Effects of predation on status of Arctic grayling at Red Rock Lakes National Wildlife Refuge, Montana
by Laura Marie Katzman

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in Fish and Wildlife Management
Montana State University

Abstract:
Arctic grayling have undergone a recent decline in abundance at Red Rock Lakes National Wildlife Refuge. Predation by other fish species is a potential factor influencing this decline. I quantified predation on early life stages of Arctic grayling in Red Rock Creek and Upper Red Rock Lake in 1995 and 1996. No Arctic grayling eggs were found in the stomach contents of mottled sculpin, white suckers, and juvenile Yellowstone cutthroat trout x rainbow trout hybrids captured in 1995 and 1996. The diet of brook trout and adult cutthroat hybrids was 0.1% and 0.2% by weight Arctic grayling eggs, respectively, which was an estimated 2.0% and 34.2% of the Arctic grayling eggs available in 1995. The diet of brook trout was 2.3% by weight Arctic grayling eggs in 1996 or 14.1% of those available. No age-0 Arctic grayling were found in the stomach contents of brook trout or juvenile Yellowstone cutthroat trout x rainbow trout hybrids captured in 1995 and 1996. The diet of mottled sculpin was 0.2% by weight age-0 Arctic grayling in 1996 or 5.9% of those available. No juvenile Arctic grayling were found in the stomach contents of burbot, brook trout, and Yellowstone cutthroat trout x rainbow trout hybrids captured in Upper Red Rock Lake. In addition, the potential predators did not aggregate at the mouth of Red Rock Creek during the age-0 grayling outmigration.

Burbot are one of the potential predators of Arctic grayling in Upper Red Rock Lake and investigations into the age structure and growth rates of burbot have been limited in Montana. Age and growth data is necessary to determine the effects of predation by a population. Thus, I collected this information on Red Rocks burbot. The oldest burbot captured was 10 years old, the longest 906 mm, and the heaviest 5.5 kg.

The proportional stock density was 66 indicating a balanced population. Burbot grew more rapidly in summer than winter. Burbot otoliths formed opaque zones during fall and winter, opposite most temperate latitude fish species which form opaque zones in spring and summer. The opaque zone has often been associated with the period of fast growth, but the translucent zone was laid down during the period of fast growth for burbot at Red Rocks. Burbot captured were generally in good condition with mean relative weights ranging from 88 to 126 over all length classes and seasons in 1996.

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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

Arctic grayling have undergone a recent decline in abundance at Red Rock Lakes National Wildlife Refuge. Predation by other fish species is a potential factor influencing this decline. I quantified predation on early life stages of Arctic grayling in Red Rock Creek and Upper Red Rock Lake in 1995 and 1996. No Arctic grayling eggs were found in the stomach contents of mottled sculpin, white suckers, and juvenile Yellowstone cutthroat trout x rainbow trout hybrids captured in 1995 and 1996. The diet of brook trout and adult cutthroat hybrids was 0.1% and 0.2% by weight Arctic grayling eggs, respectively, which was an estimated 2.0% and 34.2% of the Arctic grayling eggs available in 1995. The diet of brook trout was 2.3% by weight Arctic grayling eggs in 1996 or 14.1% of those available. No age-0 Arctic grayling were found in the stomach contents of brook trout or juvenile Yellowstone cutthroat trout x rainbow trout hybrids captured in 1995 and 1996. The diet of mottled sculpin was 0.2% by weight age-0 Arctic grayling in 1996 or 5.9% of those available. No juvenile Arctic grayling were found in the stomach contents of burbot, brook trout, and Yellowstone cutthroat trout x rainbow trout hybrids captured in Upper Red Rock Lake. In addition, the potential predators did not aggregate at the mouth of Red Rock Creek during the age-0 grayling outmigration.

Burbot are one of the potential predators of Arctic grayling in Upper Red Rock Lake and investigations into the age structure and growth rates of burbot have been limited in Montana. Age and growth data is necessary to determine the effects of predation by a population. Thus, I collected this information on Red Rocks burbot. The oldest burbot captured was 10 years old, the longest 906 mm, and the heaviest 5.5 kg. The proportional stock density was 66 indicating a balanced population. Burbot grew more rapidly in summer than winter. Burbot otoliths formed opaque zones during fall and winter, opposite most temperate latitude fish species which form opaque zones in spring and summer. The opaque zone has often been associated with the period of fast growth, but the translucent zone was laid down during the period of fast growth for burbot at Red Rocks. Burbot captured were generally in good condition with mean relative weights ranging from 88 to 126 over all length classes and seasons in 1996.

