# DEVELOPMENT AND APPLICATION OF A BIOENERGETICS MODEL FOR THE PLAINS KILLIFISH (Fundulus zebrinus) AND RED RIVER SHINER (Notropis bairdi)

by

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# ABSTRACT

I studied bioenergetics models as a method of predicting fish assemblage change after anthropogenic modifications within the upper Wichita River Basin, Texas. I determined the critical thermal maximum, and consumption and respiration rates for the salt-tolerant plains killifish *Fundulus zebrinus* and the salt-intolerant Red River shiner *Notropis bairdi*. This information was used to develop a bioenergetics model for both species and facilitate the comparison of growth rates under different temperatures and salinities. My results show the plains killifish, and most likely all other salt-tolerant fish, to have increased growth and a metabolic advantage over the Red River shiner, and most likely all other salt-intolerant fish under the conditions expected from implementation of chloride control structures. Bioenergetics models provide a viable method for predicting fish assemblage changes after anthropogenic alterations of the physical and chemical properties within the Wichita River.

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# CHAPTER I

# BACKGROUND

## Introduction

I conducted research to develop bioenergetics models for two stream fish species to use in determination of the effects of chloride control structures on the fish assemblage of the Wichita River, which is presented in Chapter II. In Chapter I, I provide background information that leads to the decision to conduct this research. This background information is provided here, in a separate chapter, to (1) provide the reader with the information needed to understand the processes affecting the environment in this region, (2) understand the motivation of the U.S. Army Corp of Engineers to construct chloride control structures on the Wichita River, and propose construction of several others, and (3) understand why bioenergetics models were chosen to understand the effects of these structures on the fish assemblage.

## Chloride Control

During the Permian Period, extensive inland seas covered the area of the Wichita River basin (U.S. Army Corp of Engineers 1994). When these seas retreated, marine evaporites were deposited (Sonnenfeld 1984). Dissolution of exposed marine deposits by surface flows and dissolution of subterranean marine deposits by ground waters results in high loading of dissolved solids, particularly sodium chloride, into the Wichita River (U.S. Army Corp of Engineers 1994). The high chloride concentration in the upper

portions of the river limits the usefulness of water as a supply for agricultural, industrial, and municipal purposes. To make the water more suitable for human use, the U.S. Army Corp of Engineers has constructed three chloride-control structures on this river and has proposed construction of several others (Irelan and Mendieta 1964; U.S. Army Corp of Engineers 1994).

Chloride control facilities constructed by the U.S. Army Corp of Engineers are designed to intercept saline flows and prevent them from contributing to the salt load of the river. The chloride control structures proposed for construction and currently in place on the Wichita River include a combination of dikes, inflatable weirs, and pumps to dispose of the salt by exporting it to brine disposal lakes and by injecting it into deep, permeable strata. When rains fall on the watershed, the river becomes swollen with fresh water, which is allowed to flow downstream to be collected for agricultural, municipal, and industrial use. During times of low flow, the river discharge is dominated by an influx of saline groundwater. This saline water is blocked by dikes and inflatable weirs, is collected, and pumped via a pipeline to a brine control lake or deep injection well. This removes much of the salt load within the stream making the water more desirable for human use.

Two chloride control structures are currently operational in the Wichita River Basin. A low-flow, inflatable collection dam (Bateman Dam) on the South Fork of the Wichita River became operational in 1987 with collected brine water pumped to a brine collection lake (Truscott Brine Lake) (U.S. Army Corp of Engineers 1994; Echelle et al. 1995). An evaluation of the effectiveness of Bateman Dam by Keller et al. (1988)

determined the structure was successful in removing 86%, or approximately 152 metric tons per day, of the chloride load from the South Fork of the Wichita River. Truscott Brine Lake is located on a tributary of the North Fork of the Wichita River and is designed to hold brine collected from Bateman and Lowrance Dams (U.S. Army Corp of Engineers 1994). Lowrance Dam is a low-flow inflatable dam located on the Middle Fork of the Wichita River and is expected to be operational with the installation of pumps and pipelines (U.S. Army Corp of Engineers 1994). An additional low-flow, inflatable dam is proposed for construction on the North Fork of the Wichita River (U.S. Army Corp of Engineers 1994).

The operation of chloride control facilities is expected to substantially reduce salinity and alter natural flow regimes in Wichita River Drainage (U.S. Army Corp of Engineers 1994). Most major rivers in North America have been modified by human activities and this has resulted in changes in fish assemblages in these rivers (Spence and Hynes 1971; Neill and Magnuson 1974; Stanford and Ward 1979; Anderson et al. 1983; Ross et al. 1985; Minns et al. 1996; Gordo and Cabral 2001). As the human population grows and the demand for water increases, modification of rivers and streams will continue especially in arid regions (Ostrand and Wilde 2001, 2002).

## Fish Assemblages

Previous studies have shown fish assemblages in streams to be affected by many of the streams characteristics such as size, alkalinity, woody debris, water clarity, dissolved oxygen concentration, water temperature, floods, and salt concentrations

(Huntsman 1942, 1946; Bailey 1955; Barlow 1958; Feldmeth et al. 1974; Tramer 1977; Matthews et al. 1982; Karr and Freemark 1985; Minckley and Mefee 1987; Resh et al. 1988; Poff and Ward 1989; Rutledge and Beitinger 1989; Taylor et al. 1993; Fausch and Bramblett 1991; Barinaga 1996; Ostrand and Wilde 2001, 2002). In some sections of the Wichita River, salinity exceeds that of seawater (Taylor et al. 1993; U.S. Army Corp of Engineers 1994) and summer temperature can reach the upper tolerances of many fish species (Matthews and Zimmerman 1990; Taylor et al. 1996). The fish fauna of the Wichita River is adapted to the variable salinity and flow regimes of the river and its tributaries with the salinity tolerances of these fish often defining the composition of the local fish assemblage (Echelle et al. 1972a; Taylor et al. 1993). Due to their adaptations to these extreme environments, native fishes have a competitive advantage over non-native fishes (Matthews and Zimmerman 1990).

Chloride control structures on the Wichita River may alter stream salinity, decrease mean flows, and confine fish to isolated pools with increasing water temperature. An increase of 3 to 4°C (and possibly even less) would almost undoubtedly have a negative effect on local fish populations (Matthews and Zimmerman 1990). Eaton and Scheller (1996) projected that global warming will increase air temperatures by 3.4°C in the Wichita River basin area. Matthews and Zimmerman (1990) believed the plains killifish in the entire southern Great Plains and the Red River shiner in the Red River Drainage, Texas, face extinction in the event of major warming. Chloride control structures likely will cause physical or chemical alterations to the Wichita River that may

result in the physiological tolerance of the fish being exceeded or reduction of the competitive advantage of the native fishes.

## Study Fish

Two fishes native to the Wichita River were chosen to determine if confinement in pools would affect their persistence in the fish assemblage. The plains killifish and the Red River shiner represent different groups within the Wichita River fish assemblage based on salinity tolerance (Ostrand and Wilde 2001, 2002). The plains killifish can tolerate conductivities up to 140,000 $\mu$S/cm (micro Siemens per centimeter) (Echelle et al. 1972a) and is representative of a group of fishes characterized by a high salinity tolerance (> 30,000 $\mu$S/cm). The Red River pupfish (Cyprinodon rubrofluviatilis) is the second member of this group in the Wichita River (Ostrand and Wilde 2002). The Red River shiner is representative of a group of fishes characterized by a lower salinity tolerance (< 30,000 $\mu$S/cm). Other members of the lower salinity tolerant group within the Wichita River are the red shiner (Cyprinella lutrensis), speckled chub (Macrhybopsis aestivalis), and the plains minnow (Hybognathus placitus) (Ostrand and Wilde 2002).

The plains killifish is native to the Great Plains from Missouri to Wyoming, and south to the Colorado River, Brazos River, Galveston Bay, and Rio Grande drainages of Texas and Mexico (Page and Burr 1991). Due to its popularity as bait, the plains killifish has been introduced into several western river drainages (Fuller et al. 1999). The plains killifish reaches a maximum length of 130 millimeters (Boschung et al. 1997) and matures in its second summer, with few individuals surviving to reproduce after their

third summer (Minckley and Klaassen 1969). The plains killifish spawns when water temperatures reach 27°C (Koster 1948).

The plains killifish feeds primarily on animals such as chironomid larvae, copepods, and nematodes; however, a large portion of its diet is indigestible material (Minckley and Klaassen 1969). The plains killifish feeds by engulfing substrate to consume buried prey. This results in the ingestion of a large amount of sand. Minckley and Klaassen (1969) found sand in 80 to 100% of the plains killifish digestive tract samples. In addition, plains killifish consume filamentous algae which Echelle et al. (1972b) found in 40 to 70% of digestive tract samples. Because it was found intact in the posterior intestine, it is believed to be indigestible by the plains killifish. The plains killifish feeds primarily during the day, but may also feed at night. Echelle et al. (1972b) believed that the observed feeding chronology of plains killifish reflected metabolic needs.

The native range of the Red River shiner is limited to the Red River Drainage from southwest Arkansas to western Oklahoma and northwest Texas, but it has been introduced into the Cimarron River in the Arkansas River Drainage, southern Kansas and Oklahoma (Page and Burr 1991). No study of the diet of the Red River shiner has been published. Marks et al. (2001) studied the diet of the smalleye shiner (Notropis buccula), which is closely related to the Red River shiner. The smalleye shiner and Red River shiner occupy similar niches within the Brazos River and Wichita River, respectively (Echelle et al. 1972a). Diets of these two species are likely to be similar. Marks et al. (2001) found plant materials in as many as 41% and sand in as many as 100%, of the

smalleye shiners they examined. The smalleye shiner fed primarily on animal items, but at times also consumed large quantities of substrate, detritus, and plant materials. The Red River shiner reaches a maximum length of 80 millimeters (Page and Burr 1991) and has an upper salinity limit only slightly above 32,000 $\mu$S/cm (Echelle et al. 1972a).

## Bioenergetics Models

The plains killifish is representative of salt-tolerant species and the Red River shiner of salt-intolerant species. Because of this, different growth rates can provide an insight into possible fish assemblage shifts that may occur in the Wichita River upon implementation of chloride control structures. Bioenergetics models provide a method to determine the effect of stream characteristics on the growth of individual fish species. By comparing growth predictions of individual species, an understanding of the potential fish assemblage change can be gained. Bioenergetics models have not been developed for the plains killifish or the Red River shiner. Therefore, I developed bioenergetics models to measure the effects of differing temperature and salinity, which may occur as a result of chloride control structures, on the growth rates of these fishes.

Bioenergetics is the study of energy consumption rates, loss rates, transformations, and uses (primarily metabolism) as functions of the whole organism (Brett and Groves 1979). The study of bioenergetics in fish has been growing rapidly since Winberg's (1956) paper on the energy budget of fish. Bioenergetics models have been developed to determine the allocation of energy to various uses in fishes. These models are essentially weight-balance equations based on the first law of

thermodynamics, conservation of energy, and divide consumed energy among growth, metabolism, and waste products (Winberg 1956; Brandt and Hartman 1993). Because the budgeting-constraint forces the energy budget to be balanced, error propagation is limited (Bartell et al. 1986).

Bioenergetics models have been developed for over 30 species of fish (Wahl and Stein 1991; Karås and Thoresson 1992; Hanson et al. 1997; Duffy 1998; Railsback and Rose 1999). Many specific applications have motivated development of bioenergetics models (Brandt and Hartman 1993; Hanson et al. 1997; Madon and Culver 1993; Hartman and Brandt 1995; Whitledge and Hayward 1997; Chipps et al. 2000; Hayes et al. 2000). Bioenergetics models have been developed to assess problems of fisheries management (Stewart et al. 1981, 1983; Stewart and Ibarra 1991), understand effects of thermal stress (Hill and Magnuson 1990; Railsback and Rose 1999), and understand food web dynamics (Stewart and Binkowski 1986; Hayward and Margraf 1987; Kitchell and Hewett 1987; Lyons and Magnuson 1987; Hewett 1989; Hewett and Stewart 1989). These assessments typically have focused on single fish species. Only Lyons and Magnuson (1987), who looked at the effects of walleye predation on small littoral-zone fishes, used bioenergetics models as a means to study an entire fish assemblage. Several bioenergetics models have been developed; however, Hewett and Johnson's (1987) Wisconsin model has been used most often because it is readily accessible as the computer program "Fish Bioenergetics 3.0" (Ney 1993). The Wisconsin bioenergetics model and equations presented here are from this program developed by Hanson et al. (1997).

Winberg (1956) developed the first model of an energy budget for fish, which separated the energy consumed by an organism as:

$$\text{consumption} = \text{growth} + \text{respiration} + \text{waste}. \quad (1)$$

Because the components form a balanced equation, determinations (or well-founded estimates) of any three components, growth, metabolism, waste, and consumption, allow the fourth to be calculated by difference. All errors associated with the three determinations; however, become a pooled error in the fourth component (Solomon and Brafield 1972; Brett and Groves 1979). Although Winberg's equation can be solved for any component, it typically is solved for growth or consumption (Ney 1993).

In this thesis I measured consumption directly and used the bioenergetics model to solve for growth. The basic equation for consumption is:

$$C = (CA \times W^{CB}) \times p \times f(T), \quad (2)$$

where C is the specific consumption rate measured as grams of prey per gram of fish per day ($g\ g^{-1}\ d^{-1}$), p is the proportion of maximum consumption, and f(T) is a temperature dependence function. The quantity $CA \times W^{CB}$ is the maximum specific consumption rate or $C_{max}$ ($g\ g^{-1}\ d^{-1}$) and is composed of CA which is the intercept of an allometric weight function (discussed later), W the fish weight (g), and CB the slope of an allometric weight function. For clarity, I will use the abbreviation pc for proportion of maximum

consumption (p in the bioenergetics model) and the abbreviation p for probability of statistical significance.

For determination of the temperature dependence function [f (T)], I used consumption equation two from Hanson et al. (1997) which determines the temperature dependence for warm water species. This equation is:

$$f(T) = V^{x} \times e^{(X \times (1-V))}, \quad (3)$$

$$\text{where } V = (CTM - T) / (CTM - CTO), \quad (4)$$

$$X = (Z^2 \times (1 + (1 + 40 / Y)^{0.5})^2) / 400, \quad (5)$$

$$Z = LN (CQ) \times (CTM - CTO), \text{ and} \quad (6)$$

$$Y = LN (CQ) \times (CTM - CTO + 2). \quad (7)$$

In these equations, CTO (consumption thermal optimum) is the laboratory temperature preferendum for consumption, CTM (consumption thermal maximum) is the maximum water temperature above which consumption ceases, and CQ is the water temperature dependent coefficient, which is an approximation of $Q_{10}$, the rate at which the consumption function increases over relatively low water temperatures.

Metabolism consists of three general components: standard respiration, activity-dependent respiration, and specific dynamic action. Standard metabolism is the energy used for respiration and is often referred to as respiration. The basic equation for respiration with an activity-dependent metabolism multiplier is:

$$R = RA \times W^{RB} \times f(T) \times ACT, \quad (8)$$

where R is the specific respiration rate measured as the gram of oxygen per gram of fish per day (g $O_2$ $g^{-1}$ $d^{-1}$), RA is the intercept of the allometric weight function, W is fish weight (g), RB is the slope of the allometric weight function, f(T) is the temperature dependence function, and ACT is the activity multiplier.

For determination of the temperature dependence function [f (T)], Respiration Equation 2: Temperature dependent with activity multiplier as presented by Hanson et al. (1997) was used. This equation is:

$$f(T) = V^{X} \times e^{(X \times (1-V))}, \quad (9)$$

$$\text{where } V = (RTM - T) / (RTM - RTO), \quad (10)$$

$$X = (Z^2 \times (1 + (1 + 40 / Y)^{0.5})^2) / 400, \quad (11)$$

$$Z = LN(RQ) \times (RTM - RTO), \text{ and} \quad (12)$$

$$Y = LN(RQ) \times (RTM - RTO + 2). \quad (13)$$

In these equations, RTO (respiration thermal optimum) is the water temperature corresponding to 0.98 of the maximum respiration rate, RTM (respiration thermal maximum) is the maximum water temperature above which respiration ceases, and RQ is the water temperature dependent coefficient (RQ), which is an approximation of a $Q_{10}$, the rate at which the respiration function increases over relatively low water temperatures.

