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**HABITAT SELECTION AND MOVEMENT OF A STREAM-RESIDENT
SALMONID IN A REGULATED RIVER AND TESTS OF
FOUR BIOENERGETIC OPTIMIZATION MODELS**

by

Mark D. Bowen

**A dissertation submitted in partial fulfillment
of the requirements for the degree**

of

DOCTOR OF PHILOSOPHY

in

Aquatic Ecology

Approved:

**UTAH STATE UNIVERSITY
Logan, Utah**

1996

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ABSTRACT

Habitat Selection and Movement of a Stream-Resident
Salmonid in a Regulated River and Tests of
Four Bioenergetic Optimization Models

by

Mark D. Bowen, Doctor of Philosophy

Utah State University, 1996

Major Professor: Dr. Chris Luecke
Department: Fisheries and Wildlife

A bioenergetics model was constructed for stream-resident drift-feeding salmonids. Model predictions of surplus power (energy available per unit time for growth and reproduction) were not statistically distinguishable from observations of surplus power in three laboratory studies. Of 40 experimental trials in these three studies, the model correctly predicted surplus power in 39 cases ($p \leq 0.05$).

I collected observations of rainbow trout (*Oncorhynchus mykiss*) focal velocity and physical habitat availability in the Green River of northeastern Utah, USA (1988-1990). In the winter of 1988, Flaming Gorge Dam generated hydropower and delivered an unstable discharge regime with a higher mean discharge to the Green River. During 1989 and 1990, Flaming Gorge Dam's operation was curtailed

by drought. Therefore, the Green River exhibited a more stable discharge regime with lower mean daily discharge.

During winters exhibiting the stable discharge regime, all size classes of rainbow trout selected slower focal velocities than under an unstable winter discharge regime. Season had less influence on microhabitat selection of large fish than smaller individuals. Rainbow trout larger than 33 cm (total length) find and use positions with low focal velocities and high velocity shear regardless of season. In contrast, during the summer, fish less than 33 cm TL find and use positions with much higher focal velocities and greater velocity shear compared to the winter.

Four bioenergetic models were tested with the focal velocity use data. Two optimal goal models produced excellent fits ($r^2 = 0.91$ and 0.93) to observed focal velocity use of rainbow trout larger than 33 cm TL. These results were consistent with the hypothesis that large rainbow trout were finding optimal focal velocity positions in stable discharge summers and under both discharge regimes in winter.

Rainbow trout movement was quantified along two scales with radio-telemetered fish: 1) weekly observations generated estimates of distances moved at intervals greater than one day and 2) multiple observations of a fish in one day produced estimates of distances moved over hours. I found an unstable discharge regime significantly reduces movement measured weekly ($F = 11.10$, $P = 0.0019$); hourly movement rates (m/h) were also reduced ($F = 5.90$, $P = 0.0273$).

DEDICATION

I dedicate this work to my parents, James P. Bowen and Nelda R. (Gilley) Bowen. My father's interest in the natural world ignited my interest in ecology. And, his unfailing support saw me through some of the most trying periods of my graduate career. My mother's focus on scholarly endeavor encouraged my continuing education. After many parents would have resigned their support, my mother continued to advocate the completion of my doctorate.

Mark D. Bowen

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Many colleagues contributed to this research. The most significant contributions were made by my committee. They were Drs. Chris Luecke (major professor), David Beauchamp, James Haefner, Mark Ritchie, and Wayne Wurtsbaugh. Other faculty that made significant contributions were Mrs. Susan Durham and Drs. John Bissonette, Layne Coppock, Barrie Gilbert, Charles Hawkins, William Helm, David Roberts, Robert Taylor, and Rebecca Wheeler. Graduate students who made contributions to this study were David Branson, Mike Buntjer, Jon Chase, Yvette Converse, Ron Englund, Randall Filbert, James Hogue, Keith Lawrence, Don McIvor, Terry Shrader, and Steve Zucker. Agency personnel who contributed to this research were James Johnson (UDWR), Robert Williams (U.S. BOR), Steve Brayton (UDWR), and Doug Young (UDWR).

I thank four people who helped me to develop a more engaging understanding of life: Susan Geer, Michael Larkin, Liliane Stacishin, and Anthony Wasowicz.

Mark D. Bowen

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CHAPTER 1

INTRODUCTION

This research had two principal goals. First, I sought to understand the mechanisms influencing the habitat selection of salmonid fishes living in streams. Second, I tried to explain the distribution of a single species in a stream exhibiting divergent and known discharge patterns. This second goal permitted me to evaluate the influence of body size and discharge regime on the distribution of rainbow trout (*Oncorhynchus mykiss*) in the regulated Green River, UT.

The distribution of stream-resident salmonids has been well studied. Physical factors such as "velocity, turbulence, and cover" have long been tied to stream salmonid distributions (Chapman, 1966). In addition to these physical parameters, Chapman also recognized important biotic factors such as prey availability, and competition among individual salmonids. Since this seminal work of Chapman, many researchers have investigated the abiotic and biotic controls on salmonid distributions.

The distribution of stream-resident salmonids depends, at least in part, upon the physical habitat available. For example, gradient and depth influence the distribution of brown trout, *Salmo trutta* (Kennedy and Strange, 1987). However, "optimal combinations of depth and velocity" were chosen over positions with more preferred values of either factor alone (Shirvell and Dungey, 1983). This selection for depth-velocity combinations may provide a favorable energy acquisition rate and cover from avian predation. Cover from predation (Fausch,

1993) and current (MacMahon and Hartman, 1989; Fausch 1993) are both important, especially for juvenile salmonids. In addition, current velocity and velocity shear preference are often linked to juvenile and adult salmonid habitat use (Chapman and Bjornn, 1969; DeGraaf and Bain, 1986; Morantz et al., 1987). Temperature commonly causes seasonal habitat shifts by individuals (Chapman and Bjornn, 1969; Rimmer et al., 1983; Swales et al., 1986; Chisholm et al., 1987), and is an important influence on salmonid distributions.

Salmonid distributions are also affected by biotic factors. Drifting invertebrate prey are an important part of the diets of stream-resident salmonids (Waters, 1969; Griffith, 1974; Bachman, 1984) and can influence salmonid distributions (Gibson and Galbraith, 1975). Prey abundance can be a more important influence on distribution than physical habitat variables such as cover (Wilzbach, 1985). However, salmonid habitat use may be affected simultaneously by prey availability and physical variables such as current velocity (Wańkowski and Thorpe, 1979). The relative importance of each may be difficult to determine because prey availability and current velocity can covary.

Competition among individuals can also determine habitat use. Some species are competitively superior to others. For example, in one set of laboratory experiments, Fausch and White (1986) found juvenile coho salmon (*Oncorhynchus kisutch*) dominate juvenile brook trout (*Salvelinus fontinalis*), which in turn dominate juvenile brown trout. When individuals of the same species

compete for positions in a stream, size and previous residency are important determinants of the winner (Jenkins, 1969). Competition and food availability can interact. When food is scarce, the number of conspecifics present at a site may be reduced through increased aggression of dominant residents and voluntary emigration of subordinants (Symons, 1971). Competition may also be mediated by discharge. Age 1+ brown trout are favored in years experiencing drought over 0+ age brown trout in the stream Jörlandaån in Sweden (Bohlin, 1977). Thus, prey availability and competition are known influences on salmonids. Yet these biotic factors interact with each other and physical variables such as cover, current velocity, and discharge.

An energetic optimization hypothesis can relate all these physical and biotic variables to salmonid distributions. In addition, energetic optimization hypotheses can be used to assess the relative importance of factors in determining the distribution of stream-resident salmonids. This hypothesis suggests stream salmonids might choose positions with low current velocities that are near areas of high velocity to maximize access to invertebrate drift (Fausch and White, 1981). The energetic optimization hypothesis developed from two threads within the ecological literature: optimization theory and energetics modeling. Optimization theory was first applied by MacArthur and Pianka (1966) to an ecological problem. They distinguished between animals choosing between patches of prey and choosing between individual prey items within a single patch. The early work

of MacArthur and Pianka was soon applied to empirical phenomena. Early tests in terrestrial (Krebs et al., 1974) and aquatic (Werner and Hall, 1974) environments suggested optimization theory was a useful approach to foraging and perhaps other behavioral studies. However, numerous criticisms have been leveled at the optimization approach. Gould and Lewontin (1979) suggested researchers employing optimization theory may ask the wrong question or ignore alternative explanations for phenomena under consideration. Furthermore, Pierce and Ollason (1987) asserted that optimal strategy existence is untestable. Several authors have provided telling responses to these criticisms (Beatty, 1980; Krebs and McCleery, 1984; Stephens and Krebs, 1986).

Since this debate, many researchers have tested behavioral optimization models in light of the criticisms. Many of these tests can be found in the aquatic biology literature. For example, Dill (1978) found that predicted optimal territory sizes agreed with observed territory size for salmonids in laboratory and field situations. In addition, optimization theory can be used to predict habitat selection of sunfish under a variety of experimental conditions (Werner and Hall, 1979; Werner et al., 1981; Mittelbach, 1981; Werner et al., 1983).

A second body of work, energetics modeling, was developed and applied to issues of fish growth and production. These models depend on a balanced energy equation (Winberg, 1956) and are used to predict how environmental variables affect the consumption and growth of individuals. These models have

been used to assess the impact of fish populations on their prey resources (Stewart et al., 1983), and to assess the effects of environmental variables on fish growth processes. For example, in Kitchell et al.'s (1977) simulations of walleye growth, summer temperatures had a greater effect on walleye (*Stizostedion vitreum*) growth than did variations in food quality. Elliot (1976) showed that body size and temperature influence all components of a brown trout's energy budget. Brett et al. (1969) and Elliot (1976) found that as a fish's ration decreased, optimal temperatures for growth decreased. Production of anadromous sockeye salmon (*Oncorhynchus nerka*) was evaluated by Brett (1986). He observed high mortality of smolts reaching the ocean and demonstrated that only about 10% of the individuals in a cohort survive. However, during their stay at sea, these individuals produce 96% of the biomass that eventually returns to spawn and die. Energetics models can also be important tools when applied to the management of populations. Stewart et al. (1983) applied a bioenergetic model of growth and in situ swimming speed to predict gross conversion efficiency of lake trout, *Salvelinus namaycush*, in Lake Michigan. Stewart et al. concluded that slow production of lake trout individuals and resulting time-lagged predation pressure make manipulation of lake trout stocking densities an ineffective tool for moderating fluctuations in prey fish densities. Stewart et al.'s efforts showed that an energetics model may be used to evaluate growth and can then be extended to evaluate effects of that growth on other species through the food web.

Other examples serve to demonstrate how energetics models can be used to analyze trophic relations. Johannsson et al. (1994) showed that freshwater shrimp, *Mysis relicta*, could compete with planktivorous fish for metalimnetic zooplankton in Lake Ontario. Rudstam et al. (1994) evaluated the effect of two coregonids on invertebrate prey in Lake Michigan. Their energetic model explained the observed predation-rate increase on benthic prey species.

In addition to analysis of trophic interactions, energetics models have been used to analyze behavioral decisions of individuals. Several of these models are syntheses of optimization theory and energetics and have been developed for stream-resident salmonids. Fausch (1984) found rank of a position's potential profit was nearly identical to the dominance rank of juvenile coho salmon inhabiting the position in a laboratory stream. Similarly, a bioenergetic model was used to determine the positions in an Alaskan stream that maximize net energy intake for Arctic grayling, *Thymallus arcticus*. Solitary grayling were found in predicted optimal positions (Hughes and Dill, 1990). Further modeling results and tests suggest that grayling "locate and rank positions based on their profitability" (p. 1999, Hughes, 1992). Finally, Hill and Grossman (1993) developed a model that predicted habitat use of rainbow trout (53-125 mm standard length). They found good agreement between predicted and observed focal velocities in a stream in North Carolina. These studies demonstrate how optimization theory and energetics modeling have been synthesized to analyze position choice by stream-

resident salmonids. I used this synthesized optimization/energetics approach to evaluate rainbow trout habitat selection below Flaming Gorge Dam.

Background

In 1985, Dr. William T. Helm of Utah State University (USU) and James Johnson of the Utah Division of Wildlife Resources (UDWR) cooperatively conceived of a multifaceted research project to protect the productive Flaming Gorge Dam tailwater trout fishery. The United States Bureau of Reclamation (USBOR) planned a rewind of the generators in Flaming Gorge Dam that would increase the maximum flow rate through the dam from 119 to 139 m³/s. While this small increase in maximum discharge might seem trivial to a large-river salmonid biologist, there was reason to believe that the increase might not be inconsequential.

The foremost reason for concern about the rewind, as it was called, was that in some years rainbow trout stocked the same year returned to fishermen's creels in far smaller proportions than in most years. Along with these overwinter mortality events, UDWR biologists noticed many small, dead fish in the river.

To alleviate the fish kills, rainbow trout fingerlings were stocked in May at 15 cm average total length (TL) instead of 11.4 cm TL. These fish grew 2.5 cm per month on average and when winter arrived these fish had grown to a mean TL of 33 cm. UDWR biologists believed the larger size at stocking had eliminated the

winter fish kills but no one was certain. No fish kill had occurred since the new stocking policy had started in 1985. But what if the peaking power regime of the dam changed? This question motivated Helm and Johnson to propose and oversee studies of trout population demographics, microhabitat use, and movement. Studies of rainbow trout included predation on the invertebrate drift (Filbert, 1991), natural recruitment to the fishery (Modde et al., 1991), and laboratory experiments concerning rainbow trout bioenergetics (Lawrence, 1991).

I investigated microhabitat use and movement of rainbow trout. To understand these aspects of rainbow trout use, I developed a bioenergetics model that used the laboratory experiments (Lawrence, 1991) as a validation test. The rainbow trout predation and invertebrate drift data (Filbert, 1991) were then used to augment the bioenergetics model to predict optimal positions of rainbow trout in the field. Finally, I tested the model and various optimization hypotheses in the Green River using my observations of microhabitat use and movement.

This dissertation describes these three steps. Chapter 2 describes the bioenergetics model I developed to predict energetic flux in rainbow trout from 5 to 1500 g in wet weight. Chapter 3 describes how the model was adapted to predict positions in the field and the optimization hypotheses and space allocation schemes I tested. Chapter 4 discusses the weekly and diel movements of rainbow trout and the influence of fish size and discharge regime on these movements.

Two principal contributions to the fields of bioenergetics and stream ecology are made in Chapter 2. First, a general model that predicts energetic flux in stream-resident salmonids is developed. This model requires known food input rates, temperature, current velocity at which the fish is swimming (i.e., focal velocity), and the fish's size to predict energetic flux of individual trout. The second contribution was confirmation the bioenergetics model for stream-resident salmonids correctly predicts a highly significant number of experimental trials from original research reported in the literature. All previous confirmation attempts have taken place with bioenergetics models for lake fishes; two of these models have been confirmed (Rice and Cochran, 1984; Beauchamp et al., 1989) and one has failed (Wahl and Stein, 1991). I present a bioenergetics model for stream-dwelling salmonids that was confirmed with independent experimental results. To my knowledge, all stream fish models published to date have been validated or tested by the same authors that developed the model (Fausch, 1984; Hughes and Dill, 1990; Hughes, 1992; Hill and Grossman, 1993).

In Chapter 3, I demonstrate, for the first time, that optimal habitat selection theory may be extended to include lotic salmonids greater than 33 cm TL in summer and winter. Also the theory can predict focal velocity use in stable and unstable discharge regimes. Surprisingly, I also find that a random-lottery space-allocation scheme predicts fish positions better than a dominance hierarchy scheme.

In Chapter 4, I show that the movement rate (m/h) of rainbow trout decreases in a winter with an unstable discharge regime. This decrease means that productivity of the fishery will decrease because fish will be less able to track energetically advantageous positions. Finally, in Chapter 5, I review the major conclusions and discuss the implications of Chapters 2 through 4.

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CHAPTER 2
A BIOENERGETICS MODEL FOR
DRIFT-FEEDING SALMONIDS

Abstract

A bioenergetics model is presented for stream-resident drift-feeding salmonids. Model predictions of surplus power (energy available per unit time for growth and reproduction) were not statistically distinguishable from observations of surplus power in three different laboratory studies (Hutchins, 1974; Grayton and Beamish, 1977; Lawrence, 1991). Of 40 experimental trials in these three studies, the model correctly predicted surplus power in 39 cases ($P \leq 0.05$). This energetics model can be used to predict the distribution of focal velocities of salmonids, to develop hypotheses about the relative fitness of various decision rules that can be used by individuals, and to determine the number of microhabitat positions that could successfully support trout in a given stream.

1. Introduction

An understanding of the mechanisms influencing distribution of drift-feeding salmonids is important for conservation and effective management. Models can provide efficient, low-cost, and powerful tools to investigate the variables affecting the distribution of organisms. An individual-based bioenergetics model

can yield testable hypotheses that provide a basis for understanding the distribution of drift-feeding salmonids.

An individual-based bioenergetics model requires a measurable currency that relates to fitness. Power is one such currency; it measures the energy acquired or lost by an animal per unit time. "Surplus power" is the energy remaining for reproduction or growth after basal and active metabolic costs have been met. Ware (1982) argued surplus power directly relates to an animal's fitness (Ware, 1982) and may be a useful currency for models that are based on natural selection processes. Using surplus power as an energetic currency is equivalent to the energy-optimizing procedure of optimal foraging models (Stephens and Krebs, 1986).

The purpose of this study was to develop an individual-based energetics model for determining the surplus power available to drift-feeding salmonids at different current velocities, rations, and temperatures. Field measurements of current velocity, ration, and temperature could then be used to evaluate the energetic quality of specific stream locations available to an individual. If we can evaluate a specific location's quality, we can estimate the effect of anthropic manipulations that alter stream habitat. Also, we can evaluate the energetic trade-offs involved in the selection of different stream locations.

The energetic advantage of some positions in a stream over others has been estimated by a few individual-based bioenergetics models for drift-feeding

salmonids. All bioenergetic models for drift-feeding salmonids have used empirical observations of swimming and metabolic costs to estimate parameters in curve-fitted equations. For example, Hill and Grossman (1993) predicted optimal locations in a stream and found rainbow trout (*Oncorhynchus mykiss*) used these locations more frequently than sub-optimal locations. Other studies have relied on ranking positions in a stream according to energetic benefit. These ranks are then compared to the individual rank of fish in a dominance hierarchy. The correlation of these two sets of ranks provides indirect evidence that optimal microhabitat location can explain the distribution of drift-feeding salmonids in a laboratory stream (Fausch, 1984) or in the field (Hughes and Dill, 1990; Hughes, 1992).

None of these modelers have subjected their estimates of energetic costs to validation with data collected by researchers other than the original authors. In this chapter, I develop a model that calculates the energetic change in a salmonid's body given the fish's body size, the food acquisition rate, and the temperature of the water. I then tested the model against experimental data obtained from the literature. Initial model predictions did not agree with the experimental data. However, a refined version of the model produced predictions that fit the empirical data well.

2. Methods

I constructed a model and compared model predictions to independent observations. The purpose of the model was to estimate surplus power: the energy

available, per unit time, for growth and reproduction. The model (FLUX1) was adapted from Elliot's (1976a) balanced energy equation. All components were measured in Joules (J)/d:

$$E_t = E_m + E_a + E_g \quad (1)$$

where

E_t = total energy input,

E_m = maintenance energy, the amount of energy required to maintain a fish at a growth rate of 0 J/d including losses through waste products,

E_a = energy expended through activity,

E_g = surplus power, the energy available for growth and reproduction.

Maintenance energy was estimated by the empirical equation developed by Elliot (1976a):

$$E_m = (aM^b)(e^{cT}) \quad (2)$$

where a, b, and c are dimensionless empirical constants (see Table 2.1 for values),

M = wet mass (g),

T = temperature (°C).

The cost of swimming activity was estimated with Ware's (1978) equation:

$$E_a = fhADV^3 / 2i \quad (3)$$

where i is dimensionless empirical constant (see Table 2.1 for value),

E_a = the energy expended on swimming activity (J/d),

f = density of water (g/cm³) at a specified temperature,

- h = conversion of ergs/s to J/s,
- A = wetted surface area (cm^2) for trout = $0.28(L^{2.11})$ and for salmon $A = 0.23(L^{2.14})$, where L is the total length of the fish (cm) (Webb, 1976, 1977),
- V = focal velocity (cm/s) is the swimming speed of the fish,
- D = drag coefficient (dimensionless) = $10.56 / R$, where R is the Reynold's number (dimensionless) for the fish's body (Webb, 1975, p. 61). $R = \rho LV / j$, where j is the viscosity of water at a given temperature ($\text{g}\cdot\text{cm}^{-1}\cdot\text{s}^{-1}$),
- i = efficiency (dimensionless) of converting chemical energy into propulsive power.

I estimated the components of the energy budget from empirically derived curve-fitted equations and first principles of biomechanics and physiology.

Parameters for these curve-fitted equations were estimated using empirical data found in the literature. No parameter estimates (Table 2.1) were derived from the validation data.

2.1 Validation data

The empirical data used for validation were obtained from the literature. I used all experimental data that met the following requirements: The initial mean energetic content of fish could be determined; the mean and standard deviation (sd) of final energy content of fish used in a trial could be resolved; energy in the food (either a pelleted food or natural prey), swimming speed, and temperature were

reported for each trial; trials were of 10 or more days duration; and the data were collected for a salmonid species. Three laboratory studies met these requirements. First, Hutchins (1974) performed 28 trials with juvenile coho salmon (*Oncorhynchus kisutch*) that were starved or fed live housefly (*Mus domesticus*) larvae. The juvenile coho were forced to swim in current velocities of 0 to 27 cm/s (0 to 4.2 Body Lengths/s). Second, Grayton and Beamish (1977) completed six trials with sub-adult rainbow trout fed 2% of wet weight or to satiation with a dry pelleted diet. These sub-adult rainbow trout were required to swim 10.3 to 11.5 cm/s (0.8 to 1.2 Body Lengths (BL)/s). Third, Lawrence (1991) performed six trials with adult rainbow trout fed 75% or 100% of "maintenance" requirements with a dry pelleted diet. These three studies provided 40 experimental trials for validation. For each trial, I calculated the mean and sd of surplus power (J/d) acquired by a set of individuals during each experimental trial (Table A.1 in the appendix).

2.2 Statistical analysis

Experimental observations were compared statistically to model predictions of surplus power. I calculated the difference between a predicted value and the mean of observed surplus power acquired per day. This difference was divided by the standard deviation of the experimental surplus power. This quotient provided a measure of the distance between the predicted value and the experimental mean measured in units of standard deviation. A *P* value for each comparison was

computed as the area under the Student's t curve for values as extreme or more extreme than the observed difference. If the P value for the test was ≤ 0.05 , I concluded that the model had failed for that particular experimental trial.

I summarized the outcomes of these 40 tests by counting the number of trials in which the model passed. The cumulative binomial probability of this many or more trials passing was computed (IMSL, 1991). Henceforth I refer to this cumulative binomial probability as the grand " P " value for a model run. If the grand P value was ≤ 0.05 , less than 95% of model predictions agreed with empirical observations, and I concluded the model had failed on that set of runs. If, however, the grand P value was > 0.05 , I concluded that the model was "confirmed" (Reckhow and Chapra, 1983) with an acceptance criterion of 0.05.

2.3 Validation test results (FLUX1)

The model, FLUX1, was run using the initial conditions presented in the validation data (Table A.1 in the appendix). FLUX1 misclassified nine cases out of 40 (Figure 2.1). I therefore concluded model predictions deviated significantly from experimental observations (grand $P = 0.00013$). Model terms and structure were then examined to determine why the model failed.

3. Model refinement

3.1 Changes to Model Structure

To refine the model, I compared the estimates of maintenance costs, E_m , to empirical observations. The model estimates of maintenance costs were considerably lower than the observed sum of energy lost through the following components of the energy budget: excretory products (Elliot, 1976b), standard metabolism (Beamish, 1964), and apparent heat increment (the energetic cost of digesting food) (Beamish et al., 1986; Beamish and Trippel, 1990). The model's estimates of swimming costs, on the other hand, were similar to actual measurements of swimming costs (Brett, 1964; Rao, 1968). I therefore refined the model by expanding E_m .