CHAPTER 1

GENERAL INTRODUCTION

Two geographically isolated and genetically divergent populations of Arctic grayling *Thymallus arcticus* historically occurred south of Canada and Alaska in Michigan and Montana (Kaya 1992). The Michigan population was extirpated in about 1936 (McAllister and Harrington 1969). In Montana, only three indigenous stocks remain (Kaya 1992). One is fluvial, consisting of less than 2000 individuals (Kaya 1992) in the Big Hole River. The Big Hole River population was recently petitioned for listing as endangered. Another population, in the Madison River in the vicinity of Ennis Reservoir is adfluvial, but occupies a manmade reservoir. The only known indigenous lacustrine population of Arctic grayling in the contiguous United States inhabits the Upper and Lower Red Rock Lakes of Red Rock Lakes National Wildlife Refuge. This genetically unique population of Arctic grayling has undergone a recent decline in abundance. Historically, thousands of Arctic grayling spawned in 12 streams of the upper Centennial Valley (Nelson 1954; U. S. Fish and Wildlife Service 1978; Unthank 1989), but by 1976 spawning appeared to be limited to Odell and Red Rock creeks (Unthank 1989). In 1994, only 10 spawners were trapped in Odell Creek (Mogen 1996a), and only 241, 85, and 140 spawners were trapped in Red Rock Creek in 1994, 1995, and 1996, respectively (Mogen 1996b).

Postglacial salmonid communities are typically fragile and highly susceptible to disruption or destruction by habitat changes and introductions (Behnke 1972). Habitat degradation, water diversions, and introduced species have likely contributed to the decline of Arctic grayling at Red Rocks (Nelson 1954; Unthank 1989). Overgrazing of riparian vegetation resulted in bank erosion, which increased sedimentation and adversely affected spawning habitat and egg survival. Water diversions dewatered streams and resulted in the loss of large numbers of grayling when they became stranded in diversion ditches (U. S. Fish and Wildlife Service 1978). All streams in Montana from which Arctic grayling have disappeared contain one or more introduced salmonids including rainbow trout *Oncorhynchus mykiss*, brook trout *Salvelinus fontinalis,* and brown trout *Salmo trutta*, and repeated attempts to reintroduce grayling where these species are abundant have failed (Kaya 1990). The Arctic grayling population declined at Red Rock Lakes National Wildlife Refuge subsequent to the introduction of rainbow trout in 1899 and brook trout in 1915 (Nelson 1954).

A combination of habitat changes and introduced species may have enhanced sizes and abundances of predatory fish. Predation could thereby be contributing to the decline and may be precluding the recovery of Arctic grayling at Red Rock Lakes National Wildlife Refuge. Potential introduced predators of Arctic grayling include Yellowstone cutthroat trout *Oncorhynchus clarki bouvieri* x rainbow trout *O. mykiss* hybrids and brook trout. Native potential predators include burbot *Lota lota,* mottled sculpin *Cottus bairdi*, white suckers *Catostomus commersoni*, and longnose suckers *Catostomus catostomus.* Yellowstone cutthroat trout x rainbow trout hybrids are large at Red Rocks; all adult cutthroat hybrids trapped in Red Rock Creek during the spawning runs of 1994, 1995, and 1996 exceeded 300 mm in total length (TL) (Mogen 1996b).

Cutthroat hybrids have attained lengths up to 795 mm TL and weights up to 6.1 kg at Red Rocks (Mogen 1996b). Cutthroat hybrids have increased in abundance since the 1960s; only 34 cutthroat hybrids were caught at a weir operated in 1963 (U. S. Fish and Wildlife Service 1978), but by 1996, 438 were caught at a weir (Mogen 1996b). Large brook trout up to 483 mm TL and 1.7 kg in weight inhabit Upper Red Rock Lake (this study) and brook trout outnumbered Arctic grayling caught by anglers in the 1930s and 1940s (U. S. Fish and Wildlife Service 1978). Burbot are abundant in Upper Red Rock Lake and attain lengths up to 906 mm and weights up to 5.5 kg.