Specific dynamic action (SDA) comprises the energetic costs of processing and assimilating food (i.e., digestion, absorption, transport, and deposition of consumed energy). Beamish (1974) found specific dynamic action to be relatively independent of temperature and food ration. The bioenergetics model measures the amount of energy used for the energetic cost of processing and assimilating food as a proportion of assimilated energy (S). The equation for S is:

$$S = SDA \times (C - F), \tag{14}$$

where S is the proportion of assimilated energy lost to specific dynamic action, SDA is the specific dynamic action, C is the specific consumption rate (g $g^{-1}$ $d^{-1}$), and F is the specific egestion rate (g $g^{-1}$ $d^{-1}$).

Wastes consist of egestion (non-assimilated energy, fecal waste) and excretion (loss due to osmosis, nitrogenous waste). The equation that was used for egestion (F) determines it as a proportion of consumption (Hanson et al. 1997):

$$F = FA \times C, \tag{15}$$

where F is egestion (g $g^{-1}$ $d^{-1}$), FA is the constant proportion of egestion, and C is the specific consumption rate (g $g^{-1}$ $d^{-1}$). The equation that was used for excretion (U) determines it as a proportion of consumption (Hanson et al. 1997), and it is:

$$U = UA \times (C - F), \quad (16)$$

where U is excretion (g $g^{-1}$ $d^{-1}$), UA is the constant proportions of excretion, C is the specific consumption rate (g $g^{-1}$ $d^{-1}$), and F is egestion (g $g^{-1}$ $d^{-1}$).

Energy is utilized by a fish in either its various bodily functions or is lost as waste products. This energy utilization is presented in the bioenergetics scheme of food use (Figure 1) presented by Niimi and Beamish (1974). Energy is consumed (C) and partitioned among various uses. Not all of the consumed energy is usable and some is lost to fecal waste (F). As energy is assimilated and metabolized, energy is lost to specific dynamic action (SDA) and nitrogenous waste (U). After losses are accounted for, the remaining energy can be used for basic bodily functions such as metabolism (R), growth (G), and activity (ACT). Growth is accomplished only after the energy requirements of all other bodily functions have been met and was measured as weight (g).

## Summary

Chloride control projects may change the physical and chemical characteristics of the Wichita River, and these changes can affect the growth and persistence of the local fish assemblage. An understanding of how different environmental characteristics affect fish growth can yield an insight to the possible effects of chloride control projects on the fish assemblage. Bioenergetics models can be a useful tool in understanding the response of fish weight under different environmental conditions, but they have not been developed for the plains killifish and the Red River shiner. Therefore, I developed a

bioenergetics model to measure the effects of differing temperature and salinity, which may occur as a result of chloride control structures, on the growth rates of these fishes.

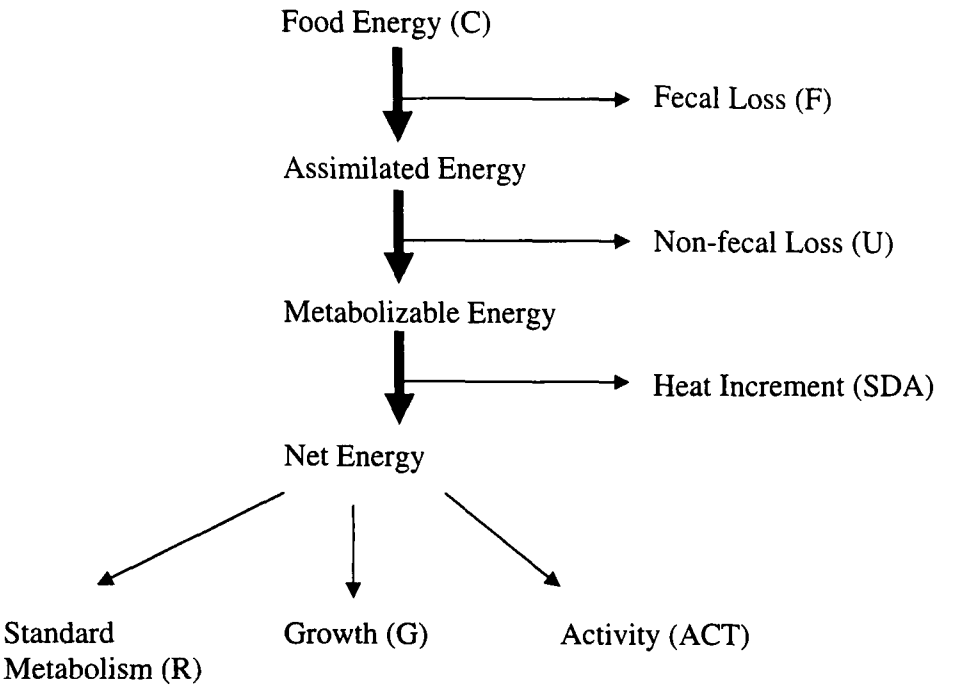


Figure 1. – A modification of the energy utilization web of food consumption for bioenergetics proposed by Niimi and Beamish (1974). Line thickness represents relative amount of energy used for each process.

# CHAPTER II

# METHODOLOGY

The physical (e.g., temperature) and chemical (e.g., salinity) characteristics of a water body affect food consumption rates and growth of fish (Adams and Breck 1990). Bioenergetics models can be a valuable tool in assessing the effects of habitat alteration on the growth of fishes because they can be used to predict growth and consumption rates under different temperatures and conductivities. Herein, I develop bioenergetics models to assess the possible effects of altered thermal and chemical variables, created by man-made water diversion structures, on the fish assemblage of the Wichita River, Texas.

Most major rivers of the world, as well as the Wichita River, have been modified by human activities and this has resulted in changes in fish assemblages in these rivers (Spence and Hynes 1971; Neill and Magnuson 1974; Stanford and Ward 1979; Anderson et al. 1983; Ross et al. 1985; Minns et al. 1996; Gordo and Cabral 2001). As the human population grows and the demand for water increases, modification of rivers and streams will continue, especially in arid regions (Ostrand and Wilde 2001, 2002). The Army Corps of Engineers has altered the Wichita River in an attempt to meet this human demand for water in the north-central region of Texas (U.S. Army Corps of Engineers 1994).

During the Permian Period, extensive inland seas deposited marine evaporites, particularly sodium chloride, in the area of the Wichita River Drainage basin (Sonnenfeld 1984, U.S. Army Corps of Engineers 1994). Chloride control facilities were constructed

to remove the salt to make the water useful for agricultural, industrial, and municipal purposes (Irelan and Mendieta 1964; U.S. Army Corps of Engineers 1994). Chloride control facilities alter the physical and chemical characteristics that affect the fish assemblage within a stream (Spence and Hynes 1971; Minns et al. 1996). Native fish inhabiting intermittent streams, such as the upper Wichita River, are adapted to variable water temperature, water level, salinity, and dissolved oxygen concentration. Due to their adaptations to these extreme environments, native fishes have a competitive advantage over non-native fishes (Matthews and Zimmerman 1990). Man-made structures alter the natural environment and may reduce the mean levels of these stream characteristics, thereby reducing the competitive advantage of all or certain species of native fish.

Two native fish of the Wichita River were chosen as study fish to determine if implementation of chloride control structures would affect the fish assemblage. The plains killifish and the Red River shiner represent different groups within the Wichita River fish assemblage based on salinity tolerance (Ostrand and Wilde 2001, 2002). The plains killifish is representative of a group of fishes that has a high salinity tolerance (> 30,000 $\mu$S/cm). The only other example of this group within the Wichita River is the Red River pupfish (Cyprinodon rubrofluviatilis). The Red River shiner is representative of a group of fishes that have a low salinity tolerance (< 30,000 $\mu$S/cm). Other examples of the low salinity tolerant group within the Wichita River are the red shiner (Cyprinella lutrensis), speckled chub (Macrhybopsis aestivalis), and the plains minnow (Hybognathus placitus).

The plains killifish is representative of salt-tolerant species and the Red River shiner of salt-intolerant species and differences in growth rates between them can provide an insight into possible fish assemblage shifts that may occur in the Wichita River. An understanding of how differing environmental characteristics affect fish growth can yield an insight to the possible effects of chloride control projects on the fish assemblage. Bioenergetics models as a tool can be useful in understanding the response of fish weight under differing environmental conditions.

Bioenergetics models have not been developed for the plains killifish and the Red River shiner. Therefore, I developed a bioenergetics model to measure the effects of differing temperature and salinity on the growth rates of these fishes. My objectives were to: (1) develop simple bioenergetics models for the plains killifish and the Red River shiner, (2) assess predicted growth of each species, (3) determine if their food consumption changes with increasing salinity, and (4) to predict the possible shift in fish assemblage composition that occurs as a result of chloride control structures based on the data collected to meet the previous three objectives. To meet these objectives I specifically posed the following null hypotheses: $Ho_1$: there is no difference in the predicted growth rates of the plains killifish and Red River shiner, $Ho_2$: for each species, temperature has no effect on growth rates at fixed food rations, and $Ho_3$: for each species there is no difference between consumption at low and high salinity.

The first null hypothesis $H_{01}$ states that given identical initial weights, food rations, and environmental temperatures, both species will grow at the same rate. To test $Ho_1$, predicted growth of each species was compared under identical initial weight,

temperature, and food ration scenarios. The second null hypothesis $H_{02}$ states that both species grow at a identical rate at different temperatures. To test $Ho_2$, predicted growth of each species was compared under identical initial weight and food ration scenarios and at differing temperatures. The third null hypothesis $H_{03}$ states that consumption does not differ between species under conditions of low and high salinity. To test $Ho_3$, laboratory estimates of food consumption for each species, under low and high salinity concentrations, were compared.

## Study Area

The Wichita River drains 9,032 $km^2$ of north-central Texas and is a tributary of the Red River, which forms the boundary between Oklahoma and Texas (U.S. Army Corps of Engineers 1976). Three locations (Figure 2) on the North Fork of the Wichita River were chosen as study sites because they currently are unaffected by chloride control structures. The site farthest upriver (33° 57.13' N latitude, 100° 4.12' W longitude) is located east of Hackberry, Texas. The middle site (33° 51.97' N latitude, 99° 52.12' W longitude) is located west of Foard City, Texas. The farthest downstream site (33° 47.23' N latitude, 99° 35.78' W longitude) is located northeast of Gilliland, Texas. Latitude and longitude for study sites were obtained using Microsoft Streets and Trips (2000).

## Methods

### Model Development

I collected 250 specimens of plains killifish and Red River shiner from the North Fork of the Wichita River, Texas, and transported them to Texas Tech University on 16 March 2001. At the time of the collection of laboratory fish, the water temperature was 14.2 °C and the conductivity was 12,600 µS/cm. In the laboratory, fish of both species were separated into seven holding aquaria and quarantined for a minimum of two weeks at a photoperiod of 16L:8D in aerated 75-liter glass aquaria. Holding aquaria for each species consisted of an aquarium at each of five experimental temperatures (5, 15, 25, 30, and 35°C) and 3000 µS/cm, one aquarium with small fish (< 50 mm) at 25°C and 3000 µS/cm to determine consumption and respiration rates of small fish, and one aquarium at 25°C and 30,000 µS/cm to determine consumption and respiration rates at high conductivity. Water temperatures in the aquaria were changed at a maximum rate of 1°C per day until the desired experimental temperature was reached. Concurrent with the change to the desired experimental temperature, conductivity was changed at a maximum rate of 1000 µS/cm per day until the desired final conductivity had been reached. Water quality parameters (e.g., pH, temperature, ammonia, and nitrate) in the holding aquaria were monitored daily during the first week of quarantine and weekly thereafter for the remainder of the laboratory period.

Fish were fed Wardley Total Tropical Gourmet Flake Blend food ad libitum until the desired experimental temperature and conductivity had been reached. Fish were held an additional minimum of two weeks at the desired experimental temperature and

conductivity to allow the fish to acclimate. During this acclimation period, all fish were fed San Francisco Bay Brand bloodworms ad libitum. Laboratory experiments, which began after the acclimation period, included determination of consumption rates, respiration rates, and upper incipient lethal temperature. Fish wet weights after all experiments, as well as the amount of wet food added and remaining, were determined with an electronic analytical balance to the nearest 0.0001 g. After each experiment, fish were measured to the nearest 1 mm.

To determine food consumption rates, eleven individuals of each species were placed in separate 12-liter aquaria filled with water in equal temperature and conductivity to that in the holding aquaria. Each 12-liter aquarium was placed inside a 2725-liter bath in which temperature was regulated by a Frigid Units, Inc., D1-100 chiller/heater. Food was withheld from all fish for 24 hours prior to initiation of consumption experiments (Hartman and Brandt 1995, Duffy 1998). Fish were then fed bloodworms ad libitum during the 24-hour consumption experiment. Total consumption (gram of prey per day; g $d^{-1}$) was calculated by subtracting food remaining from total food added during the 24 hour consumption experiment.

During the experiment, species specific consumption data were gathered specifically for specific consumption rate (C, g $g^{-1}$ $d^{-1}$), maximum specific consumption rate (Cmax, g $g^{-1}$ $d^{-1}$), optimum temperature for consumption (CTO, °C), water temperature (T, °C), and fish weight (W, g). The upper incipient lethal temperature (CTMax, °C) was assumed to be the maximum temperature at which food consumption (CTM, °C) occurred because consumption ceases after death. I used nonlinear regression

to determine the slope and intercept of the weight-specific consumption function of specific consumption on fish weight. This was used in the determination of Cmax in the equation:

$$Cmax = CA \times W^{CB}, \quad (17)$$

where CA is the intercept and CB is the slope of the allometric weight function. Species-specific values of CA, CB, CTO, CTM, C, and W for each of the five experimental temperatures were fit using the computer program SAS (version 8) to determine the best fit for CQ (Appendix A).

To determine respiration rates, twelve closed static-respirometers were constructed by placing a cap on one end of a clear 7.62 cm diameter PVC pipe approximately 15.2 cm long. A threaded cap was placed on the other end to allow access to the inside of the respirometer. An YSI-85 meter was calibrated for measurement of dissolved oxygen concentrations prior to each experiment. To prevent overestimation of SDA, food was withheld from the fish for 24 hours prior to the respiration experiment (Mathur and Robbins 1971). One fish was placed in each of twelve respirometer chambers for 15 minutes before the beginning of a trial with the open end covered by a screen mesh. The confinement period prior to the experiment allowed the fish time to acclimate to the enclosed space. The respirometer was sealed and placed in a water bath at the acclimation temperature of that fish. After 30 minutes, the dissolved oxygen level

was measured to the nearest 0.01 mg $l^{-1}$. This procedure was repeated for the fish from each of the seven holding aquaria.

During this experiment, data were gathered specifically for specific respiration rate (R, g $O_2$ $g^{-1}$ $d^{-1}$), T, and W. Hanson et al. (1997) suggest approximating RTO with CTMax when developing parameter sets for adults of new species. The development of CTMax is discussed later in this section. Hanson et al. (1997) also suggested setting RTM about 3°C greater than RTO. I assumed RTM for both species was 3°C greater than RTO. I used power regression to determine the slope and intercept of the weight-specific respiration function of specific respiration rate on fish weight. This was used in the determination of RA and RB in the equation:

$$R = RA \times W^{RB}, \tag{18}$$

where RA is the intercept and RB is the slope of the allometric weight function. Species specific RA, RB, RTO, RTM, R, and W for each of the five experimental temperatures were fit using SAS to determine the best fit for RQ (Appendix A).

I used the method of Hutchison (1961) to measure CTMax, which yields the upper incipient lethal temperature as recommended by Hanson et al. (1997). The CTMax was defined as the temperature fish began to lose equilibrium as a result of thermal stress and consequently failed to maintain an upright position. Twelve individuals of each species were acclimated to 35°C. Each fish was placed in an individual 500 milliliter

beaker and heated at a rate of 0.5°C per minute using a water bath. Beakers were aerated to insure uniform heat transfer and prevent oxygen depletion.

Previous studies found bioenergetics models to be insensitive to errors in egestion (F), excretion (U), and specific dynamic action (SDA) (Kitchell et al.1977, Bartell et al. 1986, Hewett and Johnson 1992). Therefore, I used estimates for these parameters suggested by Hanson et al. (1997). The estimates were a constant proportion of consumption equal to 0.15 for egestion, 0.1 for excretion, and 0.175 for SDA. Table 1 provides a complete list of the parameter estimates used in the bioenergetics model for each species.

