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Investigations of Forage Fish and Lake Trout Salvelinus Namaycush Interactions in Flaming Gorge Reservoir, Wyoming-Utah

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INVESTIGATIONS OF FORAGE FISH AND LAKE TROUT *SALVELINUS NAMAYCUSH* INTERACTIONS IN FLAMING GORGE RESERVOIR, WYOMING-UTAH

by

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Daniel L. Yule

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

ABSTRACT

Investigations of Forage Fish and Lake Trout
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in Flaming Gorge Reservoir

by

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Major Professor: Dr. Chris Luecke
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I investigated the interaction of lake trout (*Salvelinus namaycush*) and their dominant forage fish populations, Utah chub (*Gila atraria*) and kokanee salmon (*Oncorhynchus nerka*), in Flaming Gorge Reservoir, Wyoming-Utah. Through bioenergetics modeling, I quantified the consumption dynamics of the lake trout population. From hydroacoustics analyses, I quantified the density and biomass of the two dominant forage fish populations.

In Chapter II, I report the results of the energetics analysis. The objective of this chapter was to understand the role of lake trout predation in recent changes in fish assemblage structure of the reservoir. Through lake trout diet analysis and exploration of forage fish growth rates, I quantified the duration of time that chubs and kokanee are vulnerable to lake trout predation. Faster growth rates of kokanee greatly reduce the duration of time that

this species is vulnerable to predation relative to Utah chubs. Although chubs are more fecund than kokanee, this advantage in reproductive potential may not make up for differences in duration of vulnerability. I predict that kokanee will make up an even larger proportion of the total fish assemblage of the reservoir in future years.

In Chapter III, I compare annual estimates of lake trout consumption demand to biomass estimates of forage fish. I used vertical gill net sampling, beach seine surveys, and hydroaocustics to assess the distributions and biomasses of the Utah chub and kokanee populations. Biomasses of pelagic Utah chubs and kokanee were calculated to be 83 300 and 209 000 kg, respectively. Energetics analyses indicated that between 1985 and 1989 the lake trout population consumed 79 000 kg of chub and 196 000 kg of kokanee per year. These results suggest that forage fish populations should decline in future years. Annual consumption demand of lake trout between 400 and 600 mm (137 000 kg) exceeded biomass estimates of forage fish of useable size (22 000 kg), suggesting that this size-class of predator is currently food-limited. High occurrence of invertebrate prey taxa in the diet of small predators supports this food-limitation hypothesis. The lack of small pelagic forage fishes may reduce the ability of lake trout to recruit to sizes that are accessible to anglers and of value to the fishery. (132 pages)

CHAPTER I

INTRODUCTION

One of the principal factors limiting survival and growth of game fish in lakes and reservoirs is the availability of food (Ney and Orth 1986). Fisheries managers of reservoir systems attempt to balance the demand of anglers for quality fishing with the ecological constraints of the reservoir itself. These managers have often been forced to make decisions without knowledge of the support capacity of a system, but recent advances in fisheries management are reducing this problem. First, bioenergetics models of fish growth processes have helped managers understand the consumption demand of fish populations. Secondly, advancements in the science of hydroacoustics have allowed fisheries biologists to better quantify the abundance of pelagic fishes. By using bioenergetics in concert with hydroacoustics, consumption demand can be compared to forage availability. This comparison offers insight into the support capacity of an aquatic ecosystem, providing the knowledge from which sound management decisions can be made.

When rivers are impounded to form reservoirs, the equilibrium that existed among the physical, chemical, and biological components of the natural river system is destroyed. Nature has provided no reservoir species; thus, the biotic communities which develop, or those that

humans establish after impoundment, are not evolutionarily prepared for interaction in their man-made ecosystem. Moreover, asynchrony frequently exists in reservoirs between the annual production of phytoplankton and zooplankton populations (Noble 1986). This asynchrony in plankton production can result in dramatic fluctuations in the abundance of fish year-classes, since fish rely on plankton at the time year-class strength is established. Piscivorous fish species, however, tend to be longer-lived than prey species; thus, predation pressure often remains constant despite an occasional poor year of piscivore recruitment (Mills et al. 1987). If production of forage fish does not match concurrent consumption demand, a collapse in forage base resources can occur (Ney and Orth 1986).

Examples of predator-prey interactions of large lentic systems ending in such failure have been documented in the recent fisheries literature: for example, the striped bass (*Morone saxatilis*)-threadfin shad (*Dorosoma petenense*) interaction of Lake Powell, Utah-Arizona (Gustaveson et al. 1986); and the salmonine-alewife (*Alosa pseudoharengus*) interaction of Lake Michigan (Kitchell and Crowder 1986).

During the 1980s the population of striped bass in Lake Powell increased. This increase had deleterious effects on the population of threadfin shad, which was unable to absorb the increase in predation. Annual trawl

catches of shad during the late 1970s and early 1980s indicated that the shad population had distinct, but decreasing, population peaks occurring at three-year intervals: 1978, 1981, and 1984. Large year-classes of bass were recruited between 1981 and 1984 and likely caused, by virtue of their predation pressure, the decreasing trend in the number of shad collected in the trawls from the peak years. Trawl catches revealed that the shad population had virtually no recruitment of young-of-year (yoy) into the pelagic zone in 1985. Physical condition and growth rates of striped bass declined in direct response to the absence of the pelagic shad population (Gustaveson et al. 1986).

Alewife have historically experienced great population oscillations in the Lake Michigan system. Managerial decisions to plant increasingly large numbers of piscivorous salmonids in the 1970s and early 1980s were undertaken largely without regard to the salmonids food supply (Eck and Wells 1983). This trend raised questions about the potential overexploitation of alewife by salmonids. Stewart et al. (1981) predicted that increasing numbers of piscivorous salmonids would result in a decline in the alewife population. In accord with their prediction, adult alewife biomass, estimated to be 110 000 metric tons in 1975, fell to 20 000 by 1984 (Scavia et al. 1986).

The declining forage fish availability in Lake Powell and Lake Michigan is significant because similar events appear to be occurring in Flaming Gorge Reservoir (FGR) (Fig. 1.1). Recent spring trend netting conducted by the Wyoming Game and Fish Department (WG&FD) and the Utah Division of Wildlife Resources (UDWR) has suggested that the population of Utah chub (*Gila atraria*), historically the prominent forage fish of lake trout (*Salvelinus namaycush*) in the reservoir (Schmidt et al. 1979), has declined dramatically. For example, near the head of the reservoir, the number of Utah chub caught per gill net set has declined from 53 fish in 1983 to 14 in 1990 (Fowden et al. 1991). At the same time, catch rates have fallen to nearly zero at sampling stations near the dam where chubs had once been abundant (Varley and Livesay 1976). A similar decline in the number of Utah chubs captured has been observed in annual spring purse seine sampling (Fowden et al. 1991). In 1978, an average of 166 chubs were caught per haul, but by 1990 this value had fallen to 37.

Since the reservoir began to fill in 1962, millions of kokanee salmon (*Oncorhynchus nerka*) fry have been planted into the system (S. Brayton, UDWR, Dutch John, UT, pers. comm.). Initially these planted fish exhibited only marginal success; however, by the late 1970s, naturally-reproducing populations had been established. The number of kokanee captured in annual purse seine trend netting

increased from 0.1 per haul in 1978 to 54 by 1983. Since that time, the average number per haul has declined to 20 (Fowden et al. 1991).

Both trend gill net and purse seine catches indicate that both the Utah chub and kokanee populations in the reservoir have declined. Unfortunately, high variances associated with both monitoring programs make statistical evaluation of trends difficult.

Over time, the reservoir has experienced dramatic changes in fish assemblage structure. From the initial filling in 1962, through the late 1960s, the reservoir supported one of the outstanding rainbow trout (*O. mykiss*) fisheries in the western U.S. (Varley and Livesay 1976). However, by the early 1970s, this fishery had declined. Schmidt et al. (1979) felt the decline was caused by piscivorous species like rainbow and brown trout (*Salmo trutta*) preying on stocked rainbow trout fingerlings. Varley and Livesay (1976) attributed the decline to interspecific competition following a 20-fold increase in the reservoir's Utah chub population from 1963 to 1970. Since rainbow trout plantings have consistently failed to meet management criteria for success, less emphasis has been placed on this fishery (B. Wengert, WG&FD, Green River, WY, pers. comm.).

In the early 1970s, management initiated an intense stocking program of fingerling brown trout. At the time, it was hoped that brown trout would be better able to

utilize the chub forage base of the reservoir. By the mid-1970s, brown trout had replaced rainbow trout as the dominant piscivore in the system. During the late 1970s, the reservoir supported one of the premiere brown trout fisheries in the United States.

Substantial natural reproduction of lake trout was documented by gill net catches in the mid-1970s. By virtue of this reproduction, and the pre-piscivore growth advantage lake trout exhibited over brown trout, managers virtually ceased stocking of brown trout into the system by the late 1970s (D. Dufek, WG&FD, Lander, WY, pers. comm.). During the 1980s, the reservoir was considered one of the premiere lake trout fisheries in North America. In recent years, however, the estimated harvest of "trophy" lake trout, or those individuals greater than 760 mm, has declined from 3 000 fish in 1986 to 1 500 in 1990 (Fowden et al. 1990). In an attempt to increase the harvest of trophy lake trout back to earlier levels, a 660 to 914 mm slot-limit was initiated in January, 1990. The current regulations allow anglers to harvest two lake trout per day. One fish less than 660 mm, and one greater than 914 mm can be harvested, but all fish between 660 and 914 mm must be released. The likelihood of more lake trout larger than 660 mm remaining in the system due to this slot-limit, as well as the declining numbers of forage fish, was the principal reason for initiating this

study to compare available forage fish biomass to piscivore consumption demand.

Questions concerning consumption demand and forage availability are not new to the study of fisheries. Recent advances in fish physiology, energetics, and assessment techniques of forage fish populations have enabled ecologists to simulate the effects of predation on forage resources. In this thesis, I report how bioenergetics modeling techniques and hydroacoustics fish population assessment techniques were used to compare lake trout consumption demand to forage fish biomass in FGR.

Bioenergetics modeling techniques have been used to estimate total consumption of a population given information on growth, diet, thermal history, abundance of the field population, and relationships of body size and temperature to respiration rates. Stewart et al. (1983) developed an energetics model for lake trout which they applied to the Lake Michigan population. Their objective was to reconstruct food consumption from observed growth in the system. The summation of daily growth, metabolism, and waste losses provided an estimate of daily consumption for the average lake trout. Forage consumption by the average individual was extended to the entire population using a model that incorporated mortality rates from both harvest and natural causes.

Lyons and Magnuson (1987) used bioenergetics modeling techniques to assess the effects of predation by juvenile

walleyes on the population dynamics of darters (*Percidae*) and minnows (*Cyprinidae*) in Sparkling Lake, Wisconsin. They examined this effect by comparing observed mortality of the two forage fish families, based upon catch per unit effort in standard bag seine hauls, to the numbers of each family consumed by walleye, predicted by a walleye energetics model (Kitchell et al. 1977). From these comparisons, they quantified what proportion of the mortality for each family was attributed to walleye predation.

Hydroacoustics is a well-established technique for assessment of fish abundance (Thorne 1983). It is a relatively inexpensive way to obtain quantitative data on the abundance and biomass of fish populations (Burczynski et al. 1987). Burczynski and Johnson (1986) used a combined dual-beam/echo integration technique to obtain abundance estimates, length frequency, and distribution data of a sockeye salmon (*O. nerka*) population in Cultus Lake, B.C. Similar techniques were used by Burczynski et al. (1987) to assess abundance, biomass, and distribution of rainbow smelt (*Osmerus mordox*) in Lake Oahe, North Dakota-South Dakota.

In Chapter II, I report how the Stewart et al. (1983) model was applied to the FGR lake trout population to estimate their annual consumption demand of different forage fish species and size-classes. Specifically, I report how information that was used as input to the model

(i.e., diet proportions, prey caloric content, thermal history, and abundance of the field population) was collected and analyzed. Chapter II then describes how energetics modeling was used to understand the role lake trout predation may have played in recent changes in fish assemblage structure observed in trend netting operations.

The third chapter describes how hydroacoustics sampling was used to estimate the abundance and biomass of the epilimnetic, metalimnetic, and hypolimnetic forage fish communities. Data regarding seasonal distribution patterns of forage fish, collected by vertical gill net sampling, and beach seine surveys is also reported. Estimates of total annual lake trout consumption demand from Chapter II are compared to forage fish biomass estimates to quantify what proportion of available biomass is consumed annually. From these comparisons, insight was gathered as to which size-classes of lake trout are most likely experiencing current shortages in forage fish of ingestible size.

The fourth chapter reports how bioenergetics modeling techniques were used to estimate the production of the epilimnetic and metalimnetic forage fish communities of the reservoir. The current version of the bioenergetics model of fish growth, by Hewett and Johnson (1987), quantifies production using the same principles as an Allen curve (1971) from external input of growth, abundance, and survivalship of a population of interest.

By comparing consumption estimates of lake trout to production estimates of forage fishes, insight into the potential for current levels of lake trout predation to cause a decline in forage base resources of the reservoir was obtained.

The Appendix is a compilation of tables which contain information used in the bioenergetics and hydroacoustics analyses. The casual reader will have little use for this data; however, it has been included for ambitious readers that wish to obtain exact values used in the respective analyses.

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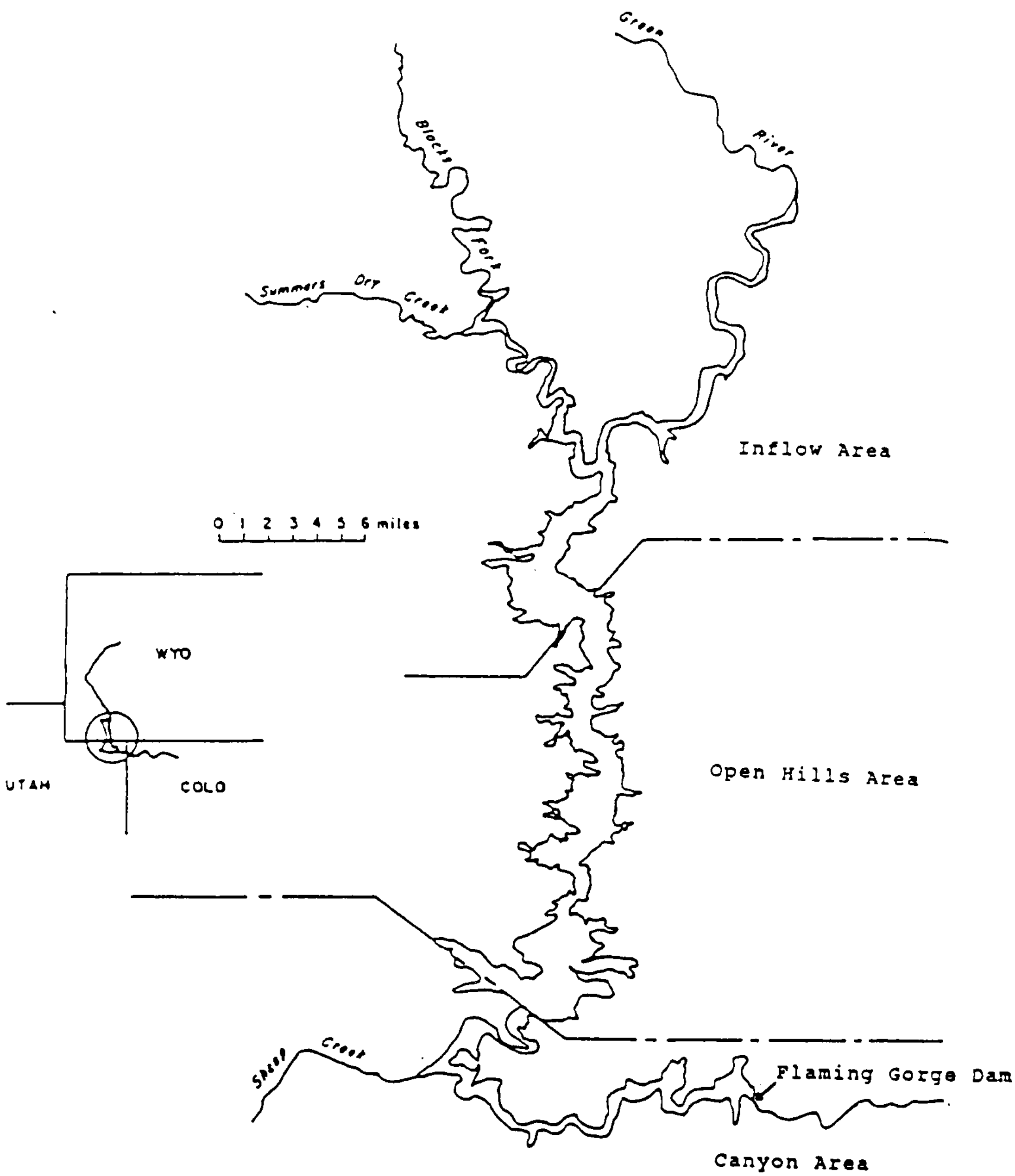

FIG. 1.1. Map of Flaming Gorge Reservoir, Wyoming-Utah.

CHAPTER II

THE ROLE OF LAKE TROUT PREDATION IN RECENT CHANGES IN FISH ASSEMBLAGE STRUCTURE OF FLAMING GORGE RESERVOIR, WYOMING-UTAH

Synopsis

Spring purse seine sampling suggests that the density of Utah chub, *Gila atraria*, historically the most abundant pelagic fish in Flaming Gorge Reservoir, has declined 4-fold in the past 12 years. During the same period, the density of kokanee, *Oncorhynchus nerka*, has increased 200-fold (Fowden et al. 1991), making them the most abundant pelagic fish in FGR. The objective of this study was to understand how lake trout, *Salvelinus namaycush*, predation may have affected population dynamics and relative abundances of Utah chub and kokanee in FGR. Bioenergetics modeling was used to quantify the consumption dynamics of the lake trout population. Through consideration of forage fish growth rates and acceptability limits of lake trout we quantified the duration of time that chubs and kokanee are vulnerable to lake trout predation. The dramatic growth advantage kokanee exhibit over chubs greatly reduces the duration of time that this species is susceptable to predation. We estimate that the average kokanee is vulnerable to predation by lake trout less than 600 mm total length for 2.25 years, while the average Utah chub is vulnerable to this size-class of predator for 7

years. Although chubs are more fecund than kokanee, it is unlikely that this advantage in reproductive potential makes up for differences in duration of susceptability. We predict that kokanee will make up an even larger proportion of the pelagic fish assemblage of Flaming Gorge reservoir in future years.