The refined model, FLUX2, expands the maintenance term, E_m , into three component parts: energy lost through egestion and excretion, E_e , energetic cost of standard metabolism, E_s , and the energetic cost of apparent heat increment, E_h . Once E_m was expanded, the model was similar to that of Glass (1971) with all terms measured in J/d:

$$E_t = E_e + E_s + E_h + E_a + E_g \quad (4)$$

where

E_t = total energy input,

E_e = energy lost through egestion and excretion,

E_s = energy required for standard metabolism,

E_h = energy required for apparent heat increment,

E_a = energy expended through activity,

E_g = surplus power, the energy available for growth and reproduction.

Energy lost through egestion and excretion, E_e , was estimated in different ways for salmonids fed on pelleted diets, individuals that were starved, and individuals fed a diet of natural prey items. Thirty percent of food energy was lost through egestion and excretion by fish fed a pelleted diet consisting of approximately 38% protein and 9% digestible fat (Cho and Slinger, 1980). For salmonids that were starved, Elliot's (1976b) equation was used:

$$E_e = (kM^l)(e^{mT}) \quad (5)$$

where all variables are the same as equation (2) and the parameter values for k , l , and m are found in Table 2.1. E_e for a salmonid fed on a natural diet was estimated in two steps from equations adapted from Elliot (1976a, b). First the proportion of the maximum possible ration obtained by a fish that day was determined:

$$B = C / C_{\max} \quad (6)$$

where

B = daily ration expressed as a proportion of the maximum possible ration (dimensionless),

C = daily ration (J/d),

C_{\max} = maximum possible ration = $(nM^o)(e^{pT})$, where, all variables are the same as equation (5) and the values of parameters n , o , and p are found in Table 2.1 (J/d).

The energy lost through egestion and excretion was then estimated by:

$$E_e = C((qT^r)(e^{sB}) + (tT^u)(e^{vB})) \quad (7)$$

where q, r, s, t, u, and v are dimensionless empirical constants (see Table 1 for values),

C = daily ration (J/d),

T = temperature (°C)

B = daily ration expressed as a proportion of the maximum possible ration (dimensionless).

Energy required for standard metabolism, E_s , was calculated via the equation developed by Elliot (1976a):

$$E_s = (wM^x)(e^{yT}) \quad (8)$$

where w, x, and y are dimensionless empirical constants (see Table 2.1 for values),

M = wet mass (g),

T = temperature (°C).

Elliot found that this model fit his data for brown trout when he used temperature-specific values for the parameters w, x, and y (Table 2.1). However, Elliot's equation underestimated the standard metabolism for salmonids larger than 140 g probably because the majority of Elliot's observations were made on fish < 140 g. Therefore, I collected observations on standard metabolism, mass, and temperature for salmonids > 140 g from Elliot (1976a) and Brett and Glass (1973).

I regressed standard metabolism against mass and temperature and estimated the parameters w , x , and y for salmonids larger than 140 g (Table 2.1).

The final component of metabolic cost estimated was apparent heat increment, E_h , the energy spent to digest food. E_h depends on temperature and the amount of lipid, protein, and carbohydrate in the diet (Beamish and Trippel, 1990). The diets for salmonids fed pelleted food in the validation experiments were composed of 12% lipid and 35-42% protein of gross energy content. Cho and Slinger (1980) fed a pelleted diet (protein: 42% of gross energy content; lipid: 9% of digestible energy) similar in composition to those diets fed in the validation experiments. Cho and Slinger found E_h was 15% of gross energy input at 7.5 °C, 10% at 10 °C, 9% at 15 °C, and 11% at 20 °C. I used these values for all experiments conducted with pelleted diets. One set of validation experiments (Hutchins, 1974) was conducted with natural prey. For these trials, I used values for E_h reported by Beamish and Trippel (1990) for a diet composed of 37.2% and 22% of gross energy content for protein and lipid, respectively. E_h was 6.7% at 8°C, 7.4% at 12°C, and 10.1% at 15°C. The difference between these two sets of values is probably attributable to the large difference in lipid content. However, the high value of E_h observed by Cho and Slinger at 7.5 °C (15%) could reflect inefficiency in the digestive system of rainbow trout at lower temperatures.

The energy expended in swimming activity, E_s , was estimated in exactly the same way in the second model as in the first model (Equation 3). The total amount

of energy expended in activity is derived only from the cost of swimming except in the case of focal velocities ≤ 0.1 L/s (= Body lengths per second). When focal velocity is this low, the cost of activity is that of routine activity for milling fish (Job, 1955) for a given temperature and weight.

3.2 Refined model (FLUX2) results

The second model, FLUX2, was run using the same initial conditions as those for FLUX1. FLUX2 misclassified one case out of 40 (Figure 2.2) and the grand P value for this run was 0.8714. Therefore, it was confirmed that the refined model's predictions could not be distinguished statistically from the experimental observations of surplus power (Figure 2.3). I called the second model "confirmed" because one requirement of model validation had been violated (Grant, 1986). This violation was my tuning of the model after a statistical comparison of model to empirical observations. Thus, I did not "validate" the model because of my *a posteriori* tuning. Yet, I still met the "confirmation" criteria of Rechow and Chapra (1983) by successful statistical comparison of model predictions and experimental observations.

The predicted model values were regressed on the experimental observations ($r^2 = 0.87$) with a Mean Squared Error (MSE) of 0.2489. I partitioned MSE into three components: bias due to differences between predicted values and observed means, error from the slope deviating from unity, and the residual (following Rice and Cochran [1984] and Beauchamp et al. [1989]). Bias due to

differences between means (0.00025) and error from the slope deviating from unity (0.006) were miniscule compared to the proportion of MSE contributed by random variation (0.99375). This result suggests that errors in model predictions were not systematic.

4. Discussion

The principal improvement of FLUX2 over FLUX1 was the latter had one term to estimate maintenance costs while the former used several terms to estimate each component of maintenance costs: egestion and excretion, standard metabolism, and heat increment. In the FLUX1 formulation, no refinement of components was possible because parameters for estimating maintenance ration were derived from Elliot's (1976a) empirical observations for only one species (brown trout, *Salmo trutta*) and one diet (live scuds, *Gammarus* sp.). Therefore, the maintenance term may have inaccurately predicted costs for other species and other diets. The validation data are from experimental trials for coho salmon (*Oncorhynchus kisutch*) and rainbow trout (*Oncorhynchus mykiss*) fed live housefly (*Musca domestica*) larvae or pelleted diets. The refinement of the model made it possible to estimate parameters for each component of the maintenance costs. Thus, observations of standard metabolism of sockeye salmon, *Oncorhynchus nerka* (Brett and Glass, 1973), could be included in the parameter estimation for the standard metabolism term. Also, the proximate composition of the diet used in a trial could be used to more precisely estimate the heat increment,

E_h , component (Beamish et al., 1986; Beamish and Trippel, 1990). These improvements made the second model, FLUX2, capable of predicting surplus power more accurately than the initial model, FLUX1.

My results suggest that FLUX2 could be modified to evaluate feeding positions in a stream assuming that foraging rate can be estimated (Chapter 3). If the energetic value of a feeding position can be estimated, it is possible to evaluate the fitness of behavioral decisions of individuals relative to each other. For instance, FLUX2 could be used to determine if drift-feeding salmonids optimize energetic flux over time. It may also be possible to predict the focal velocity distribution of salmonids in a stream given: temperature, the distribution of available current velocities, and energy available in the drift. The model's predictive abilities provide investigators with a tool to develop hypotheses about the relative fitness of various decision rules of individual fish. An individual-based bioenergetics model such as FLUX2 can also be modified to predict flow requirements of stream-resident salmonids (e.g., Van Winkle et al., 1996).

Stream ecosystem managers could also use the model's predictive abilities. It is possible to adapt FLUX2 to determine the number of positions in a stream that would provide sufficient energy to survive for drift-feeding salmonids of different sizes. This determination could provide a measure of stream area available to support salmonid populations. If physical and drift-feeding information were known at different discharges, FLUX2 could predict the area available to support drift-

feeding salmonid populations at different discharges.

To improve future bioenergetic models for drift-feeding salmonids, we could develop more biomechanical equations with which to estimate terms in the models rather than empirical, curve-fitted equations. I used empirical equations to improve my model because theoretical equations predicting apparent heat increment, standard metabolism, etc. do not exist. Such first-principle theoretical equations might provide a better biological basis for interpretation of results. In addition, we need laboratory studies that measure the energetic content of fish at the beginning and end of an experiment and each component of the energy budget. Specifically, laboratory studies conducted on fish larger than 300 g would be most useful. With these data we could more precisely estimate model parameters and validate models like the one I constructed. An important advancement of bioenergetics models would be application to diverse field situations. Diverse conditions and model estimates of foraging costs and energy acquisition need empirical tests. Finally, prediction of surplus power, growth, or reproductive success on a longer time scale than the one I used, 10-56 d, may require a dynamic model. A dynamic program could incorporate varying food availability and competitive pressure as seasons change.

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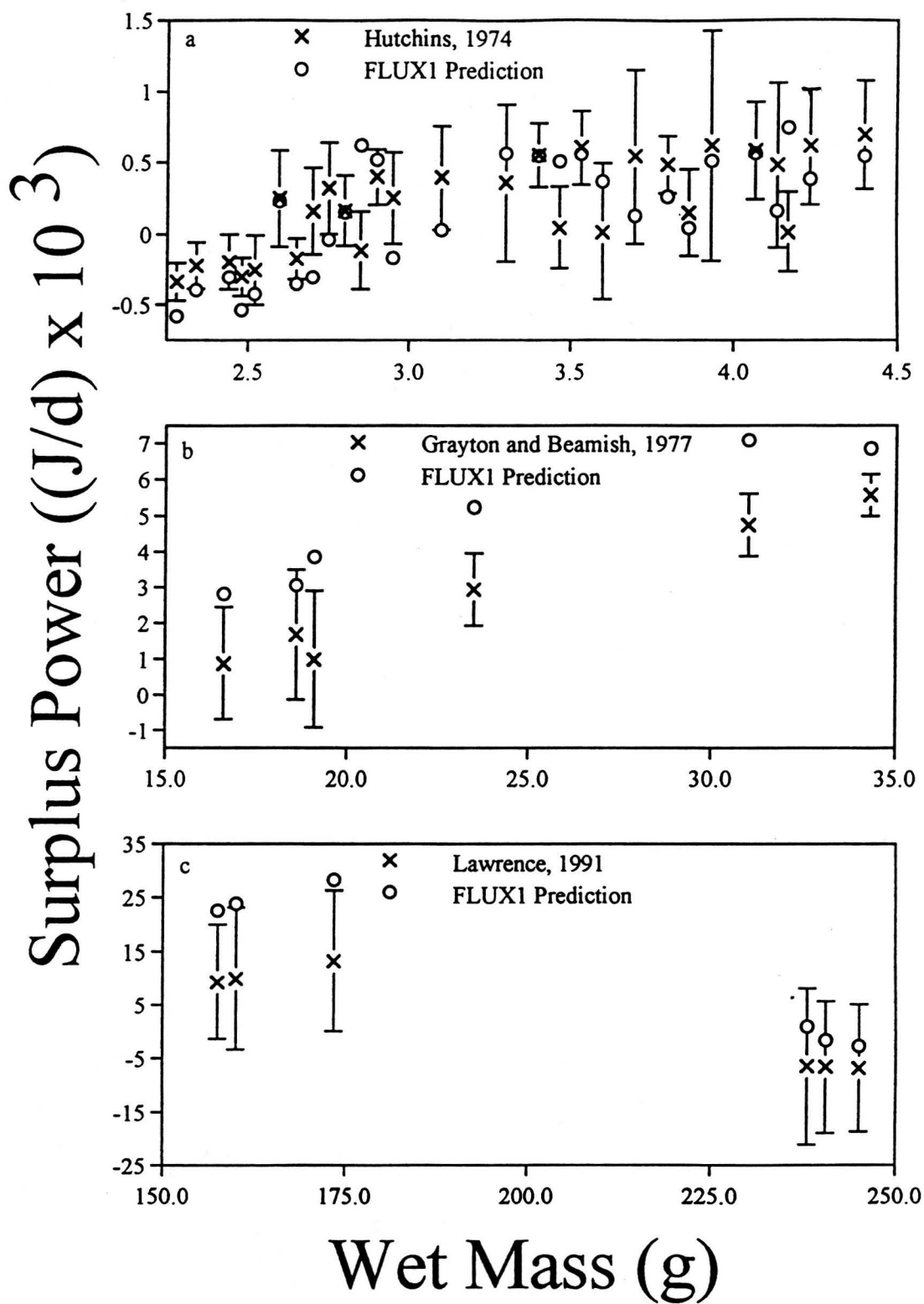
Table 2.1. Model parameter values according to temperature and weight with literature sources.

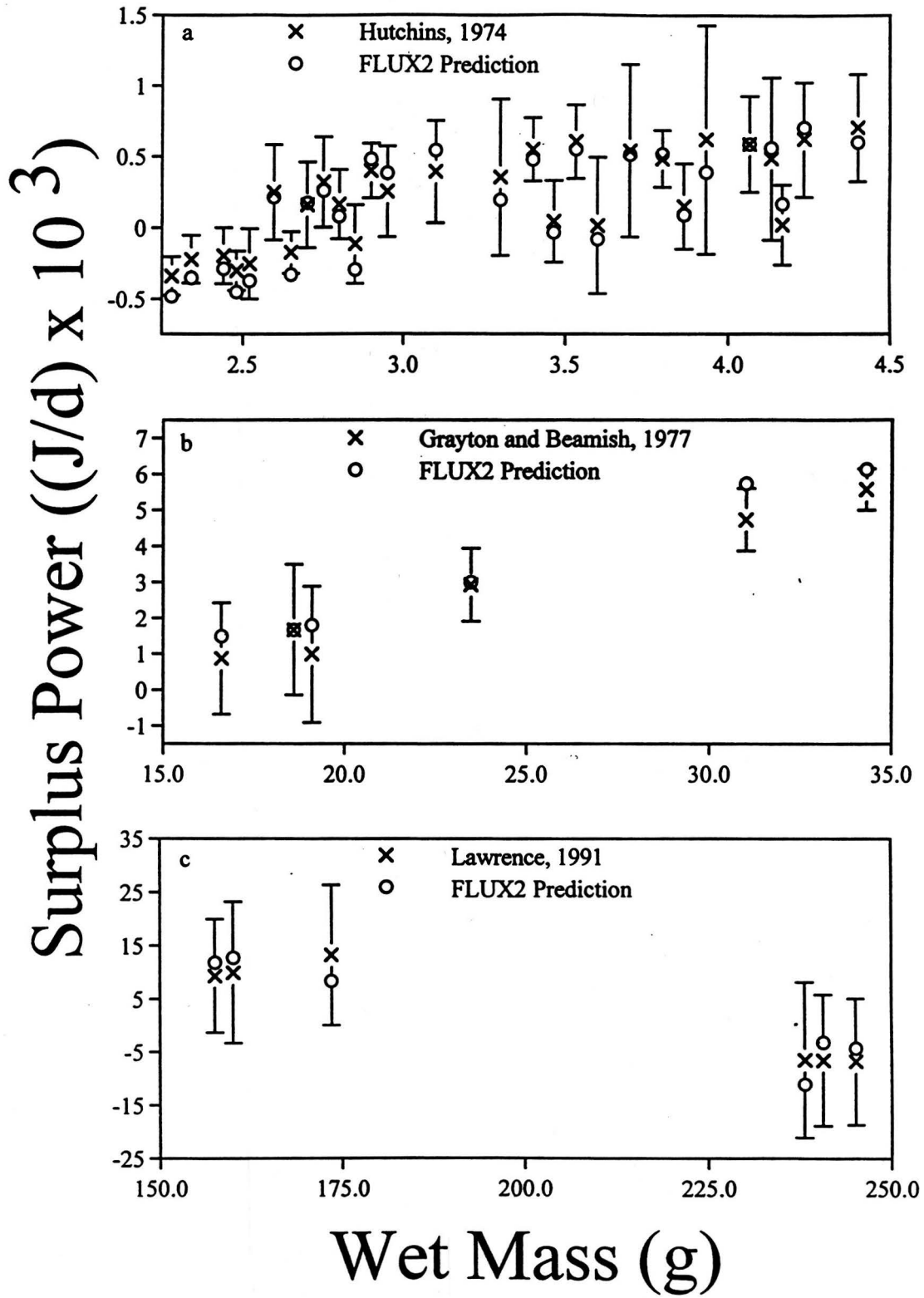
Parameter	Temperature (°C)	Mass (g)	Value	Source
a	2.0- 6.6	n/a	6.169	Elliot, 1976a
	6.6-19.5	n/a	12.031	"
b	2.0- 6.6	n/a	0.716	"
	6.6-19.5	n/a	0.737	"
c	2.0- 6.6	n/a	0.224	"
	6.6-19.5	n/a	0.105	"
f	5	n/a	1.000	Bolz and Tuve, 1973
	15	n/a	0.999	"
h	2.0-25.0	n/a	9.99×10^{-8}	Ware, 1978
i	2.0-25.0	n/a	0.20	"
j	5	n/a	0.0151	Bolz and Tuve, 1973
	15	n/a	0.0114	"
k	3.8- 7.1	n/a	0.0051	Elliot, 1976b
	7.1-19.5	n/a	0.0477	"
l	3.8- 7.1	n/a	0.812	"
	7.1-19.5	n/a	0.801	"
m	3.8- 7.1	n/a	0.523	"
	7.1-19.5	n/a	0.223	"
n	3.8- 6.6	n/a	2.902	Elliot, 1976a
	6.6-13.3	n/a	15.018	"
	13.3-17.8	n/a	26.433	"
o	3.8- 6.6	n/a	0.762	"
	6.6-13.3	n/a	0.759	"
	13.3-17.8	n/a	0.767	"
p	3.8- 6.6	n/a	0.418	"
	6.6-13.3	n/a	0.171	"
	13.3-17.8	n/a	0.126	"
q	2.0-25.0	n/a	0.212	Elliot, 1976b
r	2.0-25.0	n/a	-0.222	"
s	2.0-25.0	n/a	0.631	"
t	2.0-25.0	n/a	0.026	"
u	2.0-25.0	n/a	0.580	"
v	2.0-25.0	n/a	-0.299	"

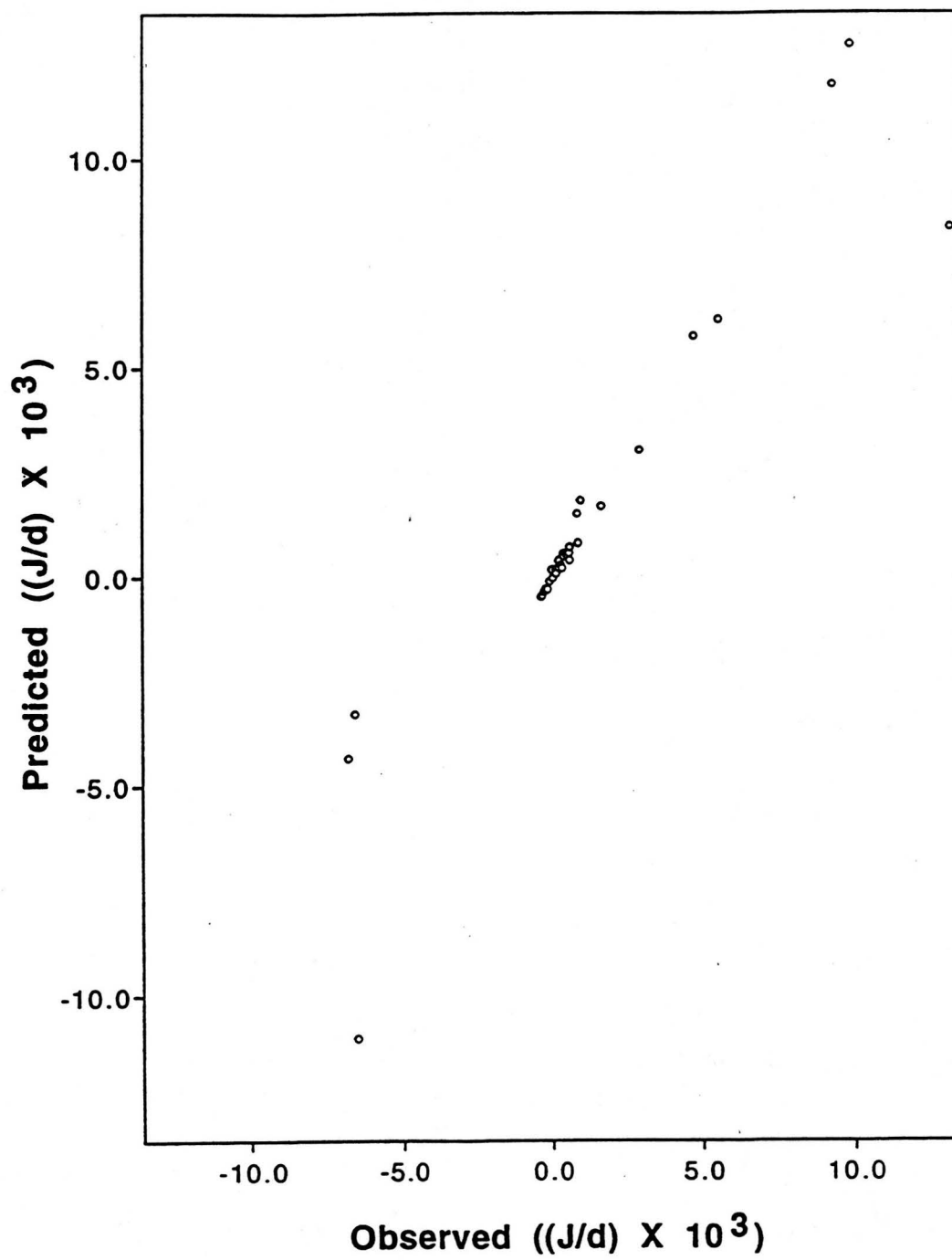
Table 2.1. Continued.

Parameter	Temperature (°C)	Mass (g)	Value	Source
w	2.0-25.0	< 140	8.277	Elliot, 1976a
	2.0-25.0	≥ 140	13.605	Bowen ¹
x	2.0-25.0	< 140	0.731	Elliot, 1976a
	2.0-25.0	≥ 140	0.662	Bowen ¹
y	2.0-25.0	< 140	0.094	Elliot, 1976a
	2.0-25.0	≥ 140	0.087	Bowen ¹

¹ Bowen: These parameter estimates are from my regression using Elliot's (1976a) model: $E_c = wM^x e^{yT}$ (see text). The data, segregated by mass, are from Elliot (1976a) and Brett and Glass (1973).







CHAPTER 3
MICROHABITAT SELECTION AND TESTS OF FOUR
HABITAT USE MODELS FOR LOTIC SALMONIDS
UNDER TWO DISTURBANCE REGIMES

Abstract. I collected observations of rainbow trout focal velocity and physical habitat availability in the Green River of northeastern Utah, USA (1988-1990). In typical years Flaming Gorge Dam generates hydropower by regulating discharge in the Green River between 21 and 120 m³/s on an hourly basis. This unstable discharge regime is a regular feature of this system. A drought occurred in 1989-1990 that reduced water in the reservoir and greatly reduced fluctuations in discharge for two years. During this drought, the Green River exhibited a stable discharge regime with lower mean daily discharge.

During winters exhibiting stable, lower mean discharges (1989-90), all size classes of rainbow trout (*Oncorhynchus mykiss*) used slower focal velocities than under an unstable winter discharge regime. Both selectivity and availability of the lowest velocity positions increased for rainbow trout in the winter, exhibiting unstable, higher mean discharges. Season had less influence on microhabitat selection of large fish than smaller individuals. Rainbow trout larger than 33.0 cm (total length) found and used positions with low focal velocities and high velocity shear regardless of season. In contrast, during the summer, trout \leq 33.0 cm TL

found and used positions with much higher focal velocities and greater velocity shear compared to the winter.