To evaluate the developed model parameters, lengths and wet weights of ten plains killifish and Red River shiners were determined before and after a 30 day feeding experiment. This was completed to determine growth on a known diet at a known temperature. Species were separated and placed in 75-liter glass aquaria and held at 25°C and 3000 μS/cm. Individuals of each species were fed a diet equal to 6% of their combined initial wet weight each day. This feeding rate was chosen because it was assumed to be sufficient for maintenance and growth among both species. For each species, mean growth determined after the 30 day feeding experiment was used in the completed bioenergetics model. Fish Bioenergetics 3.0 developed by Hanson et al. (1997), which was described in Chapter I, was used to assess the developed parameters and observed growth and in the model simulations discussed below. I assumed the observed consumption rates in the laboratory represented 100% (pc = 1.00) of Cmax in the field. The pc parameter was then adjusted downward until the bioenergetics model

predicted growth equal to that observed in experimental growth trials. This is consistent with the suggestion of Stewart et al. (1983) of adjusting laboratory estimates of Cmax downward until the developed bioenergetics model fits observed growth. I found the pc parameter, measured to the nearest 0.0001, that resulted in a percent error equal to or less than 0.01 using the equation:

$$((P - O) / O) \times 100, \tag{19}$$

where P is growth predicted by the bioenergetics model and O is observed growth during the 30 day feeding trial.

Sensitivity Analysis

I used the method of error analysis (EA) as described by Bartell et al. (1986) to measure the sensitivity of model predictions to variation in individual parameters. This method treats the nominal value of each parameter as the expected value from a normal distribution defined for that parameter. Monte Carlo simulations then are used to independently sample sets of parameters from their distributions. The normal distributions of the model parameters used were plus and minus 2, 10, and 20% of the variance of the nominal parameter values.

Pearson correlation was used to assess the effect of varying the parameter value on the model prediction of weight in the Monte Carlo simulations. Pearson correlations range from -1 to 1 for each parameter. The absolute values of the Pearson coefficients

were determined and sorted numerically from 1 to 0. The closer the absolute value of the coefficient is to 1, the greater the influence that parameter has on the variation in the final predicted growth. Parameters with a large coefficient are those that, with a relatively small change in nominal values, result in a large change in model output. These parameters should be analyzed more thoroughly in laboratory studies. This will aid in eliminating variance in the model predictions and result in a more precise, and ultimately more useful, model. Monte Carlo simulations and Pearson correlation analyses were performed using SAS. The SAS program used for sensitivity analysis is presented in Appendix B. A $p < 0.05$ for the Pearson correlation coefficient was used to determined the most influential parameters in explaining the greatest variation in final predicted weights.

Model Application

To evaluate how each species would react when placed in similar environments, identical values for pc, temperature, and initial fish weight were used. Both species were evaluated at an initial weight of 1, 2, 3, 4, and 5 g with each weight evaluated at a pc of 0.10, 0.15, 0.20, 0.25, 0.30, 0.35, 0.40, and 1.00 and each weight/pc scenario evaluated at temperatures of 5, 10, 15, 20, 25, 30, 35, and 40°C. This resulted in 320 unique initial weight, pc, and temperature scenarios. The weights were chosen because they span the observed range in weight seen in the field for both species. The pc range from 0.10 to 0.40 was chosen because it provides more realistic model predictions of fish growth based on observed growth in the laboratory (discussed further in Results). A pc of 1.00

was chosen to verify the continuation of any patterns observed by the model predictions in the 0.10 to 0.40 pc range. The temperature range (5 to 40°C) spans those experienced by fish in the Wichita River (Lewis and Dalquest 1957). Each simulation was run for a 10 day period.

Final predicted weights of both species were compared for each initial weight, pc parameter, and temperature scenario. A metabolic advantage was considered to be the outcome when the absolute value of the difference between final weights of the species was greater than 2% of the plains killifish final weight. A two percent difference in final weight was determined to be biologically important because each simulation was run for only 10 days. This increased weight could result in greater survival during the extreme summer environmental conditions. This increased weight is also biologically important if it is used during spawning, in the form of gametes, which could result in an increase in fecundity and recruitment.

The effects of increased temperature on each species were assessed individually by regressing final predicted weights for each successive temperature, with a constant pc parameter. For example, final predicted weight for the plains killifish with an initial weight of 1 g, pc of 0.10, and at a temperature of 5°C was regressed on the final predicted weight for the plains killifish with an initial weight of 1 g, pc of 0.10, and at a temperature of 10°C. This was done for final predicted weights between each successive temperature (5 and 10, 10 and 15, 15 and 20, 20 and 25, 25 and 30, 30 and 35, and 35 and 40°C) for each species. This was repeated for the final predicted weights based on differing pc parameters for each species. Three general outcomes are possible: (1) slope

is equal to zero implying temperature has no effect on final predicted weight, (2) slope is negative implying temperature adversely effects growth, and (3) slope is positive implying temperature positively effects growth.

Effects of salinity on each species were analyzed by regressing specific consumption and respiration for the low salinity (25°C and 3,000 μS/cm) on high salinity (25°C and 30,000 μS/cm) experiments. The slope and intercept of this regression was used to estimate the specific consumption and respiration of both species at 1, 2, 3, 4, and 5 g. The change (%) in consumption and respiration as a result of high salinity was determined at each initial weight for both species (Table 2). The computer program SAS was used to compare the slope and intercepts of the high and low salinity experiments.

Field Study

Conductivity was measured with an YSI-85 meter from the three study sites on a biweekly schedule from 11 June 2001 to 1 September 2001. During each visit, fish were collected, identified to species, and enumerated from three pools at each site. Fish were collected with a 1.2 × 3.1-meter and 1.2 × 9.2-meter seine, both with a 6.3 mm stretch measure mesh. From 9 July 2001 to 1 September 2001, a HOBO Temp recording thermometer was installed at each site to obtain local daily water temperature. The thermometers were placed in the deepest portion of the river, which was believed to be the coolest possible refugia, for each study site. Data collected during the field studies were used to document the environmental conditions the study fish live in, provide a

temperature data set for use in a bioenergetics modeling simulation, and determine species composition and abundance through the summer period.

Table 1. – List of the parameters, their definitions, source, and values used in the development of a bioenergetics model for the plains killifish (pk) and Red River shiner (rrs). The letter "a" denotes parameters whose value depended on the values of other parameters within its determination. The letter "b" denotes parameters that had different values depending on the simulations ran. The measurement "g $g^{-1}$ $d^{-1}$" is equal to gram of prey per gram of fish per day. The measurement "g $O_2$ $g^{-1}$ $d^{-1}$" is equal to gram of oxygen per gram of fish per day.

| Parameter | Definition | pk | rrs | Source |
|---|---|---|---|---|
| | Consumption | | | |
| C | specific consumption rate (g $g^{-1}$ $d^{-1}$) | a | a | |
| CA | intercept of the allometric mass function | 3.5999 | 4.0330 | this study |
| CB | slope of the allometric mass function | -1.1602 | -1.0589 | this study |
| Cmax | maximum specific consumption rate (g $g^{-1}$ $d^{-1}$) | a | a | |
| CQ | water temperature dependent coefficient for consumption | 2.8847 | 3.8266 | this study |
| CTM | maximum temperature for consumption (°C) | 43.0 | 41.6 | this study |
| CTO | optimum temperature for consumption (°C) | 35.0 | 35.0 | this study |
| f(T) | temperature dependence function | a | a | |
| pc | proportion of total consumption | b | b | |
| T | water temperature (°C) | b | b | |
| W | fish weight (grams) | b | b | |

Table 1. – Continued

| Parameter | Definition | pk | rrs | Source |
|---|---|---|---|---|
| | Respiration | | | |
| ACT | activity multiplier | 1.0 | 1.0 | this study |
| R | specific respiration rate (g $O_2$ $g^{-1}$ $d^{-1}$) | a | a | |
| RA | intercept of the allometric mass function | 0.0453 | 0.0247 | this study |
| RB | slope of the allometric mass function | -0.5359 | -0.1252 | this study |
| RQ | water temperature dependent coefficient for respiration | 1.5965 | 1.5350 | this study |
| RTM | maximum temperature for consumption (°C) | 46.0 | 44.6 | Hanson et al. 1997 |
| RTO | optimum temperature for consumption (°C) | 43.0 | 41.6 | this study |
| S | proportion of Specific Dynamic Action | a | a | |
| SDA | specific dynamic action | 0.175 | 0.175 | Hanson et al. 1997 |
| | Egestion (fecal waste) | | | |
| F | specific egestion rate (g $g^{-1}$ $d^{-1}$) | a | a | |
| FA | constant proportion of consumption | 0.15 | 0.15 | Hanson et al. 1997 |
| | Excretion (nitrogenous waste) | | | |
| U | specific excretion rate (g $g^{-1}$ $d^{-1}$) | a | a | |
| UA | constant proportion of assimilated energy (C - F) | 0.1 | 0.1 | Hanson et al. 1997 |

Table 2. – Specific consumption (gram of prey per gram of fish per day, g $g^{-1}$ $d^{-1}$) and specific respiration (gram of oxygen per gram of fish per day, g $O_2$ $g^{-1}$ $d^{-1}$) observed at low conductivity (3,000 $\mu$S/cm) and high conductivity (30,000 $\mu$S/cm) and percent increase between conductivity levels for 1 – 5 g plains killifish and Red River shiner. For determination of slope and intercept, see Figures 8 and 9.

| | plains killifish | | | Red River shiner | | |
|---|---|---|---|---|---|---|
| | Low | High | % | Low | High | % |
| | | | Specific Consumption (g $g^{-1}$ $d^{-1}$) | | | |
| Intercept | 1.1407 | 2.9523 | | 0.0212 | 0.0201 | |
| Slope | -0.1547 | -0.4700 | | -0.0019 | -0.0006 | |
| Weight (g) | | | | | | |
| 1 | 0.9860 | 2.4823 | 152 | 0.5775 | 1.4767 | 156 |
| 2 | 0.8313 | 2.0123 | 142 | 0.4399 | 1.1462 | 161 |
| 3 | 0.6766 | 1.5423 | 128 | 0.3023 | 0.8157 | 170 |
| 4 | 0.5219 | 1.0723 | 105 | 0.1647 | 0.4852 | 195 |
| 5 | 0.3672 | 0.6023 | 64 | 0.0271 | 0.1547 | 471 |
| | | | Specific Respiration (g $O_2$ $g^{-1}$ $d^{-1}$) | | | |
| Intercept | 0.0119 | 0.0303 | | 0.0212 | 0.0201 | |
| Slope | 0.0004 | -0.0036 | | -0.0019 | -0.0006 | |
| Weight (g) | | | | | | |
| 1 | 0.0123 | 0.0267 | 117 | 0.0193 | 0.0195 | 1 |
| 2 | 0.0127 | 0.0231 | 82 | 0.0174 | 0.0189 | 9 |
| 3 | 0.0131 | 0.0195 | 49 | 0.0155 | 0.0183 | 18 |
| 4 | 0.0135 | 0.0159 | 18 | 0.0136 | 0.0177 | 30 |
| 5 | 0.0139 | 0.0123 | -13 | 0.0117 | 0.0171 | 46 |

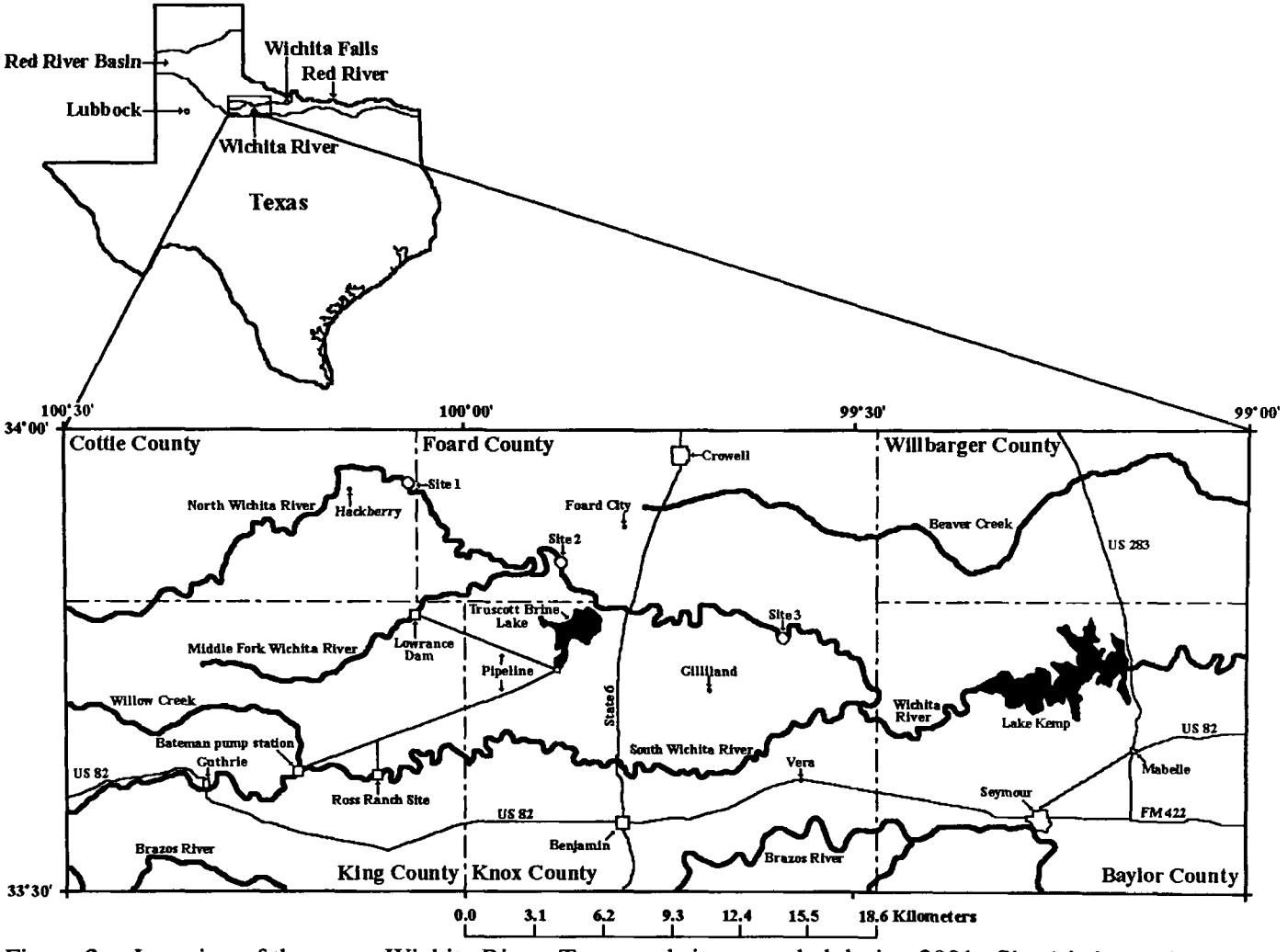


Figure 2. – Location of the upper Wichita River, Texas and sites sampled during 2001. Site 1 is located east of Hackberry, Texas. Site 2 is located west of Foard City, Texas. Site 3 is located northeast of Gilliland, Texas.

# CHAPTER III

# RESULTS

## Model Development

The greatest mean consumption occurred at 35°C for both species, so this temperature was considered to be the CTO (Figure 3). Therefore, data collected at 35°C were used to determine consumption parameters. I used nonlinear regression to determine the weight-specific consumption function of specific consumption on fish weight as:

$$Cmax = 3.5999 \times W^{-1.1602} \text{ for the plains killifish (Figure 4), and} \quad (20)$$

$$Cmax = 4.033 \times W^{-1.0589} \text{ for the Red River shiner (Figure 4).} \quad (21)$$

The best-fit estimate of CQ from species specific consumption parameters in the specific consumption equation was 2.8847 for the plains killifish and 3.8266 for the Red River shiner.

The greatest mean respiration occurred at 30°C for the plains killifish and at 35°C for the Red River shiner, and was considered to be the RTO (Figure 5). Therefore, information collected at 30°C for the plains killifish and 35°C for the Red River shiner were used to determine respiration parameters. Using nonlinear regression I determined the weight-specific respiration function of specific respiration on fish weight as:

$R = 0.0453 \times W^{-0.5359}$ for the plains killifish (Figure 6), and (22)

$R = 0.0247 \times W^{-0.1252}$ for the Red River shiner (Figure 6). (23)

The best-fit estimate of RQ from species specific respiration parameters in the specific respiration equation analyzed with SAS was 1.5965 for the plains killifish and 1.5350 for the Red River shiner.