Introduction

Bioenergetics models of fish growth have proven valuable for understanding complex food web interactions in freshwater communities. Comparisons of piscivore consumption demand to prey availability have helped fisheries ecologists understand if predation may regulate prey populations (Stewart et al. 1981, Lyons & Magnuson 1987). Model predictions have been used by researchers to forecast how changes in predator abundance might modify forage fish assemblages (Stewart et al. 1983, Kitchell & Hewett 1987). Energetics models have also allowed quantification of the relative impact of different piscivorous species (Stewart et al. 1981, Bevelheimer et al. 1985, Stewart & Ibarra 1991) and cohorts (Stewart et al. 1983) on forage fish populations. Recently, the models have been used to understand the role fish consumption plays in the seasonal population dynamics of prey species (Luecke et al. 1990).

In addition to overall effects of consumption, the size dependence of piscivory has been shown to

significantly affect the structure and abundance of prey populations (Tonn & Paszkowski 1986, Post & Evans 1989). Slow growth rates of forage fish increase the duration of time that prey are physically vulnerable to predation (Tonn et al. 1986, Adams & DeAngelis 1987). Furthermore, because piscivores tend to live longer than their prey species, predation pressure often remains relatively constant despite an occasional poor year of predator recruitment (Mills et al. 1987).

In recent years there has been a shift in the abundances and species composition of pelagic forage fishes in Flaming Gorge Reservoir (FGR). Spring purse seine sampling suggests that the density of Utah chub, *Gila atraria*, historically the most abundant pelagic fish in the reservoir, has declined 4-fold in the past 12 years (Fowden et al. 1991). During the same period, the density of kokanee, *Oncorhynchus nerka*, has increased 200-fold (Fowden et al. 1991), making them the most abundant pelagic fish in FGR (R. Whaley, Wyoming Game and Fish Department, WG&FD, Casper, WY, pers. comm.). The objective of our study was to understand how lake trout, *Salvelinus namaycush*, predation may have affected population dynamics and relative abundances of Utah chub and kokanee in FGR.

In this chapter, we examine the consumption dynamics of the lake trout population and compare these results to relative abundances and growth rates of forage fish

populations in FGR. To estimate consumption dynamics we use a bioenergetics model developed for lake trout (Stewart et al. 1983). To understand the nature of size-based lake trout/forage fish interactions we perform analyses similar to those described by Knight et al. (1984) and Ney & Orth (1986). Duration of vulnerability of the two prey species is compared to relative predatory impact by lake trout size-class to quantify how predation might influence the survivability of Utah chub and kokanee. These analyses revealed pronounced differences in relative predatory impact on chub and salmon, suggesting that predation likely played a major role in the recent shift in fish assemblage structure of the reservoir.

Study area

Flaming Gorge Reservoir, located in northeast Utah and southwest Wyoming, was created by the impoundment of the Green River behind Flaming Gorge Dam in 1962. At capacity, the reservoir is approximately 145 km long, with a surface area of 17,000 ha and a mean depth of 34 m. Traditionally the reservoir has been divided into three areas for management and study purposes (Fig. 2.1). The Canyon area extends approximately 38 km north of the dam. The reservoir in this area is characterized by deep (maximum: 122 m), well-oxygenated, thermally stratified waters (Varley & Livesay 1976), and has been classified as

mesotrophic to nearly oligotrophic (Environmental Protection Agency (EPA) 1977). The Open Hills area, which extends 48 km north of the Canyon area, is characterized by rolling terrain, greater width, moderate water depth (maximum: 61 m), with more extensive wind mixing (Varley & Livesay 1976). This area has been classified as mesotrophic to moderately eutrophic (EPA 1977). The Inflow area of FGR extends 32 km up-reservoir from the Open Hills, and is the first area to receive water from the Green and Blacks Fork Rivers. The Inflow area is relatively shallow (maximum: 24 m; Varley & Livesay 1976), and has been classified as eutrophic since the water in the summer is often turbid, with high surface temperatures and low levels of hypolimnetic dissolved oxygen (EPA 1977).

Historical review of changes in fish assemblage of Flaming Gorge Reservoir

There have aeen dramatic changes in the fish assemblage structure of FGR over time. In the decade following impoundment, the reservoir supported one of the west's premiere rainbow trout fisheries. However, by the early 1970s this fishery had declined. The demise of the rainbow trout fishery was attributed to interspecific competition following a 20-fold increase in the reservoir's Utah chub population from 1963 to 1970 (Varley & Livesay 1976). Since rainbow trout plantings have

continually failed to meet management criteria for success, and are incapable of reproducing in the system, less emphasis has been placed on this fishery (B. Wengert, WG&FD, Green River, WY, pers. comm.). The rainbow trout population is maintained, however, by annual plantings of 450,000 individuals at a mean size of 210 mm (R. Schneidervin, UDWR, Dutch John, UT, pers. comm.).

Following the decline in the rainbow trout fishery, management initiated an intense stocking program of fingerling brown trout. At the time, it was hoped that brown trout would be better able to utilize the chub forage base of the reservoir. By virtue of this stocking program, and the extensive chub forage base, FGR supported one of the best trophy brown trout fisheries in the U.S. during the late 1970s.

Concurrent to the demise of the rainbow trout fishery in the late 1960s, lake trout entered the reservoir from higher up in the drainage (Wengert 1986). By the mid-1970s substantial natural reproduction of lake trout was documented by gill net catches. By virtue of this natural reproduction, and the pre-piscivore growth advantage lake trout exhibited over brown trout, managers virtually ceased stocking of brown trout into the system by the late 1970s (D. Dufek, WG&FD, Lander, WY, pers. comm.). By the early 1980s, lake trout had surpassed brown trout as the numerically dominant piscivore in the system.

As lake trout numbers expanded, forage fish densities declined. For example, the number of Utah chub caught per gill net in the Inflow area declined from 53 fish in 1983 to 14 in 1990 (Fowden et al. 1991). At the same time, values have fallen to nearly zero at ore oligotrophic stations in the Open Hills and Canyon areas, where chubs had once been abundant (Varley & Livesay 1976).

Since the reservoir began to fill, millions of kokanee fry have been planted into the system (S. Brayton, Utah Division of Wildlife Resources (UDWR), Dutch John, UT, pers. comm.). Initially these planted fish exhibited only marginal success; however, by the late 1970s, naturally-reproducing populations had been established. The number of kokanee captured in annual purse seine netting increased from 0.1 per haul in 1978 to 54 by 1983. Since that time, the average number per haul has declined 50% (Fowden et al. 1991).

Materials and methods

Bioenergetics modeling

To apply bioenergetics modeling techniques to estimate the consumption dynamics of the lake trout population in FGR we gathered information regarding seasonal changes in lake trout feeding habits, estimates of caloric content of prey items, thermal history of lake trout, growth of lake trout, and estimates of abundance and survival rates of the population.

Lake trout diet proportions by season

Lake trout diet information was collected from May, 1990, through May, 1991. In the spring of both years (10 to 15 May, 1990, and 5 to 19 May, 1991) we worked cooperatively with both the WG&FD and the UDWR in their annual lake trout netting. Three 58 m x 2.5 m gill nets, with 29 m panels of 38 mm and 44 mm square mesh, were set at 25-minute intervals just prior to sunrise. In these small-mesh nets, most of the lake trout were captured by entangling their teeth, and few were actually gilled. Nets were pulled after fishing for one hour. Six standardized sites were sampled throughout the length of the reservoir (Fig. 2.1).

Captured fish were anesthetized in tricain methanesulfonate (MS-222), and stomach contents were removed using a stomach lavage method similar to that described by Light et al. (1983). Stomach contents were put on ice in the field, later frozen, and returned to the lab for analysis.

We also obtained 81 stomachs from angler-caught lake trout. Creel surveys were conducted at boat marinas one or two weekends a month from June through September 1990. An additional 43 stomachs of lake trout greater than 914 mm were provided by a local taxidermist. From 19 to 21 January, 1991, we collected stomachs of lake trout caught through the ice. Thin ice in the Canyon area limited our

creel surveys to the Open Hills and Inflow areas of the reservoir.

Non-fish prey items were separated under a dissecting microscope and taxa identified using the keys of Pennak (1975). Once separated, each prey taxa was blotted and weighed to the nearest 0.01 g (Metler H51 balance). Fish prey items were identified on the basis of external and/or bone morphology. Bone mounts of Utah chub, rainbow trout, and white sucker, *Catostomous commersoni*, were prepared to aid in this identification.

We calculated a seasonal aggregate percent by weight (Swanson et al. 1974) for prey taxa present in diet samples of lake trout between 400 and 600 mm, and lake trout greater than 600 mm. Aggregate percent by weight equals the percentage by weight of the i^{th} food item in the i^{th} lake trout averaged over all fish in the sample which were not empty. Seasons were delimited as follows: winter = December through February, spring = March through May, summer = June through September, and fall = October through November. The fractional composition of non-identified salmonids was proportioned to kokanee and rainbow trout based on their relative contribution to the diet in each season. Non-identified fish, which never accounted for more than 5% of the seasonal diet, were proportioned to all identifiable fish based on their relative contribution by season.

Lake trout thermal history

To estimate the thermal history of lake trout across one year, we used a combination of hydroacoustics surveys and gill net data. We estimated the temperature used by lake trout during the summer through analysis of an August, 1990, hydroacoustics survey (Yule & Luecke, submitted). Assuming all targets greater than 560 mm (-31 decibels (dB), Love (1971)) recorded were lake trout, we compared depth of a target to temperature profile data taken at the time of the sonar survey to estimate the temperature that fish was occupying at the time of sampling. Several other species are capable of reaching this length in FGR, including brown trout, rainbow trout, cutthroat trout, *O. clarki*, common carp, *Cyprinus carpio*, channel catfish, *Ictalurus punctatus*, and flannelmouth sucker, *Catastomous latipinnus*; however, Fowden et al. (1991) found that 93% of fish larger than 560 mm captured in gill net sampling during 1990 were lake trout. We estimated the thermal history of lake trout in the spring and fall by measuring the water temperature near our bottom-set gill nets with a YSI Model 54A Oxygen meter.

Lake trout growth rates

Growth rates of individual lake trout were measured by examining the change in weight of tagged individuals between tag and recapture dates. A tag-recapture study, conducted from 1985 to 1989 by the WG&FD and UDWR, was

initiated to quantify angler exploitation of the lake trout population (Wengert 1986). Lake trout were captured using sinking gill nets. Captured fish were weighed to the nearest 0.05 kg, measured to the nearest 2.5 mm, tagged with numbered Floy plastic anchor tags, and released. Return lengths and weights were obtained through creel surveys and sampling conducted in subsequent years of the study.

We entered individual growth information into the lake trout bioenergetics model to estimate the proportion of the maximum ration that the fish was consuming (p-values) to fit the observed growth rate. We ran p-value iterations on 87 returned lake trout that were tagged between 1985 and 1989 and that had been at least 6 months between capture periods. Through consideration of each fishes mean length while in the study, we divided these returns into three size-classes: 400-600, 600-800, and >800 mm. We calculated a mean p-value and associated standard deviation around that mean for the three size-classes (Appendix, Table A.8). We entered the mean p-value for the 400-600 mm size-class back into the model, and starting a fish at 521 grams (400 mm, Appendix, Table A.2), allowed the model to predict how the fish would grow over time. When the model predicted that the fish had grown into the 600-800 mm size-class, we substituted the

subsequent mean p-value, and let the model continue to predict growth over time.

Lake trout survival rates and abundance estimates

To expand individual consumption to the population level, we had to estimate the number of piscivorous lake trout in the system. To estimate the number of piscivores, we used a modified Lincoln-Peterson population estimate. This estimate required information on the number of tagged-fish-at-large, and the ratio of untagged to tagged fish harvested. We estimated the number of tagged-fish-at-large by considering the number of fish tagged each year, and estimates of survival rates predicted by a band-recovery program, BROWNIE, developed by Brownie et al. (1985). The ratio of tagged to untagged fish was determined from fish captured in the most recent creel survey (May 1988 to April 1989)(Fowden et al. 1990).

To execute the BROWNIE program we generated a tag-return matrix by year tagged since 1985. Fish that had their tags removed and were later released by anglers were not included in the matrix since they had essentially been removed from the tagging study. Their elimination selectively culls survivors from the recovery matrix, and may cause overestimation of mortality rates (Tom Edwards, Utah State University, Logan, Ut, pers. comm.). The matrix was entered into the BROWNIE program, and the program was run. The BROWNIE program has four internal

models that use the tag-return matrix as input. The program determines the efficacy of each model based on a chi-square test. The BROWNIE program produces as output, estimates of recovery and survival rates.

To estimate the number of tagged-fish-at-large on 1 May 1988, we multiplied the mean survival rate predicted by the BROWNIE program, and the associated 95% confidence intervals (95% CI), by the initial number of fish tagged each year. Thus, we had a nominal estimate of tags-at-large with an associated upper and lower bound.

The upper and lower 95% CI of the population estimate were generated through consideration of our lower and upper estimates of tagged-fish-at-large on 1 May, 1988, and by generating confidence limits around our nominal estimate of recaptures. We generated confidence limits around our nominal estimate of recaptures through the use of Pearson's formulae for confidence limits for rare events for samples greater than 25 in a Poisson frequency distribution (Ricker 1975).

Consumption estimates of lake trout

Information on diet, growth, thermal history, abundance, and survival rates of lake trout were used in the bioenergetics model. Our simulations included a 6.8% loss of individual biomass to spawning on 1 November for all fish greater than 600 mm (Stewart et al. 1983). Once the model was run, monthly estimates of consumption demand

for Utah chub, kokanee, and rainbow trout by lake trout were recorded. Summation of monthly estimates of consumption allowed derivation of seasonal and annual estimates of consumption demand.

Selectivity of diet

Species selection

Selective predation occurs when the relative frequencies of prey types in a predators diet differ from the relative frequencies in the environment (Ivlev 1961). To determine if piscivorous lake trout prefer one species of forage fish over another we used Chesson's (1978) alpha:

$$Chesson's\ \alpha = \frac{(r_i/p_i)}{\sum_{i=1}^{n}(r_i/p_i)}$$

where r_i equals proportion of prey $_i$ eaten, p_i equals proportion of prey $_i$ in the environment, and n equals number of prey species.

A Chesson's alpha of 0 indicates complete avoidance of a prey type, while a value of $1/\Sigma(r_i/p_i)$, suggests neutral selection. We defined r_i as the percent occurrence by number of kokanee, Utah chub, and rainbow trout in our lake trout diet samples of 1990 and 1991. We defined p_i as the relative proportion of these fishes

captured in pelagic vertical gill net sampling of the 3 areas of the reservoir from June through October, 1990 (Yule & Luecke, submitted). We assumed that the three species were equally active and susceptible to the vertical gill net gear.

Prey size selection

To understand the range of forage fish consumed by lake trout we performed an analysis similar to that described by Knight et al. (1984). Fish prey items in our diet samples were measured to the nearest millimeter (total, standard, or vertebral column length) and weighed to the nearest gram. Linear regression equations which related standard length and vertebral column length to total length for Utah chub and kokanee (Appendix, Table A.1) were used to estimate the total length of non-intact specimens prior to ingestion. We performed a one-tailed t-test to determine if there was a significant difference in forage fish sizes consumed by lake trout less than and greater than 600 mm.

Growth of Utah chub and kokanee cohorts

To estimate the duration of vulnerability of Utah chub and kokanee we needed to quantify their growth. Growth information of Utah chub cohorts was obtained through scale analysis of fish captured in our beach seine surveys and vertical gill net sampling of July 1990 (Yule

& Luecke, submitted). Weights of 0+ chubs in July were measaured by catching these fish in a dip net along shore and weighing them to the nearest 0.01 g. Scales from Utah chub specimens larger than 80 mm were mounted on glass slides, enlarged on a microfiche projector, and aged. Once aged, length-frequency distributions by cohort were formulated. From these cohort/length frequency distributions, we calculated a weighted mean length for each cohort. A length-weight regression equation relating total length to weight for Utah chub (Appendix, Table A.2) was used to calculate an average weight from the weighted mean length for each cohort.

Growth rates of kokanee were estimated by length-frequency analysis of fish captured in May 1990 with purse 3seines (B. Wengert, WG&FD, Green River, WY, unpublished data). Because no I+ kokanee were captured in 1990, their mean size was estimated by the length-frequency distribution of fish captured with purse seines in June, 1986 (B. Wengert, WG&FD, Green River, WY, unpublished data), assuming that growth rates of 0+ and I+ kokanee have not changed dramatically since 1986. From these length-frequency distribution data sets we calculated a weighted mean length for each kokanee cohort. A regression equation which relates total length to weight for kokanee (Appendix, Table A.2) was used to calculate cohort mean weights from the cohort weighted mean lengths. We then compared the size of prey in lake trout stomachs

to Utah chub and kokanee growth rates to quantify the duration of time that forage fish cohorts were susceptible to predation.

Results

Bioenergetics modeling

Lake trout diet proportions by season

The smaller lake trout consumed a variety of invertebrates and fish prey. In the spring and summer of 1990 lake trout between 400 and 600 mm relied primarily on chironomid (*Ablabesmyia sp.*) pupae and larvae, making up 45 and 60% of the diet by weight in these seasons (Fig. 2.2). Fish prey items constituted 33% of this lake trout size-class diet during the spring, but through the summer months this value was reduced to 5%. Crayfish (*Orconectes sp.*) were a staple of small lake trout, accounting for 16, 31, and 33% of the diet in the spring, summer, and fall of 1990. In the fall and winter, small lake trout ate more fish (27% and 47%, respectively). Zooplankton (mainly *Daphnia pulex*) was also used extensively by small lake trout during the winter (50%).

Throughout the study lake trout greater than 600 mm ate primarily kokanee (Fig. 2.2). During the spring of 1990, kokanee accounted for 52% of the diet by weight followed by Utah chub (20%), and rainbow trout (13%). In the summer, utilization of kokanee (33%) decreased

relative to consumption of Utah chub and rainbow trout. The dominant prey items of large lake trout during the winter of 1990-91 included: kokanee (76%), Utah chub (13%), and rainbow trout (7%).

We used literature values to assign caloric content to the different prey types (Appendix, Table A.10). We assumed prey caloric content to be constant across seasons. The proportion of prey items that are indigestible was placed at 3.3% for fish, and 10% for invertebrates (Stewart et al. 1983), except for crayfish we used a value of 25% (Stein & Murphy 1976). To simplify the analysis, prey items of similar caloric content were pooled: rainbow and lake trout (cannibalism was only documented twice in the winter); crayfish and amphipods (the former was by far the largest contributor).

Lake trout thermal history

A total of 34 targets greater than 560 mm (-31 dB) were sampled by our hydroacoustics gear. We estimate the mean temperature occupied by these targets to be 9.3°C ± 4.3°C sd. This is slightly warmer than the mean temperature used by lake trout captured in our summer vertical gill net sampling (8.9°C ± 1.0°C sd, n = 12). Temperature readings taken near our bottom gill nets indicated that lake trout were occupying water temperatures of 8.0°C in May and 9.0°C in October. In the winter, we assumed that lake trout occupied the warmest

available water in the reservoir (4.0°C, Bolke 1976). We used linear interpolation to model thermal history between dates when this parameter had been estimated (Fig. 2.3).

