55
	mid-lake	5.0	0.5	1.8	4.5	2.04	0.69
	mid-lake	3.2	0.8	1.1	3.6	1.84	0.49

Table 3. Dissolved oxygen (mg/l) at the top (T) and bottom (B) of the water column, water temperature (°C) at the top (T) and bottom (B) of the water column, and total water depth (m). Upper Red Rock Lake, summer 1995.

Date	Location	D.O. (T)	D.O. (B)	Temp. (T)	Temp (B)	Depth
18 July	Red Rock Crk.	9.5	---	18.2	---	---
2 August	Red Rock Crk.	9.5	---	13.0		
	Grayling Crk.	8.2	7.6	18.0	18.0	1.65
	Lake outlet	9.6	8.4	20.0	20.0	1.22
4 August	West lake	8.2	8.8	19.0	18.0	1.90
	West lake	8.3	11.1	19.0	18.7	1.54
	Lake outlet	11.4	11.4	19.9	19.9	1.20
	Mid-lake	10.1	10.2	19.0	19.2	1.75
	Mid-lake	7.8	7.9	19.2	19.0	1.70
	Mid-lake	8.5	8.2	19.3	19.1	1.60
	Mid-lake	9.8	11.3	19.2	19.0	1.68
14 August	E. lake off Red Rock Crk.	8.3	8.6	16.7	14.3	1.98
	South midlake	8.8	8.0	16.1	14.5	2.08
	Grayling Crk.	10.4	10.5	15.8	15.0	1.95
	West shore	9.3	8.8	16.0	15.8	1.77
	Outlet	12.9	13.1	17.2	17.0	1.10
15 August	Tom Crk. Bay	11.1	11.0	16.5	16.7	1.30
	South of Red Rock Creek	9.4	9.5	16.5	16.1	1.57
	E. lake off Red Rock Crk.	9.2	10.2	16.0	14.9	1.60

Table 4. Dissolved oxygen (D.O.; mg/l) at the top (T) and bottom (B) of the water column, water temperature (°C) at the top (T) and bottom (B) of the water column, total water depth (m) and ice thickness (m) at sampling stations. Stations are designated by three letter abreviation. Upper Red Rock Lake, winter 1995-1996.

Date	Location	D.O. (T)	D.O. (B)	Temp (T)	Temp (B)	Water	Ice
9 January	GRC	10.80	11.50	1.20	1.20	0.40	0.20
	OUT	15.80	15.80	0.70	0.70	---	0.00
	WML	6.40	5.10	1.00	1.90	1.37	0.25
	NML	6.40	3.35	1.0	2.00	1.55	0.25
	MEL	7.20	4.80	0.80	1.80	1.64	0.25
	EML	7.40	4.00	1.00	2.60	1.55	0.24
	BSS	7.80	3.70	1.00	3.00	1.70	0.26
	CGS	6.50	2.20	1.00	2.90	1.82	0.25
23 January	WML	6.30	4.75	1.10	2.10	1.40	0.38
	NML	7.20	6.70	1.30	3.10	1.50	0.30
	MEL	6.70	6.40	1.10	3.00	1.62	0.35
	EML	6.40	0.80	1.00	3.00	1.59	0.35
	BSS	6.40	4.80	2.00	3.80	1.68	0.35
	CGS	6.40	4.80	2.00	3.80	1.85	0.34
	RRC	7.70	7.70	0.10	0.10	0.70	0.25
	ESC	5.60	5.10	0.20	0.50	0.85	0.43
23 January	OUT	6.30	6.30	0.30	0.30	0.38	0.05
	GRC	9.20	9.20	0.20	0.20	0.52	0.32
6 February	GRC	11.30	11.30	0.25	0.25	0.62	0.40
	OUT	1.20	1.20	0.50	0.50	0.61	0.20
	ESC	3.80	3.80	0.10	0.10	0.87	0.47
	RRC	5.70	5.70	0.10	0.10	0.82	0.48
	EML	9.40	6.50	2.00	4.00	1.62	0.43
	MEL	8.50	6.60	1.50	3.00	1.67	0.43
	CGS	7.60	7.80	3.00	3.50	1.88	0.43
	BSS	8.10	0.25	2.00	3.70	1.75	0.42
	NML	7.50	6.45	0.90	3.00	1.61	0.50
	WML	6.55	5.05	0.80	2.20	1.43	0.45
20 February	WML	7.27	---	1.00	3.00	1.48	0.43

Table 4-Continued

Date	Location	D.O. (T)	D.O. (B)	Temp (T)	Temp (B)	Water	Ice
20 February	NML	11.30	---	1.00	3.20	1.65	0.51
	BSS	10.10	---	2.00	4.00	1.85	0.32
	CGS	12.50	---	2.00	4.50	1.90	0.40
	MEL	10.4	0.35	1.00	3.95	1.72	0.48
	EML	12.0	---	2.00	2.00	1.62	0.38
	RRC	8.40	---	0.00	0.00	0.70	0.50
	ESC	6.20	---	0.10	0.10	0.89	0.50
	OUT	---	---	2.00	2.00	---	0.00
	GRC	---	---	1.80	1.80	0.65	0.30
4 March	GRC	9.80	9.80	0.20	0.20	0.75	0.42
	OUT	---	---	---	---	---	0.00
	ESC	5.00	5.00	0.60	0.60	1.00	0.70
	RRC	7.20	7.20	0.50	0.50	0.75	0.55
	EML	---	0.25	2.00	4.60	1.68	0.38
	MEL	9.80	7.30	1.00	3.90	1.82	0.63
	CGS	12.30	11.80	2.80	4.50	1.97	0.40
18 March	NML	10.90	0.20	1.30	3.20	1.79	0.67
	WML	9.60	6.25	0.90	2.50	1.60	0.62
	WML	5.00	6.10	0.95	2.70	1.54	0.52
	NML	6.70	11.40	1.80	4.00	1.75	0.58
	CGS	13.20	8.45	2.50	4.90	2.03	0.42
	MEL	6.65	11.80	1.00	4.00	1.82	0.57
	EML	11.60	14.00	1.20	5.00	1.72	0.41
	RRC	9.00	9.00	0.20	0.20	0.68	0.58
	GRC	8.40	8.40	2.70	2.70	0.68	0.38