The mean of 12 CTMax measurements for the plains killifish and for the Red River shiner was 43.0 and 41.6°C, respectively. These temperatures were used to approximate RTO as 43.0°C and RTM as 46°C for the plains killifish and 41.6°C and 44.6°C, respectively, for the Red River shiner.

Sensitivity Analysis

The parameter pc had a Pearson correlation coefficient greater than or equal to 0.7949 for all tested normal distributions (2, 10, and 20%) for both species. This implies pc was strongly correlated with variation in final predicted weights. All other parameters had a Pearson correlation coefficient less than or equal to 0.2688 for all normal distributions. For the plains killifish, the parameters pc, UA, SDA, CA, and FA were the most influential ($p < 0.05$) parameters accounting for the greatest variance in the models predicted growth for all tested normal distributions (Table 3). CTM was influential ($p < 0.05$) in accounting for the greatest variance in predicted growth for the 20% normal

distribution only. For the Red River shiner, the parameters pc, UA, SDA, CA, and CTM were the most influential ($p < 0.05$) parameters, and accounted for the greatest variation in predicted growth (Table 4). CTM was influential ($p < 0.05$) in accounting for the greatest variance in predicted growth for 10 and 20% normal distributions only. For both species, no other parameters were found to be strongly correlated ($p < 0.05$) with variation in final predicted weights.

Model Application

A fungal outbreak was detected on day 20 of the 30-day feeding experiment in the plains killifish and the experiment was terminated. No disease or stress was noticed during the entire 30 days of the Red River shiner experiment. The mean initial weight for the ten plains killifish was 5.0875 g, which increased to 5.1241 after 19 days. For the Red River shiner, the mean initial weight was 2.1831, which decreased to 1.8734 after 30 days. The bioenergetics model predicted the observed growth within 0.01 percent error when pc equaled 0.3286 for the plains killifish and 0.1594 for the Red River shiner. A pc range of 0.10 to 0.40 was used in the model simulations because it encompassed both pc values and provided more realistic predictions of fish growth.

The assessment of the final Fish Bioenergetics 3.0 predicted weights determined there was a difference between predicted growth rates of the plains killifish and Red River shiner (Appendix C). The Red River shiner had a metabolic advantage at smaller initial weights and lower pc. At smaller initial weights and a high pc and larger weights at all pc, the plains killifish had a metabolic advantage. This was generally the case for

all experimental temperatures except 30 and 35°C. At 30°C, there was no difference between predicted weights at an initial weight of 5 g and a pc of 0.10 to 0.30. At all other initial weights and pc values the Red River shiner had greater growth. For the 35°C simulation, the Red River shiner exhibited greater growth at all initial weights and pc. This pattern in final weights may be explained by respiration for each species.

The plains killifish has high energetic costs associated with respiration at small sizes but this decreases as size increases. Although the energetic cost of respiration also decreases with weight for the Red River shiner, the difference between respiration costs at small and large weights is less than that of the plains killifish. This results in the plains killifish having greater respiration costs at smaller weights and lower respiration costs at larger weights when compared to the Red River shiner (Figure 7). The exceptions to this general pattern occurred at 30°C and a pc of 1.00 and at 35°C and a pc ranging from 0.30 to 0.40 where respiration was nearly equal for both species at smaller sizes and greater for the Red River shiner at larger sizes (Figure 8). The Red River shiner had greater respiration costs at large sizes for these scenarios and at all sizes at 35°C with a pc of 1.00 (Figure 8).

For both species, predicted growth rates differed as temperature differed (Appendix C). Model output of final weights for each initial weight, pc, and species generally increased with each successive temperature up to 35°C and then rapidly decreased at 40°C. This pattern of growth signifies that temperature was important in determination of growth which is to be expected because fish are ectothermic. The resulting decrease in growth as a result of the greater temperatures was larger for the Red

River shiner than for the plains killifish. This difference in decreasing growth for each species at the elevated temperatures is important because the summer environment these fish live in is often above 35°C.

Food consumption for the plains killifish and Red River shiner at high salinity was greater than that at low salinity (Figure 9). Slopes of regressions of food consumption on mass differed ($p = 0.0080$) between high and low salinity experiments in the plains killifish. Food consumption (fc) was related to mass (wt) according to the equation $fc = 2.9523 - wt*0.4700$ in the high salinity experiment, and $fc = 1.1407 - wt*0.1547$ in the low salinity experiment. For the plains killifish high salinity experiment, the intercept was 2.9523 (0.2763 standard error [SE]) and the slope was -0.4700 (0.1051 SE). For the plains killifish low salinity experiment, the intercept was 1.1407 (0.1527 SE) and the slope was -0.1547 (0.0439 SE). The slope and intercept for the high and low salinity experiments did not overlap and differed significantly. There was a 152% increase in food consumption at high salinity over that at low salinity for a 1 g plains killifish. Food consumption increased only 64% at high salinity over that at low salinity for a 5 g plains killifish. There was no significant interaction ($p = 0.1045$) between weight and salinity for the Red River shiner consumption experiments. For the Red River shiner, food consumption (fc) was related to mass (wt) according to the equation $fc = 1.8072 - wt*0.1527$ in the high salinity experiment, and $fc = 0.7151 - wt*0.1430$ in the low salinity experiment. There was a 156% increase in food consumption at high salinity over that at low salinity for 1 g Red River shiner which was

similar to the plains killifish. However, there was a 471% increase in food consumption at high salinity over that at low salinity for a 5 g Red River shiner.

Respiration for the plains killifish at high salinity was greater than that at low salinity with the exception of 5 g fish (Figure 10). Slopes of regressions of food consumption on mass differed ($p = 0.0019$) between high and low salinity experiments in the plains killifish. Respiration (R) was related to mass (wt) according to the equation $R = 0.0303 - wt*0.0036$ in the high salinity experiment, and $R = 0.0119 - wt*0.0034$ in the low salinity experiment. For the plains killifish high salinity experiment, the intercept was 0.0303 (0.0032 SE) and the slope was -0.0036 (0.0010 SE). For the plains killifish low salinity experiment, the intercept was 0.0119 (0.0019 SE) and the slope was -0.0034 (0.0005 SE). The slope and intercept for the high and low salinity experiments did not overlap and differed significantly. This decrease in respiration at 5 g is likely due to low sample size at larger weights for the plains killifish. There was a 117% increase in respiration at high salinity over that of low salinity for a 1 g plains killifish. Respiration decreased 13% at high salinity over that of low salinity for a 5 g plains killifish. There was no significant interaction ($p = 0.4437$) between weight and salinity for the Red River shiner respiration experiments. For the Red River shiner, Respiration (R) was related to mass (wt) according to the equation $R = 0.0201 - wt*0.0006$ in the high salinity experiment, and $R = 0.0212 - wt*0.0019$ in the low salinity experiment. There was a negative relationship between respiration and salinity for the Red River shiner (Figure 10). There was only a 1% increase in respiration at high salinity over that of low salinity

for a 1 g Red River shiner. Respiration increased 46% at high salinity over that of low salinity for a 5 g Red River shiner.

## Field Study

Conductivities measured during field studies ranged from 22,830 to 31,900 μS/cm at the upstream site, 2,600 to 32,740 μS/cm at the middle site, and 3,840 to 24,590 μS/cm at the downstream site (Figure 11). Conductivities exceeded 30,000 μS/cm, which is believed to be the level that excludes salt-intolerant species (Ostrand and Wilde 2001 2002), only during the July 26, 2001 sampling trip at the upstream and middle sites. The water temperatures recorded at the three study sites during the field study are presented in Figure 12. The greatest water temperature recorded in the field was 36.5°C for the upstream site, 37.8°C at the middle site, and 37.8°C at the downstream site.

The plains killifish and the Red River pupfish were the only two salt-tolerant fishes collected during field sampling (Table 5). Nine species of salt-intolerant fish were collected. Abundance of both of these groups in the upstream site showed little fluctuation between dates with the fish assemblage being dominated by salt-tolerant species throughout the sampling period (Figure 13). The fish assemblage at the middle site was dominated by salt-tolerant species until a major rain event on 13 August 2001 (Figure 14). Fish were not collected from this site on this date because of high water. After this rain event, the fish assemblage was composed equally of salt-tolerant and intolerant species. Salt-intolerant species dominated at the downstream site early but as

the summer progressed, salt-tolerant species became more dominant even though salinity decreased (Figure 15).

Table 3. Results of the error analysis for the plains killifish bioenergetics model with 2%, 10%, and 20% variance of parameter nominal numbers. Absolute values of Pearson correlation coefficients were used to rank parameters.

| | 2% | | | 10% | | | 20% | | |
|---|---|---|---|---|---|---|---|---|---|
| Rank | Parameter | Coefficient | p | Parameter | Coefficient | p | Parameter | Coefficient | p |
| 1 | pc | 0.8573 | <0.0001 | pc | 0.8277 | <0.0001 | pc | 0.7949 | <0.0001 |
| 2 | UA | 0.2688 | <0.0001 | UA | 0.2505 | <0.0001 | UA | 0.2292 | <0.0001 |
| 3 | SDA | 0.2657 | <0.0001 | SDA | 0.2478 | <0.0001 | SDA | 0.2245 | <0.0001 |
| 4 | CA | 0.2269 | <0.0001 | CA | 0.2176 | <0.0001 | CA | 0.2032 | <0.0001 |
| 5 | FA | 0.2264 | <0.0001 | FA | 0.2151 | <0.0001 | FA | 0.1803 | <0.0001 |
| 6 | CTO | 0.0452 | 0.1549 | CTM | 0.0622 | 0.0812 | CTM | 0.0848 | 0.0315 |
| 7 | CTM | 0.0411 | 0.1952 | RTM | 0.0589 | 0.0992 | RTM | 0.0696 | 0.0774 |
| 8 | RQ | 0.0409 | 0.1971 | RQ | 0.0565 | 0.1133 | RQ | 0.0459 | 0.2449 |
| 9 | RTM | 0.0348 | 0.2727 | ACT | 0.0469 | 0.1888 | RTO | 0.0373 | 0.3445 |
| 10 | RTO | 0.0330 | 0.2981 | RB | 0.0369 | 0.3019 | CQ | 0.0281 | 0.4763 |
| 11 | RB | 0.0313 | 0.3247 | CB | 0.0312 | 0.3825 | CB | 0.0261 | 0.5091 |
| 12 | RA | 0.0292 | 0.3579 | RTO | 0.0294 | 0.4104 | RB | 0.0218 | 0.5812 |
| 13 | ACT | 0.0239 | 0.4510 | CTO | 0.0161 | 0.6520 | RA | 0.0198 | 0.6162 |
| 14 | CB | 0.0181 | 0.5680 | RA | 0.0052 | 0.8845 | ACT | 0.0128 | 0.7468 |
| 15 | CQ | 0.0020 | 0.9497 | CQ | 0.0028 | 0.9382 | CTO | 0.0064 | 0.8717 |

Table 4. – Results of the error analysis for the Red River shiner bioenergetics model with 2%, 10%, and 20% variance of parameter nominal numbers. Absolute values of Pearson correlation coefficients were used to rank parameters.

| | 2% | | | 10% | | | 20% | | |
|---|---|---|---|---|---|---|---|---|---|
| Rank | Parameter | Coefficient | p | Parameter | Coefficient | p | Parameter | Coefficient | p |
| 1 | pc | 0.9202 | <0.0001 | pc | 0.88706 | <0.0001 | pc | 0.8378 | <0.0001 |
| 2 | UA | 0.2185 | <0.0001 | UA | 0.20664 | <0.0001 | UA | 0.1939 | <0.0001 |
| 3 | SDA | 0.1904 | <0.0001 | SDA | 0.14972 | <0.0001 | SDA | 0.1497 | 0.0002 |
| 4 | FA | 0.1663 | <0.0001 | CA | 0.14914 | <0.0001 | CA | 0.1401 | 0.0005 |
| 5 | CA | 0.1519 | <0.0001 | FA | 0.13748 | 0.0001 | FA | 0.1210 | 0.0026 |
| 6 | CTO | 0.0426 | 0.1799 | CTM | 0.07135 | 0.0484 | CTM | 0.0917 | 0.0228 |
| 7 | RQ | 0.0422 | 0.1839 | RTM | 0.05423 | 0.1338 | RTM | 0.0584 | 0.1475 |
| 8 | CTM | 0.0406 | 0.2015 | RQ | 0.04054 | 0.2625 | RQ | 0.0492 | 0.2225 |
| 9 | RTM | 0.0374 | 0.2391 | ACT | 0.03853 | 0.2868 | CQ | 0.0396 | 0.3261 |
| 10 | RB | 0.0305 | 0.3369 | RTO | 0.03448 | 0.3406 | CB | 0.0310 | 0.4420 |
| 11 | RTO | 0.0300 | 0.3456 | CB | 0.03309 | 0.3605 | RB | 0.0295 | 0.4651 |
| 12 | ACT | 0.0227 | 0.4755 | RB | 0.02982 | 0.4098 | RTO | 0.0178 | 0.6586 |
| 13 | RA | 0.0222 | 0.4854 | CQ | 0.01995 | 0.5815 | CTO | 0.0156 | 0.6996 |
| 14 | CB | 0.0209 | 0.5110 | CTO | 0.01795 | 0.6200 | RA | 0.0154 | 0.7024 |
| 15 | CQ | 0.0089 | 0.7794 | RA | 0.01572 | 0.6640 | ACT | 0.0139 | 0.7296 |

Table 5. – Species collected and their relative (%) abundance from upstream (1), middle (2), and downstream sites (3) on the North Wichita River. Sampling was conducted from 11 June 2001 to 1 September 2001. High river flow prevented collection in the middle site on 13 August 2001.

| | | June 11 | | | June 25 | | | July 9 | | |
|---|---|---|---|---|---|---|---|---|---|---|
| Common name | Scientific name | 1 | 2 | 3 | 1 | 2 | 3 | 1 | 2 | 3 |
| bluegill | Lepomis macrochirus | 0.0 | 0.2 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| fathead minnow | Pimephales promelas | 0.0 | 0.0 | 0.1 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.1 |
| gizzard shad | Dorosoma cepedianum | 0.0 | 0.0 | 2.3 | 0.0 | 0.1 | 0.1 | 0.0 | 0.0 | 0.0 |
| green sunfish | Lepomis cyanellus | 0.0 | 0.1 | 0.0 | 0.0 | 0.1 | 0.0 | 0.0 | 0.0 | 0.0 |
| mosquitofish | Gambusia affinis | 2.4 | 2.2 | 0.0 | 1.2 | 1.6 | 0.3 | 3.4 | 11.9 | 0.3 |
| plains killifish | Fundulus zebrinus | 29.8 | 6.9 | 3.2 | 39.8 | 27.0 | 24.0 | 41.9 | 28.3 | 61.7 |
| plains minnow | Hybognathus placitus | 0.0 | 0.0 | 10.2 | 0.0 | 0.0 | 11.0 | 0.0 | 0.0 | 0.1 |
| Red River pupfish | Cyprinodon rubrofluviatilis | 64.7 | 57.2 | 15.0 | 58.2 | 55.4 | 15.0 | 52.8 | 34.2 | 10.9 |
| Red River shiner | Notropis bairdi | 0.0 | 0.0 | 0.4 | 0.0 | 0.0 | 0.0 | 0.7 | 9.7 | 1.7 |
| red shiner | Cyprinella lutrensis | 3.2 | 33.1 | 67.0 | 0.8 | 15.4 | 48.0 | 1.2 | 15.9 | 25.2 |
| speckled chub | Macrhybopsis aestivalis | 0.0 | 0.3 | 1.7 | 0.0 | 0.4 | 1.6 | 0.0 | 0.0 | 0.1 |
| | Total | 931 | 1009 | 688 | 601 | 800 | 928 | 676 | 421 | 1574 |

Table 5. – Continued.