Lake trout growth rates

Since all previous attempts to age lake trout in FGR have been futile (Bill Wengert, WG&FD, Green River, WY, pers. comm.), we used the results of the one-year bioenergetics simulations to define lake trout age groups (Table 2.1). We converted energetics model predictions of lake trout weights (g) to lengths (mm) through the use of a lake trout length-weight regression equation ($W = 0.00000032 * L^{3.54}$, $r^2 = .95$).

Lake trout survival rates and abundance estimates

We entered the lake trout tag-return matrix (Appendix, Table A.5) into the BROWNIE program and the program was run. BROWNIE program model 0 gave the best fit to the return matrix ($X^2 = 6.01$, $p = 0.422$). Model 0 is an extension of the Seber (1970) and Robson & Youngs (1971) model in that first-year recovery rates are allowed to differ from subsequent years. Model 0 predicted that annual survivalship and rates of exploitation averaged 65% and 14%, respectively, from 1985 to 1989 (Appendix, Table A.6). This survivorship estimate was used in the bioenergetics simulations.

On 1 January, 1990, a slot-limit regulation was imposed on the lake trout fishery. The current regulation does not permit anglers to harvest individuals between 660 mm and 914 mm. To model the survivorship of lake trout in this slot-limit, we assumed anglers would comply with the regulation; thus, the only source of mortality of these fishes would result from natural causes (21% annually).

The Peterson-Lincoln estimate required information on the number of tagged-fish-at-large, and the ratio of tagged to untagged fish harvested. Between 1 May, 1988, and 30 April, 1989, an estimated 16,100 lake trout were harvested (Fowden et al. 1990), of which 95% were over 389 mm. Thus, we assumed the harvest of piscivorous lake trout to be approximately 15,300 during this interval of time. We did not correct the tag-return matrix to evaluate only piscivores since only two lake trout less than 389 mm had been marked in the five-year tag-recapture study.

Using the BROWNIE program estimates of annual survivalship we estimated that on 1 May, 1988, there were 897 tagged-fish-at-large, with upper and lower 95% CI of 748 and 1,086 fish, respectively (Appendix, Table A.7). Between 1 May, 1988, and 30 April, 1989, 114 tags from harvested lake trout were returned by anglers.

Using the modified Peterson-Lincoln estimate, we calculated that on 30 April, 1989, there were 120,500 piscivorous lake trout in FGR, with upper and lower 95% CI

of 175,300 and 83,700 fish, respectively. To estimate the initial abundances of lake trout age groups, we partitioned the piscivore abundance estimate (120,500) to the respective groups assuming a 65.0% annual survival rate, and constant recruitment over time (Fig. 2.4). Upper and lower group abundance estimates were derived by using the upper and lower estimates of piscivore abundance.

Consumption estimates of lake trout

The bioenergetics analysis indicated that the lake trout population consumed 331 metric tons (mt) of forage fish annually (range: 231 - 484 mt, Fig. 2.5). Nominal estimates of annual consumption of kokanee (196 mt) exceeded that of Utah chub (78.5 mt) and rainbow trout (58.6 mt). Lake trout greater than 600 mm exert more demand on forage base resources annually (196 mt) than do lake trout less than 600 mm (137 mt). Age groups 4-6 (586-813 mm) consume more forage fish than either smaller or larger lake trout.

Lake trout less than 600 mm consumed Utah chubs most during the winter and spring (Fig. 2.6), and primarily kokanee and rainbow trout during the fall and winter. Consumption of kokanee biomass by lake trout greater than 600 mm exceeded that of Utah chub or rainbow trout

throughout the year (Fig. 2.6). This predator size-class consumed the most forage fish during the summer and fall.

Selectivity of diet

Species selection

The standardized forage ratio (Chesson's alpha) indicated that rainbow trout were consumed in higher proportion than their proportion in the environment (Table 2.2). Kokanee were consumed in about the same proportion as their proportion in the environment.

Prey size selection

Lake trout less than 600 mm consumed forage fish between 23 and 268 mm, while lake trout greater than 600 mm consumed forage fish between 198 and 425 mm (Fig. 2.7). The mean size of forage fish ingested by lake trout less than 600 mm (118 mm ± 59 s.d.) was significantly smaller than the mean size of those eaten by lake trout greater than 600 mm (263 mm ± 69 s.d., $t = 81.9$, $t_{.001[121]} = 3.37$).

Growth of Utah chub and kokanee cohorts

Growth rates of Utah chub and kokanee were used to quantify the duration of time that the two species are vulnerable to lake trout predation. Analysis of length frequencies and scales revealed that kokanee exhibited a dramatic growth advantage over Utah chub in FGR. For

example, a I+ Utah chub measures 63 mm (3 g) in July, while the same age kokanee measures 135 mm (40 g). II+ kokanee are twice as long, and outweigh chubs of the same age by 14-fold. Faster growth of kokanee greatly reduces the time that this species is vulnerable to predation. The average kokanee will outgrow the maximum ingestibility limits of lake trout less than 600 mm in 2.25 years (Fig. 2.8), while Utah chub are vulnerable to predation by this size-class of predator for 7 years (Fig. 2.8). Moreover, the average kokanee will outgrow the maximum ingestibility limits of the largest lake trout in FGR between its third and fourth year of life, while Utah chub never grow to a size that lake trout are unable to ingest.

Discussion

Utah chub historically has been the dominant forage fish of lake trout in Flaming Gorge Reservoir (Schmidt et al. 1979). Our study revealed, however, that kokanee are now consumed more than Utah chub. Lake trout greater than 600 mm fed almost exclusively on forage fish (Fig. 2.2), while lake trout less than 600 mm consumed mostly invertebrate prey (Fig. 2.2). Our energetics analysis suggests that lake trout greater than 600 mm consume more forage fish annually than do lake trout less than 600 mm.

Calculation of a standardized forage ratio (SFR) revealed that rainbow trout are likely the preferred forage fish of piscivorous lake trout. Despite stocking

some 450,000 fish annually, the return of rainbow trout to the creel has been low (<10% annually, Steve Brayton, UDWR, Dutch John, UT, pers. comm.). Our energetics modeling suggests that lake trout consume some 58.6 metric tons of rainbow trout annually (Appendix, Table A.9). The diet analysis revealed that the average weight of rainbow trout consumed by lake trout equalled was 165 g ± 38 s.d.. It follows that lake trout consume some 360,000 rainbow trout annually, suggesting predation by lake trout is the likely cause for the poor return of stocked rainbow trout.

The SFR analysis also indicated that kokanee are selected over Utah chub. This selectivity could have occurred because of actual prey preference or because of differences in encounter rates of lake trout and forage species. Given that chub were spatially segregated from kokanee and lake trout during the summer (Yule & Luecke, submitted), it is likely that spatial overlap was largely responsible for the greater SFR of kokanee compared to Utah chub.

Growth rates of large lake trout were high compared to other lake trout populations. Growth rates of large lake trout in FGR surpassed growth rates of similar size fish in Lake Michigan even during years of high alewife, *Alosa pseudoharengus*, abundance (Eck & Wells 1983, Scavia et al. 1986). Growth of smaller lake trout was much slower than what was documented for the same size fish in Lake Michigan during the early 1970's (Stewart et al.

1983). The diet of 400-600 mm lake trout at that time consisted primarily of fish (i.e., alewives, rainbow smelt, *Osmerus mordax*, and slimy sculpin, *Cottus cognatus* (Eck & Wells 1983)). The same age fish in FGR currently rely on crayfish, chironomids, and zooplankton (Fig. 2.2). The high utilization of zooplankton during the winter (50%), despite the breakdown of the thermocline allowing small lake trout to pursue forage fish throughout the water column, suggests that small forage fishes are not available for consumption by small lake trout. Our analyses of growth rates and diets indicate that lake trout smaller than 600 mm may be experiencing a trophic bottleneck in FGR.

It is likely that this trophic bottleneck is partially a function of the growth characteristics exhibited by Utah chub and kokanee. Our study indicates that the average Utah chub is vulnerable to predation by lake trout for nearly three times longer than the average kokanee.

In recent years, kokanee have replaced Utah chub as the numerically dominant forage fish in FGR. The dramatic growth advantage kokanee exhibit over chubs results in significant differences in the duration of time that the two species are susceptible to predation induced mortality. Although chubs are more fecund than kokanee (Varley & Livesay 1976, Rieman & Myers 1991), this advantage in reproductive potential may not make up for

differences in duration of vulnerability. Our analyses of lake trout consumption dynamics and prey selectivity indicate that kokanee will likely make up an even larger proportion of the total fish assemblage of FGR in future years. If kokanee growth rates remain high, lake trout will likely experience diminished opportunity to find suitable sized forage, resulting in reduced growth and survival of lake trout in Flaming Gorge Reservoir.

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Tables and figures

Table 2.1. Bioenergetics model predictions of lake trout growth using mean p-values for the respective size-classes. Length estimated by length-weight regression (Appendix, Table A.2).

Model year	Length (mm)	Weight (g)
1	400	547
2	476	958
3	530	1394
4	586	2001*
5	696	3664
6	783	5584
7	813	6370
8	838	7119
9	863	7828
10	882	8495
11	901	9121
12	916	9706
13	931	10250
14	945	10760

* First cohort to exhibit 6.8% loss to spawning.

Table 2.2. Summary of Chesson's alpha calculations.

Species	r_i	p_i	Chesson's alpha
Kokanee	0.51	0.50	0.24
Utah chub	0.23	0.47	0.12
Rainbow trout	0.08	0.03	0.64

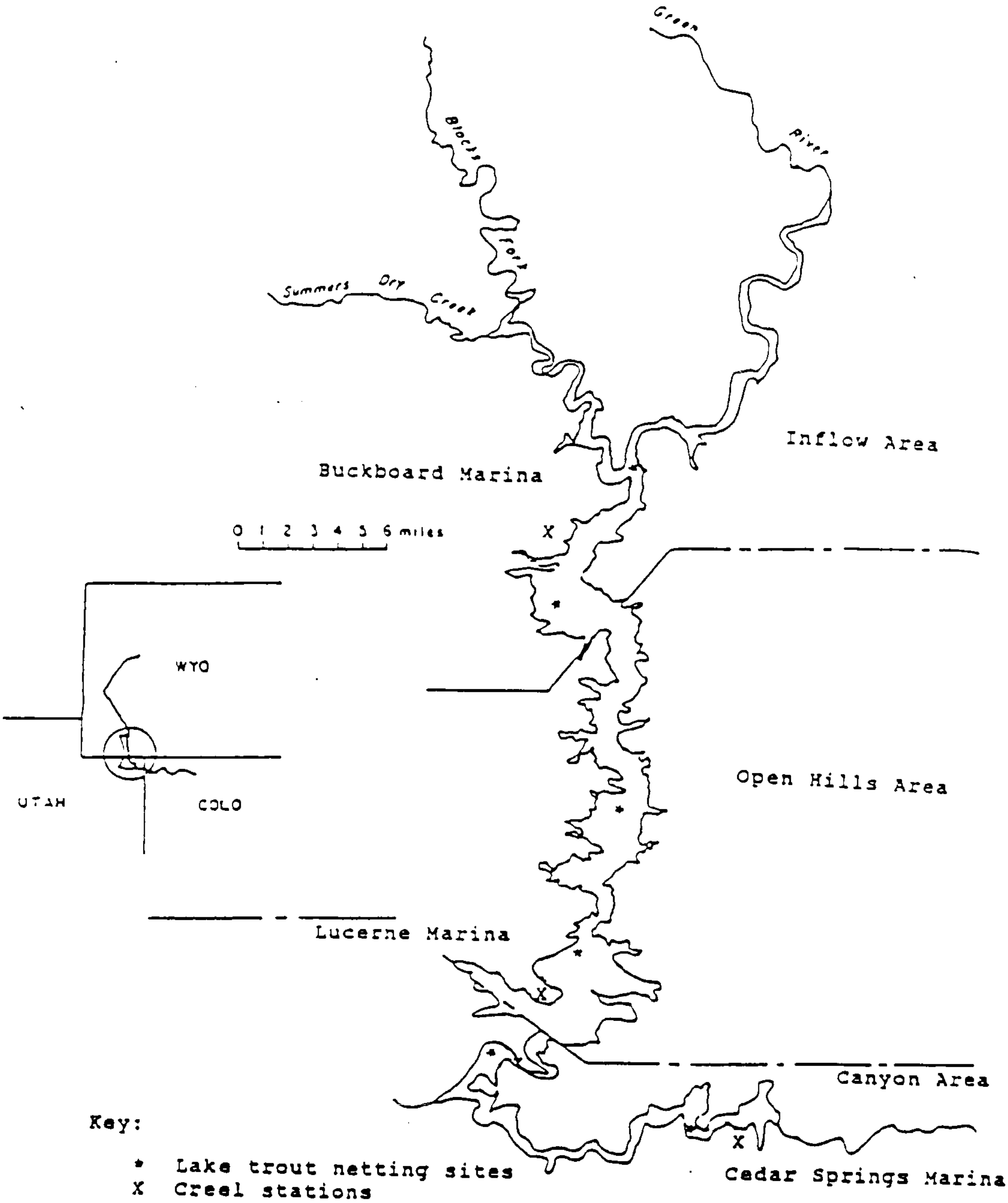


Fig. 2.1. Map of Flaming Gorge Reservoir, Wyoming-Utah, showing location of standardized lake trout netting sites and creel stations.

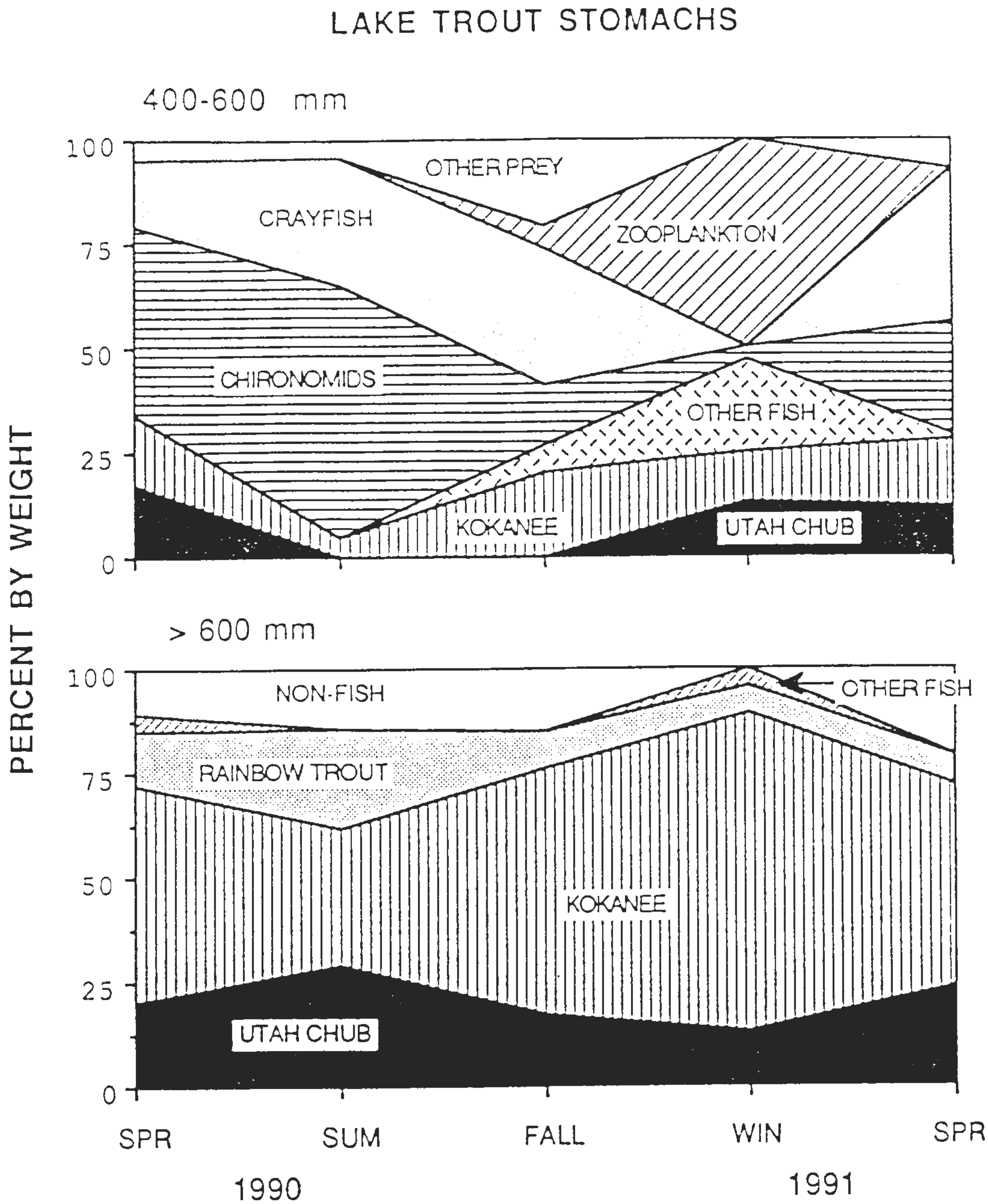


Fig. 2.2. (a) Diet of lake trout between 400 and 600 mm, and (b) diet of lake trout greater than 600 mm during five seasons. Diet expressed in aggregate percent by weight (Swanson et al. 1974).

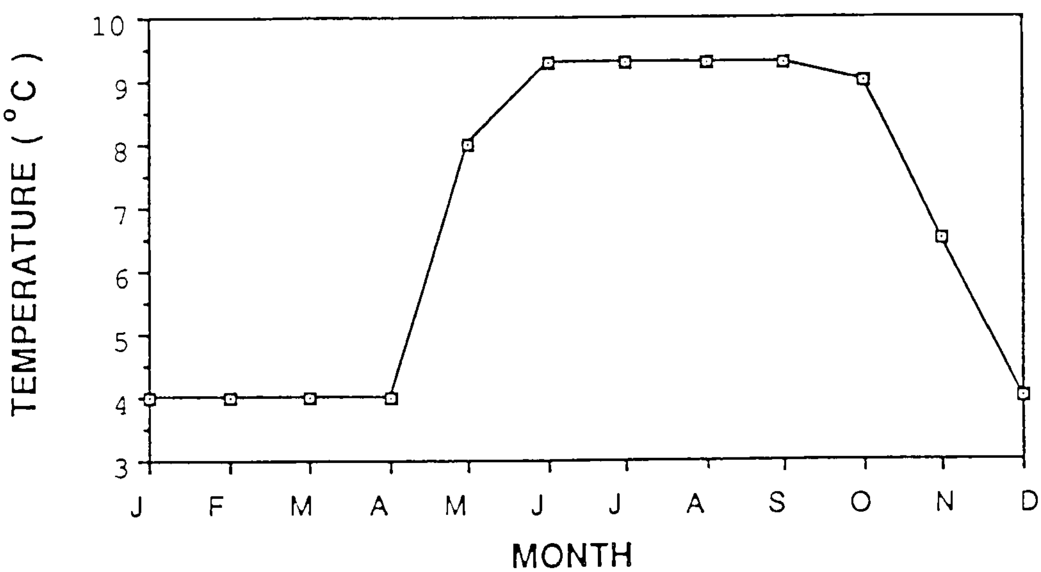


Fig. 2.3. Estimated thermal history of lake trout across one year in Flaming Gorge Reservoir.