Four bioenergetics models were tested with the focal velocity use data. Two optimal goal models produced excellent fits ($r^2 = 0.91$ and 0.93 , for both $P < 0.01$) to the observed focal velocity use of rainbow trout larger than 33 cm TL. These results were consistent with the hypothesis that large rainbow trout were seeking and finding optimal focal velocity positions in stable discharge summers and under both discharge regimes in winter.

Introduction

Optimization theory provides a general approach to study habitat selection in fishes. For example, "optimal habitat selection theory" has successfully predicted habitat selection in both laboratory and field experiments. In a spatially predictable laboratory environment, convict cichlids (*Cichlasoma nigrofasciatum*) conformed to a distribution predicted from optimal prey patches and dominance ranks of individual fish (Grand and Grant, 1994). In two field experiments, habitat use by some sizes of bluegill sunfish (*Lepomis macrochirus*) corresponded to predicted optimal habitats. (Mittelbach, 1981; Werner et al., 1983). However, in one field experiment, Eurasian perch (*Perca fluviatilis*) habitat use matched predicted optimal habitat use qualitatively, but not quantitatively (Persson and Greenburg, 1990).

Only three studies have predicted optimal habitat use and tested these predictions with lotic fishes. All three studies involved stream-resident salmonids. First, in a laboratory stream, coho salmon (*Oncorhynchus kisutch*), and brook (*Salvelinus fontinalis*) and brown trout (*Salmo trutta*) parr competed for and used positions that offered maximum potential profit. The largest individuals in a given trial used the optimal positions and exhibited the highest specific growth rates (Fausch, 1984). Second, in a field experiment, habitat use of subadult rainbow trout (*Oncorhynchus mykiss*) in a North Carolina stream matched energetically optimal habitats in all four seasons of the year (Hill and Grossman, 1993). Third, in another field experiment, the dominance rank of adult Arctic grayling in an Alaskan stream matched the rank of a position's energetic profitability (Hughes and Dill, 1990; Hughes, 1992). Optimal habitat selection theory then has successfully predicted habitat use in five species of lotic salmonids, three life stages, and two distinct geographic areas.

Optimal habitat selection theory predicts habitat selection assuming individuals choose habitats to increase fitness. Fitness is measured by some currency, subject to constraints on ability to obtain the currency. The theory is then tested by comparing theoretical predictions to actual habitat selection.

While optimal habitat selection theory can predict aspects of lotic salmonid habitat selection, its general usefulness is not completely known. For example, the theory has not been tested for adult salmonids larger than 36 cm TL (total length).

Neither has the theory been tested for habitat selection under different disturbance regimes.

Disturbance is any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources or the physical environment (White and Pickett, 1985; Resh et al., 1988). In the Green River below Flaming Gorge Dam, discharge fluctuations are not a disturbance by this definition. Rather, discharge change is a regular feature of the environment below a dam operated principally for hydropower production. The disturbance I studied was the drought of 1989-1990; this climatic variation interrupted the normal operation of the dam and imposed two years of severely limited discharge fluctuations and lowered the magnitude of the daily mean discharges. The drought, a discrete event in time, disrupted population structure of rainbow trout in the Green River and changed resource predictability. Therefore, the drought exactly meets the three criteria for a disturbance under the definition of White and Pickett (1985).

Disturbance has influenced organisms at many levels of organization (Pickett and White, 1985). Minckley and Meffe (1987) described behavioral differences in species responding to discharge fluctuations. They showed that these behavioral differences affected fitness. Greenberg (1994) found that the magnitude of discharges influenced brown trout habitat use in artificial streams. The results of these two studies suggested that stream-resident salmonids' habitat use could be

influenced and perhaps even controlled by disturbance in the form of discharge changes.

I investigated the influence of disturbance, season, and body size on habitat use by developing optimization hypotheses for rainbow trout, a stream-resident salmonid, and testing these hypotheses with empirical observations of rainbow trout habitat use. I tested the generality of the optimal habitat selection theory in three steps. First, I used optimal habitat selection theory to develop four competing hypotheses (following Platts, 1964). Each of the four hypotheses was used to predict habitat use of rainbow trout in the Green River for two discharge regimes, two seasons, and three size groups. Second, I determined rainbow trout use in the Green River for the same combinations of discharge regime, seasons, and size groups. Third, I compared the four theoretical predictions of habitat use to the actual rainbow trout habitat use.

Here, I show that two of the four optimal hypotheses produced predictions that were consistent with the distribution of rainbow trout greater than 33 cm TL but not for smaller fish. These predictions were accurate for the larger trout under the two discharge regimes and two seasons studied. Further analysis showed that one model, Optimal Goal/Random Lottery for space, consistently performed better than the Optimal Goal/Dominance Hierarchy model or either Relaxed Goal model. The optimal goal was to choose the best position available in a reach at a given discharge. The relaxed goal was to satisfy some suboptimal criteria related to

survival (fish ≤ 33.0 cm TL) or reproduction (fish > 33.0 cm TL). These results suggest that optimal habitat selection theory can be extended to include fish larger than 36 cm TL in winter and summer. Also, the optimal habitat selection theory can explain the distribution of lotic salmonids under stable and unstable discharge regimes. However, in environments that involve high densities of stream-resident salmonids, the optimal habitat selection theory may fail for some fish. These fish may be those less experienced in tracking position availability through time or space or smaller fish constrained by temperature or other factors, from using energetically advantageous microhabitats characterized by high focal velocity.

Models

In this section, I describe the basic model and the four hypotheses/models I derive from that basic model. Then, for each derived model, I describe how the predicted focal velocities are determined. Finally, I describe how the predicted focal velocity-frequency distributions were determined. These frequency distributions were used for statistical analysis of model predictions.

Basic model

The basic model consists of the physiological model described in Chapter 2 with alterations to fit the field situation. Recall that the refined physiological model is similar to that of Glass (1971):

$$E_t = E_e + E_s + E_h + E_a + E_g \quad (1)$$

where

- E_t = Total energy input,
- E_e = Energy lost through egestion and excretion,
- E_s = Energy required for standard metabolism,
- E_h = Energy required for apparent heat increment,
- E_a = Energy expended through activity,
- E_g = Surplus power, the energy available for growth and reproduction (Ware, 1982).

The first alteration to the basic model was a change in the measure of currency. Instead of J/d I measured all terms in J/h during daylight hours.

Next, I altered how I determined E_p to incorporate drift and size selectivity data. First, I estimated a trout's scanning area (SA) as a one half of a semicircle perpendicular to the axis of the fish according to the following equation:

$$SA = \pi((1.2)(RD))^2 / 2 \quad (2)$$

where, the constant 1.2 is suggested by (Dunbrack and Dill, 1984; p. 1182), RD = reaction distance = $12(P)(1-(e^{-0.2*FL}))$ (Hughes and Dill, 1990) and P is prey size (1-9.5 mm) and FL is the fork length of the predator. Second, I calculated feeding speed of a trout as the mean of the focal speed and the fastest current velocity within 1 m of a fish. Third, I used Filbert's (1991) data to estimate energy available

in the drift ($(\text{J}\cdot\text{h}^{-1}\cdot\text{cm}^{-1}\cdot\text{s}^{-1}\cdot\text{cm}^2)$; discussed in Prey Availability). Fourth, I used Filbert's (1991) selectivity data to determine what proportion of the available energy in each prey size class was actually eaten by the fish ($(\text{J}\cdot\text{h}^{-1})$; discussed in Fish Stomach Data). Fifth, I summed energy entering the gut from each prey size class to determine the total energy input (J/h). Finally, I did not allow the feeding rate to exceed the maximum daily consumption rate as determined by Chapter 2, Equation 6.

Four derived models

Four variants of the basic model were evaluated. The four models were produced from unique combinations of two different optimization goals and two space allocation schemes. The optimization goals were the "optimal" and the "relaxed goal" (see discussion of satisficing in Nonacs and Dill, 1993). The optimal goal models assumed that, given a choice, a rainbow trout would choose the best position available. The relaxed goal models assumed that, given a choice, a trout would select the first position it encountered that met some suboptimal condition.

The relaxed goal criterion depended on the size of the trout and season. In winter, the relaxed goal for trout ≤ 33 cm TL was to find a location that would allow a fish to maintain lipid content at a minimum of 2.7% of wet weight: 2.7% was the lowest value ever observed among Green River rainbow trout in 120 sampled fish (unpublished data). In summer, the relaxed goal for trout less than 33

cm TL was to grow at a rate of approximately 0.6 g/d from date of stocking to winter (1 January). This rate was hypothesized (personal communication, J. Johnson) to be the minimum necessary required for small trout to survive the winter. This rate is unsubstantiated however; no data exist to improve it.

The relaxed solution for rainbow trout larger than 33 cm TL was to find a location that would allow them to acquire 46% of total body energy content during the prespawning period (ca. 335 d in the Green River). This value was the mean of energetic cost of reproduction, in male, 44%, and female brown trout, 48% (Lien, 1978).

I modeled two space allocation schemes: dominance hierarchy and random lottery. The dominance hierarchy allowed the largest fish in a reach to evaluate all positions first and then select a position. That position was then removed from the "available" positions for all subsequent evaluations by other, smaller fish. This procedure was then repeated with the next smaller fish until all fish were assigned a position. In the random lottery scheme (Sale, 1978), a fish was selected at random. The model then evaluated all positions for this fish, and allowed it to fill a position. The position filled by this fish was then removed from the "available" positions for all subsequent evaluations by other fish.

For each empirical fish observation, Model 1 (optimal, dominance) evaluated every position measured in the physical habitat availability data set collected at the same discharge and reach as the fish. The model evaluated each

measured position in three macrohabitats (one riffle, run, and eddy complex) for the largest fish to the smallest. All fish were assigned a position, and frequency distributions of predicted focal velocities were constructed for each size class.

Model 2 (optimal, random) was the optimization model with a random-lottery space-allocation scheme. For each fish, selected randomly, this model evaluated every position in a reach. The model placed the fish in its optimal position and this position was no longer available to subsequent fish. This procedure was repeated until all fish were placed into unique positions. Because too few iterations of the random selection of fish could produce bias, I executed a Monte Carlo simulation.

To determine the number of Monte Carlo replicates, in a trial series the model was run 20, 40, 60, 80, 100, and 200 times and the "average position" was determined for each fish for each number of iterations. Average focal velocities were compiled into predicted focal velocity-frequency distributions for each size class. The average velocity-frequency distributions stabilized at 80 iterations. Consequently, all further Monte Carlo simulations used 80 replicates.

Model 3 (relaxed goal, dominance) took the largest fish first and began evaluating positions selected at random. As soon as the model determined a position would meet the relaxed goal of a fish, the fish was assigned that position. Alternatively, if no position met the relaxed goal, then the best available position was assigned. This position was then removed from the "available" positions for all

subsequent evaluations by other, smaller fish. Then, this procedure was executed for the second largest fish and so on until all fish were loaded into unique positions. All fish were loaded 80 times and the average position was determined from these runs. The average positions were compiled into predicted focal velocity-frequency distributions for each size class.

Model 4 (relaxed goal, random) selected a fish at random. Then the model evaluated positions selected at random until the fish was loaded into a position that met the relaxed goal or the best position available. A second fish was selected at random and the procedure was replicated. This process continued until all fish were loaded into unique positions.

Eighty times the model determined the average position obtained by each fish and each fish was run 80 times. These 6400 predictions were used to determine the average positions for each fish and were compiled into one predicted velocity-distribution for each size class.

Methods

Study site

Flaming Gorge Dam regulates discharge (Q) and temperature of the Green River in the Uinta mountains, Daggett County, UT, USA. Mean elevation of the Green River in the study area is 1,672 m and has an average gradient of 1.6 m/km.

Discharge (Q) is regulated between 22.6 m³/s and 120.6 m³/s. Discharge variability changed considerably during the period in which this work was conducted. Daily maxima, means, and minima varied greatly in 1988 but not 1989 or 1990 (Figure 3.1 a-d). Discharge routinely varied up to five fold within a day during 1988 but not in 1989 or 1990 (Figure 3.1 e-h).

The depth of the water releases from the dam regulates thermal variation in the Green River. In winter, hourly water temperatures varied little, remaining between 2.25 and 5.5 °C from late December to late April. Hourly summer temperatures ranged from 7 to 16 °C but mean monthly summer temperatures ranged from 11 to 13 °C from June to October.

The macrobenthic invertebrate fauna was dominated by amphipods, insects, and fly larvae. *Gammarus* sp., *Baetis* spp., chironomids, and *Simulium* spp. were the numeric dominants in the drift. The vertebrate fauna was relatively depauperate, being composed of only six species common in the study area. Salmonid species dominate the community in terms of numbers and biomass. The salmonids are, in order of numeric dominance, rainbow trout, brown trout, cutthroat trout (*Oncorhynchus clarki*), and brook trout. Mountain whitefish and common carp were far less frequent than any of the trout.

During this study, the trout fishery of the Green River was principally maintained through stocking 25,000 15-cm (Mean TL) rainbow trout fingerlings each May (personal communication, S. Brayton).

I categorized fish into three size classes (Table 3.1): size 1, rainbow trout stocked in the current year; size 2, rainbow trout stocked in the immediately previous year; and size 3, rainbow trout stocked in all other years.

Physical habitat availability

Current velocity profiles of all major macrohabitat types (riffle, runs, and eddies) were completed at three discharges in two reaches. At each macrohabitat site, I established 6 to 14 transects perpendicular to the thalweg and spaced at uniform intervals within a macrohabitat (7 to 20 m). At every 2 m along these transects, I recorded current velocity at three depths: 0.2 and 0.8 of the water column's total depth and bottom. This procedure resulted in 1080 or more current velocity measurements distributed systematically throughout every macrohabitat sampled. I sampled at three discharges: 1) 22.6 m³/s (Mode of Q in 1989 and 1990), 2) 73.6 m³/s (Mode of Q in 1988) and 3) 99.1 m³/s. The two reaches sampled included: Reach 1 located 0-6.8 km below dam (kb dam) and Reach 2 located 10.5-14.5 kb dam.

Prey availability

Drift data were obtained from Filbert (1991). Filbert collected samples in winter, 30 January 1988 to 07 February 1988, and summer, 18-20 July 1988. These data were used to estimate food availability throughout the study. Therefore, I assumed these sampling dates are representative of all three years.

Because trout are principally visual predators (Ware, 1973), I used only data from samples collected during daylight hours: 45 minutes after dawn and at midday (1330 h). Weighted means of the average daily discharge were provided for 24 h prior to and during sample periods: 67.1 m³/s in winter and 45.4 m³/s in summer. Only a brief description of drift collection methodology is included here. Filbert (1991) provides a complete account of the drift collection methodology.

Three consecutive samples were taken in a riffle at 1.0, 0.75, and 0.5 m in depth. Associated current velocity observations were obtained with each sample. The net aperture was 0.093 m² and mesh size was 450 μm. Drift samples were cleaned, enumerated, and identified to genus (except Oligochaeta and Chironomidae, which were identified to family). Invertebrates were measured and assigned to 1-mm size categories.

I then determined the drift rate in energy (J/h) in each size class passing through the feeding window. First, proportions of each size class comprised by different taxa were calculated. Second, dry weight of invertebrates was estimated from wet weight (unpublished data, C.P. Hawkins). Third, dry weights were converted to energy equivalents (Cummins and Wuycheck, 1971). Fourth, I determined the energetic value in each size class passing through the drift net aperture. Finally, I standardized the value to derive the energy available in each size class per unit area ($\text{J}\cdot\text{h}^{-1}\cdot\text{cm}^{-1}\cdot\text{s}^{-1}\cdot\text{cm}^2$).

Fish stomach data

Filbert collected fish stomach data simultaneously with drift data collection. Fifteen to 20 rainbow trout were electroshocked 50-200 m downstream of the drift sampling location. Each stomach and the complete intestine were removed and stored in 70% ethanol. All intact invertebrates were identified as above, measured, and assigned to 1-mm size categories.

The stomach content data were combined with the values derived from the drift data, i.e., the energy available in each size class ($\text{J}\cdot\text{h}^{-1}\cdot\text{cm}^{-1}\cdot\text{s}^{-1}\cdot\text{cm}^{-2}$). To determine the energy in each prey size class eaten by the fish, I multiplied the total caloric value available in each prey size category passing through the feeding window by the feeding speed (cm/s), the scanning area (cm^2), and the proportion of that prey size category found in the trout stomachs (Filbert's size selectivity data). The energy obtained by the fish from each size group was summed to obtain the total energy acquired by the fish per hour. Important assumptions inherent in this calculation are that energy in the drift increases linearly with feeding speed, encounter rate variability for different prey sizes is integrated into the proportion of prey actually found in the gut, and various sizes of trout select the same size and taxonomic composition of prey from the drift.

I also used these estimates of energy acquired by trout to predict the amount of time required to satiate rainbow trout in the Green River. First, I

estimated the dry weight of *Gammarus sp.* required to satiate brown trout (Elliot, 1975). Second, I used drift availability data of Filbert (1991) and the feeding function of the bioenergetics model to predict the time to satiation (h) for rainbow trout in each size class, in reaches 1 and 2, and in winter and summer. This estimate assumes that rainbow and brown trout require the same weight of prey to become satiated.

Focal velocity use

With scuba gear, I entered the river 25 m downstream of the area to be sampled. I visually selected fish to sample in the order the fish were encountered. I measured the 10-second average focal velocity (V_F) for individual rainbow trout with a Montedoro-Whitney PVM-2A current meter. Maximum velocity (V_{Max}) was determined as the 10-second average velocity of the fastest point among six points on a sphere 1 m from each fish's focal point. Then, I calculated the velocity shear ($\text{cm}\cdot\text{s}^{-1}\cdot\text{cm}^{-1}$) between the focal and V_{Max} points ($V_{Max} - V_F / d$; following Hayes and Jowett [1994]) where d = the distance between the two points. I visually estimated the total length of the fish. Field assessment of this technique showed I was capable of obtaining the length of a trout ± 1 cm. Focal velocity observations were converted to body lengths per second (BL/s) by dividing the focal speed (cm/s) by total body length (cm). Focal velocity observations were then compiled into frequency categories 0.5 BL/s in width. Frequency distributions were prepared for

each size class in each of the four field seasons: winter 1988; winter 1989; summer 1989; winter 1990.

All focal velocity observations were obtained between 0830 and 1630 h. These observations were conducted in the same macrohabitats as physical-habitat-availability measurements: at least one riffle, one run, and one eddy in each of the two study reaches. I noted the discharge (Q) and temperature associated with each focal velocity observation. Focal velocity observations were conducted over the entire range of discharges available in 1988. Discharges of three magnitudes, 22.6, 73.6, and 99.1 m^3/s , were delivered 12 times over the course of the winter. Each time, I requested and received a stable discharge for 10 h, beginning at 0700 h. So, I collected observations in each macrohabitat at each discharge level four times. Focal velocity observations were conducted four times in each macrohabitat at the only available discharge in 1989-90, 22.6 m^3/s .

Statistical analysis

To determine how well predicted frequency distributions fit observed patterns, I calculated the correlation coefficients (r) and coefficients of determination (r^2) (Sokal and Rohlf, 1981) between the predicted and observed frequency distributions for each combination of field season (4) and size class (3). I also evaluated the assumptions of correlation coefficient determination: both the

observed data (X) and model predictions (Y) were normally distributed and visual inspection indicated the Y variate changed monotonically with X.

To summarize these statistics, I compiled model predictions for size class 1 from all four field seasons combined to produce a summary r^2 for each size class. Then, I compiled model predictions for each field season with all size classes combined. Finally, for each model I combined all seasons and sizes to produce a summary r^2 for each model.

Results

Discharge regime changed during this study. This change produced a natural experiment and provided me the opportunity to test the generality of the optimal habitat selection theory under different disturbance regimes. Discharge fluctuated frequently in 1988; such a discharge regime is common below hydropower-producing dams. When the drought occurred, this disturbance curtailed dam discharge fluctuations in 1989 and 1990 and changed the population size structure (Figure 3.2). Two components of the disparities between the unstable discharge regime and the stable regime were apparent. First, the mean discharge during daylight hours was significantly greater in 1988 ($58 \text{ m}^3/\text{s}$) than in 1989 ($23 \text{ m}^3/\text{s}$) or 1990 ($25 \text{ m}^3/\text{s}$). Second, fluctuations occurred more often and were usually larger in 1988 ($\text{sd} = 27.6 \text{ m}^3/\text{s}$) than in 1989 ($\text{sd} = 5.83 \text{ m}^3/\text{s}$) or 1990 ($\text{sd} = 10.14$).

Higher mean discharges in 1988 resulted in increased availability of higher current velocities (Table 3.2). Furthermore, fluctuations in discharge changed the spatial distribution of current velocities. Therefore, the different discharge regime in 1988 meant that different physical microhabitats existed in time and space. The resulting environment was less predictable temporally and spatially compared to the disturbed years of 1989 and 1990.

Microhabitat use

The different discharge regimes and field seasons allow comparisons between winters with different discharge regimes, and between winter and summer seasons with stable discharges. Henceforth, when I discuss the influence of discharge regime on habitat use and selection, the discussion relates solely to three winter field seasons. The winter of 1988 was the most unstable and, in comparison, the winters of 1989 and 1990 were relatively stable. Thus, discussions of seasonal differences in microhabitat use and selection are limited to stable discharge regimes.

Discharge regime changed microhabitat use as measured by focal velocity and velocity shear. For every size class, an unstable discharge regime (winter 1988) meant more fish in higher focal velocity categories than during a stable discharge regime (winters of 1989 and 1990). This effect was most pronounced for Size Class 1 (Table 3.2). Size Class 2 and 3 fish used positions exhibiting lower velocity

shears under an unstable discharge regime than under a stable regime. Size Class 1 fish used lower mean velocity shear than Size Class 2 or 3 regardless of the discharge regime (Table 3.3).

In the winters when the discharge regime was stable, all size classes of fish were distributed similarly with regard to focal velocity (Table 3.2). In the summer when discharge was stable and warmer (1989), rainbow trout in Size Class 1 were found in higher velocity habitats than winter. However, use of the lowest velocity positions increased in summer for Size Classes 2 and 3.

In winter and summer, fish of Size Class 3, and sometimes Size Class 2, found positions with equivalent or higher velocity shear than Size Class 1. This tendency was most striking under a stable discharge regime in winter (Table 3.3).

Microhabitat selection

Fewer discharge fluctuations in 1989 and 1990 increased the relative availability of lower velocity positions (Table 3.2). Therefore, if use did not change we would expect the selectivity index in these lower velocity categories to be lower in the winters of 1989 and 1990. However, use of low velocity habitats by all size classes of fish in the stable winters increased more than availability, resulting in higher selectivity values for positions exhibiting velocities less than one BL/s.

Season also influenced focal velocity selection. In the winters when the discharge regime was cold and stable, all size classes of fish preferred similar low-

velocity microhabitats (Table 3.2). In contrast, summer produced markedly different results in selection by different size classes. Size Class 1 fish showed increased selectivity in all categories above 1 BL/s. Size Class 2 individuals exhibited a mixed shift in preference; selectivity increased in the lowest velocity category and for positions with velocities 1 to 2 BL/s. Size Class 3 fish showed preference for the lowest two velocity categories.

Model fit to observed microhabitat use

The models allowed fish to select a position with a focal velocity from the same available velocity-frequency distribution as fish in the field. From the standpoint of selectivity index calculations, predicted focal velocity use and actual focal velocity use were drawn from the "same environment." Therefore, instead of selectivity, I compared use from actual observations and predictions from the models.

The optimality models work best but model 4 (Relaxed Goal/Random Lottery) also does well (Table 3.4). However, model 4 fails to perform adequately for all size classes during summer (Table 3.4).

