

AN EVALUATION OF THE FOOD WEB DYNAMICS AND PREDATOR PREY
INTERACTIONS IN SCOFIELD RESERVOIR

by

Lisa K. Winters

A thesis submitted in partial fulfillment
of the requirements for the degree

of

MASTER OF SCIENCE

in

Ecology

Approved:

Phaedra Budy
Major Professor

Chris Luecke
Committee Member

Dan MacNulty
Committee Member

Mark R. McLellan
Vice President for Research and
Dean of the School of Graduate Studies

UTAH STATE UNIVERSITY
Logan, Utah

2014

UMI Number: 1584350

All rights reserved

INFORMATION TO ALL USERS

The quality of this reproduction is dependent upon the quality of the copy submitted.

In the unlikely event that the author did not send a complete manuscript and there are missing pages, these will be noted. Also, if material had to be removed, a note will indicate the deletion.



UMI 1584350

Published by ProQuest LLC (2015). Copyright in the Dissertation held by the Author.

Microform Edition © ProQuest LLC.

All rights reserved. This work is protected against unauthorized copying under Title 17, United States Code



ProQuest LLC.
789 East Eisenhower Parkway
P.O. Box 1346
Ann Arbor, MI 48106 - 1346

Copyright © Lisa K. Winters 2014
All Rights Reserved

ABSTRACT

An Evaluation of the Food Web Dynamics and Predator Prey

Interactions in Scofield Reservoir

by

Lisa K. Winters, Master of Science

Utah State University, 2014

Major Professor: Dr. Phaedra Budy
Department: Watershed Sciences

Aquatic food webs are comprised of complex spatial and temporal interactions within and among trophic levels. Human manipulations, such as construction of reservoirs, enhance uncertainties in our understanding of aquatic food web structure. Reservoirs are novel ecosystems which contain a unique composition of species. Species introductions into reservoirs may disrupt interactions within an already complex and poorly understood food web.

In Scofield Reservoir in central Utah, a rapidly expanding population of Utah chub poses a detrimental threat to the blue-ribbon trout fishery. The Utah Division of Wildlife Resources has recently stocked cutthroat trout and tiger trout (a brown trout x brook trout hybrid) to potentially reduce Utah chub numbers as well as to enhance the sport fishery. I used standard fisheries techniques to describe food web interactions and to assess the potential for these piscivorous trout to control the expanding Utah chub

population, as well as to determine sport fish performance and quantify diet overlap amongst top predators.

Using bioenergetics modeling, I estimated very high rates of Utah chub consumption by cutthroat trout and tiger trout. These two species collectively display control of Utah chub, as the chub population is no longer exponentially increasing. Cutthroat trout and tiger trout are likely not food limited and convincingly exhibit high performance, as abundance of Utah chub is still extremely high. Both diet and stable isotope analysis showed significant overlap between these top piscivores in the reservoir, but also substantial overlap between cutthroat trout and rainbow trout with respect to Utah chub. Analysis of rainbow trout suggested this species is performing poorly; rainbow trout had extremely low catch rates and never switched to a piscivorous diet at larger sizes. Utah chub and rainbow trout had similar diet compositions, and thus rainbow trout may be competing (poorly) for food and space resources. This study contributes to our understanding of interspecific interactions among these unique assemblages of top predators in this artificial system. This research also provides knowledge to fisheries managers tasked with providing optimal sport fisheries in these artificial and dynamic systems, as well as expanding on our extremely limited knowledge of tiger trout ecology.

(125 pages)

PUBLIC ABSTRACT

Evaluating the Food Web Dynamics of Valuable Trout

Species in Scofield Reservoir, Utah

Reservoirs are artificial, dynamic, and highly manipulated systems, where the appearance of either intentionally or unintentionally introduced species may disrupt interactions within an already complex food web. In some situations, a top predator fish may be stocked as a biological control agent, if these fish-eating predators monopolize on the nuisance and unwelcome prey. Scofield Reservoir, Utah has historically been an extremely popular blue-ribbon fishery. However, a recent decrease in rainbow trout catch and increase in the minnow, Utah chub, have made it difficult to find a balance between providing the public with a trophy sport fishery and maintaining an ecologically sustainable system. In this context, it is important for fisheries managers to understand how these stocked top predators may interact with each other, as well as with their prey, to maximize fish performance and enhance and maintain the sport fishery.