| Common name | Scientific name | July 26 | | | August 13 | | | September 1 | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | 1 | 2 | 3 | 1 | 2 | 3 | 1 | 2 | 3 |
| bluegill | Lepomis macrochirus | 0.0 | 0.0 | 0.0 | 0.0 | - | 0.0 | 0.0 | 0.0 | 0.0 |
| fathead minnow | Pimephales promelas | 0.0 | 0.0 | 0.0 | 0.0 | - | 0.0 | 0.0 | 0.0 | 0.0 |
| gizzard shad | Dorosoma cepedianum | 0.0 | 0.0 | 0.0 | 0.0 | - | 0.1 | 0.0 | 0.0 | 0.0 |
| green sunfish | Lepomis cyanellus | 0.0 | 0.0 | 0.0 | 0.0 | - | 0.0 | 0.0 | 0.0 | 0.0 |
| mosquitofish | Gambusia affinis | 1.4 | 22.6 | 0.8 | 3.4 | - | 0.2 | 0.0 | 2.6 | 2.2 |
| plains killifish | Fundulus zebrinus | 34.3 | 30.0 | 54.7 | 46.3 | - | 44.3 | 42.7 | 50.0 | 68.6 |
| plains minnow | Hybognathus placitus | 1.4 | 0.3 | 0.8 | 0.0 | - | 3.5 | 0.0 | 0.9 | 0.6 |
| Red River pupfish | Cyprinodon rubrofluviatilis | 62.8 | 44.0 | 21.8 | 50.3 | - | 48.8 | 49.1 | 0.0 | 21.8 |
| Red River shiner | Notropis bairdi | 0.0 | 3.1 | 1.5 | 0.0 | - | 3.0 | 3.8 | 37.7 | 2.8 |
| red shiner | Cyprinella lutrensis | 0.0 | 0.1 | 18.5 | 0.0 | - | 0.1 | 4.4 | 8.8 | 3.9 |
| speckled chub | Macrhybopsis aestivalis | 0.0 | 0.0 | 1.7 | 0.0 | - | 0.1 | 0.0 | 0.0 | 0.1 |
| | Total | 1259 | 753 | 1896 | 1082 | 0 | 1062 | 888 | 228 | 821 |

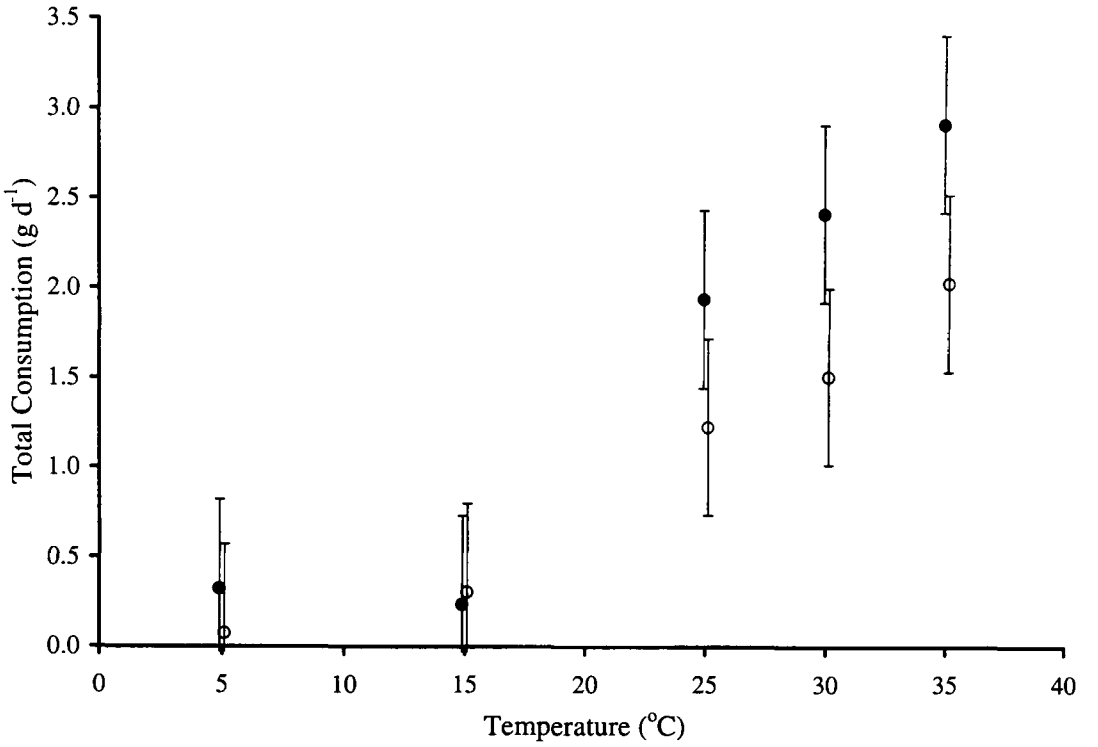


Figure 3. Mean total consumption (grams of prey per day, g $d^{-1}$) by the plains killifish (closed circles) and Red River shiner (open circles) at each of five experimental temperatures measured during laboratory studies.

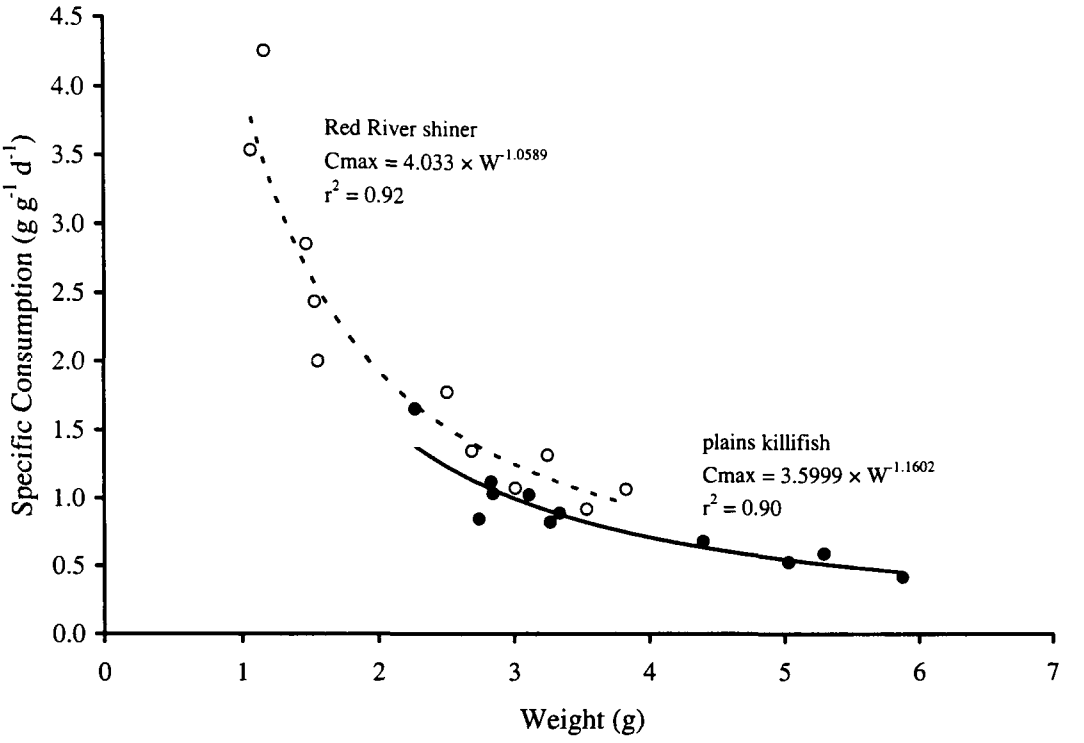


Figure 4. – Specific consumption (gram of prey per gram of fish per day, g $g^{-1}$ $d^{-1}$) of plains killifish (closed circles) and Red River shiner (open circles) at 35°C.

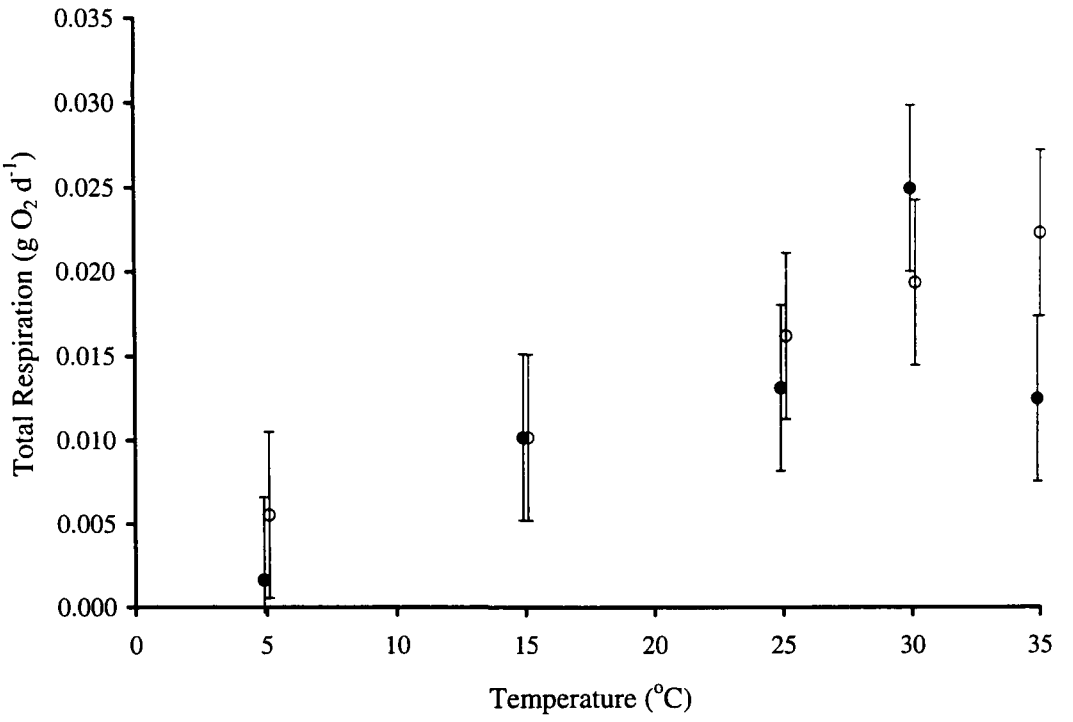


Figure 5. – Mean total respiration (gram of oxygen per day, g $O_2$ $d^{-1}$) by the plains killifish (closed circles) and Red River shiner (open circles) at each of five experimental temperatures measured during laboratory studies.

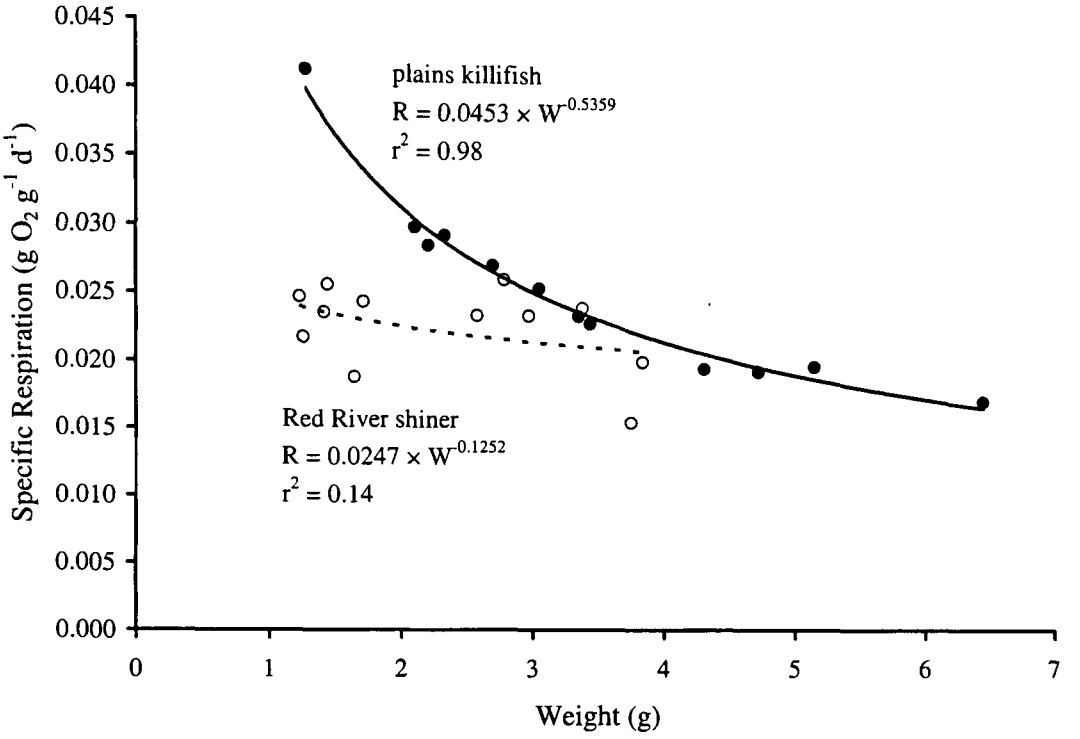


Figure 6. – Specific respiration (gram of oxygen per gram of fish per day, g $O_2$ $g^{-1}$ $d^{-1}$) for the plains killifish (closed circles) and Red River shiner (open circles) at 35°C.

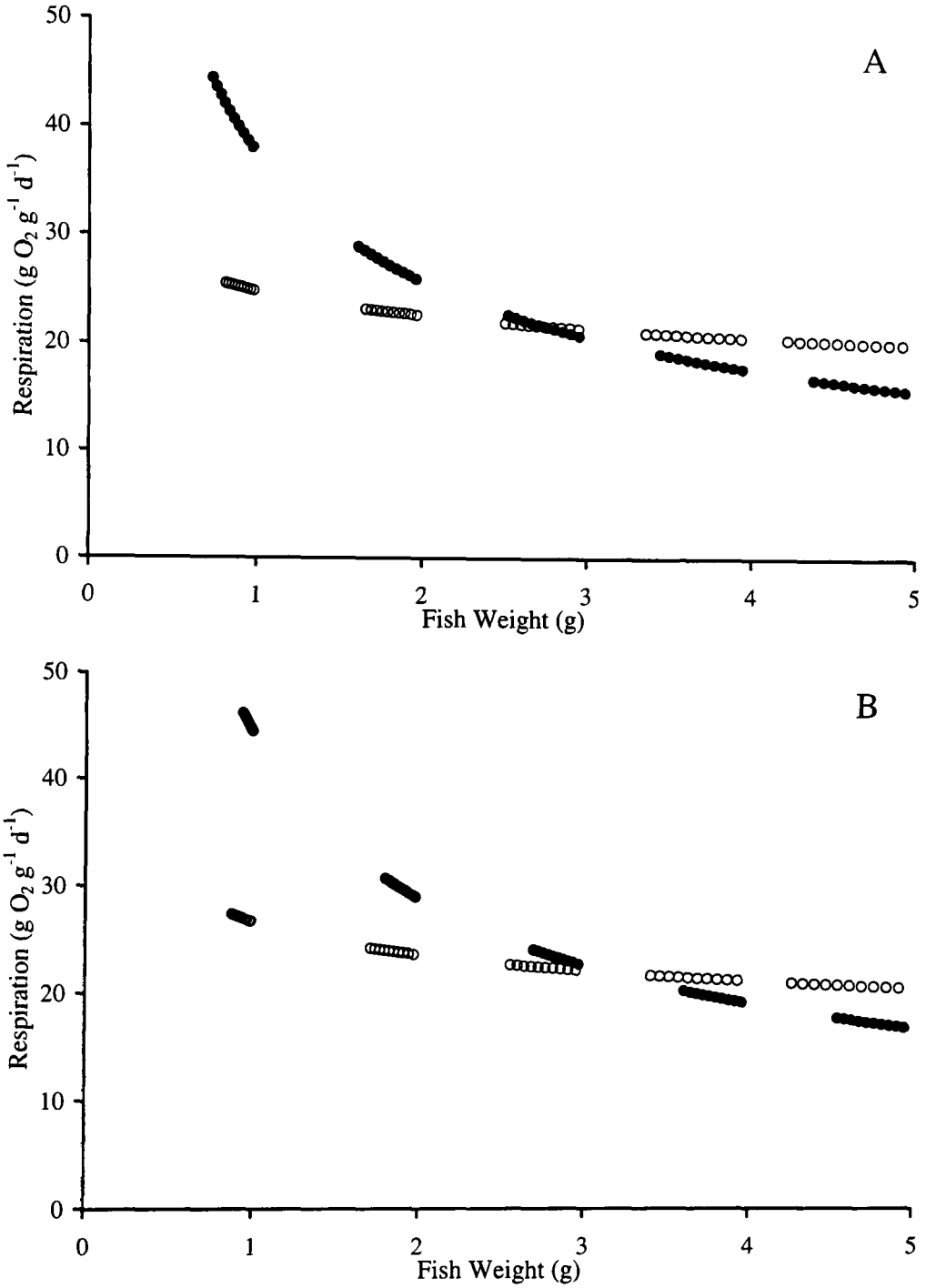


Figure 7. – Example of the general pattern of respiration rates (gram of oxygen per gram of fish per day, g $O_2$ $g^{-1}$ $d^{-1}$) observed for the plains killifish (closed circles) and the Red River shiner (open circles). Both graphs are for 5°C, with proportion of consumption equal to 0.10 (A) and 1.00 (B).