I examined the potential role of predation in the decline of Red Rocks Arctic grayling. Most of the Arctic grayling remaining at Red Rock Lakes National Wildlife Refuge spawn in Red Rock Creek. Therefore, I examined predation on Arctic grayling eggs and age-0 Arctic grayling in Red Rock Creek (Chapter 2). I also investigated predation on juvenile Arctic grayling in Upper Red Rock Lake (Chapter 3).

An important native piscivore in Upper Red Rock Lake is the burbot. Although burbot have palatable and nutritious flesh, they have generally been regarded by sport fishermen as "rough" fish (Scott and Crossman 1973; Becker 1983; Nelson and Paetz 1992). Because of this lack of interest by fishermen, fishing regulations for burbot have generally been liberal until recently and little has been learned about burbot. Bag limits on burbot were set for the first time in the central and eastern fishing districts of Montana in 1994 (Montana Department of Fish, Wildlife, and Parks 1994) and little has been learned about burbot in Montana. Biological information on burbot is necessary to determine the effects of their predation on Arctic grayling. Many recent studies have used bioenergetics to quantify predation (Ruggerone and Rogers 1992; Beauchamp 1995; Beauchamp et al. 1995; Rudstam et al. 1995). The model requires growth data to generate consumption estimates and information on age structure is necessary to apply the consumption estimates to a population. Because burbot are a potential predator of Arctic grayling and little data on burbot exists in Montana, I collected biological information such as the age structure and growth rates of burbot in Upper Red Rock Lake (Chapter 4).

Goals of my study were to (1) quantify the mortality of Arctic grayling eggs and age-0 Arctic grayling in Red Rock Creek caused by predation, (2) quantify the mortality of juvenile Arctic grayling in Upper Red Rock Lake caused by predation, and (3) determine the age structure and growth rates of burbot in Upper Red Rock Lake.

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CHAPTER 2

EFFECTS OF PREDATION ON ARCTIC GRAYLING EGGS AND AGE-0 ARCTIC GRAYLING IN RED ROCK CREEK

Introduction

Arctic grayling *Thymallus arcticus* have undergone a recent decline in abundance at Red Rock Lakes National Wildlife Refuge. Predation by other fish species is a potential factor influencing this decline (Chapter 1). The high fecundity of fishes implies a high rate of mortality during the egg or larvae stage of life (Braum 1978). Streambed conditions (e.g., sedimentation) can decrease salmonid egg survival (Beschta and Platts 1986; Everest et al. 1987) and stochastic events such as high discharge can reduce survival of eggs and early larval stages (Strange et al. 1992). Starvation caused by the inability of larvae to procure food when they shift from yolk to exogenous food causes additional mortality (Braum 1978). Recently, increasing importance has been placed on predation as the primary cause of mortality of fish eggs and larvae (Rothschild 1986; Bailey and Houde 1989).

Five potential piscivorous fishes either reside in Red Rock Creek or migrate to Red Rock Creek from Upper Red Rock Lake to spawn during the period of Arctic grayling spawning and emergence. Some introduced juvenile Yellowstone cutthroat trout *Oncorhynchus clarki bouvieri* x rainbow trout *O. mykiss* hybrids rear in Red Rock Creek, but most adult cutthroat hybrids reside in Upper Red Rock Lake and only enter Red Rock Creek during their spawning run. Other potential predators in Red Rock Creek are nonnative brook trout *Salvelinus fontinalis* and native mottled sculpin *Cottus bairdi*. Potential migratory predators are adult Yellowstone cutthroat trout x rainbow trout hybrids and native white suckers *Catostomus commersoni*.

Rainbow trout, brook trout, suckers, and sculpin are common fish egg predators (Ellis and Roe 1917; White 1930; Dineen 1951; Becker 1983; Dion and Whoriskey 1993; Biga 1996). Brook trout have been documented to consume Arctic grayling eggs in Red Rock Creek (Nelson 1954).

Predation can be an important source of mortality for juvenile fish (Ruggerone and Rogers 1992; Beauchamp et al. 1995; Gibson and Robb 1996). Rainbow trout, cutthroat trout, and sculpin prey upon juvenile salmonids (Ricker 1941; Hunter 1959; McCart 1967; Foerster 1968; Tabor and Chan 1996). Brook trout have been reported to eat age-0 Arctic grayling at Red Rocks (Nelson 1954) and in the Big Hole River drainage (Streu 1990). Predatory fish consume large numbers of migratory age-0 fish as they move to nursery lakes (Foerster 1968; Beauchamp 1995). Two- to three-week-old Arctic grayling migrate from Red Rock Creek to Upper Red Rock Lake and may be especially vulnerable to predation during this time.