I used gill nets to capture fish and collect samples to answer key questions: 1) which of the three trout stocked in the reservoir (cutthroat trout, rainbow trout, or tiger trout) has the greatest potential to reduce Utah chub numbers, 2) what is the relative performance of these three trout, and 3) how do these three top predators interact with each other within this system? To answer these questions, I used energetic modeling to predict how many chub an average trout of each species was consuming. Additionally, I used length-weight relationships to estimate the healthiness of each species and calculated metrics of diet overlap to determine if these fish were food- or space-limited, which may constrain fish performance. Results of my study indicated that Utah chub density in the reservoir was extremely high, and chub made up the majority of the catch. Rainbow trout, in contrast, were caught very infrequently. Additionally, rainbow trout contributed little to the biological control of Utah chub, whereas cutthroat trout and tiger trout populations consumed millions of Utah chub each year, and appeared to be keeping the chub population in check. Diet overlap between cutthroat trout and tiger trout was high due to shared Utah chub prey, but since this prey is in excess, they are likely not competing for resources. Alternatively, rainbow trout relied heavily on aquatic invertebrates and zooplankton. Rainbow trout may be performing poorly in the reservoir because they compete for food or space with the abundant Utah chub. These results will help fisheries professionals manage unique assemblages of sport fish, as well as provide pertinent knowledge to the fields of reservoir ecology and biological control.

DEDICATION

This thesis is lovingly dedicated to my dad, whose unexpected year-long battle with brain cancer, during the time of this graduate research, was a most unwelcomed experience. What I learned, to never take anything for granted, true strength, compassion, and bravery in the face of adversity, are lessons much greater than what is represented by this thesis. My dad's support, encouragement, and enthusiasm for all of my adventures will never be forgotten. I will forever cherish the moments that are now memories, the years spent tagging alongside my dad, whether hiking or fishing, always instilling a curiosity and love of nature within me.

ACKNOWLEDGMENTS

Funding and support of this project was provided by Utah Department of Natural Resources, Division of Wildlife Resources (UDWR; Federal Sport Fish Restoration, Grant number F-134-R, Project 1) and US Geological Survey, Utah Cooperative Fish and Wildlife Research Unit, in-kind. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the United States Government. Permitting assistance was provided by Suzanne McMullin (UDWR) and Jenna Daniels of the Institutional Animal Care and Use Committee (IACUC) at Utah State University. This research was conducted under State of Utah COR number 1COLL8712 and IACUC protocol number 1544.

This work would not have been possible without the help and support of many people, to whom I am deeply grateful. Thank you to my advisor, Phaedra Budy, for her advice and guidance throughout this process, and for teaching me what being a fish ecologist is all about! I would like to thank my committee members, Chris Luecke and Dan MacNulty, for their time, support, and insightful advice. I thank Paul Birdsey, Justin Hart, Calvin Black, and Craig Walker from UDWR for their assistance, guidance, and enthusiasm for this project.

I am deeply indebted to all the members of the Fish Ecology Lab at Utah State University who critiqued my work, guided my thoughts, and generally entertained me. In particular, I appreciate the other graduate students who allowed me to paint our office walls “honey toast” yellow. I am grateful for Gary Thiede, for assisting me in most everything, from logistics and analysis, to taste-testing my baked goods.

This research would not have been possible without the hard work of technicians, lab mates, friends, and volunteers, both in the field and the lab: Michael Yarnall, Dan Weber, Konrad Hafen, Bryce Roholt, Hannah Moore, Jared Baker, and Brie Estrada. I also thank Susan Durham for assistance with statistical analyses. I am grateful to Enid Kelley and Brian Bailey for keeping me on track in ways I didn't know existed, and for making checking my mailbox such a joy.

To my friends and family, thanks so much for your moral support, patience, encouragement, and shoulders to lean on along the way. I could not have accomplished this without each and every one of you.

Lisa K. Winters

CONTENTS

	Page
ABSTRACT.....	iii
PUBLIC ABSTRACT.....	v
DEDICATION	vi
ACKNOWLEDGMENTS.....	vii
LIST OF TABLES	x
LIST OF FIGURES	xi
CHAPTER	
1. INTRODUCTION.....	1
2. UNWELCOME INVADERS AND TROUT PREDATORS: EFFECTIVE BIOLOGICAL CONTROLS IN A WESTERN RESERVOIR?.....	3
Introduction	3
Methods.....	11
Results	19
Discussion	26
Management Implications.....	35
References	36
3. QUANTIFYING THE FOOD WEB IMPACTS OF INTRODUCED PISCIVORES IN RESERVOIR FISH ASSEMBLAGES	74
Introduction	74
Methods.....	81
Results.....	85
Discussion.....	90
References	97
4. SUMMARY	112

LIST OF TABLES

Table	Page
2.1 Summary of trout stocking from 2005-2012.....	51
2.2 Wet weight energy density estimates of individual predators and prey items used for bioenergetics simulations.....	52
2.3 Length categories (mm TL) proposed for trout species found in Scofield Reservoir	53
2.4 Seasonal catch rate (CPUE), an index of relative abundance, calculated as the number of fish, per net, per hour, for Cutthroat Trout, Rainbow Trout, Tiger Trout, and Utah Chub in Scofield Reservoir, Utah	54
2.5 Predator abundance and density (fish/ha) estimates based on hydroacoustics surveys in August 2011 and June 2013.....	55
2.6 Annual Utah Chub consumption (g) estimates per individual predator for a representative size class of Cutthroat Trout, Rainbow Trout, and Tiger Trout for the 2011 – 2012 simulation year	56
2.7 Bioenergetic efficiency expressed as a percentage of the realized maximum possible consumption rate, determined with the Fish Bioenergetics 3.0 model (Hanson et al. 1997)	57
2.8 Condition (K_{TL}) of Cutthroat Trout, Rainbow Trout, and Tiger Trout captured in Scofield Reservoir during 2012.....	58
2.9 Relative return rates of Cutthroat Trout stocked in Scofield Reservoir and recaptured from summer 2011- autumn 2012.....	59
2.10 Relative return rates of Rainbow Trout stocked in Scofield Reservoir and recaptured from summer 2011 – autumn 2012	60
2.11 Stock density index ranges for Scofield Reservoir trout species.....	61