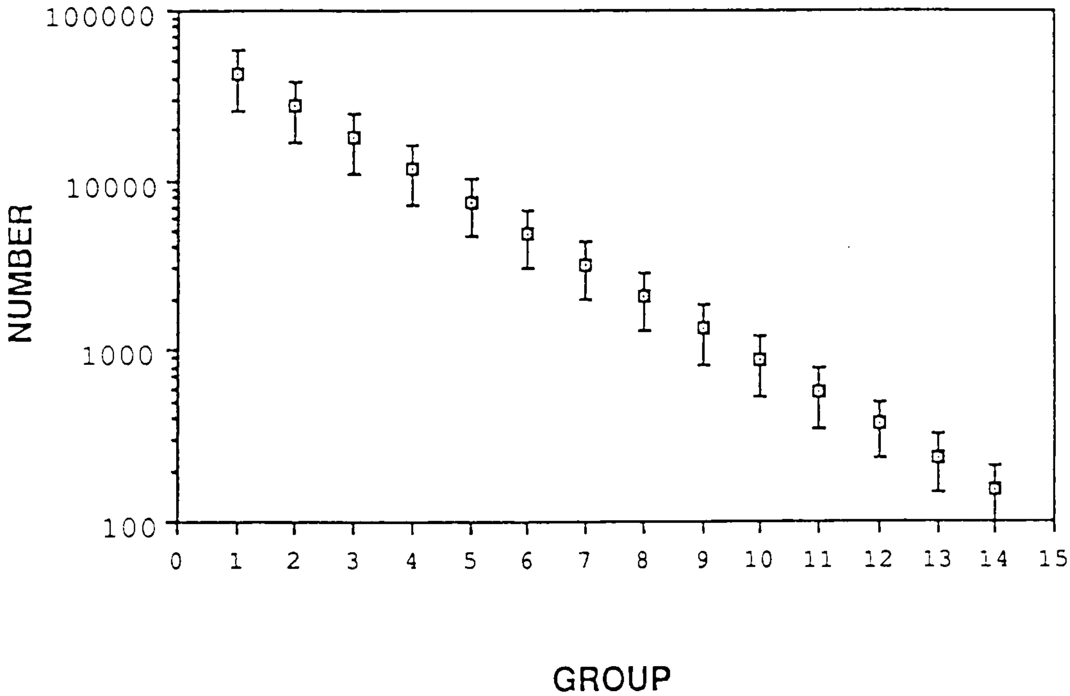


Fig. 2.4. Abundance estimates of lake trout groups in Flaming Gorge Reservoir.

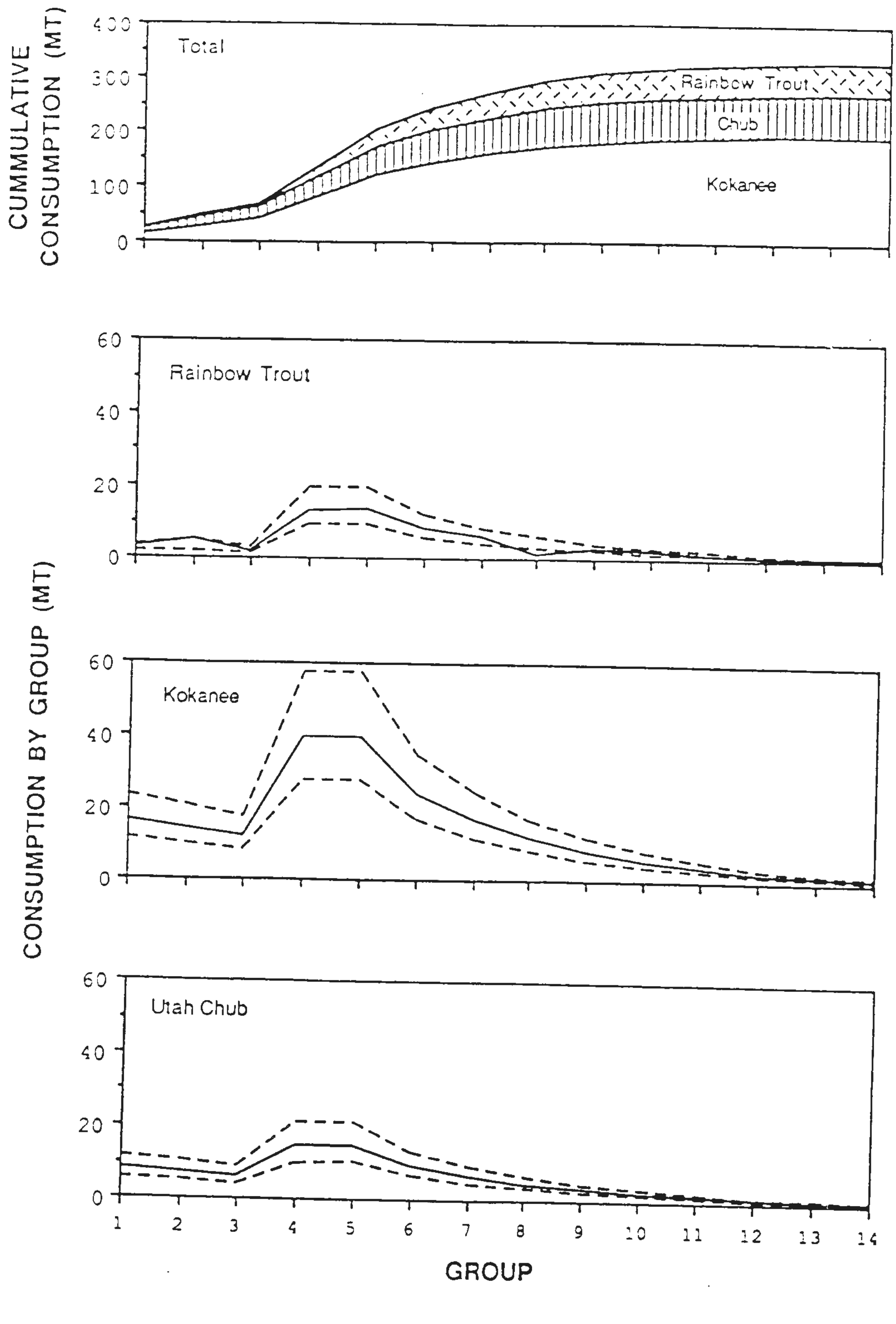


Fig. 2.5. Estimates of annual lake trout consumption of Utah chub, rainbow trout, and kokanee by lake trout group. Dashed lines represent upper and lower consumption estimates by group.

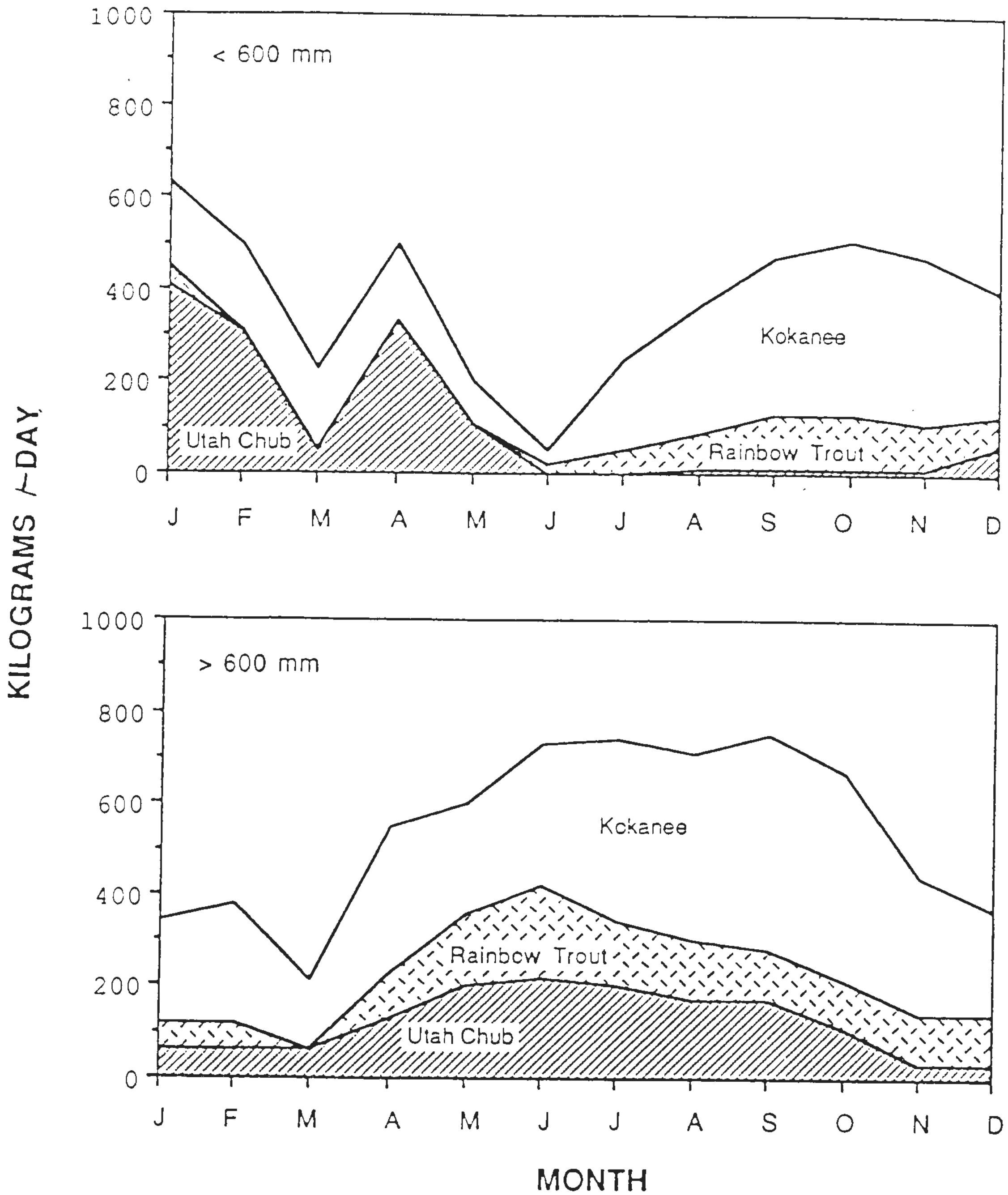


Fig. 2.6 (a) Bioenergetics model prediction of daily consumption by month of Utah chub, rainbow trout, and kokanee by lake trout between 400 and 600 mm, and (b) lake trout greater than 600 mm in Flaming Gorge Reservoir.

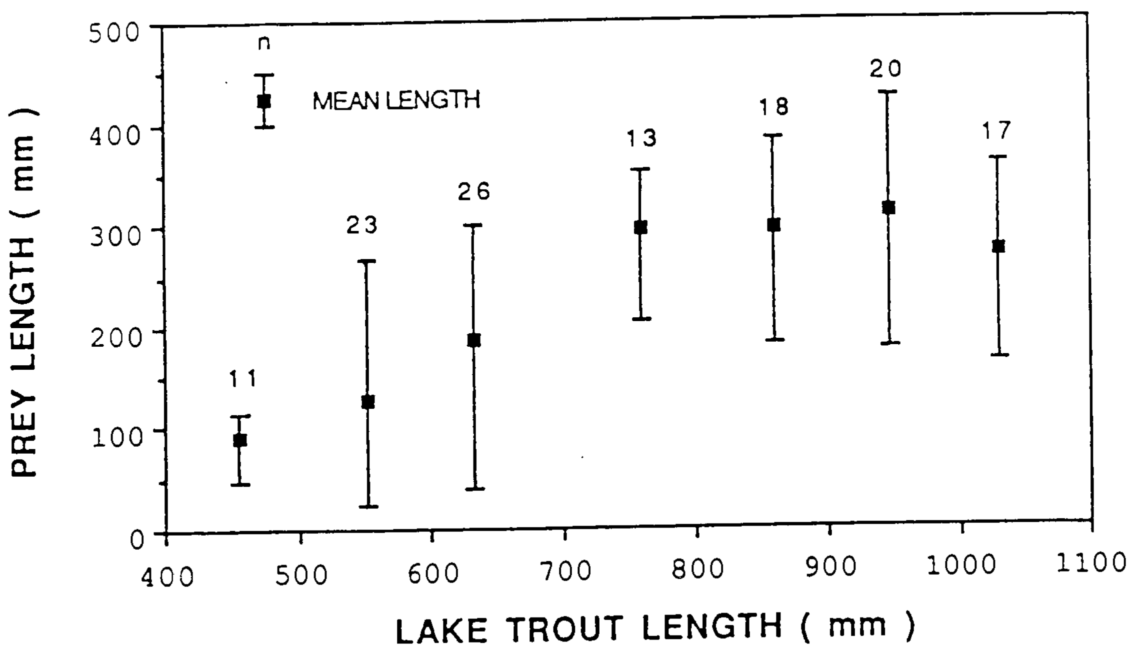
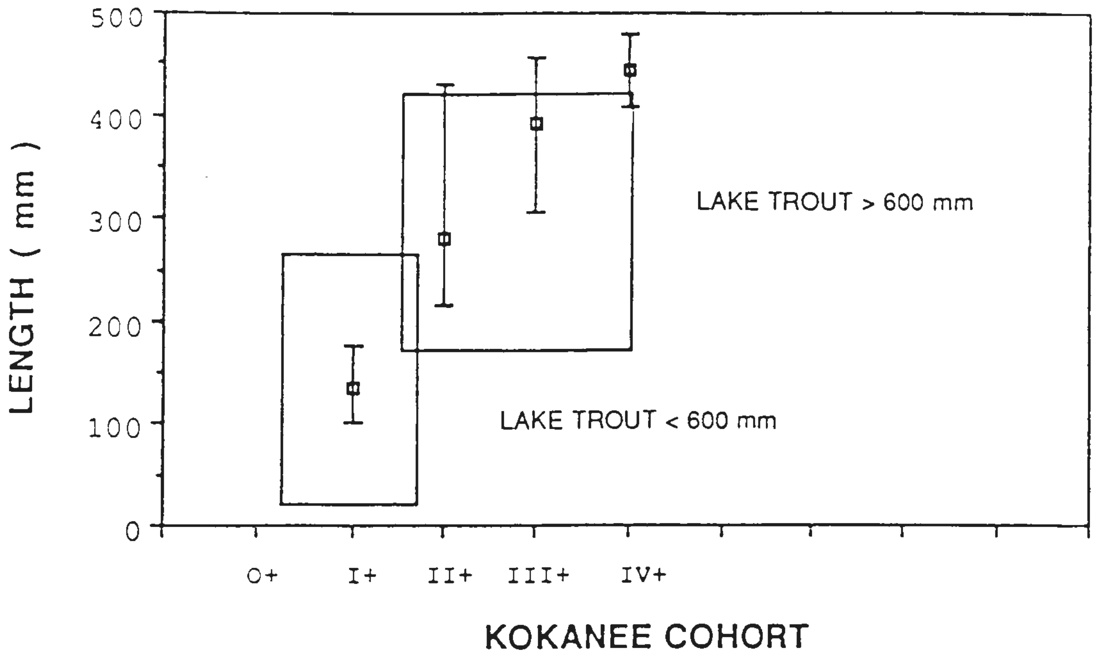


Fig. 2.7. Relationship between lake trout total length and the size of prey fishes consumed. Error bars represent range.



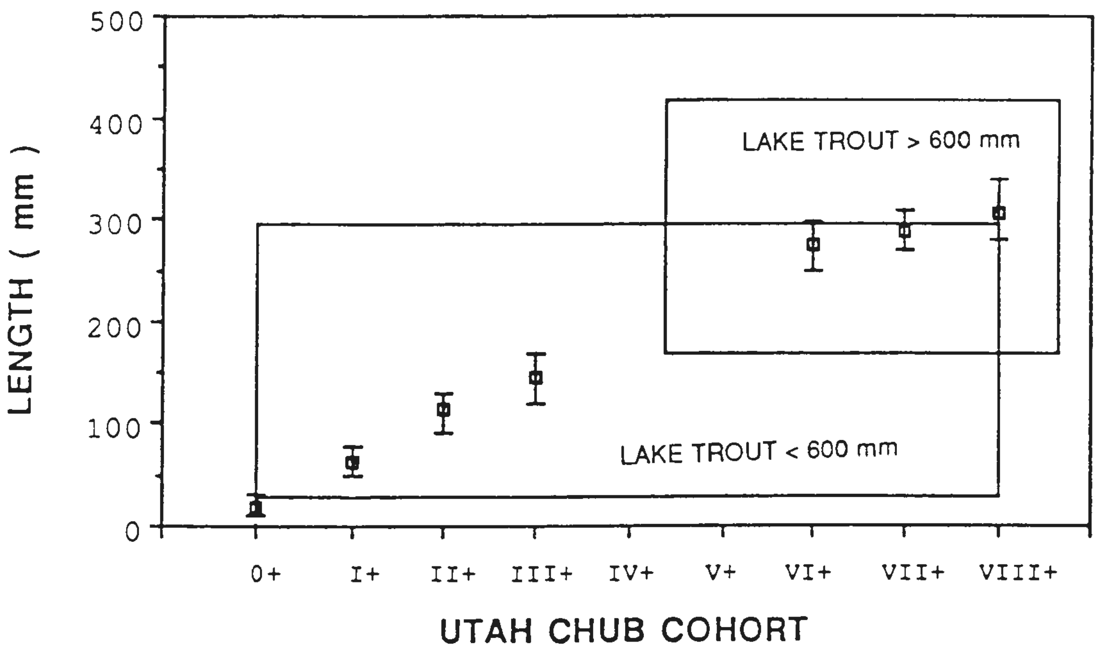


Fig. 2.8. (a) Growth of kokanee, and (b) growth of Utah chub versus acceptability limits of lake trout less than, and greater than 600 mm in Flaming Gorge Reservoir.

CHAPTER III

COMPARISON OF LAKE TROUT *SALVELINUS NAMAYCUSH* CONSUMPTION TO ACOUSTIC ASSESSMENT OF FORAGE FISH BIOMASS IN FLAMING GORGE RESERVOIR, WYOMING-UTAH

Abstract

During the last decade, purse seine and gill net monitoring programs of forage fish populations in Flaming Gorge Reservoir, Wyoming-Utah, have documented a 4-fold decline in the density of Utah chub (*Gila atraria*), and a 50% reduction in the density of kokanee salmon (*Oncorhynchus nerka*). These declines initiated this research to compare estimates of annual lake trout (*Salvelinus namaycush*) consumption demand to estimates of forage fish biomass. Lake trout consumption demand was quantified using a bioenergetics model developed for the species by Stewart et al. (1983). We used vertical gill net sampling, beach seine surveys, and hydroacoustics to assess the distributions and biomasses of the Utah chub and kokanee populations. Two-way ANOVA (depth and area) indicated significant difference in fish densities among different areas of the reservoir ($f_{3,70} = 9.88$, $p \leq 0.0001$), but no overall differences between epilimnetic and metalimnetic densities of fish ($f_{1,70} = 0.04$, $p > 0.05$). Biomassess of pelagic Utah chub and kokanee were calculated to be 83 300 and 209 000 kg, respectively.