I quantified predation on early life stages of Arctic grayling in Red Rock Creek. Specific objectives of the study were to (1) determine the temporal availability of Arctic grayling eggs and age-0 Arctic grayling to predators in Red Rock Creek, (2) identify predators of Arctic grayling eggs and age-0 Arctic grayling in Red Rock Creek, (3) quantify consumption of Arctic grayling eggs and age-0 Arctic grayling by predators in Red Rock Creek, and (4) estimate the mortality of Arctic grayling eggs and age-0 Arctic grayling caused by predation in Red Rock Creek.

Study Site

Red Rock Creek is a third-order headwater of the Missouri River located in the Centennial Valley of southwestern Montana. The creek flows out of the Centennial Mountains, which rise over 3,000 m, forming the Continental Divide, the southern border of the Centennial Valley, and the Montana-Idaho boundary. Red Rock Creek flows into Upper Red Rock Lake, which lies at an elevation of 2,015 m. After leaving Upper Red Rock Lake, the creek flows to Lower Red Rock Lake, downstream of which it is called the Red Rock River.

Throughout most of its length, Red Rock Creek meanders over a gentle gradient. In my study area, from the mouth of Red Rock Creek in Upper Red Rock Lake to the confluence of Corral Creek, Red Rock Creek has a sinuosity of 2.0, a gradient of 0.1%, and an average width of 7 m.

Red Rock Creek flows through various land ownership and riparian vegetation before entering Upper Red Rock Lake. Red Rock Creek originates in timbered National Forest, flows through state land, and then through heavily grazed private property where riparian vegetation is primarily sage *Artemisia* spp. Next the creek flows through more state land, which is also grazed, but where willow *Salix* spp. dominates the riparian vegetation. Finally, Red Rock Creek enters Red Rock Lakes National Wildlife Refuge where both wetlands and *Salix* spp. make up the riparian zone. Most of my study area lies inside Refuge boundaries. Red Rock Lakes National Wildlife Refuge was established in 1935 for the protection and maintenance of trumpeter swans *Cygnus buccinator* and other waterfowl.

Native fish species other than those mentioned previously and that occur in low numbers in Red Rock Creek include longnose suckers *Catostomus catostomus*, burbot *Lota lota,* mountain whitefish *Prosopium williamsoni*, and long-nosed dace *Rhinichthys cataractae*.

Methods

Temporal Availability of Arctic Grayling Eggs and Age-0 Arctic Grayling to Predation in Red Rock Creek

Arctic grayling eggs were vulnerable to predation from the onset of spawning until the eggs hatched. The timing of spawning was determined by monitoring the spawning migration, temperature, and flow.

The spawning migration was monitored daily by censusing the numbers of Arctic grayling that moved through a weir located just upstream of the Elk Lake Road bridge (Mogen 1996a, 1996b) (Figure 2.1). Spawning occurred between the peak of upstream and downstream movements in 1994 (Mogen 1996a) and I assumed similar spawning timing related to peak upstream movements through the weir in 1995 and 1996.

Temperature and flow data were examined to help determine when Arctic grayling spawned because no clearly defined peak in their downstream movement through the weir was evident in 1995 and their downstream movement was not monitored in 1996. Spawning of lacustrine populations of Arctic grayling in Montana usually occurs during high flows at stream temperatures between 4.4°C and 10.0°C (Kaya 1990). The peak spawning of Arctic grayling in Red Rock Creek in 1994 occurred during peak runoff at mean daily temperatures ranging from 5.0 to 11.0°C (Mogen 1996a). Mean daily water temperatures were measured with an electronic temperature logger near the known spawning area in Red Rock Creek [between the confluences of Antelope (13.4 km from the mouth of Red Rock Creek) and Corral creeks (14.6 km from the mouth of Red Rock Creek) (Mogen 1996a) (Figure 2.1)]. Flow information was obtained from Mogen (1996a, 1996b).

Degree-days were calculated with temperature logger data to estimate when Arctic grayling eggs initiated hatching. The shortest time reported in the literature required for hatching is 133 degree-days (Nelson 1954) and for emergence is 3 days (Kaya 1990). Therefore, I estimated that emergence began when 133 degree-days plus 3 days elapsed after the estimated initiation of spawning.

I attempted to confirm the timing of the emergence of Arctic grayling and of their migration from the creek to the lake by drift netting, dip netting, and seining. This helped me determine when age-0 Arctic grayling were available to predation in the creek.