For Size Class 1, no model produced significantly high coefficients of determination (r^2) for more than one field season. For all four models, model predictions did not match habitat use by Size Class 1 in three seasons out of four (see Table 3.4 and Figures 3.3a-3.6a and 3.7a-3.10a). The primary reason the

models fail for Size Class 1 is that they predict less habitat use in the slowest velocity category (0-0.5 BL/s) compared to the second category (0.5-1.0 BL/s). This prediction results from the lack of energetically advantageous positions in the lowest velocity category because very few positions have 0-0.5 BL/s focal velocity and velocity shear greater than $25 \text{ cm} \cdot \text{s}^{-1} \cdot \text{cm}^{-1}$. However, all four models predicted microhabitat locations well for Size Classes 2 and 3, with model 2 (Optimal/Random Lottery) performing slightly better than any other model (Figures 3.3-3.6, 3.7-3.10).

All models performed well for both stable and unstable discharge regimes during winter (Table 3.4). However, overall the optimal goal models predicted the distribution of Size Classes 2 and 3 rainbow trout best under disparate discharge regimes (Table 4; Figures 3.3-3.6 and 3.7-3.10).

The optimal goal models performed well regardless of season, but the relaxed goal models did poorly in summer (Table 3.4). Because the relaxed goal models failed in the summer, I concluded that models 1 and 2 were more general in application than models 3 and 4. To determine if model 1 or 2 was superior, I compared their performance under different seasons. For the winters of 1989 and 1990 and the summer of 1989, models 1 and 2 produced equally good fits (Figures 3.4-3.6).

To differentiate between models 1 and 2, I performed an *a posteriori* analysis. I changed the frequency category width to 0.2, 0.3, and 0.4 BL/s from the

original value of 0.5. I ran models 1 and 2 with each of these three new widths. At all interval widths, Model 2 always performed better than model 1 (Figure 3.11). Model 2 appears to do better because, as the resolution is increased, model 1 (Optimal/Dominance) fails more often for Size Classes 2 and 3 in the unstable winter of 1988 (Table 3.5).

Discussion

Microhabitat use and selection

Flaming Gorge Dam operates to provide power to the western U.S. Like Glen Canyon Dam downstream, the tailwaters of such peaking power regimes experience regular, large diel fluctuations (Budhu, 1994). Even small daily fluctuations (1.6-5.1 m³/s) from a dam can change habitat availability and influence rainbow trout habitat use (Pert and Erman, 1994). The diel fluctuations of Flaming Gorge Dam produce discharge fluctuations an order of magnitude greater than those observed by Pert and Erman. When water levels in Flaming Gorge Reservoir are low, due to drought, discharges are smaller in magnitude and fluctuate less. The winter of 1988 exhibited an unstable discharge regime and produced higher mortality in Size Class 1 (up to 81%; Modde et al., 1991), and changed the population structure.

Discharge fluctuations in the winter influenced rainbow trout focal velocity use most for Size Class 1 and least for Size Class 3. Size Class 1 fish used higher

focal velocities than Size Classes 2 and 3 during the period of high and fluctuating discharge (winter 1988). At least two explanations for this phenomenon are possible. First, the proportion of available current velocities was shifted to the right by higher discharge in 1988. This shift in availability has a disproportionately greater effect on small fish compared to larger fish (Table 3.2, Column 2 and Column 5). Second, in winters with unstable discharge, Size Class 1 fish may be less able to track changing locations of desirable lower current velocities. This second explanation is supported by the results of Greenberg (1994). He found that, at higher discharges in an artificial stream, juvenile brown trout will select areas of lower velocity when possible.

Selectivity of focal velocities indicated that the inability of smaller fish to track profitable positions was more important than the shift in current velocity availability. In the most stable winters, small fish tracked and used low-velocity positions sufficiently to offset an increase in availability. Therefore, the increased selectivity exhibited by smaller fish for low-velocity positions during stable winters (Table 3.2, Columns 4, 7, and 13) suggests that small fish had difficulty tracking optimal energetic positions during periods of unstable discharge. This explanation is consistent with the findings of Grand and Grant (1994). They showed convict cichlids use optimal prey patches in a spatially predictable laboratory environment.

Seasonal changes in position choice were less pronounced for larger fish compared to smaller fish. For example, Size Class 3 fish need not accept high focal

velocities in summer to use high velocity shears as Size Class 1 fish must do. In winter and summer, under a stable discharge, Size Class 3 fish select positions with low focal velocity and high velocity shear. In summer, Size Class 1 fish find and use positions with much greater velocity shear but must also accept greater focal velocities. Greater velocity shear allows a fish to swim at a lower velocity than that at which it feeds. Thus, high velocity shear conveys an energetic advantage over positions with lower velocity shear.

Higher temperatures or increased food availability (Filbert, 1991) may have made it possible for Size Class 1 fish to use higher velocities during summer. Able to accept higher focal velocities, Size Class 1 fish may then have been capable of taking advantage of positions with higher velocity shears. However, since the discharge regime was stable throughout 1989, I do not know if Size Class 1 fish can find and use these faster positions if discharge fluctuates during the summer.

Model fit to observed microhabitat use

The optimal goal models predicted the focal velocity use of Size Class 2 and 3 in winter and summer and in stable and unstable discharge regimes. These results are consistent with the hypothesis that adult fish were seeking and finding optimal positions.

Specifically, model 2 (Optimal/Random Lottery) performs better than model 1 (Optimal/Dominance) under most circumstances. The most notable

exception to this is that model 1 performs as well in stable winters (1989 and 1990) as model 2 (Tables 3.4 and 3.5). Understandably, the dominance hierarchy space-allocation scheme works best when discharge change is infrequent.

Larger, presumably more dominant individuals tracked optimal positions under an unstable discharge regime during winter. This result was not consistent with the results of Grand and Grant (1994). They found that both dominant and subordinate fish were unable to track optimal prey patches in spatially unpredictable laboratory environments. However, Grand and Grant worked with juvenile fish, whereas the larger fish in this study, Size Class 2 and 3 individuals, were adults.

No model worked well for Size Class 1. Size Class 1 fish used higher velocities than the model predicted. Similarly, Mittelbach (1981) found bluegill sunfish < 100 mm (standard length) did not use predicted optimal habitats. He suggested this was due to size-selective predation risk. This explanation seems unlikely for Size Class 1 fish in the Green River. Less than 0.1% of the fish in the river could prey upon the smallest fish in Size Class 1. In addition, avian predators would be ineffective because over 80% of the river has a depth of 1 m or more. While the behavior of Size Class 1 individuals could be restricted due to perceived risk, predation pressure seems unlikely to be influencing habitat selection in Size Class 1 rainbow trout. If predation pressure is not the cause, there are explanations in two areas: biological and modeling artifact.

Two biological explanations could account for the inability of any model to predict optimal habitat use by Size Class 1 fish. First, these smaller fish have less experience than larger fish and are unable to find or track advantageous positions as well as their larger counterparts. Second, many positions with high velocity shear also require the trout swim at a focal velocity greater than 1.0 BL/s for a Size Class 1 fish. These small fish seemed unwilling to use positions with high focal velocity and high velocity shear except in the summer (Table 3.2). The bioenergetics models should have successfully predicted Size Class 1 habitat use if the second explanation were correct because the models took into account focal velocity and velocity shear. These results then suggest the lack of experience is the more likely biological explanation for the observed pattern.

The inability of the Optimal/Random Lottery (OR) model, and perhaps all four derived models, to predict Size Class 1 habitat use could have been a modeling artifact. In *a posteriori* analyses of the OR model, an explanation was suggested that could explain the failure of this model to predict habitat use by Size Class 1. In addition, these analyses suggested a limitation of the bioenergetics approach. I found the model output was more dependent on energetic costs than benefits of foraging. For example, in Figure 3.12, the OR model and the OR cost component alone make very similar predictions of habitat use by all size groups in the winter of 1988. The benefit component makes qualitatively different predictions from the combined model. In addition, the cost component alone

predicts the habitat use of rainbow trout better than the benefit component alone (Tables 3.6 and 3.7). These results suggest that energetic costs influence model predictions much more than benefits derived from foraging. The importance of costs to OR model predictions may be derived from three sources. First, the estimates of drift do not reflect actual food availability in the Green River, and this component of the model simply adds another source of variation to model predictions. Second, the fish cannot evaluate or predict food availability at any position in the river. Third, foraging benefits could be sufficiently high, at positions throughout the river, to provide for trout growth. In this last case, if small fish can find enough food to eat, then they might minimize the cost function and not balance foraging benefits and energetic costs. To test this, I compared OR model predictions in the two reaches. Because there was more energy available in reach 2 drift, trout ≤ 33 cm TL will be satiated much more quickly in reach 2, 2.9 h, than in reach 1, 17.3 h (Table 3.8). Then, if it is true that these small fish are cost minimizing when food is not limiting, the OR model should fit best when food is abundant, as in reach 2. But, the OR model predictions in reach 1 are consistently better than in reach 2 when compared to actual habitat use by small rainbow trout (Tables 3.9 and 3.10). Therefore, I concluded the OR model does not seem to fail for small rainbow trout because abundant food in the Green River leads to cost minimizing by these small fish.

An important limitation of the bioenergetic approach was also suggested by the *a posteriori* analyses. The amount of variance accounted for by the model depends upon the metric (absolute focal velocity (cm/s), relative focal velocity (BL/s), or velocity shear ($\text{cm}\cdot\text{s}^{-1}\cdot\text{cm}^{-1}$)) modeled and the interval width chosen for the statistical comparisons. I chose, *a priori*, to evaluate the models' performance in predicting focal velocity in body lengths per second. In addition, I compiled habitat use and model predictions into histograms with an interval width of 0.5 BL/s for statistical comparisons. The choices of metric and interval, in part, could explain the failure of the OR model to predict habitat use of Size Class 1. Rainbow trout ≤ 33 cm TL might react to focal velocity at a smaller scale than the 0.5 BL/s interval. Then, the interval width chosen may have been too coarse to allow a valid comparison of small trout habitat use and model predictions. To test the importance of these *a priori* choices, I compared the summary r^2 for different metrics and interval widths. I found absolute focal velocity (cm/s) least sensitive to the choice of interval (Figure 3.13). In contrast, velocity shear was the most sensitive metric to choice of interval width. My choice of relative focal velocity (0.5 BL/s intervals) appears intermediate in sensitivity. However, I am not aware of any data with which to evaluate whether or not the 0.5 BL/s interval was too coarse for a valid statistical comparison of OR model predictions and habitat use of rainbow trout ≤ 33 cm TL.

In conclusion, several possible explanations exist for the failure of the OR model to predict habitat use by rainbow trout in Size Class 1. Three explanations seem the most reasonable. First, the small trout were incapable of tracking, finding, and using optimal positions perhaps because they have less information about the system. Second, food availability is actually quite important in the position choice of small trout and the model depends much more on costs than benefits. Third, the choice of metric (Focal Velocity, BL/s) and interval width (0.5 BL/s) for statistical comparisons could have provided a test that was improperly scaled to the scale of response used by the fish. Therefore, future research should investigate more than one metric, consider their robustness, and evaluate choice of interval width.

Conclusions

Discharge fluctuations during winter tend to make it more difficult for fish of Size Class 1 to find and use preferred positions. Thus, changes in discharge decrease the energetic return of rainbow trout less than 33 cm TL in the winter. Productivity of the fishery, then, is decreased by a heavily fluctuating discharge regime, as in the winter of 1988.

A large proportion of Size Class 1 fish moves into positions exhibiting higher velocities in summer to achieve greater velocity shears and higher energetic return. Size Class 3 trout do not need to move because they have found and are using positions with low focal velocities and high velocity shear.

Optimal habitat selection theory may be extended to include lotic salmonids greater than 33 cm TL in summer and winter. Also the theory can predict focal velocity use in stable and unstable discharge regimes.

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Table 3.1. Range of rainbow trout sizes by class in the Green River below Flaming Gorge Dam: 1988 to 1990.

Size	Summer	Winter
Class 1		
Total Length (cm)	≤ 30.5	≤ 33.0
Wet Weight (g)	≤ 312.5	≤ 394.8
Class 2		
Total Length (cm)	30.5- 40.6	33.0- 43.2
Wet Weight (g)	312.5-730.5	394.8-878.5
Class 3		
Total Length(cm)	> 40.6	> 43.2
Wet Weight (g)	> 730.5	> 878.5

Table 3.2. Matrices of velocity availability (proportion of observed), use (proportion of observed), and selectivity (Chesson's [1983] α) for rainbow trout in the Green River, UT. Velocity categories have 0.5 Body Lengths/s in range, only midpoints are reported. Neutral selection has $\alpha = 0.143$.

Velocity Midpt. (BL/s)	Winter 1988			Winter 1989			Summer 1989			Winter 1990			
	Available	Use	α	Available	Use	α	Available	Use	α	Available	Use	α	
Size Class 1	0.25	0.221	0.365	0.188	0.328	0.627	0.397	0.285	0.159	0.055	0.320	0.513	0.300
	0.75	0.109	0.336	0.351	0.142	0.253	0.370	0.118	0.178	0.150	0.140	0.368	0.492
	1.25	0.086	0.164	0.215	0.107	0.120	0.233	0.096	0.267	0.277	0.107	0.118	0.208
	1.75	0.064	0.077	0.136	0.085	0.000	0.000	0.076	0.168	0.220	0.082	0.000	0.000
	2.25	0.060	0.048	0.091	0.079	0.000	0.000	0.068	0.099	0.145	0.078	0.000	0.000
	2.75	0.055	0.010	0.019	0.068	0.000	0.000	0.058	0.079	0.137	0.068	0.000	0.000
	>3.25	0.405	0.000	0.000	0.191	0.000	0.000	0.299	0.050	0.016	0.206	0.000	0.000
Size Class 2	0.25	0.256	0.349	0.182	0.376	0.541	0.310	0.381	0.630	0.370	0.368	0.579	0.357
	0.75	0.127	0.384	0.403	0.161	0.320	0.427	0.162	0.185	0.255	0.158	0.351	0.505
	1.25	0.091	0.209	0.309	0.117	0.126	0.233	0.117	0.130	0.247	0.115	0.070	0.138
	1.75	0.073	0.035	0.064	0.097	0.009	0.020	0.097	0.055	0.128	0.095	0.000	0.000
	2.25	0.073	0.023	0.042	0.087	0.000	0.000	0.088	0.000	0.000	0.087	0.000	0.000
	2.75	0.075	0.000	0.000	0.058	0.000	0.000	0.059	0.000	0.000	0.060	0.000	0.000
	>3.25	0.305	0.000	0.000	0.104	0.004	0.010	0.096	0.000	0.000	0.117	0.000	0.000
Size Class 3	0.25	0.294	0.474	0.266	0.415	0.589	0.345	0.414	0.533	0.326	0.414	0.656	0.444
	0.75	0.141	0.289	0.338	0.173	0.250	0.350	0.175	0.467	0.674	0.173	0.344	0.556
	1.25	0.099	0.211	0.349	0.131	0.143	0.265	0.129	0.000	0.000	0.131	0.000	0.000
	1.75	0.092	0.026	0.047	0.108	0.018	0.040	0.111	0.000	0.000	0.108	0.000	0.000
	2.25	0.095	0.000	0.000	0.073	0.000	0.000	0.073	0.000	0.000	0.072	0.000	0.000
	2.75	0.078	0.000	0.000	0.051	0.000	0.000	0.053	0.000	0.000	0.050	0.000	0.000
	>3.25	0.201	0.000	0.000	0.049	0.000	0.000	0.045	0.000	0.000	0.052	0.000	0.000

Table 3.3. Mean velocity shear use by rainbow trout in the Green River.

Size	Winter, 1988 $\text{cm}\cdot\text{s}^{-1}\cdot\text{m}^{-1}$	Winter, 1989 $\text{cm}\cdot\text{s}^{-1}\cdot\text{m}^{-1}$	Summer, 1989 $\text{cm}\cdot\text{s}^{-1}\cdot\text{m}^{-1}$	Winter, 1990 $\text{cm}\cdot\text{s}^{-1}\cdot\text{m}^{-1}$
Class 1	22.8	22.1	48.0	24.5
Class 2	20.2	40.0	43.2	37.9
Class 3	32.3	48.4	43.3	50.4

Table 3.4. Matrix of r^2 values for all models compared to empirical data. Model predictions and empirical data were placed into categories with increments of 0.5 BL/s. Values in the SEASON row and SZ CL column are summary values for those variables. Value in the bottom right corner of each matrix is the summary value for the model. The final matrix is the sample size of empirical observations contained in each cell of the above matrices. Symbols are *: $P \leq 0.05$; **: $P \leq 0.01$; NS: $P > 0.05$.

Size	Winter 1988	Winter 1989	Summer 1989	Winter 1990	SZ CL
Model 1: Optimal, Dominance					
Class 1	0.7644 **	0.1778 NS	0.0615 NS	0.4138 NS	0.5427 NS
Class 2	0.7721 *	0.8167 *	0.9648 **	0.9460 **	0.9719 **
Class 3	0.6473 *	0.8320 **	0.4950 NS	0.7574 *	0.7607 *
SEASON	0.7849 **	0.9553 **	0.7381 *	0.9838 **	0.9073 **
Model 2: Optimal, Random Lottery					
Class 1	0.8305 **	0.2792 NS	0.0605 NS	0.4423 NS	0.7067 *
Class 2	0.6584 *	0.8664 **	0.9182 **	0.9456 **	0.9612 **
Class 3	0.7728 **	0.9441 **	0.7369 *	0.8681 **	0.8927 **
SEASON	0.7624 *	0.8643 **	0.6806 *	0.8704 **	0.9297 **
Model 3: Relaxed Goal, Dominance					
Class 1	0.6055 *	0.0724 NS	0.0402 NS	0.4138 NS	0.2972 NS
Class 2	0.6417 *	0.6670 *	0.0029 NS	0.8949 **	0.8660 **
Class 3	0.7530 *	0.8320 **	0.0110 NS	0.7574 *	0.7824 **
SEASON	0.8702 **	0.7655 **	0.0792 NS	0.8588 **	0.7683 **
Model 4: Relaxed Goal, Random Lottery					
Class 1	0.8556 **	0.1956 NS	0.1773 NS	0.3224 NS	0.4264 NS
Class 2	0.6083 *	0.8785 **	0.0022 NS	0.9542 **	0.9748 **
Class 3	0.7895 **	0.9361 **	0.0132 NS	0.8628 **	0.9328 **
SEASON	0.8256 **	0.8448 **	0.0113 NS	0.8306 **	0.9010 **
Sample Size					
Class 1	104	83	101	76	364
Class 2	86	222	54	114	476
Class 3	38	56	15	32	141
SEASON	228	361	170	222	981

Table 3.5. Matrix of r^2 values for all models compared to empirical data. Model predictions and empirical data were placed into categories with increments of 0.3 BL/s. Values in the SEASON row and SIZE column are summary values for those variables. Value in the bottom right corner of each matrix is the summary value for the model. The final matrix is the sample size of empirical observations contained in each cell of the above matrices. Symbols are *: $P \leq 0.05$; **: $P \leq 0.01$; NS: $P > 0.05$.

Size	Winter 1988	Winter 1989	Summer 1989	Winter 1990	SZ CL
Model 1: Optimal, Dominance					
Class 1	0.7983 **	0.0219 NS	0.1945 NS	0.2543 NS	0.3087 NS
Class 2	0.4301 NS	0.3520 NS	0.9336 **	0.6856 *	0.8186 **
Class 3	0.4805 NS	0.7923 **	0.6907 *	0.8244 **	0.8122 **
SEASON	0.7974 **	0.9348 **	0.5703 *	0.8480 **	0.8279 **
Model 2: Optimal, Random Lottery					
Class 1	0.9628 **	0.0696 NS	0.1832 NS	0.2598 NS	0.4790 NS
Class 2	0.4881 NS	0.4886 NS	0.7405 *	0.7433 *	0.7849 **
Class 3	0.6304 *	0.8465 **	0.8403 **	0.8684 **	0.8513 **
SEASON	0.8000 **	0.6831 *	0.2763 NS	0.7297 *	0.8458 **

Table 3.6. Matrix of r^2 values for the Optimal/Random Lottery's cost component. Model predictions and empirical data were placed into categories with increments of 0.5 BL/s. Values in the SEASON row and SIZE column are summary values for those variables. Value in the bottom right corner of matrix is the summary value for the model. The final matrix is the sample size of empirical observations contained in each cell of the above matrices. Symbols are *: $P \leq 0.05$; **: $P \leq 0.01$; NS: $P > 0.05$.

Size	Winter 1988	Winter 1989	Summer 1989	Winter 1990	SZ CL
Class 1	0.7160 *	0.8478 **	0.0595 NS	0.9197 **	0.8681 **
Class 2	0.4198 NS	0.8872 **	0.9182 **	0.9532 **	0.9092 **
Class 3	0.6270 *	0.9381 **	0.7369 *	0.8681 **	0.8438 **
SEASON	0.5814 *	0.9480 **	0.6917 *	0.9747 **	0.9312 **

Table 3.7. Matrix of r^2 values for the Optimal/Random Lottery's benefit component. Model predictions and empirical data were placed into categories with increments of 0.5 BL/s. Values in the SEASON row and SIZE column are summary values for those variables. Value in the bottom right corner of matrix is the summary value for the model. The final matrix is the sample size of empirical observations contained in each cell of the above matrices. Symbols are *: $P \leq 0.05$; **: $P \leq 0.01$; NS: $P > 0.05$.

Size	Winter 1988	Winter 1989	Summer 1989	Winter 1990	SZ CL
Class 1	0.6918 *	0.9680 **	0.0302 NS	0.6714 *	0.9590 **
Class 2	0.5228 NS	0.5767 *	0.9576 **	0.0003 NS	0.7014 *
Class 3	0.6853 *	0.5158 NS	0.6472 *	0.0000 NS	0.6383 *
SEASON	0.7476 *	0.7254 *	0.7188 *	0.3450 NS	0.8891 **

Table 3.8. Optimal/Random Lottery model predictions of time to satiation (h) for rainbow trout feeding at 45 cm/s in the Green River.