Energetics analyses indicated that between 1985 and 1989 the lake trout population consumed 79 000 kg of chub, and 196 000 kg of kokanee per year. These results suggest that forage fish populations should continue to decline in future years. Annual consumption demand of lake trout between 400 and 600 mm (137 000 kg) exceeded biomass estimates of forage fish of useable size (22 000 kg), suggesting that this size-class of predator is currently food-limited. High occurrence of invertebrate prey taxa in the diet of small predators supports our food-limitation hypothesis.

Introduction

Recent advances in fish physiology, energetics, and assessment techniques of fish populations have enabled ecologists to more precisely examine the effects of predation on forage fish populations. Comparisons of consumption dynamics of piscivores to available forage fish in Lake Michigan indicated that forage fish populations were likely to decline due to predation (Stewart et al. 1981, 1983). This prediction caused fisheries managers to reduce the number of stocked piscivores which likely helped stabilize forage populations (Kitchell and Crowder 1986; Scavia et al. 1986; Brandt et al. 1991; Stewart and Ibarra 1991).

In other systems, predation by piscivorous fish has resulted in collapse of forage fish populations. During

the late 1980s, the population of striped bass (*Morone saxatilis*) increased in Lake Powell, Utah-Arizona. This increase led to a collapse in the threadfin shad (*Dorosoma petenense*) population, which was unable to absorb the associated increase in predation. The quality of the striped bass fishery declined in response to the near absence of the shad population (Gustaveson et al. 1986). In Lake Oahe, North Dakota-South Dakota, yellow perch (*Perca flavescens*) and black bullhead (*Ictalurus melas*), which had dominated trawl catches in the mid-1960s, were essentially absent by 1970. Predation by walleye (*Stizostedion vitreum vitreum*) was suggested as the likely cause for their decline (Nelson and Boussu 1974).

Similar declines in forage fish appear to be occurring in Flaming Gorge Reservoir (FGR), Wyoming-Utah. Recent trend netting, conducted by the Wyoming Game and Fish Department (WG&FD) and the Utah Division of Wildlife Resources (UDWR), suggests that the density of Utah chub (*Gila atraria*), historically the prominent forage fish of lake trout (*Salvelinus namaycush*), has declined 4-fold in the last decade (Schmidt et al. 1979; Fowden et al. 1991). Moreover, during the same period the density of kokanee (*Oncorhynchus nerka*) has declined by 50% (Fowden et al. 1991).

The decline in forage fish densities, as evidenced by trend netting, initiated this research project to compare estimates of piscivore consumption demand to estimates of

forage fish biomass. The objectives of this study were 1) to assess the distribution and biomass of forage fish, and 2) to compare estimates of forage fish biomass to estimates of annual lake trout consumption demand.

In this chapter, we assess the distribution and biomass of forage fish by combining the results of hydroacoustics sampling with catches of fish in vertical gill nets and beach seines. Hydroacoustics is a well established and relatively inexpensive technique for assessment of fish abundance (Thorne 1983; Burczynski et al. 1987; Brandt et al. 1991). Burczynski and Johnson (1986) used a dual beam analysis to obtain abundance estimates, length frequency, and depth distribution for sockeye salmon (*O. nerka*) in Cultus Lake, B. C. We used similar techniques to assess the abundance, biomass, and distribution of Utah chub and kokanee in FGR in 1990.

We then compare estimates of forage fish availability to rates of lake trout consumption as estimated with a bioenergetics model developed by Stewart et al. (1983). The details of the energetics analysis of lake trout consumption dynamics in FGR can be found in Yule and Luecke (submitted).

Study Area

FGR, located in Northeast Utah and Southwest Wyoming, was created by the 1962 impoundment of the Green River behind the Flaming Gorge Dam. When filled to capacity,

the reservoir is approximately 145 km long, with a surface area of 17 000 ha, and a mean depth of 34 m. Traditionally, the reservoir has been divided into three areas for the purpose of management and study (Fig. 3.1). The Canyon area extends approximately 38 km north of the dam. The reservoir in this area is characterized by deep (maximum: 122 m), well-oxygenated, thermally-stratified waters (Varley and Livesay 1976); and has been classified as mesotrophic to nearly oligotrophic (Environmental Protection Agency (EPA) 1977). The Open Hills area, which extends 48 km north of the Canyon area, is characterized by rolling terrain, wider reservoir width, moderate water depth (maximum: 61 m), with more extensive wind mixing (Varley and Livesay 1976). This area has been classified as mesotrophic to moderately eutrophic (EPA 1977). The Inflow area of FGR extends 32 km up river from the Open Hills, and is the first area to receive water from the Green and Blacks Fork Rivers. The Inflow area is relatively shallow (maximum: 24 m; Varley and Livesay 1976), and has been classified as eutrophic, because the water often becomes turbid during the summer and may experience high surface temperatures and low hypolimnetic dissolved oxygen levels (EPA 1977).

FGR currently supports a sports fishery of several exotic species. Rainbow trout (*O. mykiss*), brown trout (*Salmo trutta*), cutthroat trout (*O. clarki*), kokanee salmon, largemouth bass (*Micropterus salmoides*),

smallmouth bass (*M. dolomieui*), and channel catfish (*Ictalurus punctatus*) have all been introduced into the reservoir. The renowned lake trout fishery developed from fish that entered the reservoir from higher up in the drainage during the late 1960s (Wengert 1986). The reservoir also supports several nongame fish populations, including Utah chub, white sucker (*Catastomous commersoni*), common carp (*Cyprinus carpio*), flannelmouth sucker (*Catostomous latipinnus*), redside shiner (*Richardsonius balteatus*), mountain whitefish (*Prosopium williamsoni*), and sculpin (*Cottus spp.*).

Methods

Acoustic Surveys

Hydroacoustic surveys were conducted from 16 August to 18 August, 1990. Previous sampling had indicated that thermal stratification in August tended to segregate warm-water species, such as Utah chub, from cold-water species, such as kokanee. The reservoir was divided into 6 regions based upon similarities in morphometry and productivity. Six to 9 cross-reservoir transects were conducted in each region and treated as replicates (Fig. 3.1). Surveys were conducted at night during moonless periods, and covered water where depths exceeded 5 m.

Acoustics samples were collected with a BioSonics model 105 echosounder equipped with a 420-kHz dual beam ($6x15^{\circ}$) transducer that allowed us to estimate fish sizes.

We sampled at a rate of 2 pings per second traveling at a boat speed of 4-6 m/s. Pulse width of the signal was 0.4 ms. Data were recorded directly into computer files. They were also digitized and recorded on Betamax videotape, and a paper chart was used to store a visual record of the detected targets.

Data were processed by counting echoes using dual beam information processed with Biosonics ESP Dual Beam Processor (Model 281) and software. Targets within 4° of the center axis of the sound pulse were examined for fish target criteria and used for density analysis. Target criterion was checked at 1/2 and 1/4 of the amplitude of each returned signal. Target strength (TS) of echoes returned were converted to fish length using Love's (1971) empirical formula:

$$\text{Log}(L) = (TS + 64.1) / 19.1,$$

where TS = target strength (dB), and L = fish length (cm). In this chapter we present echo count data of fish targets ranging from -51 to -33 dB, which represents fish of approximately 50-420 mm. These targets encompass size-classes of Utah chub, kokanee, and rainbow trout consumed by lake trout in the reservoir. Only echoes that met the single-target criterion of the analysis software were used to calculate densities. The proportion of targets that met the single target criterion ranged from 14 to 42% among the transects. This procedure may underestimate fish densities, but will not likely affect distribution

patterns. The region where fish targets were indistinguishable from the bottom (bottom window) was set at 0.5 m in the Canyon areas and 1.0 m in the Open Hills and Inflow areas.

To calculate forage fish abundance, we multiplied the hydroacoustics estimates of fish density in 3 depth strata by water volume of each strata obtained from a hypsographic curve of the reservoir. The 3 strata were epilimnion (0-13 m), metalimnion (13-30 m), and hypolimnion (>30 m). Our hydroacoustics system does not sample the top 2 m of water; thus, we assumed that fish densities between the surface and 2 m were equal to densities estimated from 2 to 13 m.

To estimate the biomass of forage fish, we multiplied the abundance estimate by an estimate of mean weight. Mean weight was estimated from the relative frequency of fish targets in every 2 dB size bin from -51 to -33 dB, calculating lengths from Love's (1971) equation, and calculating weights using length-weight regressions:

Species	Regression Equation	n	r^2
Utah chub	$W (g) = 0.0000091 * L (mm)^{3.07}$	104	0.944
kokanee	$W (g) = 0.000127 * L (mm)^{2.58}$	91	0.961

This analysis was further delimited by dividing the fish into two groupings: -51 to -41 dB (50 to 170 mm), and -41 to -33 dB (170 to 440 mm). These groups represent the approximate range of forage fishes eaten by lake trout of

400 to 600 mm, and greater than 600 mm, respectively (Yule and Luecke, submitted).

Vertical Gill Net Sampling

To assess the vertical distribution of forage fishes, day and night vertical gill net sets were conducted monthly from June through October 1990 at one standardized site in each of the 3 areas. The 3 locations initially chosen as vertical gill net sites included: Canyon (Mustang Ridge), Open Hills (Antelope Flats), and Inflow (North of Buckboard) (Fig. 3.1). In June, no fish were captured at the Open Hills site, thus all subsequent sampling of this area was conducted at Wildhorse Draw. The other sites remained as initially selected, except inclement weather in August forced us to net at the more protected confluence of the Inflow area. Sampling was conducted between 19 and 22 June, 17 and 20 July, 19 and 23 August, 18 and 20 September, and from 20 to 22 October, 1990. Nighttime sets were initiated at 1900 hours and pulled the following morning at 0700 hours. Daytime sets normally lasted from 0800 to 1500 hours. Between 1500 and 1900 hours, the nets were moved to the next location and reset. Six nets, 3.0 x 31 m, with square mesh sizes of 19, 25, 38, 51, 64, and 76 mm, respectively, were used from June through August. Nets were set perpendicular to shore at depths greater than 31 m when possible. In September, the 76 mm net, which had not caught fish, was

replaced with a 38 mm mesh net. Sample sizes in September and October subsequently increased. Species, depth of capture, total length in millimeters, and weight in grams were recorded for each fish captured. Temperature and dissolved oxygen profiles were measured by a YSI Model 54A Oxygen meter at the time of each net setting.

Beach Seine Surveys

To gather information about the littoral fish community, beach seine surveys were conducted monthly from June through September 1990 at standardized sites in each of the three areas (Fig. 3.1). The monthly beach seine surveys were conducted between 19 and 21 June, 16 and 19 July, 19 and 23 August, and 16 to 19 September, 1990. A 1.5 m x 31 m with 12 mm square mesh beach seine was used. Three 30 m seine hauls, parallel to the shoreline, were conducted at midday and three near midnight at each site. Approximately 1 000 cubic meters of water were sampled by each haul. Fish captured were identified to species, measured to the nearest millimeter, and weighed to the nearest gram.

Results

Acoustic Surveys

Densities of forage fishes varied significantly among areas of the reservoir if densities are expressed on the basis of surface area (Fig. 3.2). ANOVA indicated

significant differences among areas ($f_{5,36}$=9.43, $p \leq 0.001$), and a Bonferroni multiple comparison of means (Wilkinson 1988) indicated that Canyon-A and the Inflow areas were significantly different from the other regions of the reservoir.

Densities of forage fishes expressed in volumetric units also varied significantly among different regions of the reservoir (Fig. 3.2). Two-way ANOVA (depth and area) indicated significant differences among area ($f_{5,70}$=9.88, $p \leq 0.001$) but no overall differences between epilimnetic and metalimnetic densities of fish ($f_{1,70}$=0.04, $p>0.05$). The interaction term between depth and area was also not significant ($f_{5,70}$=0.50, $p>0.05$). Visual inspection of the data, however, suggests that epilimnetic and metalimnetic densities were similar in the Inflow area, but that metalimmnetic densities were higher than the epilimnetic densities in the Canyon area. Density of fish in the hypolimnion were low in the Canyon area and intermediate in the Open Hills area (Fig. 3.2). Water depth did not exceed 30 m in the Inflow area, hence no data are present for hypolimnetic densities. Visual inspection of paper charts indicated that densities of fish in the upper portion of the hypolimnion (30-40 m) were similar in the Canyon and Open Hills areas. Increased volumes of very deep water with very few fish targets in the Canyon area reduced hypolimnetic densities.

Vertical Gill Net Sampling
and Density Estimation

A total of 553 fish were caught in the vertical gill net sampling. More fish were caught from the Inflow area (316) than from the Open Hills (209) and Canyon (28) areas (Table 3.1). Kokanee were the most commonly caught species in the Canyon (39%) and Open Hills (96%) areas, while Utah chub dominated the catch in the Inflow area (77%).

The vertical gill net sampling revealed that the dominant forage fish, kokanee and Utah chub, were thermally segregated from July through September (Fig. 3.3). Significant differences in mean temperatures occupied by chubs and kokanee were observed with chubs occupying warmer waters (18.3°C) compared to kokanee (12.1°C), ($t = -3.105$, $t_{.10[153]} = 1.645$).

Temperature profile data collected in August 1990 at vertical gill net sites revealed that the depths at which the 8°C and 17°C temperature strata occurred were fairly consistent throughout the entire length of the reservoir. The depth at which water was warmer than 17°C was 13 m, while water cooler than 8°C was encountered at depths of 30 m (Fig. 3.4).

We used this thermal segregation to partition hydroacoustic targets to species. Because Utah chubs dominated the catch in water warmer than 17°C (86%), we estimated chub abundance assuming that this percentage of

epilimnetic acoustic targets was Utah chub (Table 3.2). In a similar manner we estimated kokanee abundance assuming that 76% of metalimnetic acoustic targets were kokanee. These estimates indicated that slightly more than 500 000 Utah chubs and approximately 400 000 kokanee greater than 50 mm were present in the pelagic regions of the reservoir during nighttime periods (Table 3.2).

Beach Seine Surveys

Six species of fish were captured in the beach seine surveys; however, we limit our discussion to Utah chub since they represent the only species associated with the littoral zone that was also found to a substantial degree in the diet of lake trout (Table 3.3).

In the 54 beach seine hauls conducted during the stratified period of the reservoir (16 July to 19 September) a mean of 4.8 (sd=12.9) Utah chub was captured during the day compared to 11.2 (sd=27.7) captured at night. A Mann-Whitney U-test indicated significant differences between day and night seine catches ($U=753$, $p<0.001$).

Discussion

Abundance and species composition of forage fish for lake trout varied across areas and depths of FGR during the summer of 1990. Utah chub was the most abundant species in the epilimnion (Table 3.2) and were more abundant in the Inflow compared to other areas of the

reservoir. Kokanee were the most abundant forage fish in the metalimnion and hypolimnion in all areas of the reservoir. Kokanee and rainbow trout comprised almost all of the forage fishes in the Canyon area. Biomass of pelagic Utah chub and kokanee estimated from nighttime acoustic surveys was calculated to be 83 300 and 209 000 kg, respectively (Table 3.4).

These biomass estimates can be compared to annual rates of consumption of lake trout in FGR. Consumption rates estimated from bioenergetics analyses (Yule and Luecke, submitted) indicated that the lake trout population between 1985 and 1989 consumed on average 79 000 kg of Utah chub and 196 000 kg of kokanee per year. Given that these annual consumption estimates almost match acoustic estimates of available forage (Fig. 3.5), it is unlikely that stocks of Utah chub or kokanee will be able to maintain themselves in future years.

It is likely that the lake trout population consumes a significant proportion of the annual production of forage fish in the system. A production/biomass (P/B) of 0.95 would be necessary for Utah chub to match annual lake trout consumption demand. Although this value is within the range of P/B ratios for cyprinids (Chadwick 1976; Pitcher and Hart 1982), lake trout are not the only predator which utilize chubs in FGR. A substantial population of smallmouth bass is known to feed extensively on chubs younger than IV+ during the spring and fall (B.

Wengert, WG&FD, Green River, WY, pers. comm.). In a similar manner kokanee would need to have a P/B of 0.94. This value is within the range of reported P/B ratios for *O. nerka* (Eggers et al. 1978; Sorokin and Paveljeva 1978); however, angler harvest of kokanee likely substantially reduces the availability of kokanee production for lake trout forage.

Although our analysis suggests that lake trout are overexploiting prey stocks, some caution should be taken in interpreting the acoustic estimates of forage fish availability. Acoustic estimates of fish abundance are biased towards underestimation for several reasons (Burczynski and Johnson 1986). In our surveys only 29% of acoustic targets were classified as single fish. Some of the non-classified targets were likely fish targets that failed to meet the target criteria. In the FGR surveys we only sample at night in pelagic regions where water depths are greater than 5 m. While this method encompasses most of the surface area of the reservoir, beach seine surveys indicated that Utah chub were present in the littoral zone and were more abundant inshore during nighttime hours than during the daytime. In addition to the lack of littoral zone sampling, our acoustic sampling does not include fish within 1 m of the bottom. Our surface-towed transducer might also be detected and avoided by fish residing near the surface. Vertical gill net catches indicated that

Utah chub were occasionally captured in the top 2 m of the water column.

Although uncertainties in acoustic sampling make it difficult to determine the likely magnitude of error, our estimates of forage fish abundance are likely reasonable for pelagic regions of the reservoir at night. Given that lake trout can feed under low light intensities (Scott and Crossman 1973), and that they are not likely to spend much time in warm epilimnetic waters, our acoustic estimates may provide a good means of assessing forage fishes that are available to trout during summer periods. Our analyses, however, ignore the potential contribution of the littoral zone to forage fish production.

In addition to comparing forage species abundances to lake trout consumption patterns, our acoustic and bioenergetics analyses allow us to examine size-dependent interactions between piscivorous lake trout and forage fishes in FGR. Previous research on lake trout feeding habits in the reservoir indicated that diets of lake trout varied greatly with fish length (Yule and Luecke, submitted). Small lake trout (400 - 600 mm) fed extensively on invertebrates and fish between 50 - 170 mm. Lake trout larger than 600 mm fed almost exclusively on fish ranging from 170 - 425 mm. This distinction in lake trout diets allowed us to assess the availability of forage fishes for the two size-classes.