Each 1-m long drift net used to sample larval Arctic grayling was constructed of 0.5-mm nylon mesh with a 30 x 60 cm opening that tapered down to a 1-mm mesh collection box with baffles. Drift nets were placed below the known Arctic grayling spawning area, below the Elk Lake Road bridge, and at the mouth of Red Rock Creek in 1995. In these areas, nets were placed in backwater pools, inside margins of glides, and in glides at all times of the day from early morning until 2 h after dark. The drift nets were fished for durations varying from 15 minutes to 2 days on 11 occasions from late June until early July 1995.

Drift netting was attempted again in 1996. One drift net was placed just below the known Arctic grayling spawning area and another just upstream of the Elk Lake Road bridge. The drift nets were placed in the thalweg of riffles (Mogen 1996a) and checked daily during the week of estimated emergence in late June and every 3 days during the following week in early July 1996.

Seining was conducted in 1995 in an 8-km reach of Red Rock Creek that contains gravel substrates of sizes preferred by Arctic grayling for spawning (Nelson 1954) (Figure 2.1). The seine was 1.2 m in height and 4.4 m in length with 1.6-mm mesh. The 8-km reach extended from 1.5 km below the Elk Lake Road bridge upstream to the confluence of Corral Creek. The reach was divided into three 2.7-km units. Sampling took place in one or two randomly-selected locations (located with a global positioning system instrument) within each of the 2.7-km units. Two seine hauls were conducted at the first four areas with backwater or slow-water downstream of each randomly selected location. Seining was conducted weekly from late June (when eggs were estimated to have begun hatching) until age-0 Arctic grayling began migrating to the lake in late July 1995.

In addition, sampling with the 4.4-m seine occurred in both the known spawning area and near the weir just upstream of the Elk Lake Road bridge. Sampling was conducted in four areas with backwater or slow-water in each location weekly from late June until late July 1995.

Red Rock Creek was floated once from the Elk Lake Road bridge to its mouth after detection of age-0 Arctic grayling in the margins of the mouth of Red Rock Creek in late July 1995. Backwater or slow-water habitat was sampled with a dip net (1-mm mesh) and the 4.4-m seine at 10-minute intervals of floating time. The margins of the mouth of Red Rock Creek were also dip netted and seined twice weekly for 2 weeks upon detection of age-0 Arctic grayling there.

Red Rock Creek was floated and sampled with the dip net and seine weekly during the estimated creek residency of age-0 Arctic grayling in July 1996. Four dip net hauls and two seine hauls were conducted at 10-minute intervals of floating time in backwater or slow-water habitat, in oxbows, at the creek mouth, and in the lake margin around the mouth of Red Rock Creek during each float. The first float began at the known Arctic grayling spawning area and ended at the mouth of Red Rock Creek. Successive floats proceeded from the Elk Lake Road bridge to the mouth of Red Rock Creek.

A 30-m seine was used at the mouth of Red Rock Creek in Upper Red Rock Lake to determine when age-0 Arctic grayling entered the lake. This seine consisted of 6.4-mm mesh and was 1.2 m in height. Seining was conducted north of the mouth (within 200 m of the mouth) in late August, mid-September, and early October 1995. Three seine hauls were conducted at 0300, 0900, 1500, and 2100 h each month to assess diel variation in age-0 Arctic grayling abundance.

Seining was conducted at the mouth of Red Rock Creek during the estimated age-0 Arctic grayling migration in July 1996 and continued until the grayling dispersed from the vicinity of the mouth in late August 1996. Seining also occurred after the migration in late September 1996. One seine haul was pulled across the mouth of the creek and two others were pulled north of the mouth of the creek (within 200 m of the mouth) just after sunset each sampling night. Seining occurred at dusk because grayling migrate downstream during darkness (Bardonnet et al. 1993) and all age-0 Arctic grayling captured by seining in 1995 were taken during darkness.

The duration of the stream residency of age-0 grayling captured at the mouth of Red Rock Creek in 1996 was estimated to determine their temporal availability to predation in Red Rock Creek. A regression of the total lengths of age-0 Arctic grayling captured in Red Rock Creek and at its mouth in July and August on time in days was used to determine the mean weekly growth rate of the grayling. The total length of age-0 Arctic grayling at emergence (10 mm; Kaya 1990) was subtracted from their mean total lengths at the beginning and end of their migration. The resulting lengths were divided by the mean weekly growth rate to estimate the duration of their stream residency.