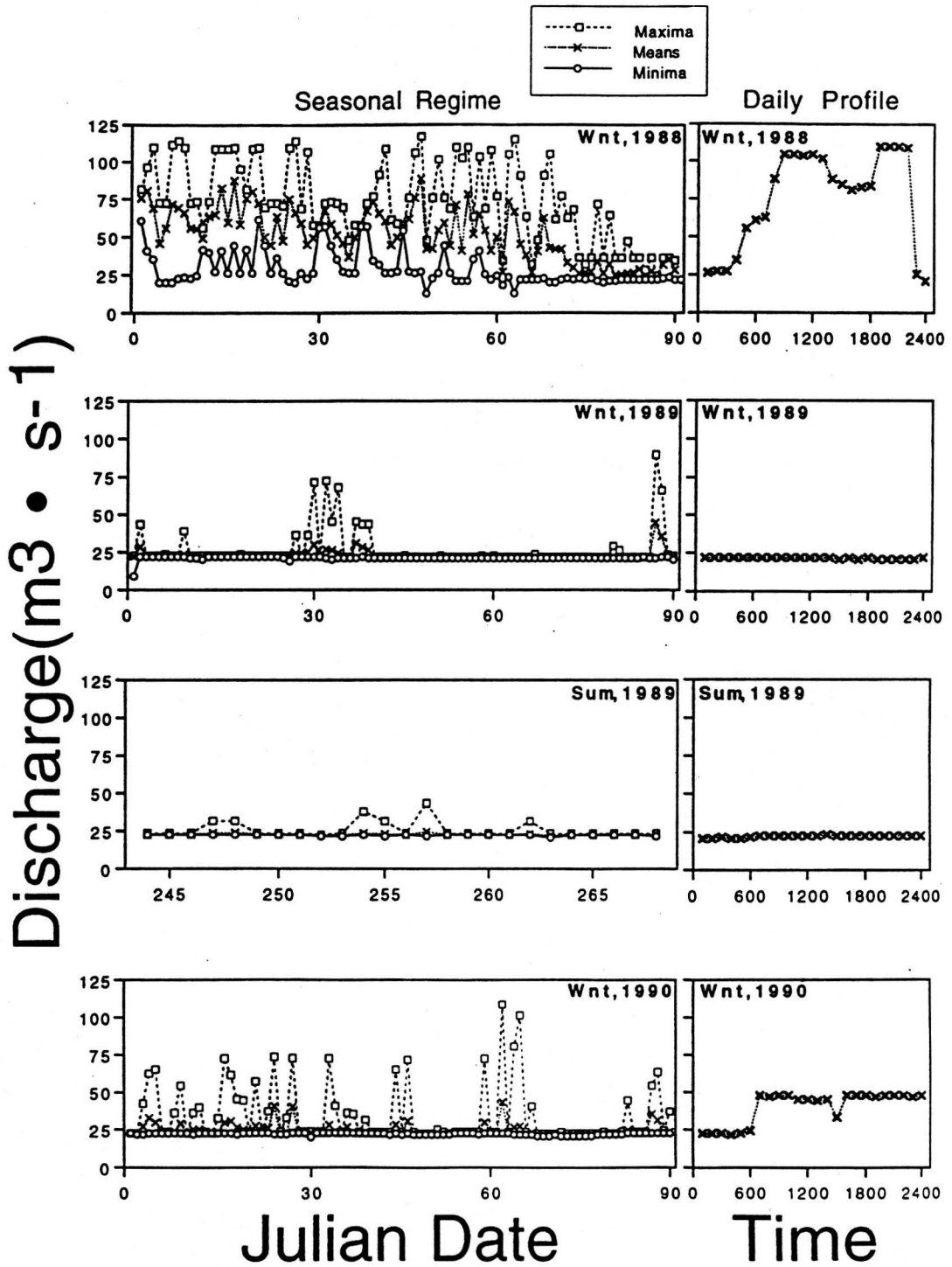
Size	Mean TL (cm)	Winter		Summer	
		Reach 1	Reach 2	Reach 1	Reach 2
Class 1	28	17.3	2.9	3.6	2.0
Class 2	37	34.6	5.8	7.3	4.0
Class 3	46	53.3	9.0	11.2	6.2

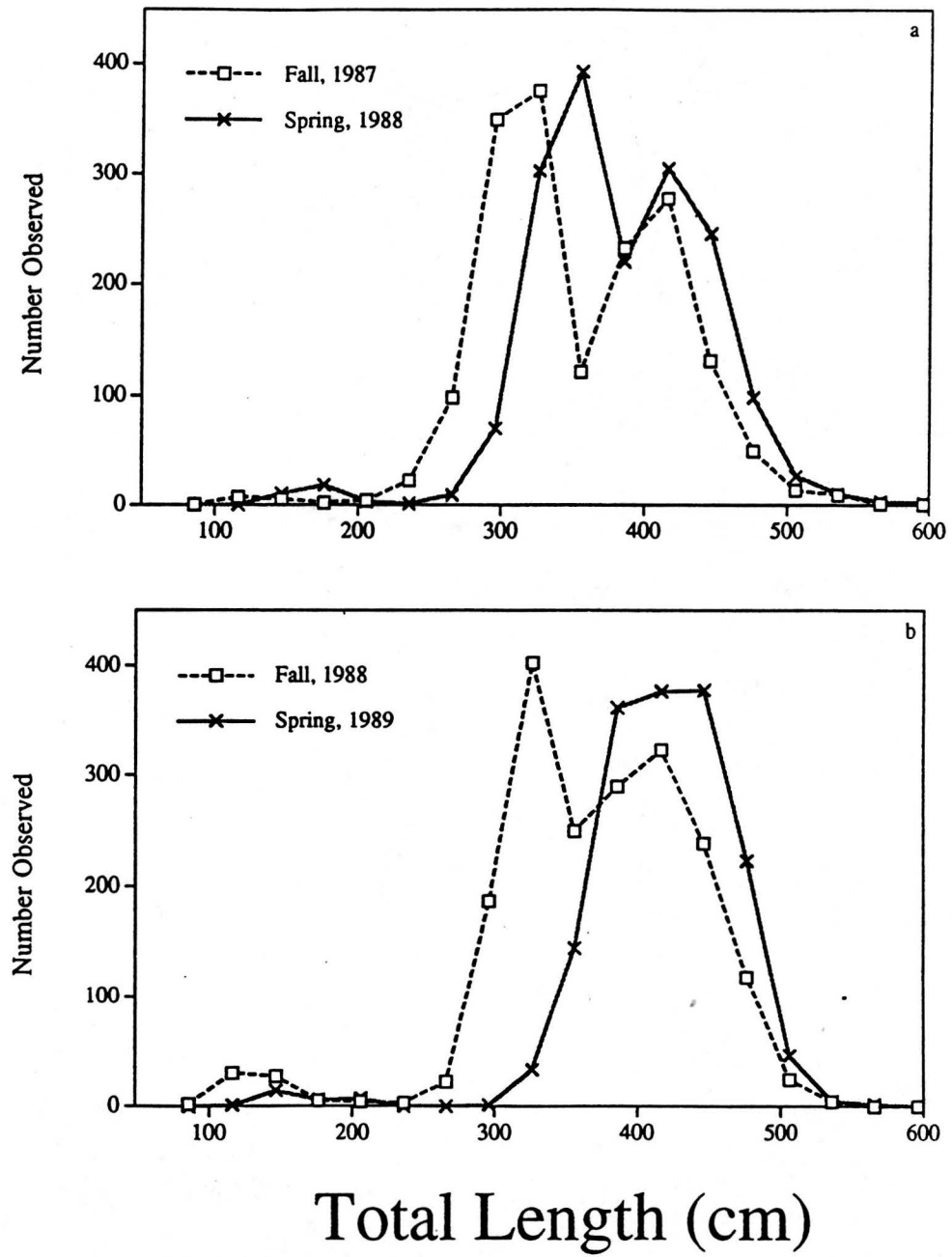
Table 3.9. Matrix of r^2 values for the Optimal/Random Lottery model for Reach 1 only. Model predictions and empirical data were placed into categories with increments of 0.5 BL/s. Values in the SEASON row and SIZE column are summary values for those variables. Value in the bottom right corner is the summary value for the model. The sample size of empirical observations contained in each of the above matrices can be found in Table 3.4. Symbols are *: $P \leq 0.05$; **: $P \leq 0.01$; NS: $P > 0.05$.

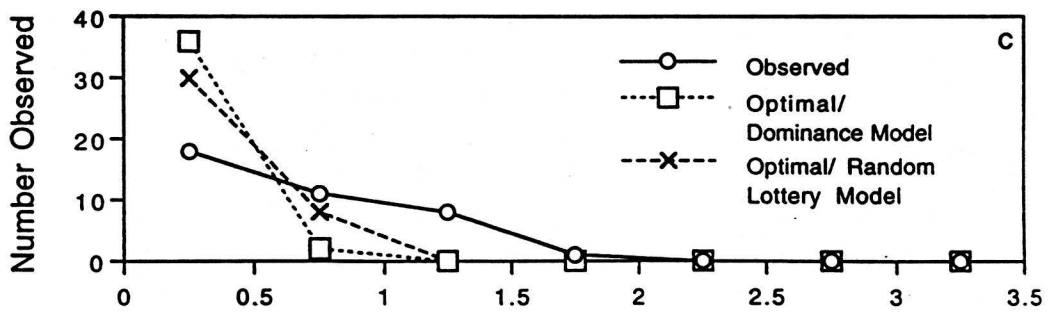
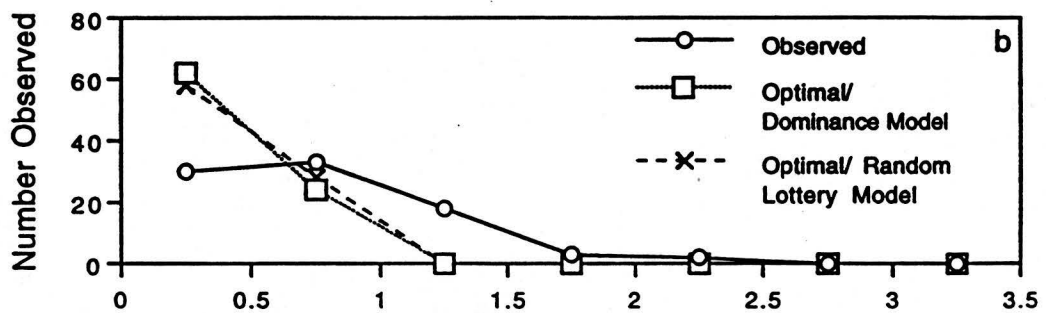
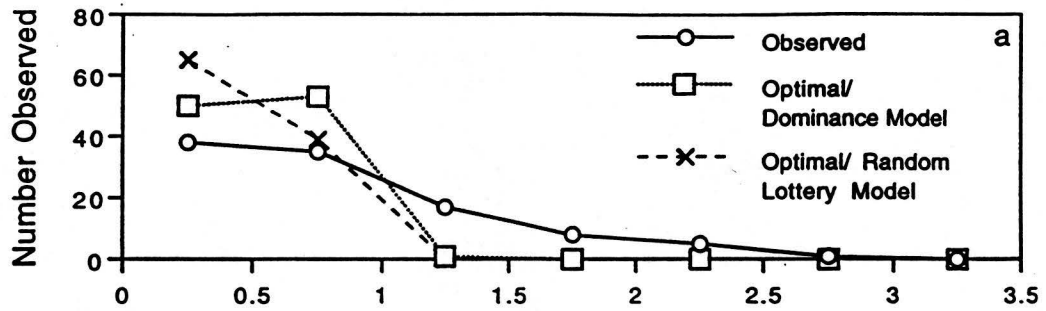
Size	Winter 1988	Winter 1989	Summer 1989	Winter 1990	SZ CL
Class 1	0.8724 **	0.4945 NS	0.2141 NS	0.4649 NS	0.8019 **
Class 2	0.6779 *	0.9792 **	0.8321 **	0.9791 **	0.9671 **
Class 3	0.4103 NS	0.7206 *	0.2045 NS	0.8299 **	0.7534 *
SEASON	0.7786 **	0.9568 **	0.7032 *	0.9031 **	0.9396 **

Table 3.10. Matrix of r^2 values for the Optimal/Random Lottery model for Reach 2 only. Model predictions and empirical data were placed into categories with increments of 0.5 BL/s. Values in the SEASON row and SIZE column are summary values for those variables. Value in the bottom right corner is the summary value for the model. The sample size of empirical observations contained in each of the above matrices can be found in Table 3.4. Symbols are *: $P \leq 0.05$; **: $P \leq 0.01$; NS: $P > 0.05$.

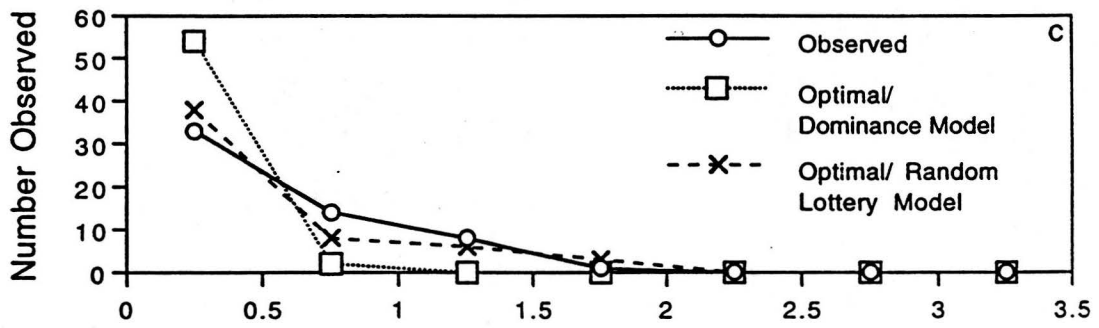
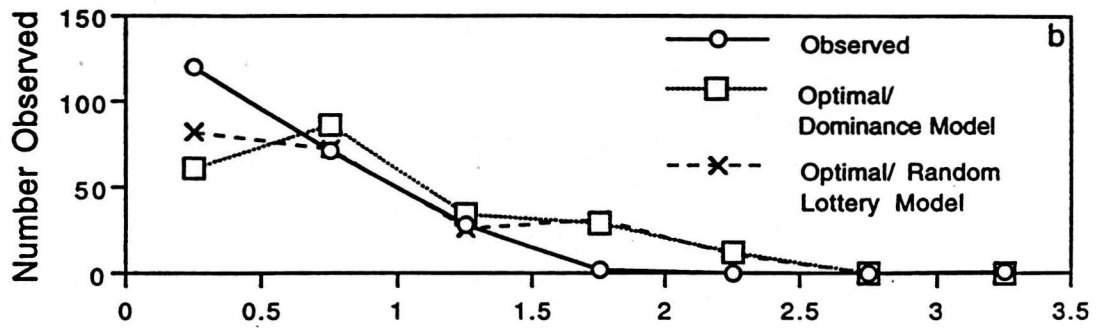
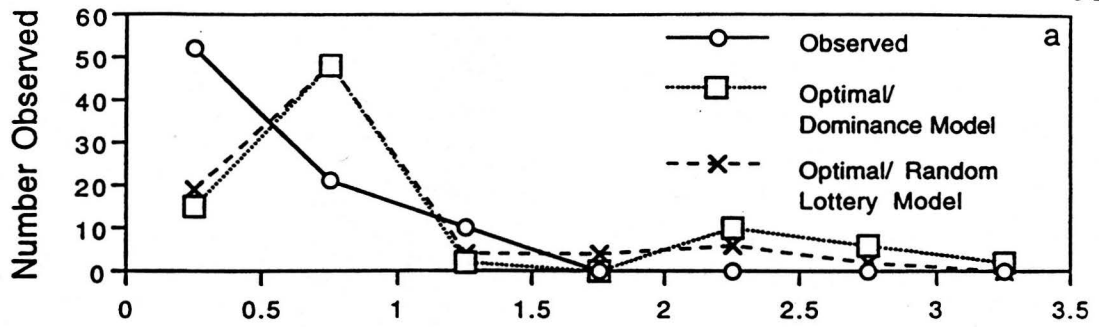
Size	Winter 1988	Winter 1989	Summer 1989	Winter 1990	SZ CL
Class 1	0.4550 NS	0.0214 NS	0.0720 NS	0.4543 NS	0.4203 NS
Class 2	0.4423 NS	0.3008 NS	0.0542 NS	0.6380 *	0.7793 **
Class 3	0.7850 **	0.5750 *	0.4358 NS	0.8920 **	0.9861 **
SEASON	0.5493 NS	0.3127 NS	0.0023 NS	0.7096 *	0.7712 **



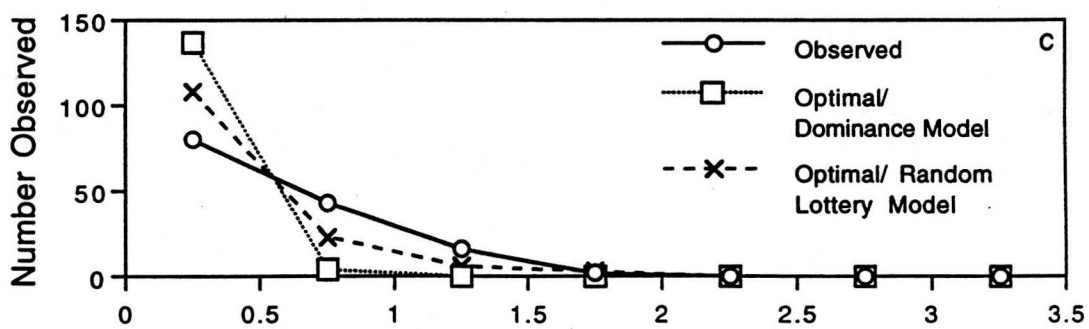
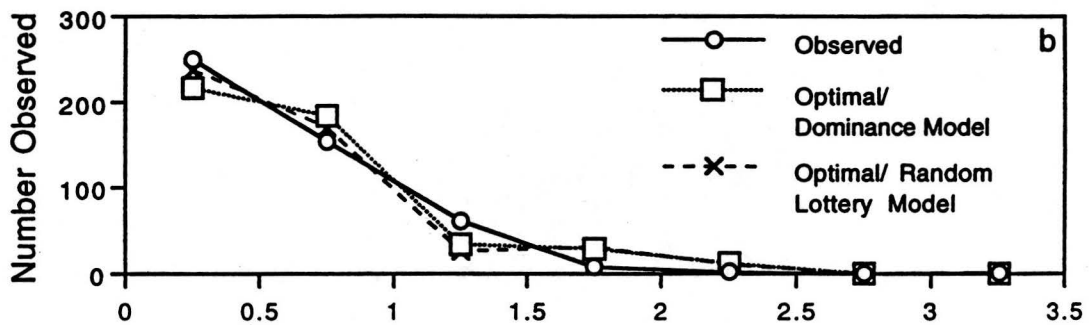
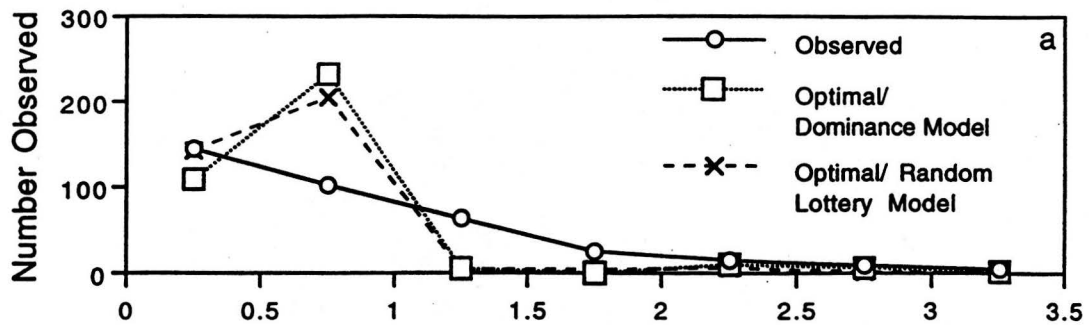




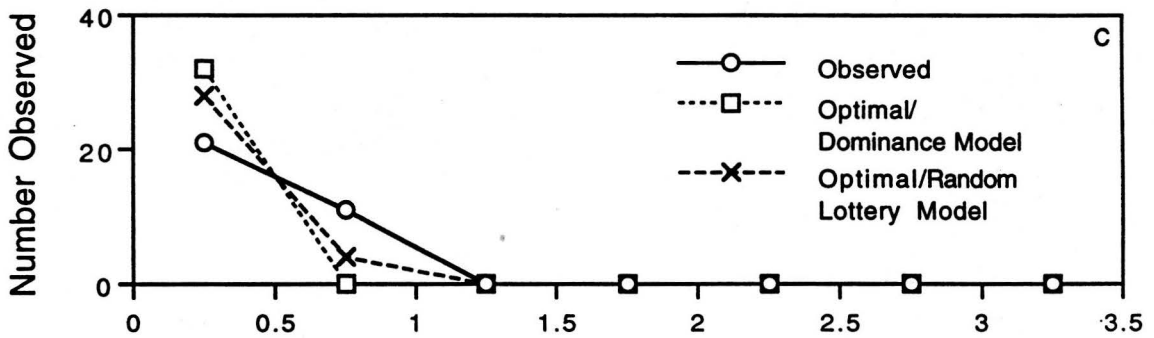
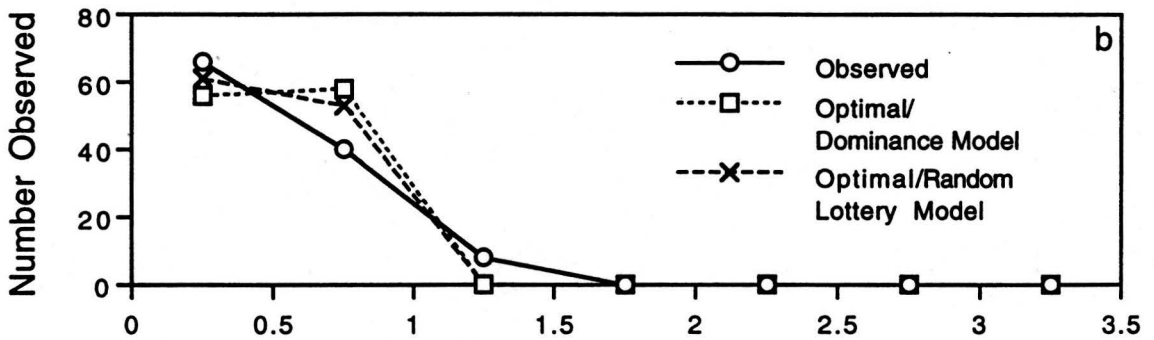
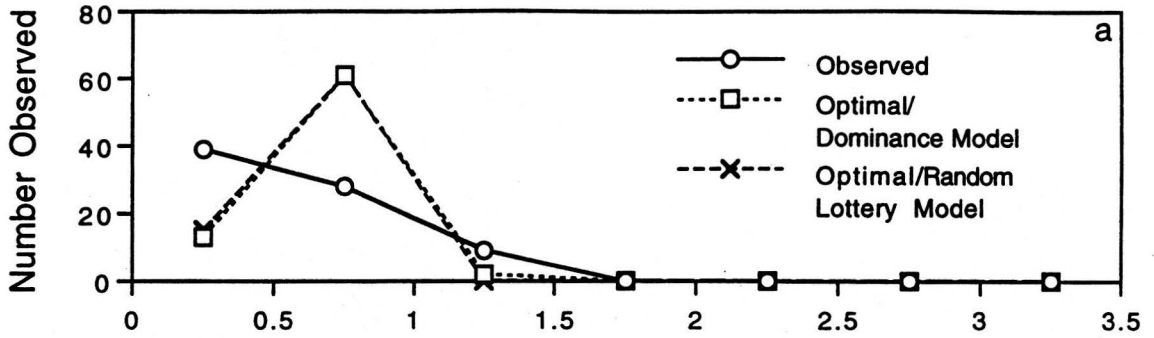
Focal Velocity (BL/s)