We used target strength measurements from the hydroacoustic survey to estimate the abundance and biomass of pelagic forage fishes available (Table 3.4). We grouped all target strengths between -51 and -41 dB and assumed that these forage fishes were suitable as forage to small lake trout. Fish with target strengths between -41 and -33 dB were assumed to be suitable to larger lake trout. These calculations allowed us to compare the availability of usable forage fish to rates of lake trout consumption. Availability of forage fish biomass was an order of magnitude greater for larger lake trout compared to smaller lake trout (Table 3.4). Consumption demand of small lake trout exceeded biomass estimates of forage fish of the size they consume (Fig. 3.5), while available biomass of forage fish between 200 and 420 mm was greater than annual consumption demand by large lake trout.

This difference in available forage biomass may explain why fish comprise such a small proportion of the diet of small lake trout in FGR. Forage fish accounted for 34%, 5%, 33%, and 47%, of the diet of small lake trout by weight in the spring, summer, fall of 1990, and the winter of 1990-91, respectively (Yule and Luecke, submitted). The lack of forage fish in the diet of these small predators is not likely a function of gape morphology since lake trout feed at much smaller sizes in other systems (Trippel and Beamish 1989; Martin 1970; Magnin and Clement 1978). Populations of lake trout where

diets of 400-600 mm individuals were composed primarily of invertebrates exhibited low growth rates (Konkle and Sprules 1986; Donald and Alger 1986).

These results suggest that forage fish populations should decline in FGR over the next several years due to predation by lake trout. Utah chub populations appear to be more vulnerable to overexploitation than do kokanee populations because biomass and annual production of this species do not approach estimates of annual lake trout consumption demand. This potential decline would be hastened as the number of lake trout greater than 600 mm increases following the initiation of the 650 to 920 mm slot-limit regulation (Luecke et al., submitted).

The kokanee population of the reservoir will likely have difficulty expanding, especially if lake trout begin to feed more on kokanee if chub numbers continue to decline. The current pattern of declining numbers of Utah chubs has resulted in larger kokanee, rather than more kokanee (Fowden et al. 1991). It is likely that this pattern will continue.

Our results also suggest that lake trout growth rates should decline especially for smaller individuals. Lake trout 400-600 mm were subsisting on invertebrate prey probably because of a lack of suitable-sized forage fishes. The lack of small pelagic forage fishes coupled with a potential decline in forage fish populations in upcoming years may reduce the ability of lake trout to

recruit to sizes that are accessible to anglers and are of value to the fishery.

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Tables and Figures

TABLE 3.1. Numbers of fish captured by vertical gill net sampling by area of Flaming Gorge Reservoir from June through October, 1990. Percent of catch by area in parentheses.

	Area		
Species	Canyon	Open Hills	Inflow
Kokanee	11 (39%)	201 (96%)	55 (18%)
Lake trout	7 (25%)	1 (<1%)	4 (1%)
Rainbow trout	5 (18%)	-	3 (1%)
Utah chub	3 (11%)	7 (3%)	243 (77%)
White sucker	2 (7%)	-	10 (3%)
Brown trout	-	-	1 (<1%)
Totals	28 (100%)	209 (100%)	316 (100%)

TABLE 3.2. Abundance estimates of the epilimnetic (0-13 m), metalimnetic (13-30 m), and hypolimnetic (30-90 m) forage fish communities in Flaming Gorge Reservoir. Prop VGN equals the proportion of fish captured from a depth strata by vertical gill net (VGN) sampling. Abundance was calculated by multiplying fish density x volume x Prop VGN.

Depth strata	Species	Prop VGN	Fish density (#/1000 m^3)	Volume (x 10^9 m^3)	Abundance (x 10^3)
0-13	Chub	0.863	0.347	1.438	431
	Kokanee	0.055	0.347	1.438	27.4
13-30	Chub	0.186	0.386	1.240	89.0
	Kokanee	0.762	0.386	1.240	365
30-90	Kokanee	-	0.009	1.049	9.44
Totals	Chub				520
	Kokanee				402

TABLE 3.3. Fish captured in beach seine sampling of Flaming Gorge Reservoir from June through September, 1990. Percent occurrence in lake trout diet is from samples collected during 1990 and 1991.

Species	Total number caught	% Day	% Night	Percent* diet occurrence
Utah chub	531	32.4	67.6	22.5
Common carp	223	49.8	50.2	2.2
White sucker	148	20.9	79.1	1.4
Smallmouth bass	55	90.9	9.1	-
Rainbow trout	22	40.9	59.1	8.7
Redside shiner	1	-	100	-
Kokanee salmon	1	-	100	51.4
	978			86.2**

* Yule and Luecke (submitted)

** Does not include sculpin (12.2%), and lake trout (1.6%).

TABLE 3.4. Abundance and biomass estimates of pelagic Utah chub and kokanee from August, 1990, acoustic survey. Abundances from Table 3.1. Mean weight (g) was calculated by calculating the frequency of fish targets in every 2 dB size bin from -51 to -33 dB, calculating lengths from Love's (1971) equation, and calculating weights using the length weight regressions from Appendix, Table A.1.

Depth (m)	Species	Abundance (X 1000)	Weight (g)	Biomass (kg X 1000)
0-13	Chub	431	76.3	32.8
	Kokanee	27.4	78.2	2.14
13-30	Chub	89.0	568	50.5
	Kokanee	365	551	201
30-90	Kokanee	9.44	643	6.1
Totals	Chub			83.3
	Kokanee			209

TABLE 3.5. Abundance and biomass estimates of pelagic forage fish available to lake trout less than, and greater than 600 mm. Estimated prey sizes are equivalent to -51 to -41, and -41 to -33 dB, for the 50 to 170, and 170 to 440 mm size-classes, respectively.

Depth (m)	Estimated prey sizes (mm)	Abundance (X 1000)	Weight (g)	Biomass (kg X 1000)
0-13	50 to 170	346	43	15.0
13-30	50 to 170	164	43	7.05
30-90	50 to 170	3.0	43	0.13
Total for lake trout less than 600 mm				22.2
0-13	170 to 440	151	709	107
13-30	170 to 440	315	709	223
30-90	170 to 440	3.7	709	2.7
Total for lake trout greater than 600 mm				333

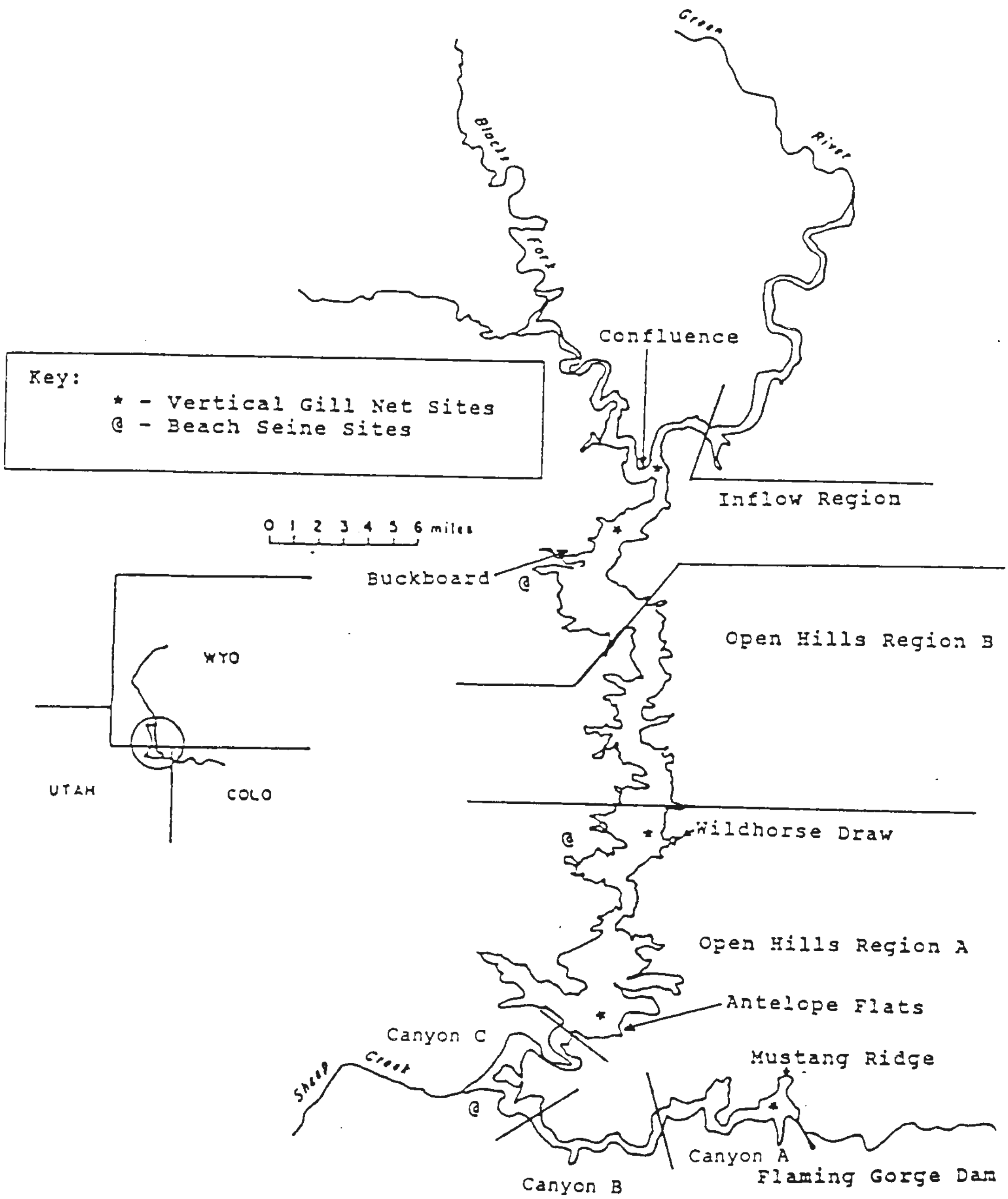


FIG. 3.1. Map of Flaming Gorge Reservoir, Wyoming-Utah, showing acoustic region demarcation, and location of vertical gill net sites and beach seine surveys.

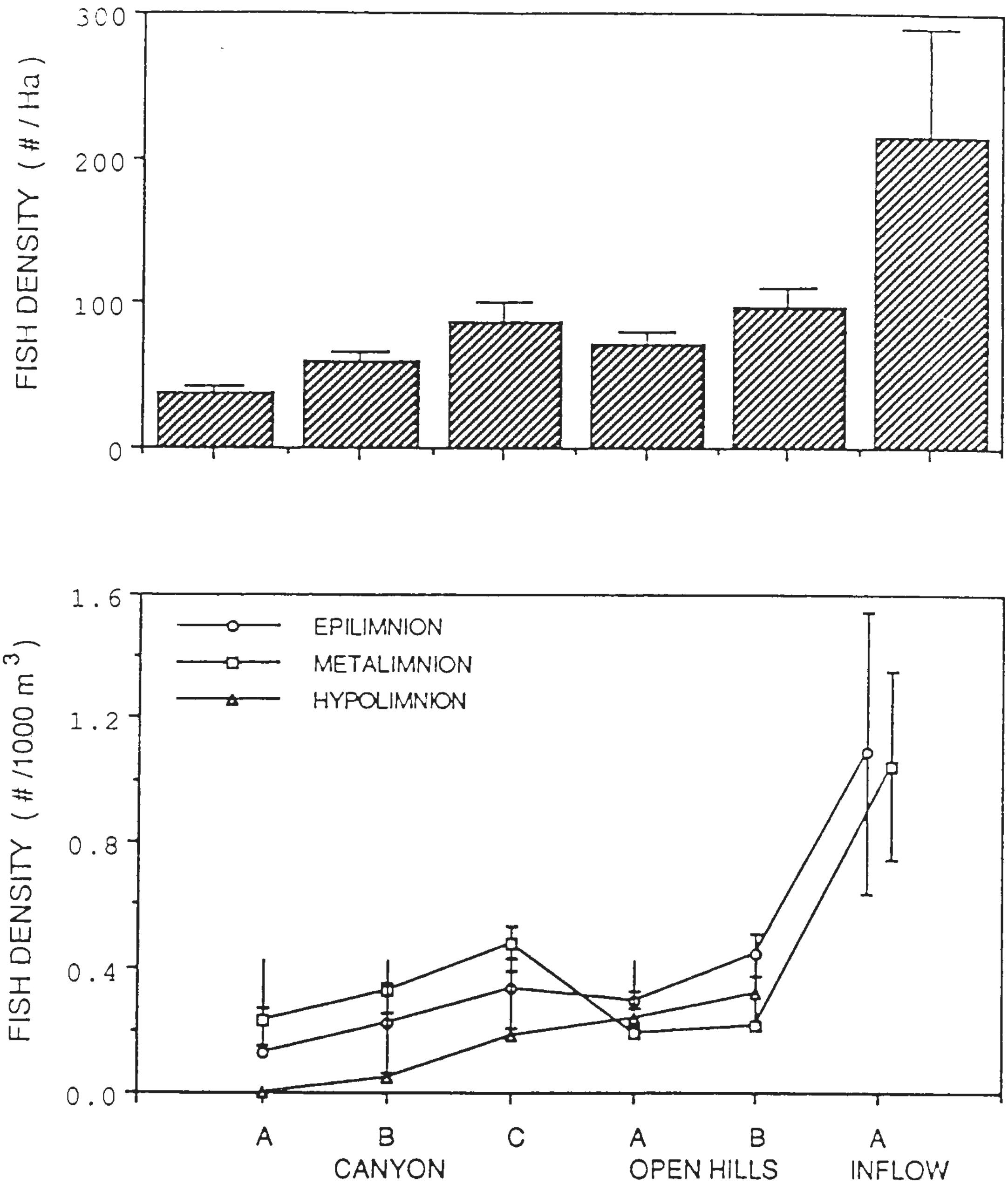


FIG. 3.2. (a) Areal densities of forage fish by region, and (b) volumetric densities of epilimnetic (0-13 m), metalimnetic (13-30 m), and hypolimnetic (30-90 m) fishes by region in Flaming Gorge Reservoir. Error bars indicate ± standard error.

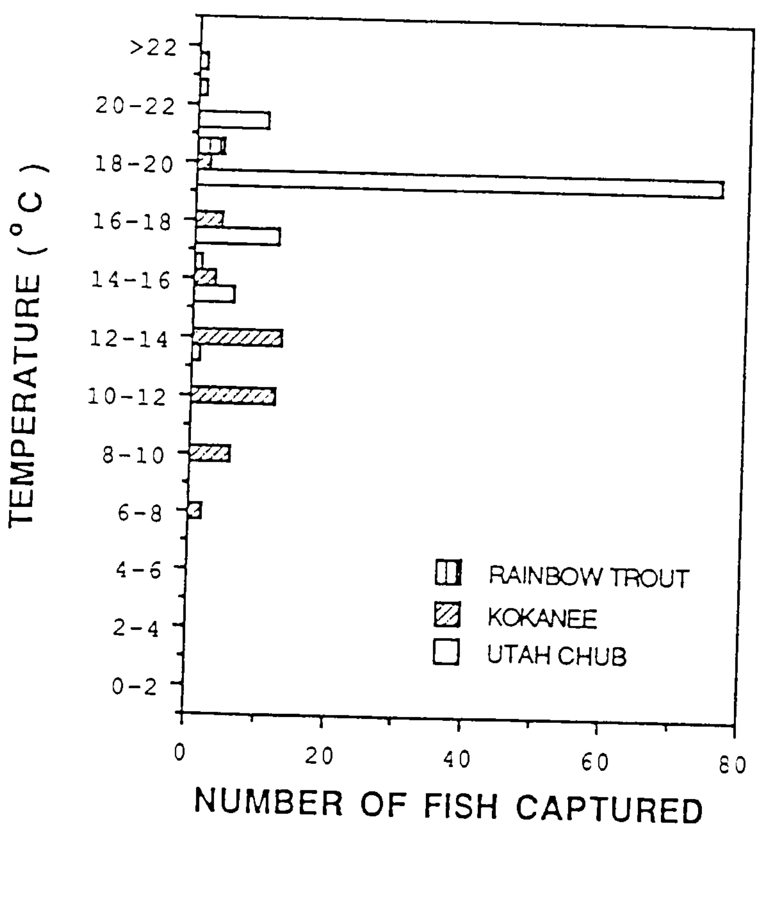


FIG. 3.3. Relationship between the number of rainbow trout, kokanee, and Utah chub captured in vertical gill net sampling of Flaming Gorge Reservoir during July and August, 1990, and temperature. All sites and dates pooled.

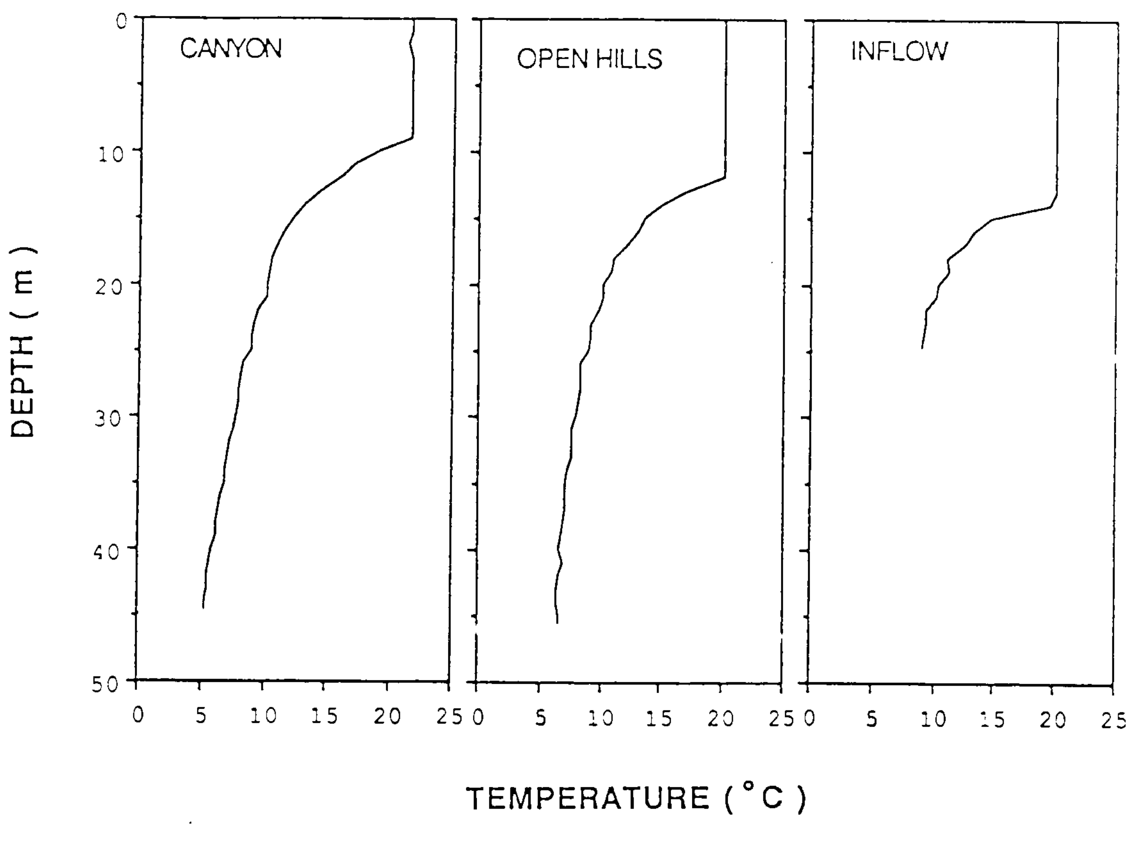
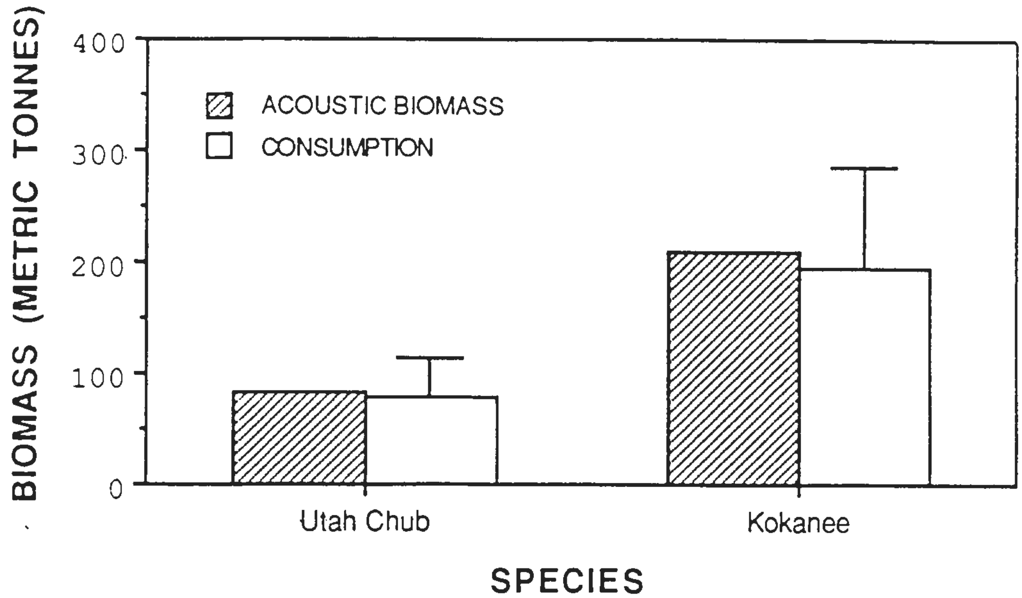


FIG. 3.4. August temperature profiles of Flaming Gorge Reservoir at vertical gill net sites.