Collection of Predators

Potential predators of Arctic grayling eggs and age-0 Arctic grayling were collected using a Smith-Root Model 15-C backpack electrofisher with pulsed direct current. A frequency of 30 to 50 pulses per second and a pulse width of 500 microseconds were used to minimize fish injuries and maximize electrofishing efficiency (W. Fredenberg, Creston Fish and Wildlife Center, personal communication). Voltages ranged from 700 to 900 volts. Electrofishing took place from the bank during high water conditions in Red Rock Creek. Swift turbid water made detecting stunned fish difficult and the greatest success was achieved by positioning the dip net downstream from the anode on the creek bottom against the bank. When flows decreased, electrofishing was conducted by both wading and from the bank. Electrofishing was conducted for 700 seconds at each location each sampling day.

Predation would likely occur in the known Arctic grayling spawning area where eggs and emerging grayling are concentrated; however, because electrofishing over recently deposited trout eggs can increase egg mortality (Dwyer et al. 1993), and not all grayling emerge simultaneously, I sampled just below and above the known Arctic grayling spawning area. Sampling was conducted once or twice weekly during the Arctic grayling spawning season, beginning in early June and continued until age-0 Arctic grayling were migrating to the lake in late July 1995.

Electrofishing also took place immediately below and above the known Arctic grayling spawning area in 1996. Electrofishing took place four times during the estimated peak of the Arctic grayling spawning season in early June and four times during the estimated stream residency of age-0 Arctic grayling in early July 1996. I electrofished in late afternoon and evening when spawning was expected to occur (Northcote 1995) to obtain egg predators in 1996.

Additional electrofishing was conducted in 1995 in randomly-selected locations in the 8-km reach of Red Rock Creek that contains gravel substrates of sizes preferred by Arctic grayling for spawning (Nelson 1954). Although the 8-km reach included the known Arctic grayling spawning area, locations randomly selected for electrofishing were away from its vicinity. Electrofishing took place weekly at one or two randomly selected locations within each of the 2.7-km units making up the 8-km reach during the Arctic grayling spawning season beginning in early June and continued until age-0 Arctic grayling were migrating to the lake in late July 1995.

The weir located just upstream of the Elk Lake Road bridge was used in 1995 to obtain stomach contents of migratory fish (Yellowstone cutthroat trout x rainbow trout hybrids and white suckers) that were potential predators of eggs in Red Rock Creek. Stomachs from potential predators trapped by the weir were sampled 3 to 5 days per week beginning when Arctic grayling started spawning in late May and continued until most Arctic grayling eggs were estimated to have hatched in late June.

All fish captured weighing less than 2,000 g were weighed to the nearest 0.1 g on an Ohaus LS 2000 portable electronic balance or to the nearest gram with 1 kg x 10 g, 500 g x 5 g, and 100 g x 1 g Pesola precision spring scales. The spring scales were used when weather conditions did not permit the use of the electronic balance. Fish weighing greater than 2,000 g were weighed to the nearest 28.3 g on a HOMS 9.1 kg x 28.3 g top-loading spring scale. The total lengths of all fish captured were measured in millimeters.

Collection and Analysis of Stomach Contents

Stomach contents were pumped using a modified 4-liter chemical sprayer (Light et al. 1983). The esophagus of each adult Yellowstone cutthroat x rainbow trout hybrid and brook trout was distended with PVC tubing of varying diameters before pumping to increase the efficiency of evacuating its stomach (Van Den Avyle and Roussel 1980). A subsample of fish (mottled sculpin, brook trout and Yellowstone cutthroat trout x rainbow trout hybrids) was sacrificed to test the efficiency of the stomach pump. Fish can be a major component of the diet of brook trout and Yellowstone cutthroat trout x rainbow trout hybrids greater than 250 mm in total length (TL) (East and Magnan 1991) and the pump may be less efficient at extracting fish than invertebrates from stomachs. Therefore, the efficiency of the stomach pump was calculated for trout both less than and greater than 250 mm TL.

Stomach contents were fixed in 10% formalin buffered with sodium bicarbonate (McMahon and Tash 1979) and stored in Whirl-Pak bags. They were sieved with 400-μm Nitex screen (Tabor et al. 1993), identified, and counted. Invertebrate prey were identified to taxonomic class or order (Thorp and Covich 1991; Merritt and Cummins 1996). Only heads or invertebrates with heads were counted in a sample with both body pieces and heads.