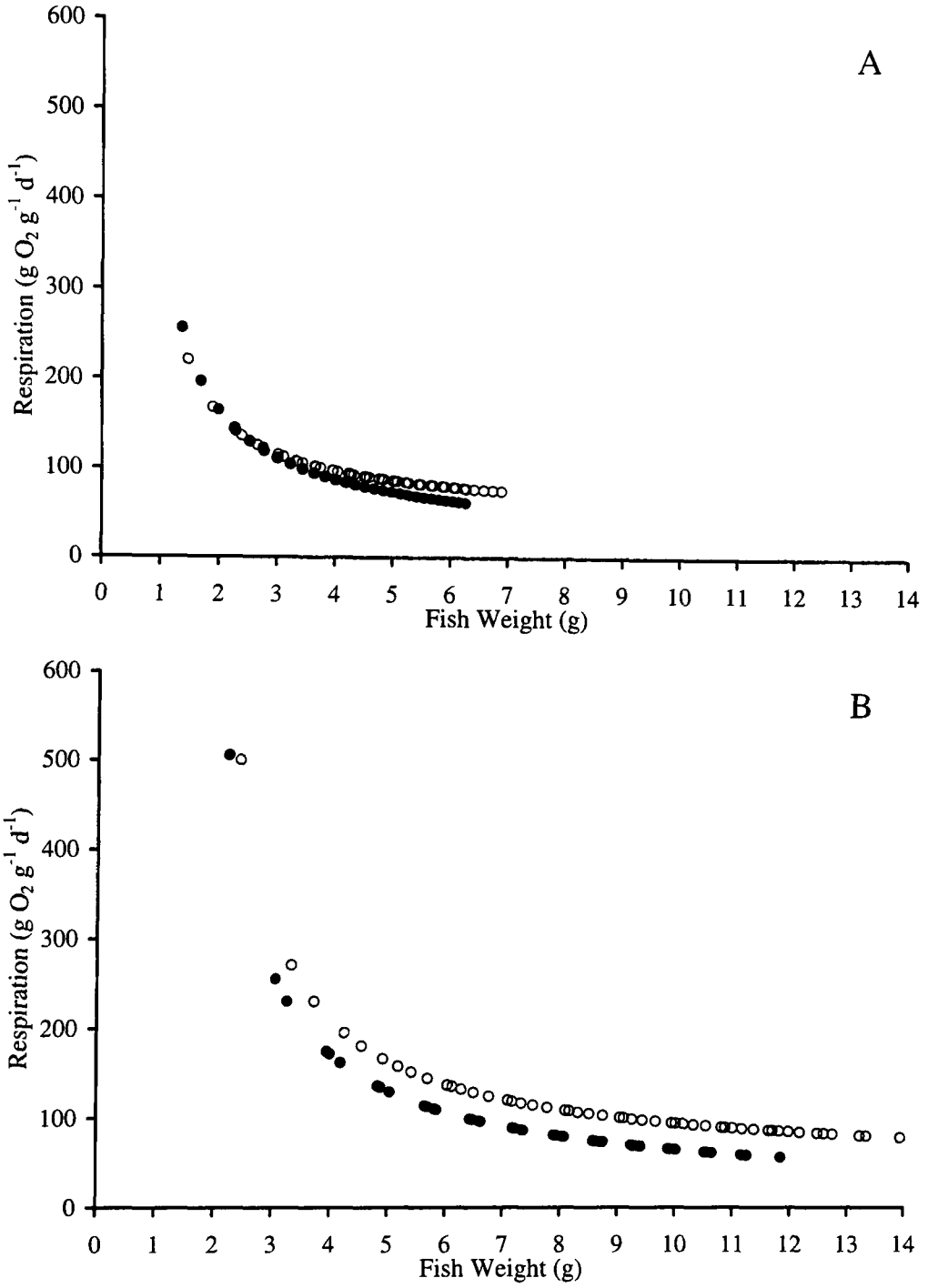


Figure 8. – Example of exceptions to the pattern of respiration rates (gram of oxygen per gram of fish per day, g $O_2$ $g^{-1}$ $d^{-1}$) observed for the plains killifish (closed circles) and the Red River shiner (open circles). Both graphs are for 35°C, with proportion of consumption equal to 0.35 (A) and 1.00 (B).

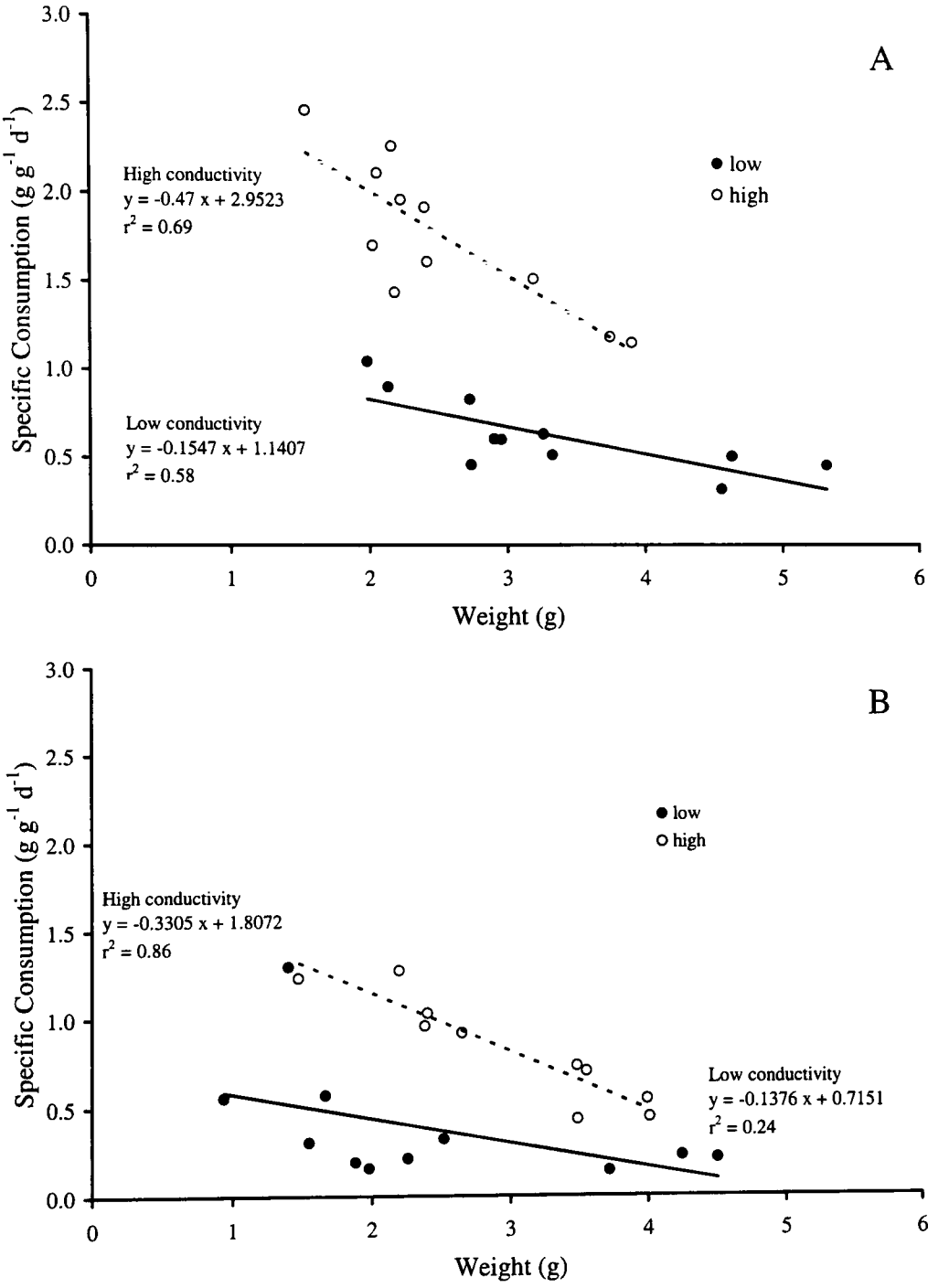


Figure 9. – Comparison of specific consumption (gram of prey per gram of fish per day, g $g^{-1}$ $d^{-1}$) of the plains killifish (A) and Red River shiner (B) at low (closed circles) and high (open circles) salinity.

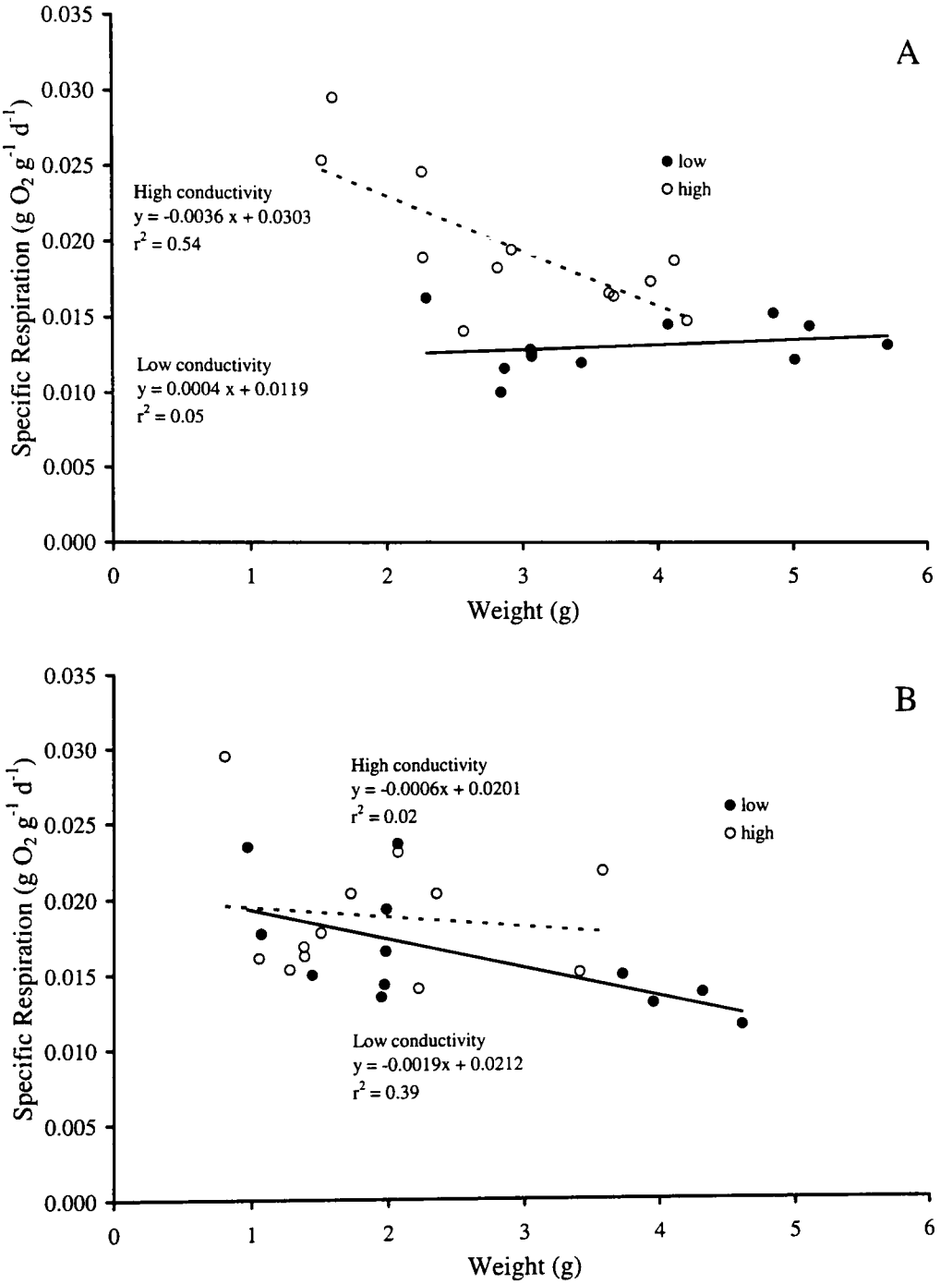


Figure 10. – Comparison of specific respiration (gram of oxygen per gram of fish per day, g $O_2$ $g^{-1}$ $d^{-1}$) of the plains killifish (A) and Red River shiner (B) at low (closed circles) and high (open circles) salinity.

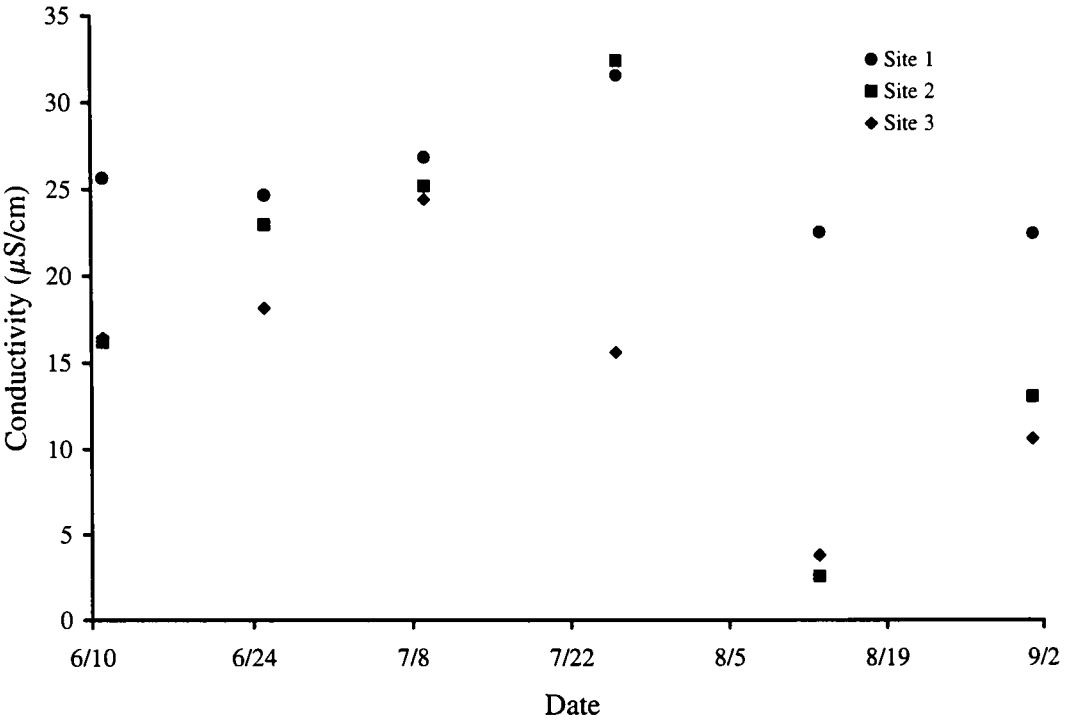


Figure 11. – Conductivity (micro Siemens per centimeter, µS/cm) measured at the upstream (1), middle (2), and downstream (3) site on the North Wichita River, during 2001.