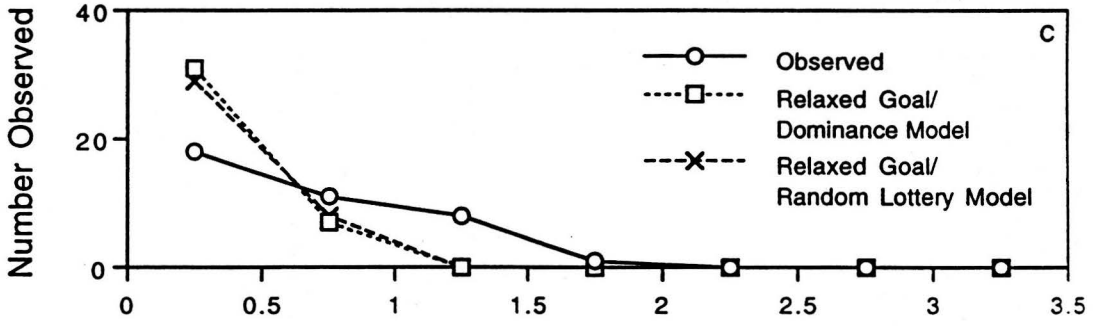
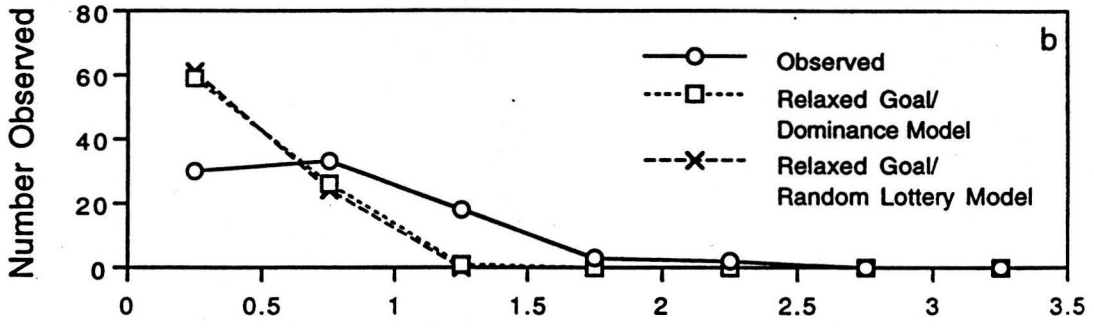
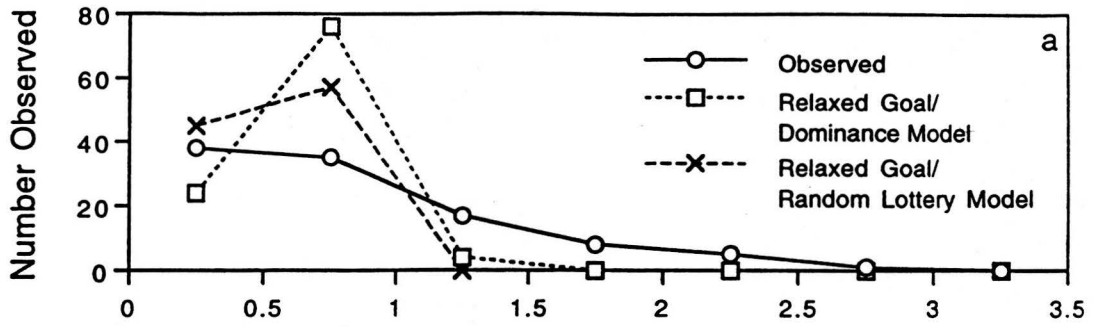
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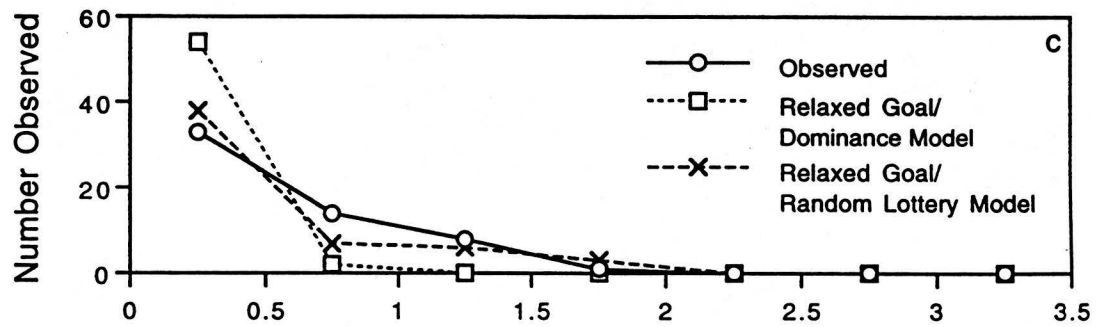
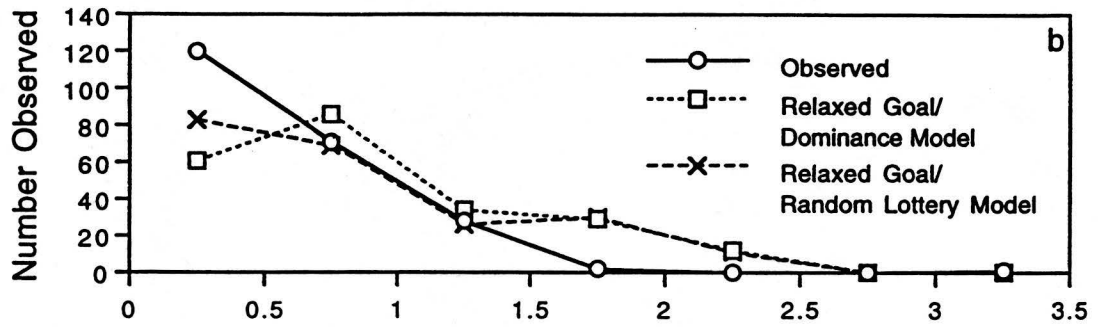
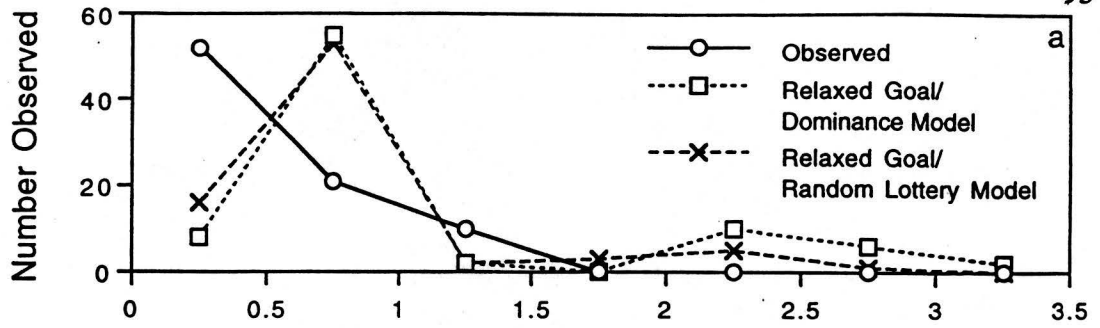


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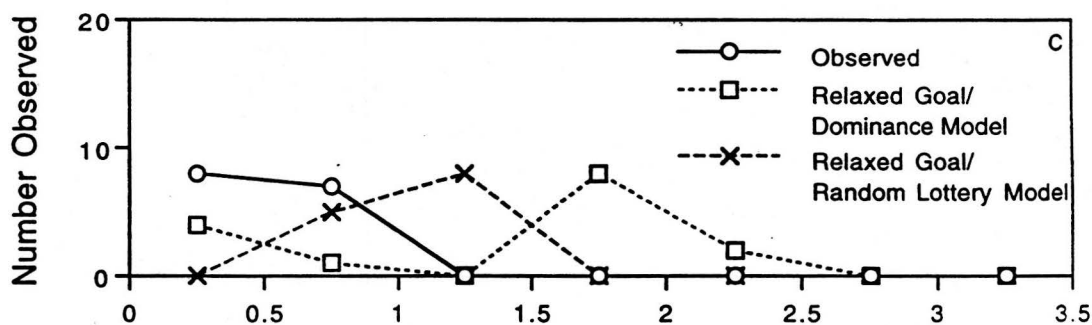
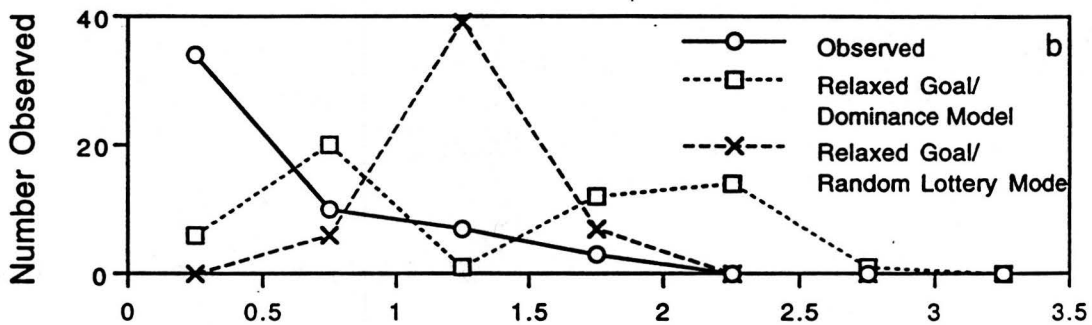
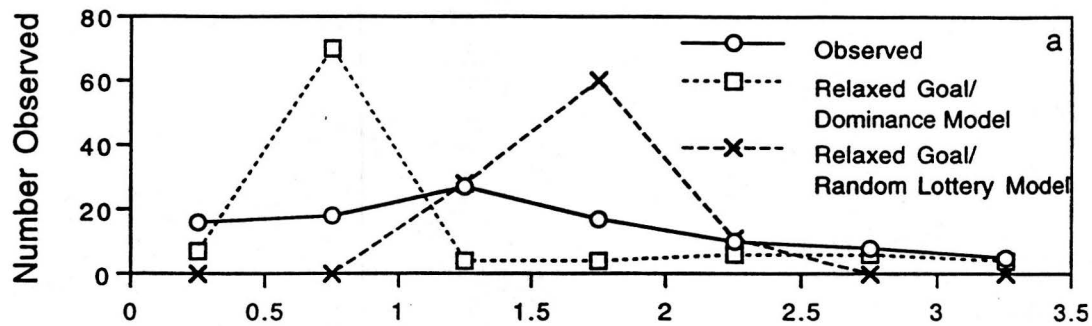


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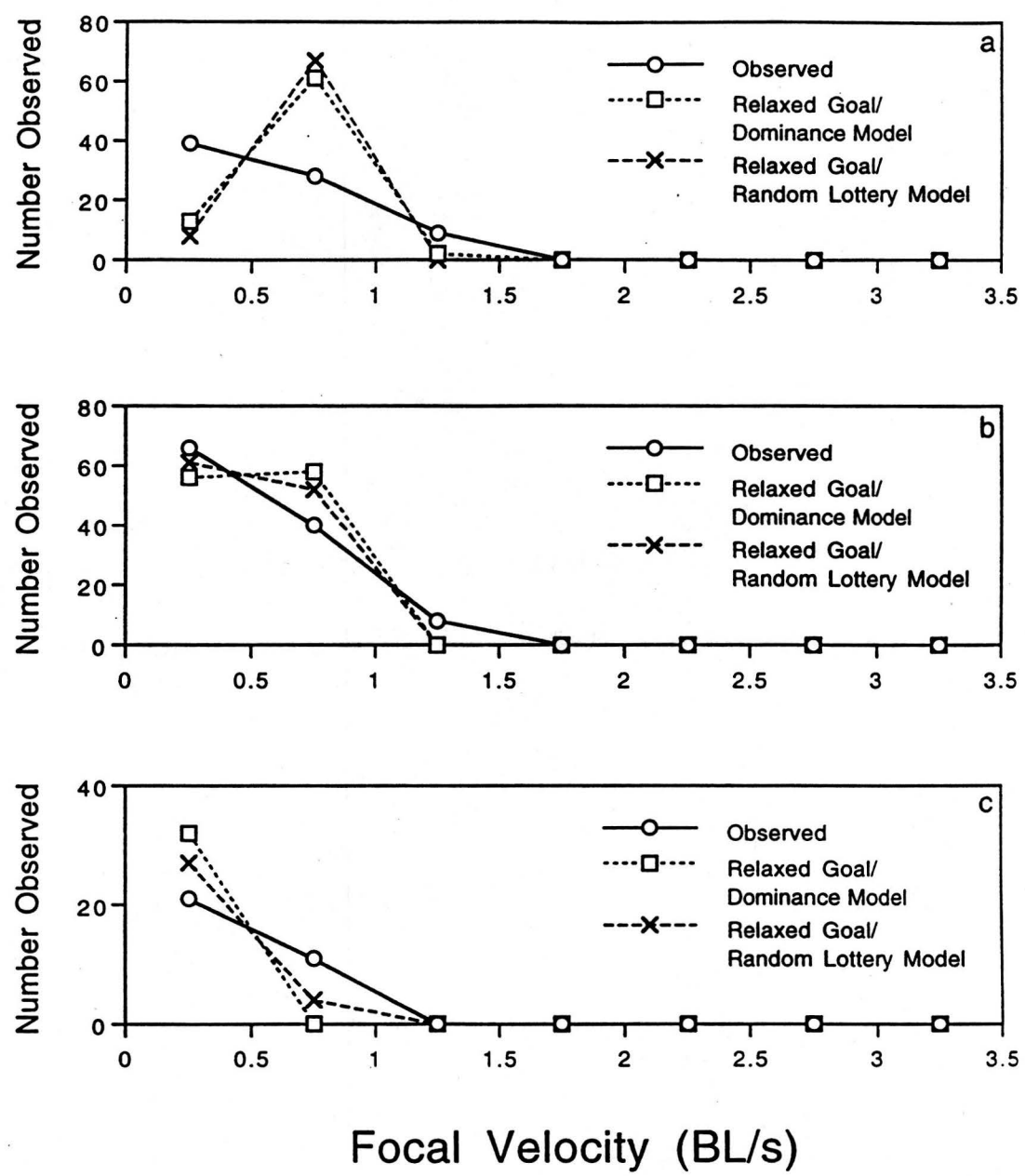


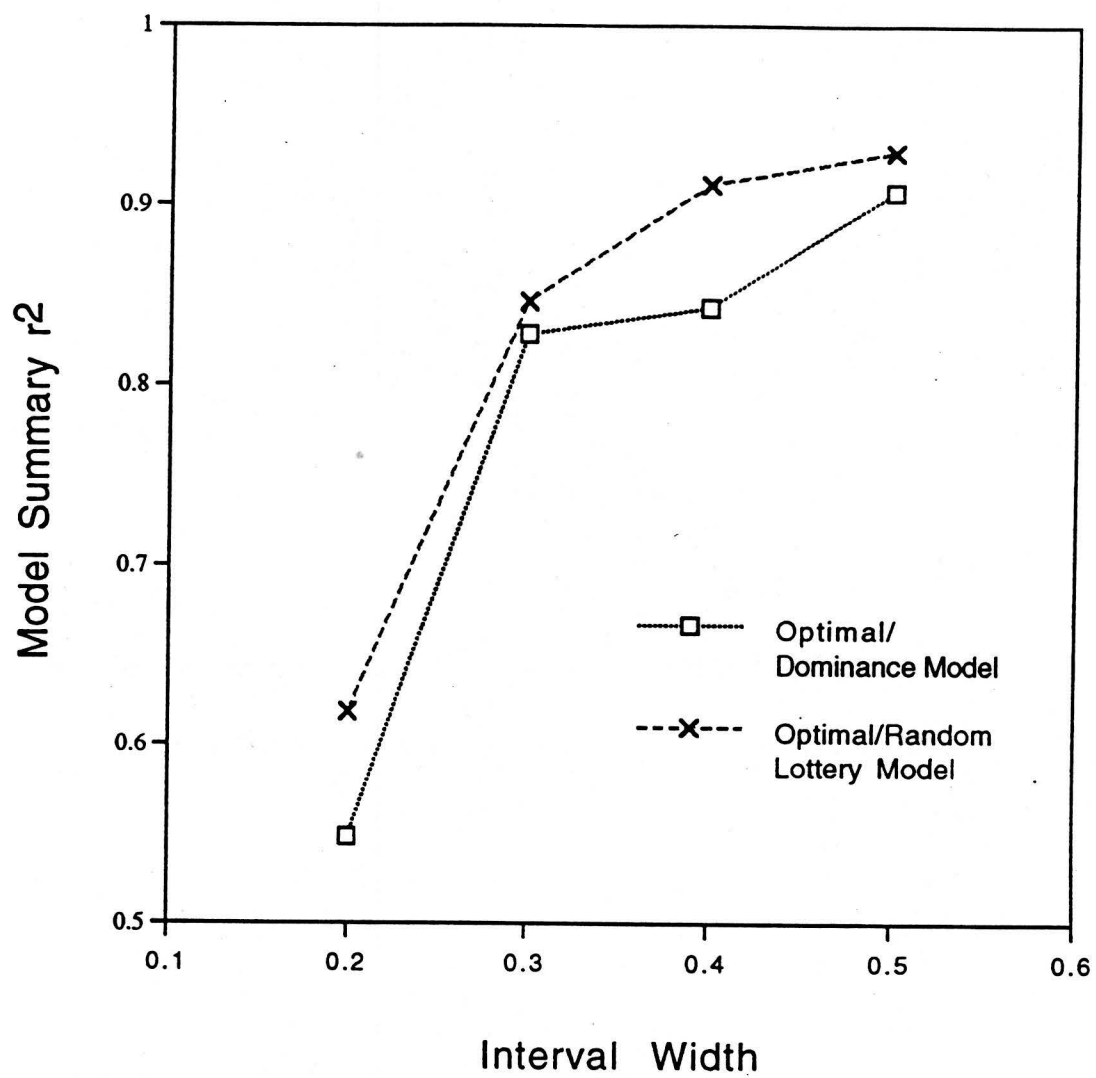


Focal Velocity (BL/s)

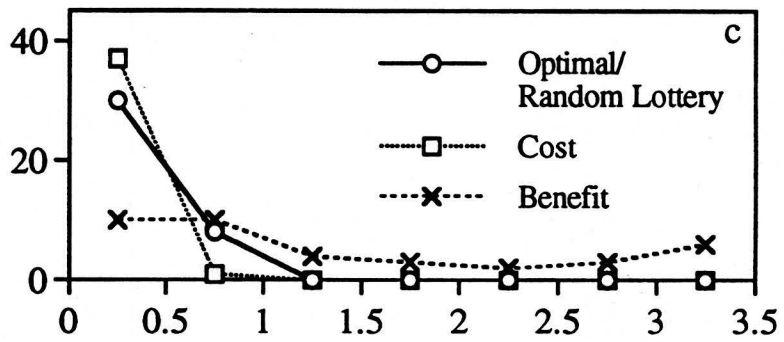
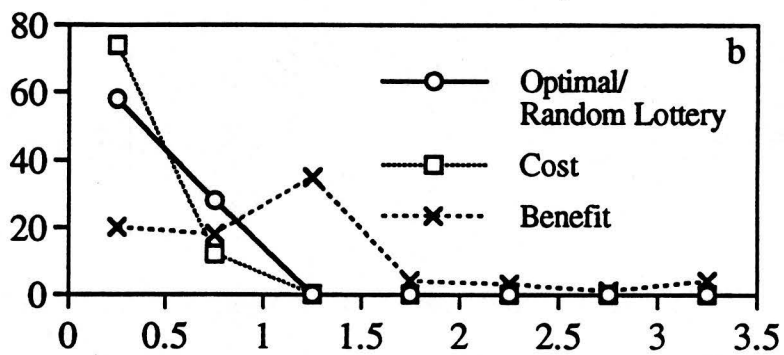
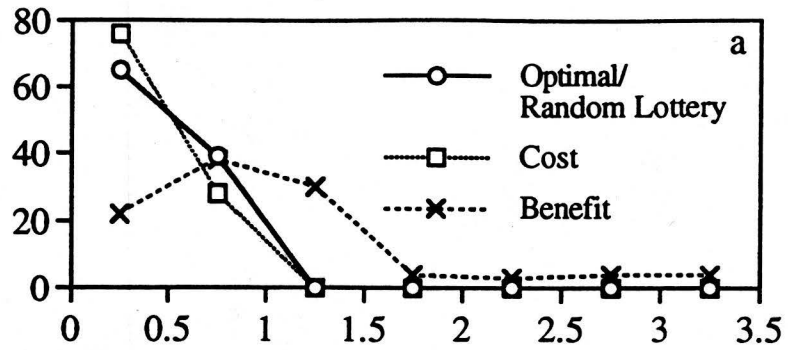


Focal Velocity (BL/s)

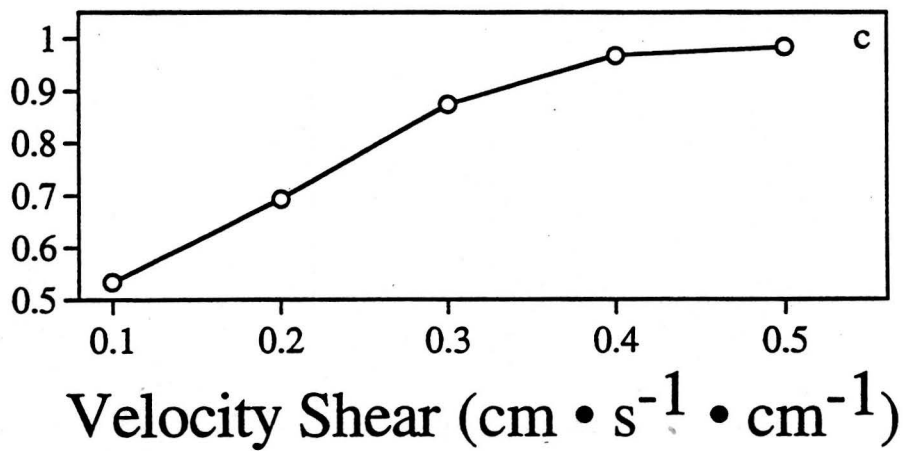
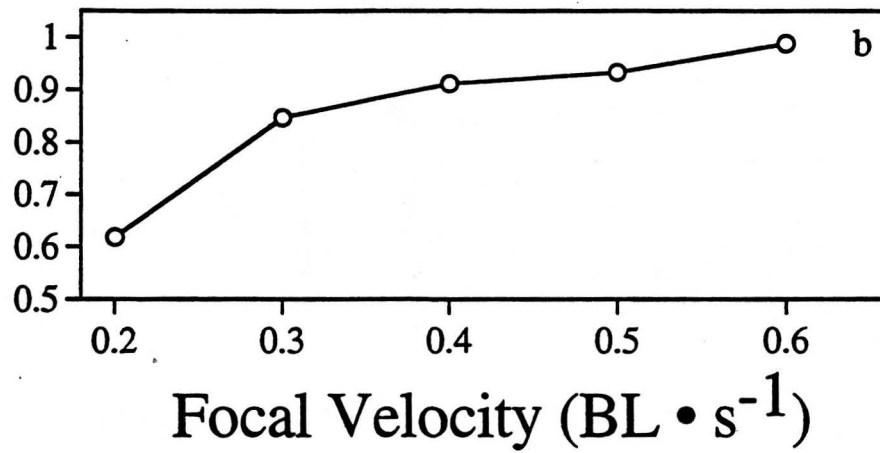
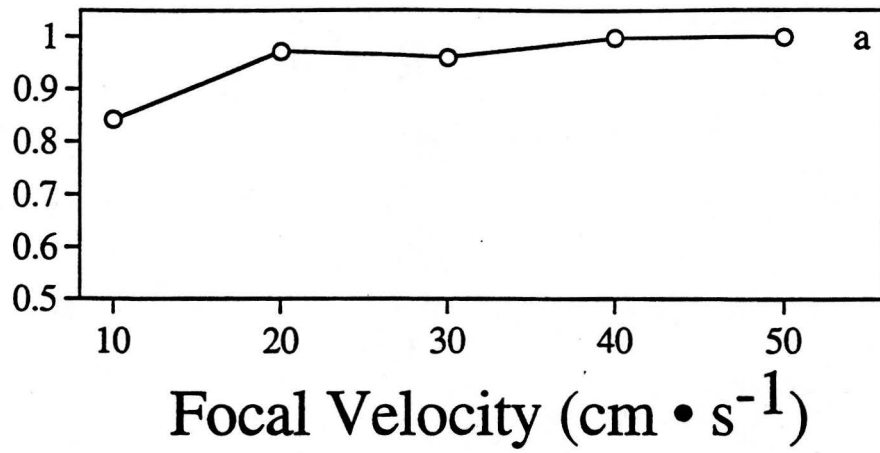




Number Observed



Focal Velocity (BL/s)

Summary r^2 

CHAPTER 4

WINTER MOVEMENTS OF RAINBOW TROUT IN THE GREEN RIVER,
UTAH BELOW FLAMING GORGE DAM

Abstract.--I evaluated the effects of fish size and discharge regime on winter movements of adult rainbow trout resident in the regulated Green River, UT. Movement was quantified along two scales with radio telemetered fish: 1) weekly observations generated estimates of distances moved at intervals greater than one d and 2) multiple observations of a fish in one d produced estimates of distances moved over hours. Body size had a weak influence on weekly movement but the power of the test was small ($1-\beta=0.34$). Body size also exhibited an influence on hourly movement. While the effect was statistically significant, I concluded the effect was equivocal biologically.

I found an unstable and higher mean discharge significantly reduced displacement (m) measured weekly ($F = 11.10, P = 0.0019$). In addition, an unstable discharge regime significantly reduced hourly movement rates (m/h) ($F = 5.90, P = 0.0273$). These results supported a habitat fragmentation theory: changes in discharge regime may isolate energetically advantageous positions and make movements between such positions more costly. I further hypothesized this would be more evident in smaller fish than larger fish because the results of Chapter 3 suggested that smaller fish habitat use is disproportionately influenced by discharge changes. The habitat fragmentation theory was supported by t-test

results. The rainbow trout most influenced by discharge changes were the smallest size group studied, ≤ 33.0 cm TL ($t = 2.3092$, $P = 0.0255$).

Regardless of the cause of movement suppression by unstable discharges, the management implications are clear. Productivity of the fishery will decrease, in winters with fluctuating discharge regimes, because fish will be less able to track energetically advantageous positions.