Fish prey were identified to genus or species (Hansel et al. 1988; Barndt 1996; Frost et al. 1996). A digestive enzyme technique was used to prepare a diagnostic bone collection to aid in the identification of fish prey in stomachs (Tabor et al. 1993). The enzyme solution consisted of 97% (by weight) lukewarm tap water, 2% (by weight) pancreatin, and 1% (by weight) sodium sulfide. Fish were immersed in the enzyme solution in individual containers and placed in a 40°C water bath under a chemical fume hood until the flesh had digested off the bones (up to 36 hours depending on fish size). After the flesh had digested, the contents were poured through a 400-μm sieve and rinsed with tap water. Diagnostic bones included cleithra, dentaries, opercles, pharyngeal teeth, otoliths, and vertebrae. Burbot and sculpin possessed the only distinctive vertebrae of the fish species found at Red Rocks. Scales were also used to identify fish prey in stomachs. Bones in stomach contents that were not diagnostic and fleshy tissue that was not attached to diagnostic bones were classified unidentifiable fish. Eggs were identified by measuring their diameters with a micrometer mounted in a dissecting microscope. Yellowstone cutthroat trout x rainbow trout hybrids, suckers, and mottled sculpin all overlap with Arctic grayling in spawning times and egg sizes. However, to estimate the maximum possible consumption of Arctic grayling eggs, all pale eggs 2.7 mm to 4.3 mm in diameter were considered Arctic grayling eggs (Scott and Crossman 1973). Orange eggs 3 mm to 5 mm, or any eggs greater than 4.3 mm in diameter were considered Yellowstone cutthroat trout x rainbow trout hybrid eggs. Demersal eggs less than 2.7 mm in diameter were classified as sucker eggs and those less than 2.7 mm in diameter occurring in an adhesive mass as mottled sculpin eggs (Scott and Crossman 1973). Plants that made up more than 10% of the stomach contents were considered a separate category. Other plant matter and unidentifiable invertebrate parts were classified unidentifiable.

Identifiable prey were blotted with paper towels and their total wet weight was obtained on an Ohaus E400D balance to the nearest 0.001 g. Unidentifiable parts were poured through a piece of Nitex screen, which was folded with the contents in its center, blotted with paper towels, and weighed. Stomach contents were quantified using percent frequency of occurrence, percent composition by number, and percent composition by weight (Hyslop 1980).

Consumption of Arctic Grayling Eggs and Age-0 Arctic Grayling

A bioenergetics model (Hanson et al. 1997) incorporating percent composition by weight was used to calculate consumption of Arctic grayling eggs. The model incorporates data on fish physiology, diet composition, energy density, and water temperature to generate consumption estimates based on a balanced energy equation:

Consumption = Metabolic Loss + Waste Loss + Growth

All computations were based on specific rates (grams of prey per gram of predator per day) and converted to rates per fish and per population (Hewett and Johnson 1992). The input needed for the model includes growth and diet composition of predator cohorts along with energy densities of diet components, species-specific physiological parameters, and water temperatures over the time period modeled. A cohort is defined as a group of similar sized fish of the same species experiencing identical environmental conditions (i.e., temperature, diet, and growth) (Hanson et al. 1997). Whereas there is individual variability in diet and growth, and thus, consumption within each cohort, the model represents the average individual in each cohort.

Parameter Estimation for Bionenergetics Modeling of Predation on Arctic Grayling Eggs and Age-0 Arctic Grayling

Predator Cohorts

Predator cohorts used for modeling predation on Arctic grayling eggs and age-0 Arctic grayling were based on lengths at age obtained from the literature (Bailey 1952; Irving 1954; Domrose 1960). Mean lengths of cohorts of Yellowstone cutthroat trout x rainbow trout hybrids at annulus formation were obtained from Yellowstone cutthroat trout x rainbow trout hybrids captured in Henry's Lake, Idaho (Irving 1954) (Appendix A, Table A.1). Henry's Lake is similar in proximity (20 km east of Upper Red Rock Lake) and elevation (1,973 m) to Upper Red Rock Lake. Henry's Lake is also shallow and productive like Upper Red Rock Lake.