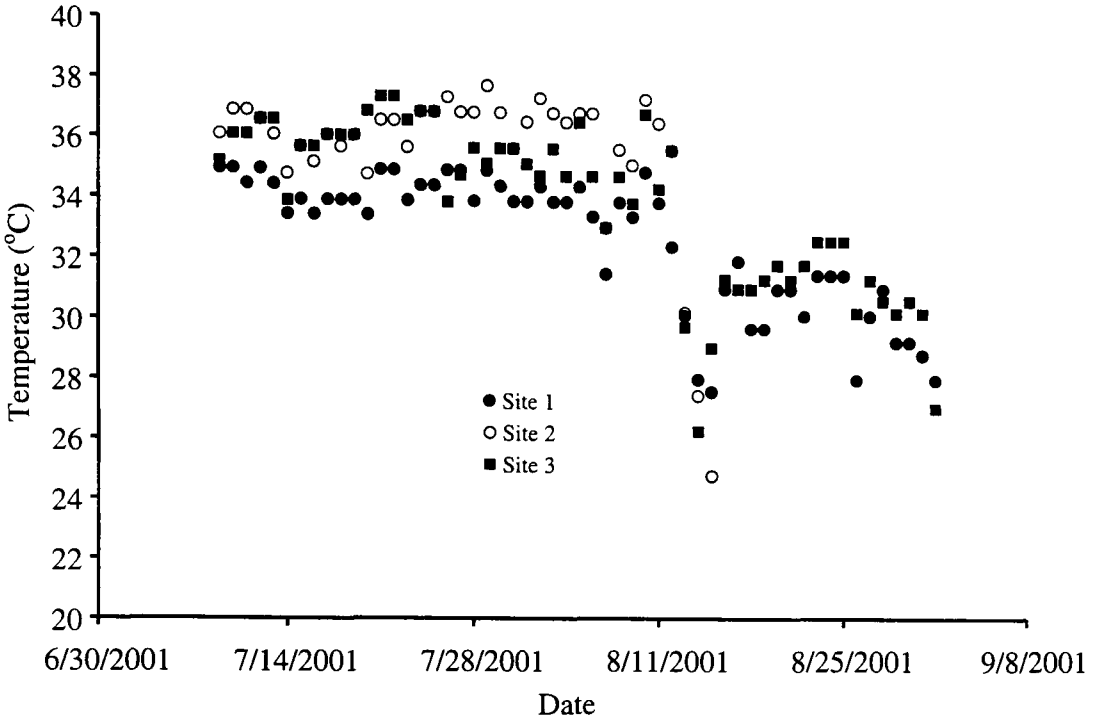


Figure 12. – Maximum water temperatures measured from the upstream (1), middle (2), and downstream (3) site on the North Wichita River, during 2001.

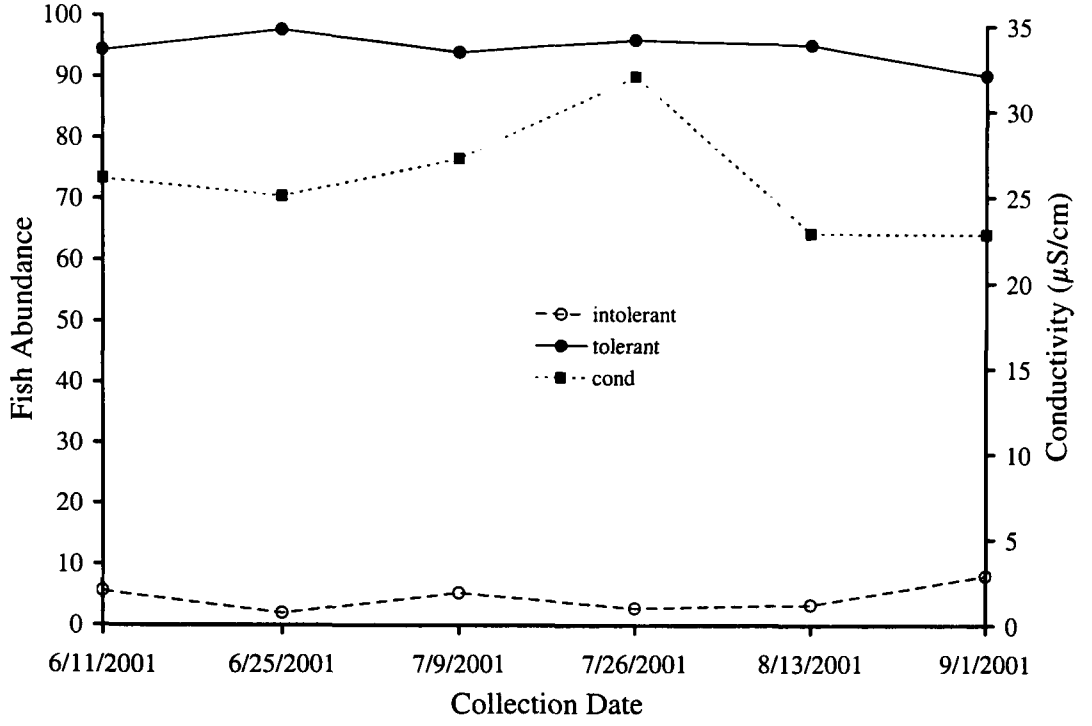


Figure 13. – Abundance of salt tolerant (closed circles) and intolerant (open circles) fishes and conductivity (micro Seimens per centimeter, µS/cm, closed squares) measured from the upstream site on the North Wichita River from 11 June 2001 to 1 September 2001.

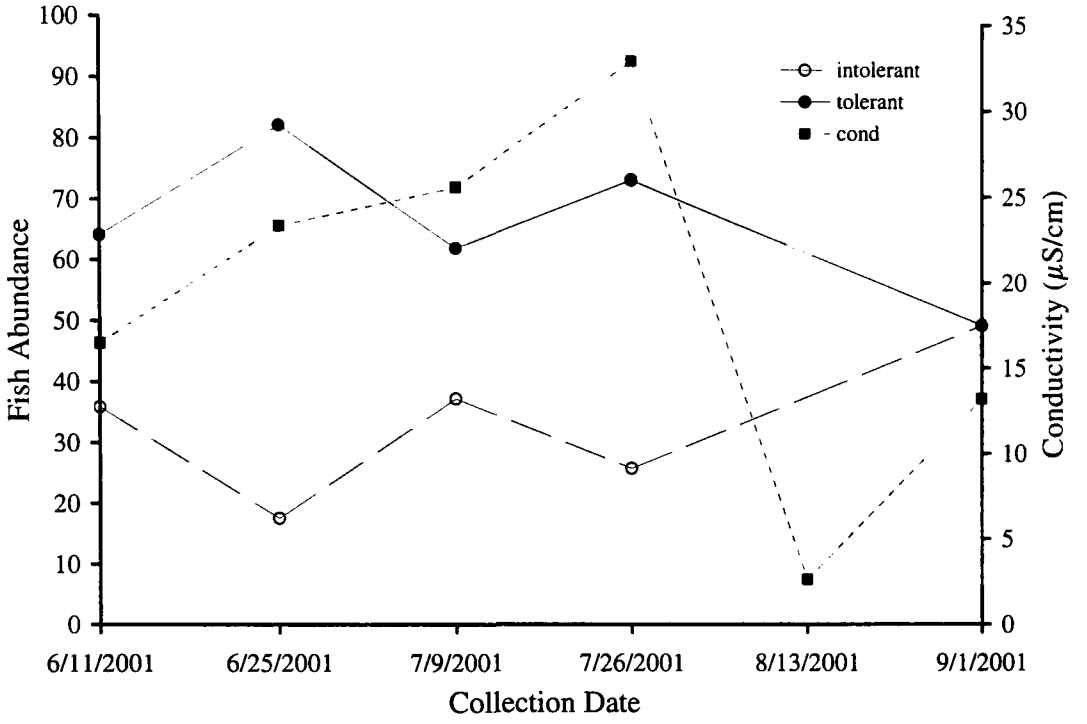


Figure 14. – Abundance of salt tolerant (closed circles) and intolerant (open circles) fishes and conductivity (micro Seimens per centimeter, µS/cm, closed squares) measured from the middle site on the North Wichita River from 11 June 2001 to 1 September 2001.

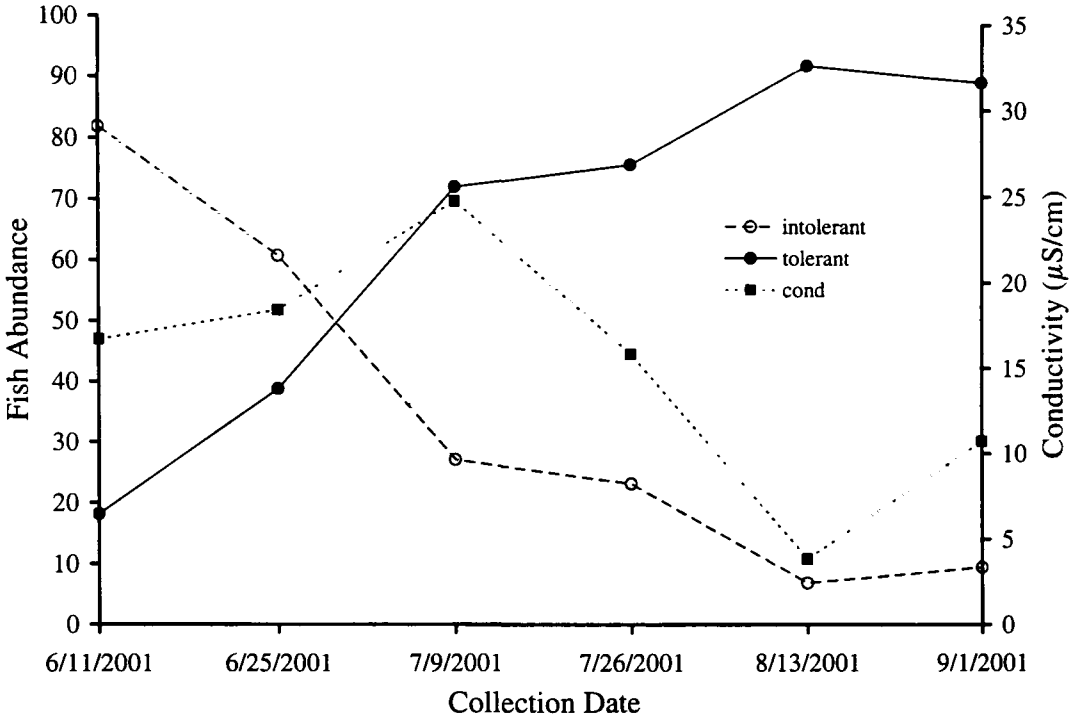


Figure 15. – Abundance of salt tolerant (closed circles) and intolerant (open circles) fishes and conductivity (micro Seimens per centimeter, µS/cm, closed squares) measured from the downstream site on the North Wichita River from June 11, 2001 to September 1, 2001.

# CHAPTER IV

# DISCUSSION

## Model Development

For each species, CA was greater and CB was less than values reported by Hanson et al. (1997) for any other warmwater species. For the plains killifish, RA was greater and RB was less than values reported by Hanson et al. (1997) for any other warmwater species. RA and RB for the Red River shiner were within the range reported by Hanson et al. (1997) for other warmwater species. All plains killifish and Red River shiner parameter values falling outside the range of values for other warmwater fish are probably indicative of the extreme environments these fish live in. Both species not only had a CTMax higher than values reported by Hanson et al. (1997) for any other warmwater species but routinely survived water temperatures at or above all other reported CTMax values. These freshwater species also experienced salinity at or exceeding saltwater environments.

## Sensitivity Analysis

The results of the EA and Pearson correlation ranking establish that the parameter pc was by far the most likely parameter associated with variance in the predicted growth for both species. Other significant ($p < 0.05$) parameters included UA, SDA, CA, FA, and CTM. CA, CTM, and pc are consumption parameters, SDA is a respiration parameter, and UA and FA are waste parameters. However, in the development of my models, I did

not directly measure SDA, UA, and FA. These parameters were found by estimating them as a proportion of consumption and therefore, are directly linked to the consumption parameters. This implies that consumption, and respiration and waste, accounts for most of the variance in the model predictions of growth and should receive the greatest effort in determination of its nominal values.

Model Application

At low salinity, the Red River shiner has a small metabolic advantage over the plains killifish, primarily at temperatures from 30 to 35°C. This small metabolic advantage may be indicative of the relatively small native range (i.e., found only in the Red River basin) and specialization of the Red River shiner as compared to the large metabolic advantage (all other temperatures) and large native range of the plains killifish (i.e., many rivers within the Great Plains). It appears the Red River shiner will experience better growth during the summer because temperatures measured in the field were often within the range of metabolic advantage for the Red River shiner (30 to 35°C). However, the water temperature in the Wichita River frequently reaches 35°C and greater during the hottest time of summer days and is well below 30°C for many months during fall, winter, and spring. During these times, larger plains killifish are at an advantage which may allow them to stockpile energy increasing their chances to survive during the harsh summer days.

For each species, there was generally an increase in final weights with each increase in temperature up to 35°C and then weights decreased at 40°C. This implies that

high temperatures increase metabolic needs reducing the amount of energy allotted for growth. High temperatures negatively affect both species but because the CTMax of the plains killifish (43.0°C) is greater than that of the Red River shiner (41.6°C), it is capable of surviving at greater temperatures. The high water temperatures can be expected to increase if chloride control structures are implemented or the current pattern of global warming continues. It is likely the Red River shiner will be extirpated first from the Wichita River because of its decreased growth at greater temperatures and its lower CTMax.

The plains killifish has less metabolic demands for respiration and waste at adult size during the cooler months and can place more energy into spawning. The plains killifish may be able to spawn earlier or more successfully, through more eggs or larger yolk sac per egg, because of its advantage in growth during cooler temperatures. With the potentially more successful spawning characteristics, the fry of the plains killifish may be better able to take advantage of resources before the fry of the Red River shiner. This may, overall, confer a metabolic advantage to the plains killifish.

The difference in predicted growth rates at identical temperatures, consumption at low and high salinity, and predicted growth rates as temperature increases for the plains killifish and Red River shiner suggests that prolonged isolation in pools will affect the composition of the fish assemblage. It is expected that species with greater temperature and salinity tolerances like the plains killifish will have a greater survivability under the conditions expected from implementation of chloride control structures. Assuming there are no sources of saline groundwater entering the stream below chloride control

structures or that sources are less saline, salinity in pools may be lower than periods prior to chloride control implementation. However, it is more likely that the extended period that the river is pooled would result in increased salinity due to evaporation.

Other physical factors besides temperature, such as stream discharge, have been found to affect fish success and recolonization rates in rivers and may affect fish assemblage compositions (Kushlan 1976; Harrell 1978; Matthews and Styron 1981; Tonn and Magnuson 1982; Schlosser 1982; Wilde and Ostrand 1999). Fish that are adapted to survive periods of low stream discharge, which occurs during droughts, in insolated areas may have a competitive advantage in regaining former population levels over fish that must recolonize from downstream (Tramer 1977). Fausch and Bramblett (1991) categorized the plains killifish as a non-colonizing species because it did not migrate far upstream after flows resumed in a creek that dried during summer drought conditions. This suggests that the plains killifish may become extirpated in the North Wichita River if they are unable to survive even one period of increased high temperature such as could occur during periods of no flow conditions. Although data on the colonizing abilities of the Red River shiner are not available, it probably can be expected that they would also be extirpated in the North Wichita River if unable to survive even one period of increased high temperatures such as those that occur in longer periods of no flow conditions.

As the volume of water within the river decreases, fish are confined to a decreasing habitat. This may increase competition for available resources such as food and make fish more vulnerable to parasites and bacterial infection (Matthews and Zimmerman 1990). Coupled with the crowding is a decrease in area of aquatic

productivity which potentially decreases food abundance. It is more likely that the plains killifish can achieve its metabolic needs more easily because the increase in food consumption in high salinity environments for it is less than that for the Red River shiner, especially at larger weights. The large increase in food consumption at high salinity for the Red River shiner makes it less likely to meet its metabolic demands especially at larger weights. The decreased food availability and increased food requirements would further stress both species however this stress is likely greater for the Red River shiner. My data suggest that the plains killifish would have a better survivability within the altered stream conditions that occur from implementation of chloride control structures.

The greatest salinity measured in the field (conductivity of 32,740 $\mu$S/cm) exceeded that in the laboratory (conductivity of 30,000 $\mu$S/cm). Ostrand and Wilde (2001, 2002) did not find mosquitofish and cyprinids in pools with a specific conductance greater than 30,000$\mu$S/cm and believed this conductivity was an important threshold determining species absence in the Brazos River. Taylor et al. (1993) found conductivity to be the most important variable responsible for the structure of fish assemblages in the upper Red River. The laboratory experiments shows the metabolic requirements of tolerating high salinity decrease with increasing weight for the plains killifish but increase with increasing weight for the Red River shiner. Although the plains killifish is a salt-tolerant species, the overall increased food consumption at each weight is expected due to the increased metabolic cost of removing excess salts from its body. The Red River shiner is a salt-intolerant species and the large increase in food consumption at high salinity indicates an increased metabolic cost of removing excess salts and increased

stress for this species in this environment. The results of increased stress are likely increased respiration and activity that accompanies searching for a more optimum environment. This same pattern was observed for respiration at differing salinity.