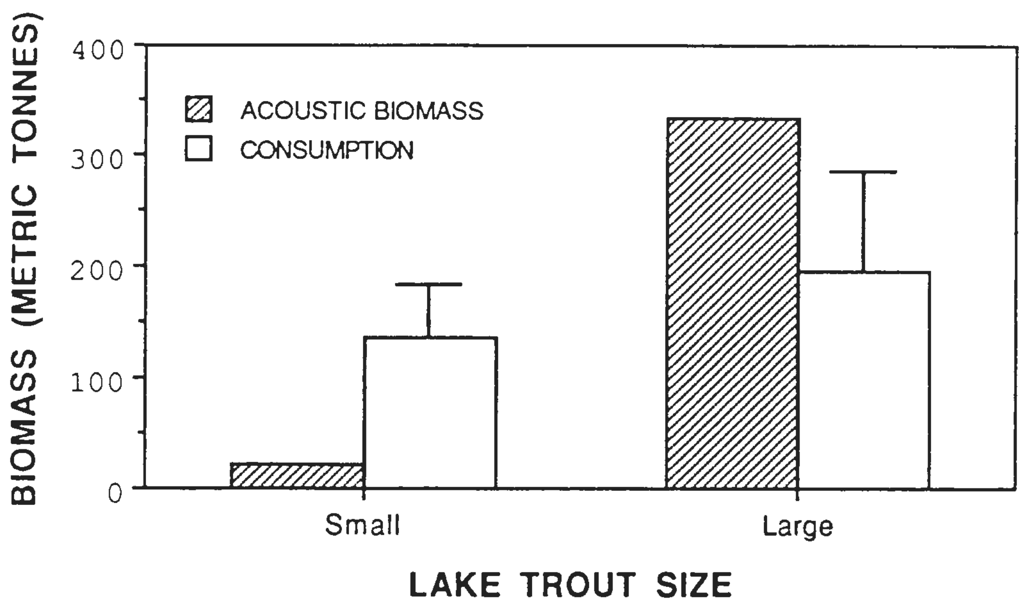


FIG. 3.5. (a) Comparison of annual lake trout consumption demand to biomass estimates of Utah chub and kokanee, and (b) comparison of annual consumption demand by lake trout less than, and greater than 600 mm to pelagic forage fish biomass of useable size. Consumption error bars indicate upper and lower estimates, derived through consideration of upper and lower 95% CI of lake trout abundance (Yule and Luecke, submitted)

CHAPTER IV

PRODUCTION OF FORAGE FISH IN FLAMING GORGE RESERVOIR

Introduction

Ivlev (1945) defined production as the total elaboration of fish tissue within one year, regardless of the fate of that tissue during the year. By comparing consumption estimates of lake trout (*Salvelinus namaycush*) to production estimates of forage fishes, some general predictions can be made regarding the potential for lake trout predation to cause a decline in forage fish abundance in Flaming Gorge Reservoir (FGR). For example, if lake trout predation removes a significant proportion of the production of Utah chub (*Gila atraria*) through the course of a year, one might expect Utah chub numbers to decline over time. Conversely, if consumption does not remove a significant proportion of Utah chub production, it is unlikely that predation by lake trout could result in a decline in chub numbers. What constitutes excessive consumption is difficult to quantify; however, determination of the relative proportion of production currently being consumed annually does allow some predictions to be made.

In this chapter, I compare estimates of annual lake trout consumption demand to production estimates of metalimnetic and epilimnetic forage fish communities in

FGR. Annual lake trout consumption was estimated using a bioenergetics approach (Chapter II). To quantify forage fish production, I used the generalized bioenergetics model for fish growth (Hewett and Johnson 1987). The model quantifies production using the same principles as an Allen curve (1971) from external input of growth, abundance, and survivalship of a population of interest. For simplicity in modeling reservoir-wide forage fish production, I assumed that the Utah chub population was representative of the epilimnion, while the kokanee (*Oncorhynchus nerka*) population was representative of the metalimnion (Chapter III).

Methods and Results

To model the production of kokanee, I utilized the bioenergetics model developed for sockeye salmon (*O. nerka*) by Beauchamp et al. (1989). Since no energetics model currently exists for Utah chub, I opted to use a model developed for another genus in the cyprinid family, the dace (*Phoxinus spp.*) (Hewett and Johnson 1987). To allow Utah chub to grow to observed adult sizes (>300 g) I adjusted the respiration parameters internal to the dace model so that they more closely conformed to a warm-water species in a lentic environment. I chose the respiration parameters recommended for yellow perch (*Perca flavescens*) (Kitchell et al. 1977).

Growth of Forage Fish

Growth information for Utah chub was obtained through scale analysis of fish captured in our beach seine surveys and vertical gill net sampling of July 1990 (Chapter III). The mean weight of 0+ chubs in July was gathered by catching these fish in a dip net and weighing them to the nearest 0.01 g on a Metler H51 balance. Scales from Utah chub specimens older than 0+ were mounted on glass slides, enlarged on a microfiche projector, and aged. Once aged, length-frequency distributions by cohort were formulated (Table 4.1). From these age/length frequency distributions we calculated a weighted mean length in July for each cohort (Table 4.2). A regression equation relating total length (mm) to weight (g) for Utah chub (Appendix, Table A.1) was used to calculate a mean weight from the weighted mean length (Table 4.2). For the bioenergetic runs, initial weights for each cohort were chosen as the calculated mean weight in July, while final weights for the one year simulations equaled the mean weight of the next oldest cohort. Since no IV+ and V+ chubs were captured in our sampling of July 1990, we used the roseyface dace/yellow perch bioenergetics model to estimate their final weights.

Growth information of kokanee for the bioenergetics simulations was obtained through analysis of an age/length-frequency distribution data set of fish captured in the May, 1990, purse seine netting (Table 4.3,

from B. Wengert, Wyoming Game and Fish Department (WG&FD), Green River, WY, unpublished data). No I+ kokanee were captured in 1990. Thus, to calculate a weighted mean length for I+ fish we utilized an age/length-frequency distribution data set from fish captured in the June, 1986, purse seine survey (Table 4.3, from B. Wengert, WG&FD, Green River, WY, unpublished data). We assumed that growth rates of 0+ and I+ kokanee have not changed since 1986. From the age/length-frequency distribution data sets we calculated a weighted mean length for each kokanee cohort older than 0+ (Table 4.4). Initial weights and final weights for the bioenergetics simulations (0+ initial weight excluded) were calculated through a regression equation relating total length to weight for kokanee (Appendix, Table A.1). We used a value of 0.03 g as the initial weight of emerging kokanee (Randall Jerik, Utah Cooperative Research Unit, Utah State University, Logan, UT, pers. comm.).

Abundance and Survivorship of Forage Fish

Abundance estimates for the Utah chub and kokanee cohorts were derived through analysis of an August 1990 hydroacoustics survey (Chapter III). We delimited our total estimates of the number of fish belonging to the respective pelagic fish communities (epilimnion and metalimnion) to cohorts through consideration of target-strength frequency distribution data sets. For example,

I+ kokanee from the 1986 purse seine had a length range of 102 to 175 mm (Table 4.4). Using Love's (1971) equation, which relates target strength to fish length, this range of fish lengths equals targets strengths from -45 to -41 decibels (dB). We calculated the relative proportion of targets in this length range to the total number of targets returned (31%), and multiplied this proportion by the total abundance estimate of the metalimnion forage fish community (454 000, Chapter III), thereby estimating the abundance of I+ kokanee in the system to be 140 300. Abundance estimates of the remaining kokanee cohorts (Table 4.5), and all of the Utah chub cohorts (Table 4.6) were calculated using the same method. To estimate annual cohort mortality rates, we divided the abundance estimate of a cohort by the abundance estimate of the proceeding cohort (estimate of survival between cohorts) and subtracted 1. We used the generalized bioenergetics model for fish growth to calculate daily mortality rates from annual mortality rates, assuming that mortality of forage fish was constant across the year.

Modeling Approach

Energetics simulations of the chub population began on 1 July, the approximate date that chubs become free-living in FGR (Varley and Livesay 1976). The chub simulations included a 6.8% loss of body mass to spawning on model date 335 (1 June) for chubs older than IV+

(Varley and Livesay 1976). Bioenergetics simulations of the kokanee population began on 1 June, the approximate date that reservoir-spawning kokanee become free-living (Randall Jerik, Utah Cooperative Research Unit, Utah State University, Logan, UT, pers. comm.).

I assumed that both chubs and kokanee fed entirely on zooplankton. I used a value of 800 cal x g^{-1} (wet weight) as the caloric content of this food type (Cummins and Wuycheck 1971).

I estimated the thermal preference of both populations from July through October (Fig. 4.1) from fish captured during our 1990 vertical gill net sampling. From 1 December through 1 March, I assumed that both chubs and kokanee occupied a temperature of 4.0°C.

Once growth, abundance, survivalship, diet, and thermal history information had been entered in the respective bioenergetics models, I used the p-fit option of the models to generate p-values by cohort. P-values are an index of what proportion of the maximum feeding rate (1 = *ad libitum*) the fish had to feed at to match observed growth. These p-values were entered back into the models and the models were run. I used the roseyface dace/yellow perch model to estimate production of all cohorts of Utah chub up through VIII+, since this species is vulnerable to lake trout predation throughout its life history (Chapter II). I used the sockeye model to estimate production of kokanee cohorts up through III+.

Production estimates of IV+ kokanee were not estimated since this cohort is not eaten by even the largest of lake trout in the system (Chapter II).

Biomass Estimates and Production to Biomass (P/B) Ratios

Biomass estimates of chub and kokanee cohorts were calculated by multiplying the cohort abundance estimate by the mean weight of the cohort in July. P/B ratios for each chub and kokanee year-class were calculated by dividing the production estimate for that cohort by the biomass estimate of that cohort. Community P/B ratios were calculated by dividing the sum of the respective cohort production estimates by the sum of the respective cohort biomass estimates.

Results and Discussion

These analyses suggest that metalimnetic production greatly exceeds epilimnetic production (Table 4.7). Metalimnetic production of small fishes (0+, and I+) is much greater than the same size fishes in the epilimnion. Greater survivability of 0+ and I+ kokanee over the same age chubs (Fig. 4.2), combined with the dramatic growth advantage of kokanee over chubs (Fig. 4.3), explains the higher production of the metalimnion. The P/B ratio of the metalimnetic community (1.6) exceeded that of the epilimnetic community (0.7) (Table 4.7). Our estimates of P/B ratios for chubs and kokanee are very similar to those

reported in the fisheries literature. P/B ratios for cyprinids usually range from 0.9 to 1.4 (Chadwick 1976; Pitcher and Hart 1982), while P/B ratios for *O. nerka* typically range from 1.2 to 2.5 (Eggers et al. 1978; Sorokin and Paveljeva 1978). The greatest P/B ratios occurred in 0+ fishes; however, the P/B of 0+ metalimnetic fishes exceeded the P/B of 0+ epilimnetic fishes by 19-fold (Table 4.7).

Consumption rates estimated from bioenergetics analyses indicate that the lake trout population between 1985 and 1989 consumed an average of 79 000 kg of Utah chub and 196 000 kg of kokanee per year (Chapter II). Biomasses of pelagic Utah chub and kokanee estimated from nighttime acoustic surveys were calculated to be 83 000 and 209 000 kg, respectively (Chapter III). Thus, a P/B ratio of 0.95 would be necessary for Utah chub production to match annual lake trout consumption demand. In a similar manner kokanee would need to have a P/B of 0.94.

These analyses suggest that Utah chub production does not match concurrent lake trout consumption demand; thus, we predict that the chub population will decline over time. Currently, kokanee production appears to be surpassing consumption demand of lake trout, suggesting that the population is capable of supporting current levels of predation. This scenario may change if lake trout begin to feed more on kokanee as the chub population declines, or if angler harvest of kokanee should increase

substantially. Fortunately, lake trout are easily harvested from FGR (Bill Wengert, WG&FD, Green River, WY, pers. comm.); thus, should available forage for lake trout in FGR become extremely limited, a liberal harvest regulation of lake trout might act to quickly reduce consumption demand. Moreover, a reduction of the number of kokanee harvested by anglers may act to provide additional forage for piscivorous lake trout in the system.

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Tables and Figures

TABLE 4.1. Length frequency distribution by cohort of Utah chub captured in beach seine surveys and vertical gill net sampling of July 1990. Class-range in mm.

Class-range	Cohort							
	I+	II+	III+	IV+	V+	VI+	VII+	VIII+
40-49								
50-59	4							
60-69	2							
70-79	2							
80-89								
90-99		1						
100-109		36						
110-119		32						
120-129		19	1					
130-139			5					
140-149			5					
150-159			4					
160-169			1					
170-179								
180-189								
190-199								
200-219								
220-229								
230-239								
240-249								
250-259						1		
260-269						3		
270-279						3	2	
280-289						2	6	1
290-299						1	2	3
300-309							2	13
310-319								8
320-329								3
330-339								1
Totals	8	88	16			10	12	29

TABLE 4.2. Weighted mean length, length range, and mean weight of Utah chub cohorts captured in beach seine surveys and vertical gill net sampling of July 1990. Weighted mean length, and length range are in mm. Mean weight in grams calculated from regression equation (Appendix, Table A.2).

Cohort	Weighted mean length (mm)	Length range (mm)	Mean weight (g)
0+	17	11-31	0.03*
I+	63	50-79	3
II+	113	90-129	18
III+	144	120-169	39
IV+	-	-	119**
V+	-	-	163**
VI+	274	250-299	277
VII+	288	270-309	323
VIII+	306	280-339	388

* 0+ chubs captured in dip net (n=44).
\- No data
** Predicted by dace/perch bioenergetics model.

TABLE 4.3. Age/length-frequency distribution of kokanee captured in purse seine sampling of June 1986, and June 1990. Class-range is in inches. I+ kokanee lengths are from June, 1986, while II+, III+, and IV+ kokanee are from June 1990 (B. Wengert, WG&FD, Green River, WY, unpublished data).

Class-range	Cohort I+	II+	III+	IV+
4.0-4.4	2			
4.5-4.9	8			
5.0-5.4	6			
5.5-5.9	8			
6.0-6.4	2			
6.5-6.9	1			
7.0-7.4				
7.5-7.9				
9.0-8.4				
8.5-8.9		2		
9.0-9.4		2		
9.5-9.9		11		
10.0-10.4		14		
10.5-10.9		11		
11.0-11.4		9		
11.5-11.9		9		
12.0-12.4		7	1	
12.5-12.9		3		
13.0-13.4			4	
13.5-13.9			2	
14.0-14.4		1	2	
14.5-14.9			10	
15.0-15.4		1	10	
15.5-15.9			9	
16.0-16.4			12	1
16.5-16.9		1	1	3
17.0-17.4			1	4
17.5-17.9			1	3
18.0-18.4				1
18.5-18.9				
19.0-19.4				
19.5-19.9				
Totals	27	71	53	12

TABLE 4.4. Weighted mean length, length range, and mean weight of kokanee cohorts captured in purse seine sampling of June, 1986 and 1990. I+ lengths from 1986, while II+, III+, and IV+ lengths from 1990. Weighted mean length, and length range was converted to mm by multiplying inches by 25.4. Mean weight in grams calculated from regression equation (Appendix, Table A.2).

Cohort	Weighted Mean Length (mm)	Length Range (mm)	Mean Weight (g)
0+	-	-	0.03*
I+	135	102-175	40
II+	279	216-429	259
III+	391	305-455	618
IV+	444	406-480	861**

\- No data.
* Weight of emerging kokanee (Randall Jerik, pers. comm.).
** Not available as lake trout forage.

TABLE 4.5. Abundance estimates of kokanee cohorts. TS (target strength) in decibels (dB). TS dist. is the number of targets of a dB range returned from the metalimnion. Relative-frequency (Rel. freq.) is the proportion of targets of a dB range returned of the total targets returned. Length in millimeters calculated using Love's (1971) equation. Cohort is age of kokanee of that length. Sum of rel.-freq. by cohort equals proportion of targets of specific cohort size. Abundances were calculated by multiplying sum of rel.-freq. by cohort by the epilimnion abundance estimate (454,000, Chapter III).