Mean lengths of cohorts of brook trout were obtained by calculating the mean length at annuli of brook trout captured in Trail Creek and the Big Hole River, Montana

(Domrose 1960) (Appendix A, Table A.2). Trail Creek is similar in size, proximity, and elevation to Red Rock Creek. It is a third-order tributary to the Big Hole River in the Jefferson River drainage that lies at about 1,950 m elevation. The section of the Big Hole River where brook trout were obtained by Domrose (1960) (about 4.8 km south of Jackson) is similar in proximity and elevation to Red Rock Creek. The Big Hole River is in the Jefferson River drainage and this section lies at an elevation of about 1,950 m.

Mean lengths at age of cohorts of mottled sculpin were obtained from mottled sculpin collected near Shed's Bridge in the West Gallatin River, Montana (Bailey 1952). The West Gallatin River is also within the upper Missouri River drainage in southwest Montana, at a somewhat lower elevation (1,465 m vs. 2,015 m). The mean lengths at age of mottled sculpin captured by Bailey (1952) in February and March were weighted by sample size to calculate the mean lengths at age prior to the growing season (Appendix A, Table A.3). Mean lengths prior to the growing season were used because they approximate mean lengths at annuli.

Predator cohort length groups were defined using ranges of lengths at age if given (Bailey 1952) (Appendix A, Table A.3). If ranges of lengths at age were not given, cohort length groups were estimated using mean lengths prior to the growing season (Irving 1954; Domrose 1960), annual growth, and the proportion of annual growth that occurred during the time period modeled. Differences in lengths at annulus formation between each cohort and its successor were calculated to obtain the annual growth of each cohort. The values midway between the length at annulus formation for each cohort and its successor were then calculated to estimate the upper and lower bounds of each cohort length group. Degree-days were used to determine the proportion of growth that occurred during the time period modeled. Growth for brook trout begins at about 4°C (Haskell et al. 1956; Dwyer et al. 1983). I assumed growth of other predators in Red Rock Creek also began at about 4°C. The number of degree-days the predators grew each year at Red Rocks was determined by calculating the sum of all degree-days over 4°C in Red Rock Creek each year (for every degree above 4°C, a degree-day was accrued). Degree-days over 4°C that occurred before and during the time period modeled were determined, as were the corresponding increments of annual growth in length for each predator cohort. Increments of annual growth in length that occurred before and during the time period modeled were added to the values midway between lengths at annulus formation for each cohort. These were the upper bounds of each cohort length group. The lower bounds were the values subsequent to the upper bound of each preceding cohort length group (Appendix A, Tables A.1, A.2).

Growth of Predator Cohorts

Starting and ending weights for each predator cohort were estimated from a combination of the literature (Bailey 1952; Irving 1954; Domrose 1960), temperature data from Red Rock Creek, and weight-length relationships of the predators from Red Rock Creek. Annual growth in length that occurred prior to the time period modeled was added to mean lengths of cohorts prior to the growing season to arrive at the lengths at the start of the time period modeled. Weight-length relationships were calculated for each predator species from Red Rock Creek as described by Anderson and Neumann (1996). The mean lengths at the start of the time period modeled were converted to weights with the weight-length relationships. These were beginning weights of cohorts used for modeling. Annual growth in length that occurred during the time period modeled was added to mean lengths of cohorts at the start of the time period modeled. The resulting lengths of cohorts at the end of the time period modeled were converted to weights with the weight-length relationship. These were ending weights of cohorts used for modeling (Appendix A, Tables A.4-A.6).

Diet Composition of Predator Cohorts

Diet components were compiled by cohort length group into categories for modeling based upon their relative importance in the stomach contents and caloric densities. Food items making up greater than 3% of the stomach contents by weight were modeled as independent diet categories. Trichopteran cases and plants were excluded from consideration because the predators at Red Rocks cannot efficiently process these items and obtain caloric energy from them. All other diet components of similar caloric content were incorporated into the model in an "other invertebrates" category. Items with energy values considerably lower or higher than the "other invertebrates" category (i.e., oligochaetes, dipterans, fish, and fish eggs) were modeled as independent diet categories.

Energy Densities of Diet Components

Energy densities of predators and prey were obtained from the literature (Cummins and Wuycheck 1971; Hanson et al. 1997). A combination of the energy densities of Trichoptera and Ephemeroptera (Cummins and Wuycheck 1971) was used for the "other invertebrates" category when modeling trout. Because these orders were consumed by brook trout in the greatest quantities by weight, invertebrate parts, which composed most of the "other invertebrates" category, were most likely from these orders.