Introduction

Animal movements influence important ecological processes such as competition, predation, and population dynamics (Merriam et al. 1991). Individuals move to acquire food, find mates, and use refugia. Because these three primary resources fluctuate with the physical and biological environment, movement patterns may also reflect environmental changes. Therefore, movement may reflect the influence of disturbance on individuals and populations (Ims et al. 1993).

Movements of stream-resident salmonids occur along several spatial scales. Small movements, less than 100 body lengths, occur when fish relocate between feeding and resting positions, seek cover, change feeding positions, or capture food. These small movements are common (Edmundson et al. 1968; Heggenes et al. 1991) and until recently were thought to be the principal type of movement exhibited by stream-resident trout (Gowan et al. 1994).

Recently, movements on two larger spatial scales have been studied in detail. First, intermediate scale movements, hundreds of a fish's body length, occur when fish switch stream reaches or move to different macrohabitats (Armstrong et al. 1994; Young 1995). Second, large-scale movements, thousands of a fish's body length, occur when fish migrate to spawning areas or new river segments (Clapp et al. 1992; Meyers et al. 1992; Young 1994). These latter two scales encompass systematic directional movements from one stream reach to another.

Trout body size may influence the movement rate along one or more of these three scales. For example, Young (1994) found larger fish, ≥ 34.0 cm total length (TL), tended to move farther than smaller individuals. He suggested that different movement patterns for different sizes of fish implied that more than one movement strategy may exist.

In addition to trout size, disturbance, in the form of discharge change, may influence movement. Three pieces of evidence suggest that discharge fluctuation may increase movement.

First, dams can fragment stream habitat. Lusk (1995) found that 19 dams on the Dyje River watershed fragmented the river's various reaches. This hydrologic fragmentation resulted in disruptions in the fish community structure. If habitats are also fragmented by dams or dam discharges then distances between fragments should increase, fragment size should decline, and total habitat area should be decreased (Andrén and Delin 1994). Therefore, if individuals are to find

energetically advantageous positions, then the distance travelled may increase in response to fragmentation. Ims et al. (1993) have shown such movement increases in male capercaillie grouse, *Tetrao urogallus*, and some male root voles, *Microtus oeconomus* (but see Johannesen and Ims 1996).

Second, stream-resident juvenile coho (*Oncorhynchus kisutch*) and chinook (*O. tshawytscha*) salmon selected and moved to different positions in the stream when discharge was changed experimentally in Kloiya Creek, B.C. (Shirvell 1994).

Third, Chapter 3 suggested an unstable winter discharge regime made it more difficult for smaller rainbow trout (≤ 33.0 cm TL) to find and use preferred positions. If discharge changes alter the location of these preferred positions, then an unstable discharge regime could increase movements by smaller rainbow trout seeking preferred positions. Also, Chapter 3 suggested larger individuals (≥ 33.0 cm TL) found and used positions that were energetically optimal, regardless of discharge regime. The location of many of these optimal positions changed with discharge fluctuations in the Green River. Thus, changing discharge might require movements of larger fish seeking energetically optimal positions.

Due to habitat fragmentation research, Shirvell's (1994) observed movements associated with discharge change, and the results of Chapter 3, I hypothesized an unstable discharge regime would increase rainbow trout movement in the Green River. As an alternative to this hypothesis, I considered the

notion that habitat fragmentation might be manifested differently than that scenario discussed in the preceding paragraphs: consider the river as an assortment of positions comprising a two-dimensional matrix. Positions preferred by rainbow trout occur in the habitat matrix in noncontiguous clumps of varying sizes. The cost of movement between these clumps, C_m , might be relatively low when mean discharge is small or discharge fluctuates infrequently such as the winters of 1989 and 1990. When the discharge regime has a higher mean or fluctuates frequently (e.g., 1988), C_m could be higher. Consequently in 1988, rainbow trout may have been less likely to attempt movements because of increased costs. I would expect these cost increases to escalate faster for smaller individuals because discharge fluctuations in 1988 influenced rainbow trout on a continuum from strong to weak for Size Classes 1 to 3, including influences on focal velocity use and velocity shear use (see Chapter 3, Results). Therefore, my second hypothesis was that movement rate would decrease in the winter characterized by higher mean discharge and more fluctuations. In addition, this decrease in movement would be more conspicuous for rainbow trout ≤ 33 cm TL (Size Class 1).

I tested these two hypotheses by evaluating the effects of body size and discharge regime on winter movements. I radio-tracked the movements of 47 rainbow trout over three winters. Movements were monitored weekly and hourly. In contrast to my first hypothesis, an unstable discharge regime (1988, Figure 3.1) significantly reduced weekly movements compared to a stable discharge regime. In

addition, the unstable discharge regime significantly reduced hourly movement rates (m/h) of all size groups. These results and others supported the hypothesis that movement between preferred habitat positions might have become significantly more costly for rainbow trout ≤ 33.0 cm TL in winters exhibiting an unstable discharge regime. My results also indicated that movement rates were weakly influenced by body size. Individuals larger than 33.0 cm TL tended to exhibit larger hourly movements than smaller fish. The largest individuals > 43.2 cm TL (Size Class 3) moved further than either Size Class 1 or 2 fish on a weekly basis but my data were unable to distinguish whether the difference was significant statistically or biologically.

Methods

The research reported in this chapter was conducted completely within three winter field seasons (1 January to 15 March: 1988, 1989, and 1990). Discharge regime changed between these 3 years. Mean discharge was smaller in 1989 and 1990 than in 1988. Also, discharge fluctuations were extremely uncommon in 1989 and 1990 but were frequent in 1988 (Figure 3.1). Water temperature did not vary between winters. From 1 January to 15 March mean daily temperature was 4°C.

Transmitter Implanting

During each winter, I implanted one group of fish between 1 December

and 11 December and began tracking this group of fish on 2 January. The second group of fish were implanted between 6 January and 16 January and tracking was initiated on 6 February. The delay between implantation and tracking allowed rainbow trout at least 3 weeks before any telemetry observations were recorded.

In three winters, I located 47 of the 77 implanted rainbow trout two or more times (61% efficiency). Of these 47, 23 of the tracked fish had been stocked 7-8 months previously and were ≤ 33.0 cm TL (Size Class 1), 10 fish had been stocked 19-20 months previously and were between 33.0 and 43.2 cm TL (Size Class 2), and 15 fish had been stocked more than 32 months previously and were > 43.2 cm TL (Size Class 3).

The entire implantation procedure required 3 d to complete. On day 1, I captured 64 rainbow trout by electroshocking and angling. Each rainbow trout received a uniquely coded spaghetti tag and the exact site of capture was noted. The fish were held overnight in a holding pen (1 m X 1 m X 2 m) in an eddy. On day 2, rainbow trout were anesthetized in a solution of tricaine methane sulfonate (660 mg/L), weighed, and measured. A transmitter (27 X 13 X 15 mm; Custom Telemetry, Athens, GA) was inserted into the body cavity through a 2-cm incision ventrolateral to the ribcage. All transmitters were checked at this time to see they were operating properly. The transmitters broadcasted on a frequency between 30 and 31 MHz, had a range up to 40 m, and a life expectancy of 45 to 60 d (personal communication, D. Stoneburner, Custom Telemetry). The rainbow trout were

again held overnight in the same eddy pen. On day 3, rainbow trout were released at their capture site.

Fish Tracking

I determined fish positions by triangulation from shore with a directional antenna (loop antenna, Advanced Telemetry Systems, Isanti, MN). Preliminary trials indicated this triangulation method allowed fish location to within 1 m in water less than 3 m deep and within 3 m in water 3 to 7 m in depth. The fish's position was marked on maps traced from aerial photos. Then I digitized the maps, made ground truth measurements of objects visible in the aerial photographs, and determined the scale conversion of the map to the river. I then used this scale conversion to calculate the distance (m) between fish positions.

Fish movements were monitored in two ways. First, I attempted to locate all the implanted fish each week. This "weekly observation" data set resulted from fish that were located at intervals greater than 1 d. I computed displacement (m) by summing the distances moved by a single fish and dividing by the number of measurements. I computed movement rate (m/d) by summing the distances moved by a single fish and dividing by the total number of d (usually 30-65) I had tracked that fish.

I also monitored movement on a second, smaller, temporal scale. The "hourly observation" data set resulted from observations that were made over a period of less than 1 d for a "focal" fish. Each week I chose two focal fish on

which to concentrate my tracking efforts. Fish were tracked on 2 d during the week they were focal animals but the frequency of location varied between winters. In 1988, I attempted to locate these focal fish twice: once during darkness and once during daylight hours. In 1989 and 1990, I located the focal fish every 3 h for two or more 24-h periods. I computed hourly displacement (m) by summing the distances moved by a single fish and dividing by the number of measurements. I computed movement rate (m/h) by summing the distances moved by a single fish and dividing by the total number of hours I had tracked that fish.

Statistical Design

I completed four two-way analyses of variance (ANOVA). The dependent variable for the first two of these ANOVAs was \log_{10} transformed displacement (m), measured weekly and hourly, and for the second two ANOVAs, \log_{10} transformed movement rate in m/d and m/h. Log transforms were required to normalize these data. All other assumptions of ANOVA were met. For each ANOVA, size class and discharge regime were the independent variables. The three size groups were allocated according to Table 3.1. Discharge regime had two states: unstable with a higher mean (winter, 1988) and stable with a lower mean (winters of 1989 and 1990). If I found significant differences in the transformed data through ANOVA, I performed a Ryan-Einot-Gabriel-Welsch multiple range test (MRT) to determine groups that were similar.

The one-tailed hypothesis that an unstable discharge regime decreased

rainbow trout movement rate was analyzed by t-test. Log transformed movement rates (\log_{10} m/d and \log_{10} m/h) in the unstable year (1988) were tested against movements in stable years (1989 and 1990) combined. I completed a t-test for each size class. This analysis differed from the two-way ANOVAs by its directional nature, specificity for the fragmentation hypothesis, and allowed me to determine if a single size group was being impacted even if the two-way ANOVA was not significant. All analyses described, ANOVAs and t-tests, were completed using the Statistical Analysis System (SAS Institute [1988]: Cary, NC, USA).

Results

The majority of Green River rainbow trout do not move systematically upstream or downstream during the winter (Table 4.1). The percentage of rainbow trout that did move systematically, 9% of individuals \leq 33.0 cm TL, 0% of fish 33.0 to 43.2 cm TL, and 20% of fish $>$ 43.2 cm TL had no strong size-dependent pattern. However, the small number of fish that moved systematically (n=5) precluded statistical analysis.

Weekly movement observations indicated that winter movements were influenced by discharge regime (Figure 4.1a). Analysis of variance indicated that weekly displacements (m), were significantly lower under a varying discharge regime compared to a stable regime (Table 4.2). However, weekly movement rate (m/d) did not change significantly with changing discharge. Body size had a

statistically weak influence on weekly movement rate ($P = 0.08$, Table 4.3). The multiple range test suggested Size Classes 1 and 3 and Size Classes 1 and 2 grouped together while Size Classes 2 and 3 did not. Size Classes ranked by means were $2 < 1 < 3$ (Figure 4.2a).

Observations of focal fish produced a measure of routine movements during winter. As expected, fish moved less when measured at intervals less than 24 h than when measured at weekly intervals (Figures 4.1b and 4.2b).

Hourly displacement varied significantly with body size (Table 4.2). The multiple range test suggested Size Classes 1 and 3 and Size Classes 2 and 3 grouped together, with the second group exhibiting larger means, while Size Classes 1 and 2 did not group together.

Hourly movement rate was significantly lower in winters with an unstable discharge regime (Table 4.3). This result was striking when viewing the means and standard errors (Figure 4.2b). The pattern of hourly movement rates was similar to patterns of weekly displacement and suggested that discharge regime was an important influence on winter movement.

Discharge regime also influenced the distribution of observed movements. For all sizes of fish, an unstable discharge regime (1988) skewed the distribution of weekly displacements to the left compared to a stable regime (Figure 4.3). Furthermore, an unstable discharge regime skewed the distribution of hourly movements to the left for Size Class 1 (Figure 4.4). Sufficient data did not exist to

plot histograms for diel movements of Size Classes 2 and 3.

I investigated one possible mechanism by which discharge regime might influence movement. The mechanism, habitat fragmentation, might occur because a fluctuating and higher mean discharge might increase movement cost between preferred positions. Increased movement costs could cause fewer movements. Therefore, I hypothesized that movement rate would decrease in the winter characterized by higher mean discharge and more fluctuations. In addition, in Chapter 3 I found discharge changes have a disproportionately greater effect on small fish. I expected movement decreases would be more conspicuous for smaller individuals (≤ 33 cm TL). One-sided t-tests for rainbow trout > 33 cm TL (Size Classes 1 and 2) showed no significant change in movement rates (m/d or m/h) in an unstable discharge regime compared to a stable one (Table 4.4). However, diel movement rate of rainbow trout ≤ 33.0 cm TL was significantly smaller in the winter of 1988. This result supports the hypothesis that movement cost may have increased in a biologically important manner for small fish. Movement rate decreased significantly only at the diel scale. Weekly movements showed no such decrease. Thus, the effect was scale dependent.

Discussion

Weekly Observations

Discharge regime influenced the winter movements of rainbow trout. The

weekly displacement data showed, when discharges were unstable (1988), all size classes of fish moved significantly less than when discharges were stable (1989 and 1990). This metric (displacement) detrended the weekly observations from an arbitrary weekly time scale. These results suggested fish tend to move farther from their previous location under a stable discharge regime compared to unstable regardless of how long it has been since the last location. The significance of discharge regime is especially interesting because for the displacement data the time between locations could add variation that is unrelated to movements on smaller time scales.

Gowan et al. (1994) argue that movements by resident-stream salmonids may not be as limited to small time and spatial scales as previously thought. In addition, Young (1994) has argued that more than one movement strategy may exist. In support of Young's contention, Pert and Erman (1994) found that rainbow trout can exhibit two patterns of movement in regulated streams. My research described here was not designed to test Gowan et al. and Young's contentions. However, I found a distinct minority of the population that moved systematically in one direction. The individuals exhibiting these movements could represent a second movement strategy that occurred at low frequency in the population.

Unlike the rare systematic migration during winter, many salmonids sometimes exhibit a seasonal shift between habitats. Examples of such seasonal

shift in macrohabitat use and the movement associated with it have been described in Arctic grayling (West et al. 1992), brown trout (Clapp et al. 1990), and cutthroat trout (Brown and MacKay 1995). Similarly, Englund (1991) showed a consistent trend by many rainbow and cutthroat trout (*Oncorhynchus clarki*) to move into and use Green River riffles in spring. These fish then stayed in these faster macrohabitats at least until October before moving to lower velocity macrohabitats such as eddies (Englund 1991). While I did not study these seasonal movements, it is important to note that they occur, to understand the movement patterns of Green River rainbow trout. The movement rates I observed in the winter were smaller than the movements required for the seasonal shifts in macrohabitat Englund observed. Therefore, Gowan et al. (1994) may be correct that resident-stream salmonids are more mobile than previously thought. However, the majority of rainbow trout in the Green River do not typically exhibit movements greater than 50 m during the winter.

The various movement rates exhibited by individuals, the differences in movement with season and species (Bjornn and Mallet 1964), and movement differences between fish in different streams (Young 1994) demonstrate that movement is a complicated response to a complex environment. Variation in individuals, life stages, and life history strategies can be overlooked. We will be best prepared to recognize the diversity in movement patterns if we think of movement as a highly plastic trait subject to change from physical and biological

characteristics of each individual fish's environment.

For example, in this study, variation in weekly movement rate was evidenced by the high coefficients of variation (V^* , Sokal and Rohlf [1981], p. 59) for the log transformed means of movement rate (m/d) for the three Size Classes (all years combined): 1) 33.06%, 2) 43.61%, and 3) 31.81%. In part, this variability may explain why the effect of body size on weekly movement rate (m/d) did not appear greater. Because the power of the test was low ($1-\beta=0.34$; Zar 1984), I concluded that this test was indecisive. Therefore, body size may influence weekly movement rate but my data would not allow me to discriminate the effect.

Hourly Observations

Analysis of movement at this shorter time scale produced conflicting results. Displacement (m) data suggested body size alone significantly influences movement. However, the movement rate (m/h) data suggested discharge regime alone significantly influenced movement. The multiple range test for the displacement data grouped Size Classes 1 and 3 and Size Classes 2 and 3 together but not Size Classes 1 and 2. Suppose body size has a significant impact on hourly movement, measured by displacement. The MRT suggests Size Class 1 and 3 are not statistically different from each other. But the data show that size 2 fish move significantly more than size 1 fish. Size Class 1 individuals may be unable to track optimal positions because of limited information about the system (suggested by

Chapter 3). Size Class 2 individuals have more information yet are subordinate to Size Class 3 fish. Therefore, Size Class 2 fish may move to and use energetically advantageous positions, as Chapter 3 suggests, but move farther than Size Class 3 fish to find them. Size Class 3 fish, presumably the most dominant fish in the system and with more information than other fish, move to and use positions that are energetically advantageous with smaller movements than those required of size 2 individuals. This argument seems plausible but unconvincing because the Dominance Hierarchy models in Chapter 3 performed more poorly than the Random Lottery models. Therefore, I concluded that body size may influence short-term displacement but the effect was equivocal.

A change in data collection methodology might have further obscured the results. In 1988, fish were located twice per day on 2 d of the same week. In 1989 and 1990, fish were located approximately every 3 h for 2 d of the same week. This disparity could result in inflated displacement values in the winter of 1988. Inflated displacement values in the unstable winter could explain why unstable discharge did not appear to suppress displacement. Due to these concerns, I had more confidence in the hourly movement rate data than the displacement data due. The change in methodology does not preclude comparisons between years. Consider, if we leave six observations out of the eight taken for each focal fish in one d in 1989-90, we retain only one observation during daylight and one during darkness. The resulting data set would have been collected identically to 1988.

Therefore, adding those six observations in each d only increases the information contained in our estimate of the mean movement rate. Additional information should only improve our ability to distinguish between means in 1988 and 1989-90 combined.

An unstable discharge regime suppressed movement rate (m/h) of all size classes of Green River rainbow trout. Yet, the decrease in movement rate was significant for only the smallest size group of fish ($t = 2.3092$; $P = 0.0255$). If this movement rate decrease was caused by increased costs of movement with discharge change, then discharge change may have functionally fragmented the habitat for these small rainbow trout. However, the lack of a significant decrease in movement rate on a weekly time scale suggested this fragmentation may have taken place only at smaller scales. In spite of these results, other hypotheses, besides fragmentation, might explain this same trend in the data.

The analysis of rainbow trout movement on small time scales must be approached with caution. Hourly displacement and hourly movement rate suggested different independent variables influenced movement in a statistically significant manner. These conflicting results suggest we should be careful what metrics and scales we choose when working with movement. I think such scale comparisons might go far to reconcile seemingly contradictory findings in recent studies (e.g., Heggenes et al. 1991; Young 1994). Young found 69% of all brown trout he tracked had home ranges greater than 50 m. In contrast, Heggenes et al.

have suggested that less than 20% of the cutthroat trout they studied ever moved more than 50 m. Young worked with individuals 25-53 cm TL and tracked fish over many kilometers. Heggenes et al. studied individuals 9-27 cm TL over a study reach less than 1 km in length. Such disparities may explain much of the variability in the views of biologists toward salmonid movements. In the Green River, the discharge regime influenced movement at different temporal scales; perhaps other independent variables produce different patterns when viewed at different scales. Careful consideration should be paid to scale problems in the design of salmonid movement studies.

The results of this study support the idea that movement patterns were, in part, influenced by habitat fragmentation due to a fluctuating Flaming Gorge Dam discharge regime. My hypothesis that fragmentation, caused by an unstable discharge regime, would decrease movement rates may not have been tested adequately. A more realistic test could be developed by a dynamic model of preferred habitat availability. Then computer-generated experimental manipulations of discharge could predict the changes in movement rates expected for each size class if fragmentation of preferred habitat does occur. Such a dynamic model was beyond the scope of the current research.

Management Implications

Discharge fluctuations or a higher mean discharge in the winter of 1988 decreased movement of rainbow trout compared to the winters of 1989-90. These results implied fish were less able to track energetically advantageous positions. Therefore, productivity of the fishery could decrease under fluctuating, higher mean discharge regimes in winter because the growth rate of rainbow trout may be retarded compared to a more stable discharge regime.

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Table 4.1.--Summary of rainbow trout biotelemetry observations. "Number of Positions" is the number of points at which the fish was found. "Number of Contacts" is the total number of times the fish was located. "DEAD" means a visual confirmation was made of the deceased fish.

Size Class	Number of positions	Number of contacts	Duration of contact(d)	Largest movement(m)	Systematic directional movement
<u>Unstable Winter (1988)</u>					
1	7	8	21	15	No
1	10	11	35	25	No
1	2	4	14	29	No
1	4	5	19	34	No
1	9	11	40	35	No
1	14	21	63	55	No
1	8	9	28	63	No
1	2	3	10	91	No
1	8	10	31	142	No
1	10	22	62	277	No
1	12	21	62	354	Yes
Dead	-	-	-	-	-
Dead	-	-	-	-	-
2	5	8	35	6	No
2	3	3	33	21	No
2	8	10	33	63	No
2	15	18	61	88	No
2	6	6	31	262	No
2	18	26	62	312	No
3	3	4	9	14	No
3	8	11	35	44	No
3	8	11	35	58	No
3	6	9	35	98	No
3	11	15	48	114	Yes
3	7	9	31	149	No
3	2	2	14	150	No
3	12	14	35	295	No

Table 4.1. Cont.

Size Class	Number of positions	Number of contacts	Duration of contact(d)	Largest movement(m)	Systematic directional movement
<u>Stable Winter (1989)</u>					
1	6	6	4	4	No
1	2	2	8	31	No
1	7	11	8	134	No
1	19	23	67	875	Yes
2	2	2	8	8	No
2	10	11	55	65	No
3	8	8	4	64	No
3	7	10	43	72	No
<u>Stable Winter (1990)</u>					
1	3	4	31	16	No
1	2	2	15	34	No
1	11	12	21	54	No
1	5	6	57	92	No
1	3	3	15	108	No
1	5	8	58	133	No
1	4	6	51	586	No
1	5	5	50	1743	No
2	5	8	29	33	No
2	4	4	50	60	No
3	14	15	52	30	No
3	7	7	65	124	No
3	5	5	58	315	Yes
3	6	6	51	523	No
3	8	8	65	1257	Yes

Table 4.2.—Analysis of variance tables for log transformed displacement measured weekly and hourly.