TS (dB)	TS dist.	Rel. freq.	Length (mm)	Cohort	Sum of rel.-freq. by cohort	Abundance
-61	154	0.046	14.9	0+		
-59	181	0.054	19.1	0+		
-57	204	0.061	24.3	0+		
-55	216	0.065	30.9	0+		
-53	242	0.073	39.3	0+		
-51	236	0.073	50.1	0+		
-49	233	0.070	63.7	0+		
-47	239	0.072	81.1	0+	0.512	232,500
-45	285	0.086	103.2	I+		
-43	356	0.107	131.3	I+		
-41	393	0.118	167.1	I+	0.309	140,300
-39	337	0.101	212.7	II+		
-37	169	0.051	270.7	II+	0.152	69,000
-35	76	0.023	344.5	III+	0.023	10,400
-33	14	0.004	438.4	IV+	0.004	1,800
Tot.	3335	1.000			1.000	454,000

TABLE 4.6. Abundance estimates of Utah chub cohorts. TS (target strength) in decibels (dB). TS dist. is the number of targets of a dB range returned from the epilimnion. Relative-frequency (Rel. freq.) is the proportion of targets of a dB range returned of the total targets returned. Length in millimeters calculated using Love's (1971) equation. Cohort is age of chub of that length. Sum of rel.-freq. by cohort equals proportion of targets of specific cohort size. Abundances were calculated by multiplying sum of rel.-freq. by cohort by the epilimnion abundance estimate (458,000, Chapter III).

TS (dB)	TS dist.	Rel. freq.	Length (mm)	Cohort	Sum of rel.-freq. by cohort	Abundance
-61	52	0.133	14.9	0+		
-59	52	0.133	19.1	0+		
-57	53	0.135	24.3	0+		
-55	56	0.142	30.9	0+		
-53	56	0.142	39.3	0+	0.685	313,800
-51	25	0.064	50.1	I+		
-49	26	0.066	63.7	I+		
-47	16	0.041	81.1	I+	0.171	78,300
-45	10	0.026	103.2	II+	0.026	11,900
-43	12	0.031	131.3	III+	0.031	14,200
-41	12	0.031	167.1	IV+	0.031	14,200
-39	13	0.033	212.7	V+	0.033	15,100
-37	7	0.018	270.7	VI+	0.018	8,200
-35	2	0.005	344.5	VII+ VIII+	0.005	2,300
Tot.	392	1.000			1.000	458,000

TABLE 4.7. Estimates of epilimnetic and metalimnetic forage fish biomass, production, and P/B ratios. Biomass estimates (metric tons) calculated by multiplying cohort abundance estimate by the mean weight of the cohort in July. Production estimates (metric tons/annually) were predicted by energetics modeling. Cohort P/B ratios were derived by dividing the estimate of cohort production by the biomass estimate for that cohort. Community P/B ratios were calculated by dividing the sum of the respective cohort production estimates by the sum of the respective cohort biomass estimates.

	Epilimnion			Metalimnion		
Cohort	Biomass	Prod.	P/B	Biomass	Prod.	P/B
O+	0.009	0.439	49	0.007	6.48	929
I+	0.235	0.545	2.32	5.61	27.6	4.92
II+	0.214	0.250	1.17	17.9	12.2	0.68
III+	0.554	1.24	2.24	6.43	1.24	0.20
IV+	1.69	0.816	0.483			
V+	2.46	1.53	0.622			
VI+	2.27	0.291	0.129			
VII+ & VIII+	0.818	0.205	0.251			
Totals	8.25	5.32	0.645	29.9	47.5	1.59

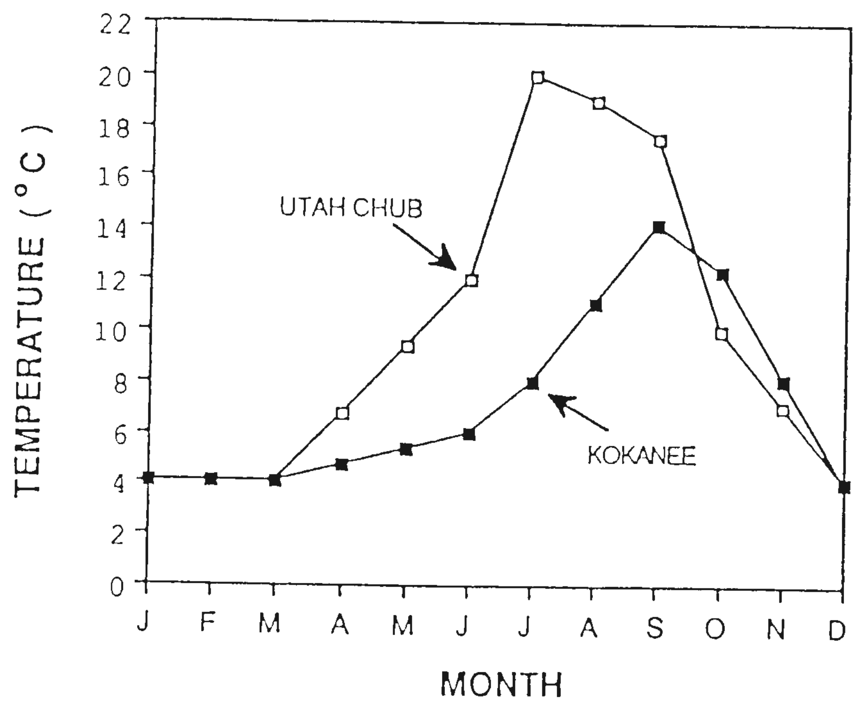

FIG. 4.1. Estimates of temperatures occupied by Utah chub and kokanee across one year. June through October estimates derived from vertical gill net sampling (Chapter III). From December through March we assumed that chubs and kokanee occupied a temperature of 4.0°C.

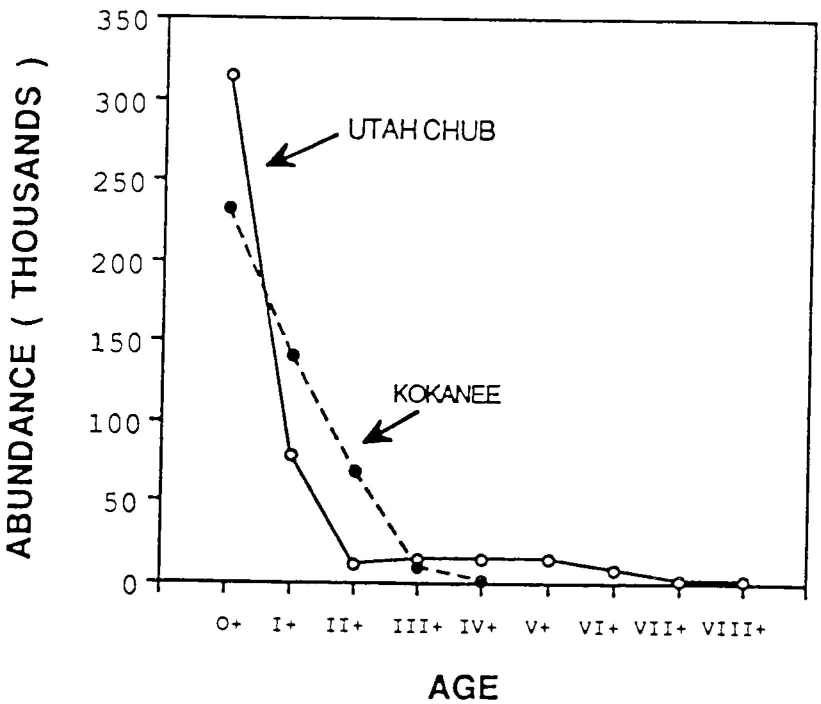

FIG. 4.2. Abundance estimates of Utah chub and kokanee cohorts in Flaming Gorge Reservoir. Data from Table 4.5 and Table 4.6.

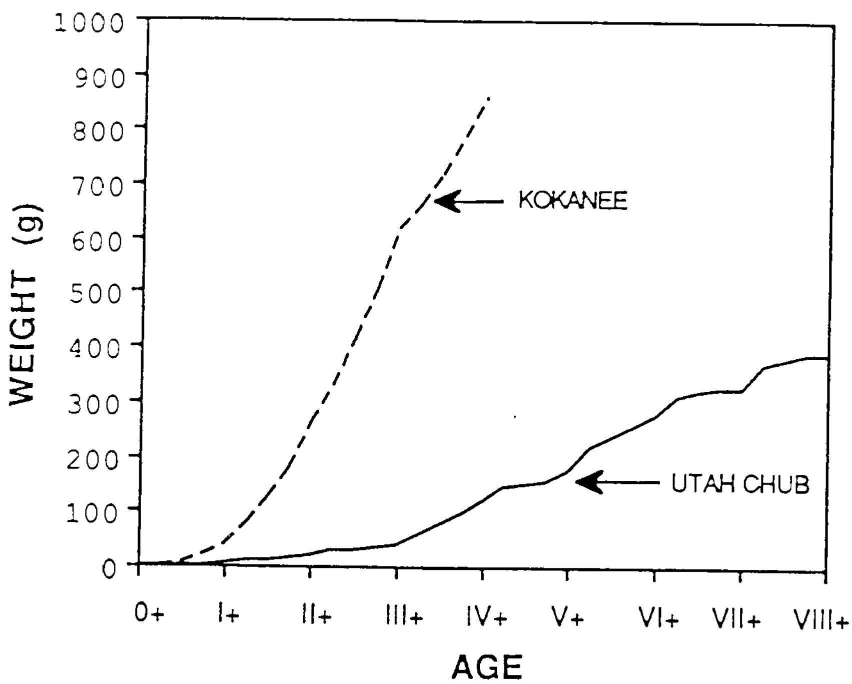

FIG 4.3. Growth of Utah chub and kokanee in Flaming Gorge Reservoir. Seasonal growth patterns predicted by bioenergetics modeling.

CHAPTER V

SUMMARY AND CONCLUSIONS

My research represents one of the first attempts to combine the results of bionergetics modeling techniques with hydroacoustic forage fish assessment techniques. The use of these two technologies allowed me to make general predictions about the future status of lake trout and their forage fish populations in Flaming Gorge Reservoir. Should these predictions hold true, this research will serve as evidence that the two technologies have advanced to the point where they can be successfully combined. By using bioenergetics in concert with hydroacoustics, consumption demand can be compared to forage availability. Such comparisons will offer insight into the support capacities of equatic ecosystems, providing the knowledge from which sound management decisions can be made.

I make the following general predictions about the future status of lake trout and their forage fish populations in Flaming Gorge Reservoir: 1) the Utah chub population will continue to decline owing to predation by lake trout, 2) the kokanee population will have difficulty expanding in the face of current levels of lake trout consumption demand, 3) growth of lake trout less than 600 mm will be slow in upcoming years owing to the current shortage of forage fish of useable size, and 4) since lake trout greater than 600 mm currently have a substantial and

suitable forage base, I predict that the newly implemented slot-limit regulation will result in an increase in trophy lake trout harvested in upcoming years. With poor growth of small lake trout, however, the long-term success of the slot-limit regulation will be minimal.

APPENDIX

TABLE A.1. Regression equations relating standard length (SL) and vertebral column (VC) length to total length (TL) for kokanee and Utah chub in Flaming Gorge Reservoir.

Species	Regression equation	n	r^2
Utah chub	TL(mm) = 1.19[SL(mm)] + 4.68	83	0.99
	TL(mm) = 1.38[VC(mm)] + 6.88	83	0.99
Kokanee	TL(mm) = 1.05[SL(mm)] + 26.8	30	0.95
	TL(mm) = 1.49[VC(mm)] - 19.3	46	0.99

TABLE A.2. Regression equations relating weight (g) to total length (mm) for Utah chub, kokanee, and lake trout in Flaming Gorge Reservoir.

Species	Regression Equation	n	r^2
Utah chub	$W = 0.0000091 * L^{3.07}$	104	0.944
Kokanee	$W = 0.000127 * L^{2.58}$	91	0.961
Lake trout	$W = 0.00000032 * L^{3.54}$	176	0.953

TABLE A.3. Diet of lake trout between 400 and 600 mm by season. Five seasons represented: spring 1990 (Sp. 90), summer 1990 (Su. 90), fall 1990, winter 1990-91 (Wi. 90-91), and spring 1991 (Sp. 91). Diet expressed in aggregate percent by wet weight. T equals less than 0.5% by weight.

Prey items	Sp. 90	Su. 90	Fall 90	Wi. 90-91	Sp. 91
Utah chub	17	0	T	13	12
Kokanee	17	5	20	12	16
Rainbow trout	0	0	3	0	0
Lake trout	0	0	0	5	0
Sculpin	0	0	T	14	1
Other fish	0	0	4	3	0
Crayfish	16	31	33	T	37
Amphipod	5	0	5	T	T
Chironomid pup.	45	54	14	0	27
Chironomid lar.	0	6	T	3	0
Zooplankton	0	T	5	50	T
Fish egg	0	0	14	0	0
Other non-fish	0	4	2	T	7
Sample size	18	25	50	30	26
Empty	3	3	14	1	0

TABLE A.4. Diet of lake trout greater than 600 mm by season. Five seasons represented: spring 1990 (Sp. 90), summer 1990 (Su. 90), fall 1990, winter 1990-91 (Wi. 90-91), and spring 1991 (Sp. 91). Diet expressed in aggregate percent by wet weight. T equals less than 0.5% by weight.

Prey items	Sp. 90	Su. 90	Fall 90	Wi. 90-91	Sp. 91
Utah chub	20	29	17	13	24
Kokanee	52	33	59	76	48
Rainbow trout	13	24	9	7	7
Lake trout	0	0	0	0	0
Sculpin	0	0	0	2	0
Other fish	4	0	0	2	0
Crayfish	0	7	8	0	13
Amphipod	0	0	0		2
Chironomid pup.	7	7	0	0	2
Chironomid lar.	4	0	0	0	1
Zooplankton	0	0	0	0	0
Fish egg	0	0	7	0	0
Other non-fish	0	0	0	0	3
Sample size	32	30	30	16	46
Empty	12	15	16	4	8

TABLE A.5. Lake trout tag-return matrix from 1985 through 1990 by year tagged.

Year	Number tagged	1985	1986	1987	1988	1989	1990
1985	357	39	51	21	16	6	2
1986	344		39	40	20	7	3
1987	313			20	18	17	5
1988	368				31	24	6
1989	357					17	10

TABLE A.6. BROWNIE program, model 0, predictions of nominal, and 95% confidence intervals (95% CI), of percent (%) survival and recovery rates of tagged lake trout by year tagged.

	Survival		Recovery	
Year	%	95% CI	%	95% CI
1985	61.2	40.2 - 82.3	****	**** - ****
1986	73.2	43.4 - 103	22.6	12.4 - 32.8
1987	64.7	31.9 - 97.5	14.2	7.6 - 20.8
1988	60.6	10.8 - 111	10.7	5.0 - 16.5
1989	****	**** - ****	8.9	1.5 - 16.3
Mean	65.0	51.8 - 78.1	14.1	10.3 - 17.9

**** - Not predicted by BROWNIE program, model 0.

TABLE A.7. Estimates of the lower 95% confidence interval (CI), nominal, and upper 95% confidence interval of tagged-lake-trout-at-large in Flaming Gorge Reservoir as of 1 May, 1988.

Lower 95% CI		(51.8% estimate of survival)		
Year	Number tagged	1986	1987	1988
1985	363	188	97	50
1986	366		189	98
1987	342			177
1988	423			423
Estimate of tagged-fish-at-large on 1 May, 1988 =				748
Nominal estimate		(65.0% estimate of survival)		
1985	363	236	153	99
1986	366		237	153
1987	342			222
1988	423			423
Estimate of tagged-fish-at-large on 1 May, 1988 =				897
Upper 95% CI		(78.1% estimate of survival)		
1985	363	284	222	173
1986	366		286	223
1987	342			267
1988	423			423
Estimate of tagged fish at large on 1 May, 1988 =				1086

TABLE A.8. Mean p-values, standard deviations (s), and sample sizes (n) of three size-classes of lake trout in Flaming Gorge Reservoir.

Size class	Mean p-value	s	n
400-600 mm	0.54	0.23	8
600-800 mm	0.55	0.18	55
800-1000 mm	0.51	0.14	24

TABLE A.9. Annual consumption estimates (metric tons) of Utah chub, rainbow trout, and kokanee by lake trout group. Lake trout sizes were estimated using length-weight regression (Appendix A.1). Lower is bioenergetics model prediction when lowest estimate of model year abundances were modeled. Nominal is when nominal abundance estimates of lake trout model years were simulated. Upper is when the upper estimates of lake trout model years were simulated. Sub-totals equal model lake trout years less than and greater than 600 mm. Grand-tot. equals sum of sub-totals.

		Utah chub			Rainbow trout			Kokanee		
Gp.	Size	low.	nom.	upp.	low.	nom.	upp.	low.	nom.	upp.
1	406	5.5	8.0	12	1.7	2.5	3.5	11	16	23
2	476	4.8	7.0	10	1.5	2.1	3.1	10	14	21
3	530	4.0	5.8	8.5	1.2	1.8	2.6	8.3	12	17
4	586	10	15	21	9.1	13	19	27	40	58
sub-tot.		24	35	51	14	19	28	56	82	119
5	696	10	15	21	9.3	14	20	27	40	58
6	783	6.3	9.0	13	5.6	8.1	12	17	24	35
7	813	4.4	6.4	9.3	4.0	5.7	8.3	12	17	24
8	838	3.1	4.5	6.5	2.8	4.0	5.8	8.1	12	17
9	863	2.1	3.1	4.5	1.9	2.8	4.0	5.6	8.1	12
10	882	1.5	2.1	3.0	1.3	1.9	2.8	3.8	5.5	8
11	901	1.0	1.4	2.1	0.9	1.3	1.9	2.6	3.8	5.5
12	916	0.6	0.9	1.3	0.6	0.8	1.2	1.6	2.4	3.4
13	931	0.4	0.6	0.9	0.4	0.6	0.8	1.1	1.6	2.3
14	945	0.3	0.4	0.6	0.3	0.4	0.5	0.7	1.1	1.6
sub-tot.		30	43	63	27	39	57	79	114	166
grand		54	79	114	41	59	85	136	196	285

TABLE A.*10*. Results of literature review to estimate caloric content of prey items consumed by lake trout in Flaming Gorge Reservoir.

Prey item	Closest relative found	Caloric content cal x g^{-1} (wet)	Ref.
Utah chub	*Cyprinidae*	1800	c
Kokanee	a	2093-2300	d
Rainbow trout	a	1452	b
Sculpin	*Cottus perplexus*	1295	c
Chironomids	*Chironomidae*	656	c
Crayfish	*Onconectes propinquus*	1472	e
Amphipods	*Amphipoda*	1058	c
Odonata	*Argia emma*	664	c
Zooplankton	*Daphnidae*	800	c
Fish eggs	*Salmonidae*	1492	c
White sucker	*Cyprinidae*	1800	c
Lake trout	a	1382	f

a - Denotes actual species.
b - Rainbow trout from Causey Reservoir, Utah (n = 108), Chris Luecke and Wayne Wurstbaugh unpublished data.
c - Cummins and Wuycheck (1971).
d - Beauchamp et al. (1989).
e - Stein and Murphy (1976).
f - Stewart et al. (1983).