Wilde and Ostrand (1999) found the fish assemblage of the Double Mountain Fork of the Brazos River changed from a primarily Cyprinidae (e.g., Red River shiner and red shiner) to a Cyprinodontidae (e.g., plains killifish and Red River pupfish) dominated assemblage after the impoundment of Lake Alan Henry. They also noted that two cyprinid species had become extirpated. Unmodified streams support a greater proportion of native fishes but as the stream becomes modified, the proportion of native fishes decreases (Minckley and Mefee 1987).

The increased temperature and salinity caused by alterations of the aquatic environment would stress adults of the Red River shiner, possibly to the point of death. If this occurs then there would be no mature fish to spawn which would eliminate new recruitment into the river, other than immigration from downstream reaches. This can be expected to occur for all species that are relatively salt and high temperature intolerant such as the red shiner, plains minnow, and speckled chub (Matthews 1987). This would reduce competition for resources for salt and temperature tolerant species, likely increasing their survivability (Hill and Holland 1971; Feldmeth et al. 1974).

In conclusion, it is likely that chloride control structures will further decrease flow and increase no flow periods and local water temperatures. This confines fish to smaller areas and will likely cause increased thermal variation. Similar fish assemblage shifts towards more tolerant species, as predicted herein, can be expected in any arid system

that experiences decreased flows. These shifts could be brought on by natural (global warming) or anthropogenic (chloride control structures, increased human water demands) causes. This can occur in any water body in arid regions throughout the world. Bioenergetics models are not site specific and can be applied to a variety of systems (Rice and Cochran 1984). Bioenergetics models can be used to predict the fish assemblage shifts in any environment where the plains killifish or the Red River shiner is found. This would encompass a larger geographic area for the plains killifish. Provided bioenergetics models are developed for local species, the method of comparing bioenergetics model predictions can be used to assess the potential fish assemblage shift due to environmental change in any system.

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# APPENDIX A

SAS CODE USED TO ESTIMATE CQ AND RQ FOR THE PLAINS KILLIFISH AND RED RIVER SHINER. PRESENTED IS THE EXACT CODE USED TO ESTIMATE CQ. TO ESTIMATE RQ, SPECIES SPECIFIC RESPIRATION PARAMETERS AND THEIR VALUES REPLACED CONSUMPTION PARAMETERS AND THEIR VALUES FOR BOTH SPECIES.

```
data pk ;
input C W T ;
infile 'C:Bioenergetics.csv';

data pk ;
set pk ;
CA  =  3.5999 ;
CB  = -1.1602 ;
CTM = 43.0 ;
CTO = 35.0 ;

proc nlin method=dud;
 model
        C=CA*W**CB*(((CTM-T)/(CTM-CTO))**(((log(CQ)*(CTM-
        CTO))**2*(1+(1+40/(log(CQ)*(CTM
        -CTO+2)))**0.5)**2)/400)*2.718281828**((((log(CQ)*(CTM-
        CTO))**2*(1+(1+40/(log
        (CQ)*(CTM-CTO+2)))**0.5)**2)/400)*(1-((CTM-T)/(CTM-CTO)))));

 parms
 CQ = 2.3 ;

run ;
```

# APPENDIX B

SAS CODE USED TO CONDUCT THE MONTE CARLO SIMULATIONS AND TO DETERMINE THE PEARSON COEFFICIENT RANKING OF THE PARAMETERS FOR THE PLAINS KILLIFISH AND RED RIVER SHINER WITH A 2%, 10%, AND 20% VARIATION IN NOMINAL PARAMETER VALUES.

```
* options ls=65;

 data one;
 no_exp=1000;
 do exp=1 to no_exp;

* FIXED PARAMETERS;
 w = 1.0;
 t = 35;

* SET SEEDS FOR RANDOM NUMBER GENERATION;
 seedp = 15864;
 seedfa = 12568;
 seedua = 69735;
 seedsda = 72436;
 seedcto = 49873;
 seedctm = 45672;
 seedrto = 60158;
 seedrtm = 09706;
 seedact = 60037;
 seedp  = 98000;
 seedca = 88327;
 seedcb = 77383;
 seedcq = 12323;
 seedra = 22312;
 seedrb = 10199;
 seedrq = 90087;

*SET MEANS AND VARIANCES FOR RANDOM PARAMETERS;

*2% OF MEAN PARAMETER VALUES;
 p_mean = 0.3286;      p_var =0.006572;
 fa_mean = 0.15;   fa_var  = 0.003;
 ua_mean = 0.10;   ua_var  = 0.002;
 sda_mean = 0.175;   sda_var  = 0.0035;
 cto_mean = 35.0;   cto_var  = 0.7;
 ctm_mean = 43.0;   ctm_var  = 0.86;
 rto_mean = 43.0;   rto_var  = 0.86;
 rtm_mean = 46.0;   rtm_var  = 0.92;
 act_mean = 1.0;   act_var  = 0.02;
 ca_mean = 3.5999;   ca_var  = 0.071998;
 cb_mean = -1.1602;    cb_var  = 0.023204;
 cq_mean = 2.8847;      cq_var  = 0.057694;
 ra_mean = 0.0453;     ra_var  = 0.000906;
```

```
 rb_mean = -0.5359;    rb_var  = 0.010718;
 rq_mean = 1.5965;     rq_var  = 0.03193;

* GENERATE RANDOM VALUES FOR RANDOM PARAMETERS;
 p  = p_mean + sqrt(p_var)*rannor(seedp);
 fa = fa_mean  + sqrt(fa_var)*rannor(seedfa);
 ua = ua_mean  + sqrt(ua_var)*rannor(seedua);
 sda = sda_mean + sqrt(sda_var)*rannor(seedsda);
 cto = cto_mean + sqrt(cto_var)*rannor(seedcto);
 ctm = ctm_mean + sqrt(ctm_var)*rannor(seedctm);
 rto = rto_mean + sqrt(rto_var)*rannor(seedrto);
 rtm = rtm_mean + sqrt(rtm_var)*rannor(seedrtm);
 act = act_mean + sqrt(act_var)*rannor(seedact);
 ca = ca_mean  + sqrt(ca_var)*rannor(seedca);
 cb = cb_mean  + sqrt(cb_var)*rannor(seedcb);
 cq = cq_mean  + sqrt(cq_var)*rannor(seedcq);
 ra = ra_mean  + sqrt(ra_var)*rannor(seedra);
 rb = rb_mean  + sqrt(rb_var)*rannor(seedrb);
 rq = rq_mean  + sqrt(rq_var)*rannor(seedrq);

 cv = (ctm-t)/(ctm-cto);
 cz = log(cq) * (ctm-cto);
 cy = log(cq) * (ctm-cto+2);
 cx = ((cz**2) * (((1+((1+(40/cy))**0.5))**2)/400));

 rv = (rtm-t)/(rtm-rto);
 rz = log(rq) * (rtm-rto);
 ry = log(rq) * (rtm-rto+2);
 rx = ((cz**2) * (((1+((1+(40/ry))**0.5))**2)/400));

 c_term= (ca *  ((w**cb) * p * (cv**cx)) *  (2.71828**(cx*(1-cv))));
 r_term = ra *   (w**rb) * (rv**rx) *  (2.71828**(rx*(1-rv))*(act));
 f_term = fa*c_term;
 u_term = ua*(c_term-f_term);
 s_term = sda*(c_term - f_term);

 growth = c_term - (r_term + s_term + f_term + u_term);

 output;
 end;

data one;set one;

proc sort;by growth;
```

```
run;

proc print;var growth act rto rtm cto ctm p ca cb cq ra rb rq;

run;

proc corr spearman pearson;var growth;with act sda fa ua rto rtm cto ctm p ca cb cq ra rb
rq;

run;

proc reg;model growth=act sda fa ua rto rtm cto ctm p ca cb cq ra rb rq/selection=maxr;

run;
```

# APPENDIX C

PREDICTIONS OF FISH GROWTH (G) AS AN INCREASE OR DECREASE FOR THE PLAINS KILLIFISH (PK) AND RED RIVER SHINER (RRS) AFTER A 10 DAY BIOENERGETICS MODEL SIMULATIONS AT ALL EXPERIMENTAL TEMPERATURES AND PROPORTION OF CONSUMPTION (PC).

5°C

| | Fish Weight (g) | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | 1 | | 2 | | 3 | | 4 | | 5 | |
| pc level | pk | rrs | pk | rrs | pk | rrs | pk | rrs | pk | rrs |
| 0.10 | -- | | -- | - | - f | - f | | -- | | -- |
| 0.15 | -- | | -- | | - g | - g | - | -- | - | -- |
| 0.20 | -- | - | - a | - a | - h | - h | | -- | | -- |
| 0.25 | -- | - | - b | - b | - i | - i | - | -- | | -- |
| 0.30 | -- | - | - c | - c | - j | - j | | -- | - | -- |
| 0.35 | -- | - | - d | - d | k | - k | | -- | - | -- |
| 0.40 | -- | - | - e | - e | | -- | - | -- | | -- |
| 1.00 | - | -- | - | -- | - | -- | - | -- | | -- |

10°C

| | Fish Weight (g) | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | 1 | | 2 | | 3 | | 4 | | 5 | |
| pc level | pk | rrs | pk | rrs | pk | rrs | pk | rrs | pk | rrs |
| 0.10 | -- | - | -- | | - g | - g | - | -- | - | -- |
| 0.15 | -- | - | -- | - | - h | - h | - | -- | | -- |
| 0.20 | -- | - | - c | - c | - i | - i | - | -- | - | -- |
| 0.25 | -- | - | - d | - d | - | -- | - | -- | - | -- |
| 0.30 | -- | - | - e | - e | - | -- | - | -- | - | -- |
| 0.35 | - a | - a | - f | - f | - | -- | - | -- | | -- |
| 0.40 | - b | - b | - | -- | - | -- | - | -- | - | -- |
| 1.00 | + | - | | -- | | -- | - | -- | - | -- |

Denotes a predicted decrease in fish weight.

-- Denotes a predicted decrease in fish weight and where the difference between the pk and rrs final weights was greater than 2% of the final predicted plains killifish weight.

\+ Denotes a predicted increase in fish weight.

++ Denotes a predicted increase in fish weight and where the difference between the pk and rrs final weights was greater than 2% of the final predicted plains killifish weight.

a, b,... Denotes predicted weights that were not statistically different from each other.

15°C

| | Fish Weight (g) | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | 1 | | 2 | | 3 | | 4 | | 5 | |
| pc level | pk | rrs | pk | rrs | pk | rrs | pk | rrs | pk | rrs |
| 0.10 | - - | - | - - | | - e | - e | - | - - | | - - |
| 0.15 | - - | - | b | - b | - f | - f | - | - - | - | - - |
| 0.20 | - - | - | - c | - c | | - - | - | - - | - | - - |
| 0.25 | - a | - a | - d | - d | | - - | | - - | | - - |
| 0.30 | - | - - | - | - - | - | - - | - | - - | - | - - |
| 0.35 | + | - | - | - - | - | - - | | - - | - | - - |
| 0.40 | + | | | - - | | - - | | - - | | - - |
| 1.00 | + + | + | + + | + | + | - | + | - | + | - |

20°C

| | Fish Weight (g) | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | 1 | | 2 | | 3 | | 4 | | 5 | |
| pc level | pk | rrs | pk | rrs | pk | rrs | pk | rrs | pk | rrs |
| 0.10 | - - | | - - | | - d | - d | - | - - | - | - - |
| 0.15 | - - | | - b | - b | - e | - e | - | - - | - | - - |
| 0.20 | + a | + a | - c | - c | - | - - | - | - - | - | - - |
| 0.25 | + + | + | - | - - | - | - - | | - - | - | - - |
| 0.30 | + + | + | + | - | - | - - | - | - - | - | - - |
| 0.35 | + + | + | + | | - | - - | - | - - | - | - - |
| 0.40 | + + | + | + + | + | + | | - | - - | - | - - |
| 1.00 | + + | + | + + | + | + + | + | + + | + | + + | + |

Denotes a predicted decrease in fish weight.

\- Denotes a predicted decrease in fish weight and where the difference between the pk and rrs final weights was greater than 2% of the final predicted plains killifish weight.

\+ Denotes a predicted increase in fish weight.

\+ + Denotes a predicted increase in fish weight and where the difference between the pk and rrs final weights was greater than 2% of the final predicted plains killifish weight.

a, b,... Denotes predicted weights that were not statistically different from each other.

25°C

| | Fish Weight (g) | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | 1 | | 2 | | 3 | | 4 | | 5 | |
| pc level | pk | rrs | pk | rrs | pk | rrs | pk | rrs | pk | rrs |
| 0.10 | - | + | -- | - | - f | - f | - j | - j | | -- |
| 0.15 | + | + + | -- | - | - g | - g | | -- | | -- |
| 0.20 | + | + + | + c | + c | - h | - h | | -- | | -- |
| 0.25 | + a | + a | + d | + d | + i | + i | | -- | | -- |
| 0.30 | + b | + b | + e | + e | + + | + | + | | | -- |
| 0.35 | + + | + | + + | + | + + | + | + + | + | + | - |
| 0.40 | + + | + | + + | + | + + | + | + + | + | + + | + |
| 1.00 | + + | + | + + | + | + + | + | + + | + | + + | + |

30°C

| | Fish Weight (g) | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | 1 | | 2 | | 3 | | 4 | | 5 | |
| pc level | pk | rrs | pk | rrs | pk | rrs | pk | rrs | pk | rrs |
| 0.10 | + | + + | - | + | -- | | -- | | - a | - a |
| 0.15 | + | + + | + | + + | | + | -- | - | - b | - b |
| 0.20 | + | + + | + | + + | + | + + | + | + + | - c | - c |
| 0.25 | + | + + | + | + + | + | + + | + | + + | + d | + d |
| 0.30 | + | + + | + | + + | + | + + | + | + + | + e | + e |
| 0.35 | + | + + | + | + + | + | + + | + | + + | + | + + |
| 0.40 | + | + + | + | + + | + | + + | + | + + | + | + + |
| 1.00 | + | + + | + | + + | + | + + | + | + + | + | + + |

- Denotes a predicted decrease in fish weight.

- - Denotes a predicted decrease in fish weight and where the difference between the pk and rrs final weights was greater than 2% of the final predicted plains killifish weight.

+ Denotes a predicted increase in fish weight.

+ + Denotes a predicted increase in fish weight and where the difference between the pk and rrs final weights was greater than 2% of the final predicted plains killifish weight.

a, b,... Denotes predicted weights that were not statistically different from each other.

35°C

| | Fish Weight (g) | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | 1 | | 2 | | 3 | | 4 | | 5 | |
| pc level | pk | rrs | pk | rrs | pk | rrs | pk | rrs | pk | rrs |
| 0.10 | - - | | | + | - - | - | - - | | - - | |
| 0.15 | - | + | + | + + | + | + + | - | + | - - | |
| 0.20 | + | + + | + | + + | + | + + | + | + + | | + |
| 0.25 | + | + + | + | + + | + | + + | + | + + | + | + + |
| 0.30 | + | + + | + | + + | + | + + | + | + + | + | + + |
| 0.35 | + | + + | + | + + | + | + + | + | + + | + | + + |
| 0.40 | + | + + | + | + + | + | + + | + | + + | + | + + |
| 1.00 | + | + + | + | + + | + | + + | + | + + | + | + + |

40°C

| | Fish Weight (g) | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | 1 | | 2 | | 3 | | 4 | | 5 | |
| pc level | pk | rrs | pk | rrs | pk | rrs | pk | rrs | pk | rrs |
| 0.10 | - - | - | - - | | - - | | - d | - d | - | - - |
| 0.15 | - - | | - - | | - c | - c | | - - | - | - - |
| 0.20 | + a | + a | - b | - b | | - - | - | - - | - | - - |
| 0.25 | + + | + | | - - | | - - | | - - | | - - |
| 0.30 | + + | + | + + | + | - | - - | | - - | | - - |
| 0.35 | + + | + | + + | + | + | - | - | - - | | - - |
| 0.40 | + + | + | + + | + | + | - | | - - | - | - - |
| 1.00 | + + | + | + + | + | + + | + | + + | + | + + | + |

Denotes a predicted decrease in fish weight.

- - Denotes a predicted decrease in fish weight and where the difference between the pk and rrs final weights was greater than 2% of the final predicted plains killifish weight.

\+ Denotes a predicted increase in fish weight.

+ + Denotes a predicted increase in fish weight and where the difference between the pk and rrs final weights was greater than 2% of the final predicted plains killifish weight.

a, b,... Denotes predicted weights that were not statistically different from each other.

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