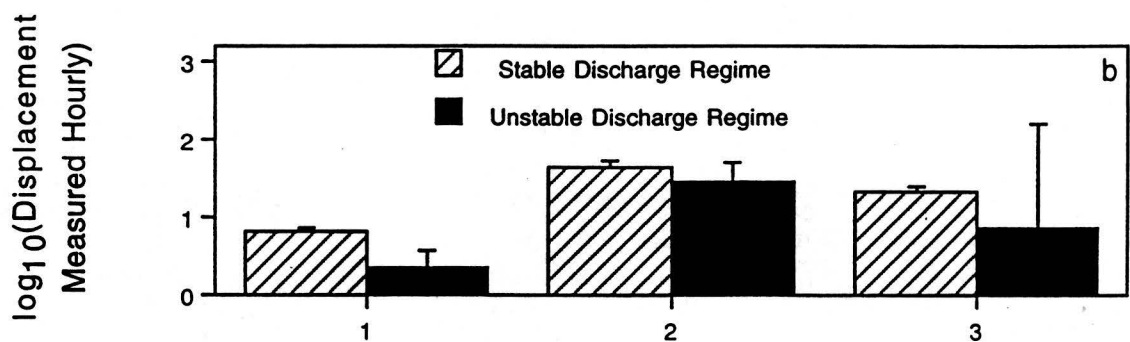
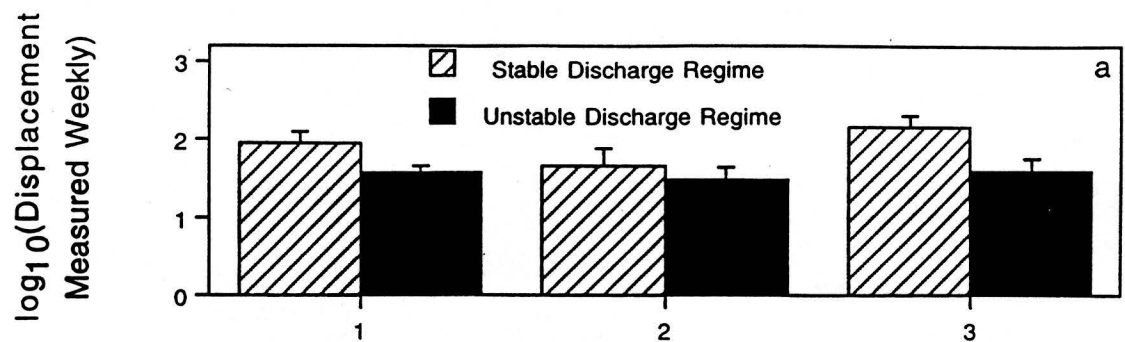
Source	df	Sum of squares	Mean square	F value	<i>P</i>
<u>Displacement (log₁₀ Weekly observations (m))</u>					
Size Class	2	0.5709	0.2854	1.78	0.1815
Discharge regime	1	1.7786	1.7786	11.10	0.0019
Size Class X					
Discharge regime	2	0.2269	0.1134	0.71	0.4987
Error	40	6.4097	0.1602		
<u>Displacement (log₁₀ Hourly observations (m))</u>					
Size Class	2	3.1335	1.5668	4.10	0.0366
Discharge regime	1	0.9377	0.9377	2.45	0.1369
Size Class X					
Discharge regime	2	0.0658	0.0329	0.09	0.9179
Error	16	6.1182	0.3824		

Table 4.3.—Analysis of variance tables for log transformed movement rate measured in m/d and m/h.

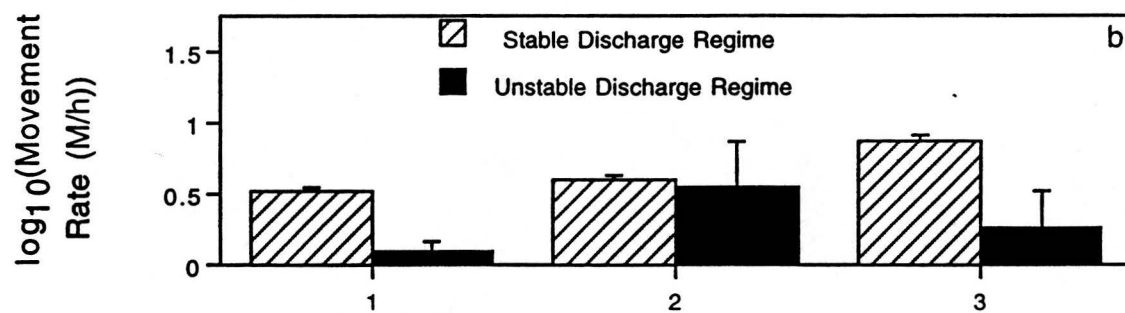
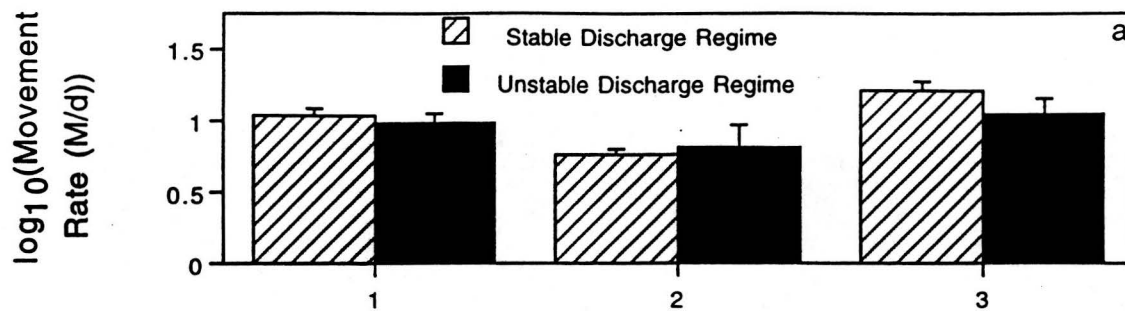
Source	df	Sum of squares	Mean square	F value	P
<u>Movement rate (log₁₀ m/d)</u>					
Size Class	2	0.6463	0.3232	2.69	0.0802
Discharge regime	1	0.0529	0.0529	0.44	0.5109
Size Class X					
Discharge regime	2	0.0697	0.0348	0.29	0.7498
Error	40	4.8060	0.1202		
<u>Movement rate (log₁₀ m/h)</u>					
Size Class	2	0.4132	0.2066	1.44	0.2657
Discharge regime	1	0.8455	0.8455	5.90	0.0273
Size Class X					
Discharge regime	2	0.1780	0.0890	0.62	0.5500
Error	16	2.933	0.1433		

Table 4.4.--Rainbow trout movement rate means and t-tests of those means. "P" is the one-sided probability of acquiring a value greater than the value of the reported t value for the hypothesis $H_1: \mu_{\text{stable}} > \mu_{\text{unstable}}$.

Size range	Size class	Unstable discharge regime mean	Stable discharge regime mean	t value	P value
<u>Movement rate (\log_{10} m/d)</u>					
≤ 33.0 cm TL	1	0.9815	1.0350	0.3535	0.3646
33.0-43.2 cm TL	2	0.8161	0.7660	-0.2169	0.5831
>43.2 cm TL	3	1.0467	1.2117	0.9004	0.1921
<u>Movement rate (\log_{10} m/h)</u>					
≤ 33.0 cm TL	1	0.0981	0.5198	2.3092	0.0255
33.0-43.2 cm TL	2	0.5482	0.5966	0.1172	0.4587
>43.2 cm TL	3	0.2593	0.8693	1.4899	0.1165

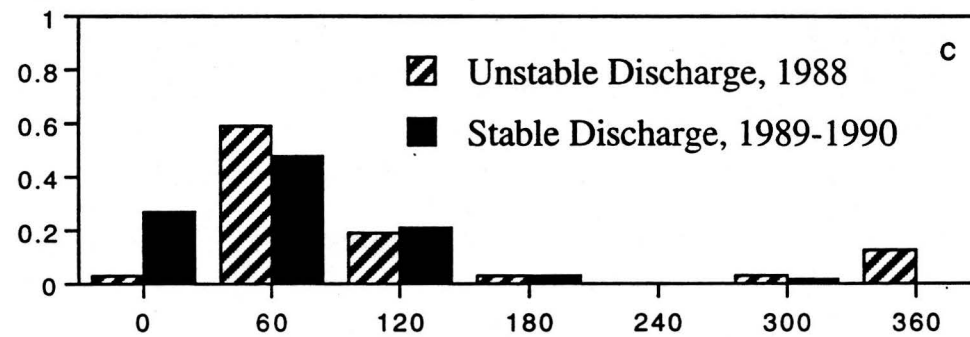
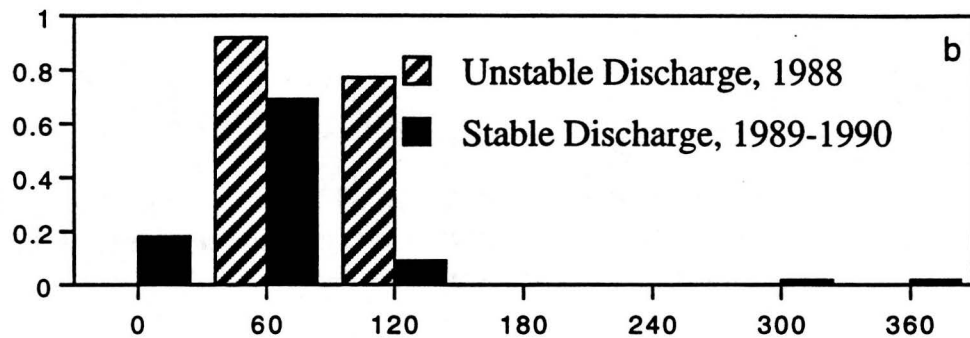
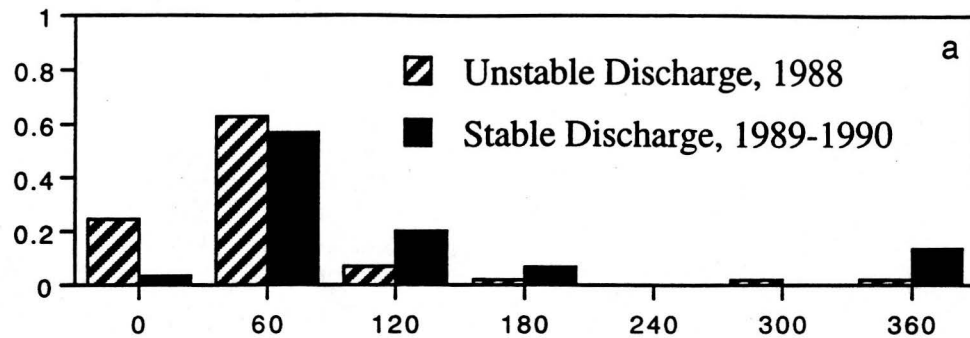


Size Class

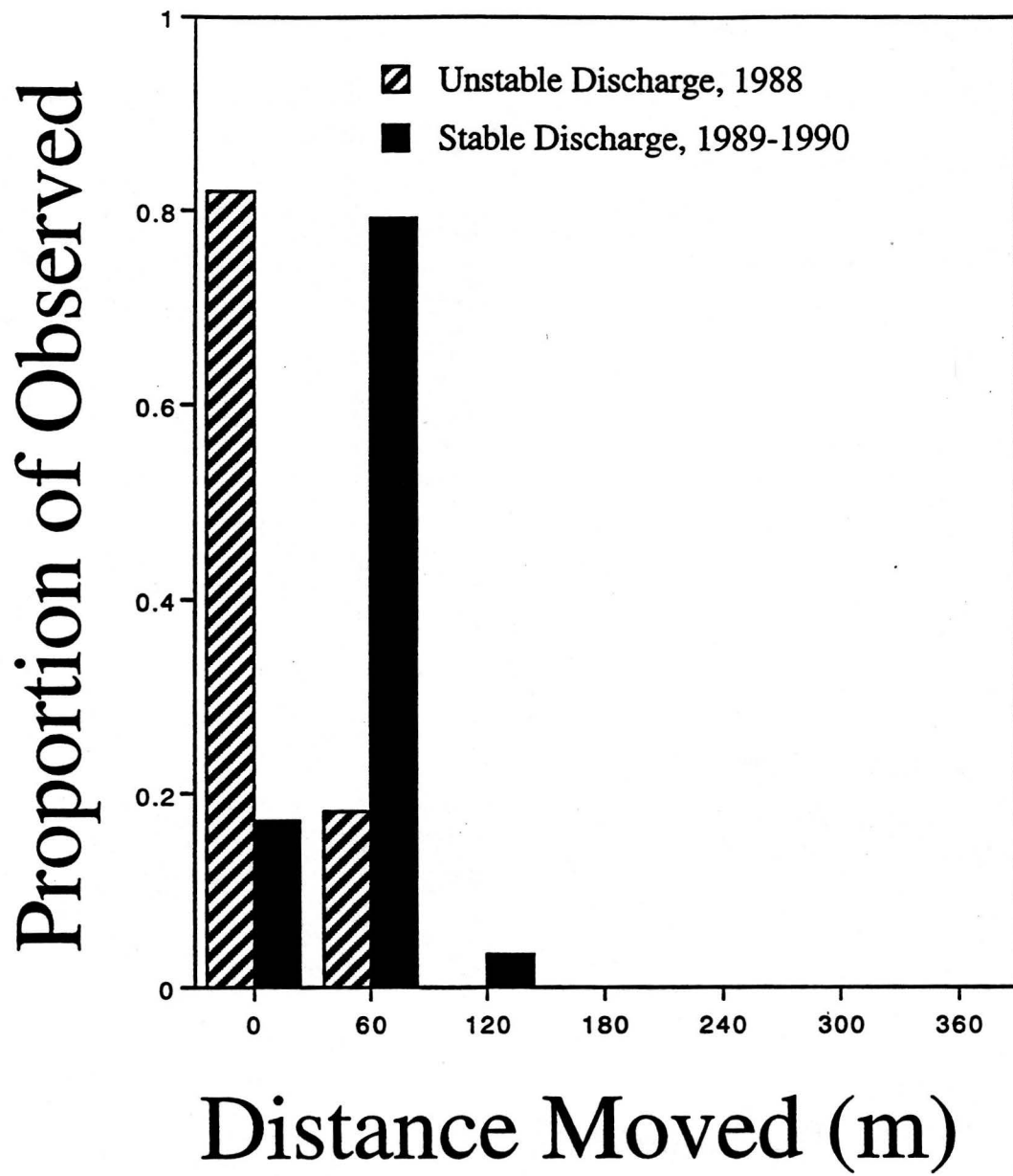


Size Class

Proportion of Observed



Distance Moved (m)



CHAPTER 5

SUMMARY

In this final chapter, I discuss the confirmation of the basic bioenergetic model with published literature data. I summarize how the model was modified to predict energetically advantageous positions in the Green River. Then the optimization hypotheses tested and the model fit to empirical observations are discussed, including the poor fit for smaller rainbow trout. I discuss possible explanations for the poor fit, including evidence from the movement data. Last, I make two management recommendations based upon the results presented in this dissertation and my experience in the Green River.

In Chapter 2, I developed two models. The first model had one mathematical term to estimate maintenance costs. This model failed to satisfactorily predict energetic flux. The second model broke the maintenance costs into three components: egestion and excretion, standard metabolism, and heat increment. Then I changed how these three terms were calculated depending on temperature, fish size (mass, g), and composition and quantity of the diet. This refinement modified the model sufficiently and the second, revised model accurately predicted the outcome of 39 of 40 experimental trials. These experimental trials were drawn from three published studies (Hutchins, 1974; Grayton and Beamish, 1977; Lawrence, 1991). These three studies comprised all known published work that

allowed the determination of energetic content of a salmonid at the beginning and end of a trial, required the fish to swim at a known constant velocity, and reported temperature, fish size, and amount and composition of the ration. In addition these three studies included trials that were conducted at temperatures from 4 to 15 °C and using fish with beginning wet mass from 6.21 to 242.00 g.

In Chapter 3, I modified the second model described in Chapter 2. First, I changed the currency from J/d to J/h. I changed to J/h because this unit of measure was more appropriate for determination of optimum feeding positions during daylight hours. I knew that I did not have sufficient data to test a dynamic program of time budget or an optimal habitat selection trajectory throughout a season. Since I wished to test predictions of optimal feeding positions, J/d was not the appropriate metric.

The second major change to the confirmed, refined model developed in Chapter 2 was a direct estimate of energy input from invertebrate drift rates. I estimated total energetic input from the size distribution of invertebrates in the drift and size-selective trout predation data of Filbert (1991).

I then used the model, adapted to predict positions in the field, to test two optimization hypotheses. I found the "optimal" hypothesis, fish choose the best position available, worked better than the "relaxed goal" hypothesis, fish choose randomly from among several positions that satisfy some fitness criterion. The optimal hypothesis worked well in different seasons and the hypothesis worked in

winters that exhibited both uniform and variable discharge regimes. However, no model worked well for fish in Size Class 1, ≤ 33 cm TL.

I believe there are two possible explanations for the failure of all models to predict the habitat use of Size Class 1 fish. First, Size Class 1 fish may be responding to other habitat characteristics than larger salmonids. However, other workers have shown that optimal habitat selection models work for small rainbow trout (Hill and Grossman, 1993) and other salmonids (Fausch, 1984; Hughes and Dill, 1990; Hughes, 1992). Second, Size Class 1 fish may be less able to find and use positions with desirable lower current velocities and high velocity shear. However, selectivity index values indicated that Size Class 1 fish preferred positions with low current velocities.

High selectivity values in the lower current velocity categories (Chapter 3, Table 2) suggest small rainbow trout appear to prefer energetically advantageous positions. But, the modeling results suggest Size Class 1 fish are not found in energetically advantageous positions. Two hypotheses present themselves that explain this phenomenon. First, small fish may be restricted from preferable positions by larger fish. Two pieces of evidence support this explanation. First, Fausch (1984) and Hughes (1992) found that larger, more dominant salmonids succeeded in finding and using more energetically profitable positions than smaller individuals. Second, videotape analysis of Green River rainbow trout (unpublished data) shows many aggressive evictions of small fish by larger fish. However, not

merge #
27
2-

enough of these latter observations existed for statistical analysis and these data must be considered anecdotal. The second hypothesis is small salmonids may prefer energetically advantageous positions but may be less able to locate them than larger fish. In Chapter 4, I showed that movement rates of Size Class 1 fish were smaller than those of larger fish. Smaller movements may be important biologically. Size Class 1 fish may be aware of fewer positions because of these smaller movement rates or because they have spent less time in the river. Therefore, incomplete information might limit Size Class 1 fish from using energetically advantageous positions. Finally, exclusion by larger fish or the inability to locate energetically advantageous positions may interact synergistically to exacerbate the difficulties faced by Size Class 1 fish.

Results of Chapter 3 indicate that the distribution of rainbow trout > 33.0 cm TL is consistent with the hypothesis that these fish are finding and using optimal positions. In addition, Size Class 2 and 3 fish are able to accomplish this regardless of the discharge regime.

Results of Chapter 4 suggest that unstable discharges suppress winter movements of all size classes over two temporal scales: intraseasonal and diel movement. In addition, I found body size may influence the diel movement pattern with Size Class 1 moving the least. However, methodology changes and the grouping of size classes by multiple range test suggested the effect of body size may be artificial.

Management Recommendations

Small fish cannot find and use energetically advantageous positions in the winter. I concluded this is most likely due to incomplete information of the environment. Small fish move less in unstable discharge regimes compared to stable; therefore, unstable discharges provide less opportunity for small fish to sample alternative habitats and to learn about their environment. To improve production of these smaller fish, I would make the following modification to the discharge regime. Especially in winter, make the discharge regime predictable. A predictable discharge regime will make it possible for trout to acquire more information about their environment.

I noticed that the optimization models determined that few positions that provided for positive growth rate were left after Size Class 2 and 3 fish were loaded into the habitat. This suggests the habitat is near saturation. Production rate of salmonids in the Green River may be slowed because of the extremely high density of fish in the river. Reducing competition, especially in winter, could increase the productivity of small fish, thus increasing the productivity of the fishery. More large fish might be taken home by anglers as long as there were small fish present to replace them. I would recommend changing the slot limit to allow anglers to keep two fish smaller than 33.0 cm TL (13 inches) and two fish larger than 45.7 cm TL (18 inches). It would not be necessary to allow this smaller slot limit year round

to reduce competition. If my calculations of the number of angler-days on the river are correct, this smaller slot could be allowed October to March and the number of Size Class 3 fish would be reduced during the winter months. This would have the added effect of attracting more anglers in economically slow months.

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APPENDIX

Table A.1. Validation data, predictions of energetic flux by model FLUX2, and *P* values for the comparison of empirical observations and model predictions (see text for discussion). Trials 1-28: Hutchins, 1974; Trials 29-34: Grayton and Beamish, 1977; Trials 35-40: Lawrence, 1991.

Trial	Temp (°C)	Focal Velocity (cm/s)	Total Length (cm)	Wet Mass (g)	Energy Content ² (J·10 ⁴)	Duration of Trial (d)	Ration (J·10 ⁴ /d)	Expt'l Flux (J·10 ⁴ /d)	sd	Model Prediction (J·10 ⁴ /d)	<i>P</i>
1	15	27.23	6.49	2.39	1.1416	12	0	-.034	.007	-.048	.071
2	15	18.37	6.42	2.44	1.1221	12	0	-.022	.008	-.035	.157
3	15	8.59	6.42	2.50	1.1410	12	0	-.020	.010	-.029	.374
4	15	25.13	6.39	2.55	1.1957	11	0	-.030	.007	-.045	.062
5	15	19.37	6.39	2.57	1.2012	11	0	-.026	.012	-.037	.365
6	15	13.65	6.42	2.65	1.2104	11	0	-.017	.007	-.033	.072
7	15	.10	6.52	2.75	1.2418	11	0	-.012	.014	-.03	.248
8	15	9.57	7.04	3.55	1.4782	11	.0458	.004	.014	-.003	.603
9	15	8.50	7.24	4.18	1.7990	11	.0776	.002	.014	.016	.338
10	15	9.71	7.16	4.07	1.5448	11	.1339	.059	.017	.059	.994
11	15	16.93	7.14	3.74	1.4421	11	.1289	.054	.030	.051	.926
12	15	27.36	7.10	3.60	1.5077	11	.0708	.002	.024	-.008	.700
13	15	25.59	7.14	3.90	1.5755	11	.0919	.015	.015	.009	.697
14	15	25.32	7.35	4.36	1.6678	11	.1644	.070	.019	.060	.594
15	15	9.48	7.09	3.77	1.4436	11	.1219	.049	.010	.052	.752
16	15	5.97	6.21	2.83	1.2569	10	.1054	.040	.010	.048	.424
17	15	11.15	6.29	3.08	1.4229	10	.1192	.039	.018	.055	.428
18	15	18.37	6.31	2.82	1.3085	10	.1019	.025	.016	.038	.443
19	15	23.67	6.25	2.72	1.3037	10	.0821	.016	.015	.018	.923
20	15	8.36	6.24	2.64	1.1898	10	.0686	.025	.017	.021	.844
21	15	16.04	6.28	2.74	1.2408	10	.0819	.032	.016	.026	.722
22	15	22.22	6.30	2.70	1.2668	10	.0664	.017	.012	.008	.554
23	15	9.27	6.72	3.37	1.3496	12	.1126	.055	.011	.048	.566

Table A.1. Cont.

Trial	Temp (°C)	Focal Velocity (cm/s)	Total Length (cm)	Wet Mass (g)	Energy Content ² (J·10 ⁴)	Duration of Trial (d)	Ration (J·10 ⁴ /d)	Expt'l Flux (J·10 ⁴ /d)	sd	Model Prediction (J·10 ⁴ /d)	P
24	15	17.97	6.76	3.53	1.3830	12	.1326	.061	.013	.055	.702
25	15	22.84	6.67	3.32	1.3910	12	.0917	.036	.027	.020	.623
26	15 ¹	9.05	7.30	4.19	1.4767	12	.1501	.062	.020	.070	.704
27	15	17.18	7.30	3.92	1.4530	12	.1146	.062	.040	.039	.595
28	15	21.42	7.34	4.07	1.4831	12	.1472	.049	.029	.056	.809
29	10	10.81	10.81	23.50	8.3479	30	.8384	.294	.051	.301	.898
30	10	10.81	10.81	34.33	10.9264	30	1.4829	.557	.029	.613	.084
31	10	10.81	10.81	31.00	9.6259	30	1.4411	.475	.043	.573	.048
32	10	10.34	10.34	16.62	6.8139	20	.4426	.088	.078	.149	.453
33	10	10.63	10.63	18.62	7.0987	20	.4817	.168	.091	.167	.991
34	10	11.47	11.47	19.12	8.0473	20	.4947	.099	.095	.181	.417
35	12	0.01	25.60	173.50	92.8190	56	3.5330	1.320	.658	.834	.501
36	12	26.25	24.20	160.00	92.8190	56	3.2581	.989	.663	1.268	.695
37	12	30.00	24.70	157.50	92.8190	56	3.2075	.930	.534	1.169	.664
38	4	0.01	28.35	238.00	170.2356	56	.4167	-.650	.731	-1.104	.568
39	4	26.25	28.43	240.50	170.2356	56	.4209	-.656	.616	-.331	.626
40	4	30.00	28.89	242.00	170.2356	56	.4236	-.679	.594	-.438	.706

² Mean energetic content of individual salmonids' bodies used in a trial at T=0.