LIST OF FIGURES

Figure	Page
2.1	Map of Scofield Reservoir, Utah showing the eight locations during which fish were sampled in 2011 and 2012 62
2.2	Utah Chub catch-per-unit-effort from 2004 until 2012 63
2.3	Abundance estimates by size class of Utah Chub and three trout species derived from hydroacoustic surveys in Scofield Reservoir on 6 June 2013 and 31 August 2011 64
2.4	Proportion of total catch, based on CPUE, for each of the trout species and Utah Chub in Scofield Reservoir 65
2.5	Seasonal diet composition of small (< 350 mm TL) and large (\geq 350 mm TL) Cutthroat Trout, Rainbow Trout, and Tiger Trout, as well as small (< 250 mm TL) and large (\geq 250 mm TL) Utah Chub captured in Scofield Reservoir 66
2.6	Length-frequency (%) distributions of Bear Lake Cutthroat Trout captured in gill nets during seasonal sampling events from July 2011 – May 2013 in Scofield Reservoir 67
2.7	Length-frequency (%) distributions of Rainbow Trout captured in gill nets during seasonal sampling events from July 2011 – May 2013 in Scofield Reservoir 68
2.8	Length-frequency (%) distributions of Tiger Trout captured in gill nets during seasonal sampling events from July 2011 – May 2013 in Scofield Reservoir 69
2.9	Mean (\pm 2SE) total length (top panel) and weight (bottom panel) at age of each trout species in Scofield Reservoir 70
2.10	Daily mean temperatures experienced by fish in Scofield Reservoir during 2011 and 2012 71
2.11	Comparison of Utah Chub abundance and annual production (Lake) versus estimates of annual Cutthroat Trout and Tiger Trout consumption of chub (Consumed) in Scofield Reservoir, using June 2013 hydroacoustic estimates of abundance 72
2.12	Relationship between total length and relative weight (W_r) of Cutthroat Trout (top), Rainbow Trout (middle), and Tiger

Trout (bottom) from Scofield Reservoir in summer of 2012	73
3.1 Map of Scofield Reservoir, Utah showing the eight locations during which fish were sampled in 2011 and 2012, denoted as black circles	106
3.2. Seasonal diet composition of small (<350 mm TL) and large (≥ 350 mm TL) cutthroat trout, rainbow trout, and tiger trout captured in Scofield Reservoir	107
3.3 Proportion of Utah chub diet contribution for each predator species in Scofield Reservoir	108
3.4 Stable isotope bi-plots for ¹³ C and ¹⁵ N of (top) large trout (≥ 350 mm TL) and large chub (≥ 250 mm TL), and (bottom) small trout (< 350 mm TL) and small chub (< 250 mm TL).....	109
3.5 Two-dimensional isotopic (δ ¹⁵ N and δ ¹³ C) niche plots of (left) large (≥ 350 mm) cutthroat trout, rainbow trout, tiger trout, and Utah chub (≥ 250 mm) from Scofield Reservoir, and (right) small (< 350 mm) cutthroat trout, rainbow trout, tiger trout, and Utah chub (< 250 mm).....	110
3.6 Relationship between cutthroat trout (top), rainbow trout (middle), and tiger trout (bottom) length with Utah chub length in Scofield Reservoir, Utah	111

CHAPTER 1

INTRODUCTION

In this thesis, I summarize my findings from an intensive two-year study of the fish community of Scofield Reservoir. In 2011, I began examining the ecological processes shaping the food web and fishery in Scofield Reservoir, historically one of the most important trout fisheries in the state of Utah and still one of the most heavily used fisheries. Anglers have historically sought after rainbow trout *Onchorhynchus mykiss*, and the fishery has been managed as a put-grow-and-take family fishery with around 600,000 rainbow trout stocked annually. However, stocking levels are now adjusted nearly every year in response to the re-discovery of Utah chub *Gila atraria*, in 2005. Despite being a native fish with a wide distribution throughout much of the state of Utah, Utah chub have high reproductive potential and fast growth rates, which are of concern when found in high numbers with valuable sport fish. Tiger trout *Salmo trutta X Salvelinus fontinalis*, fingerlings were stocked in 2005 as a potential biological control agent for the Utah chub, and have since proven to be one of the more highly desirable sport fish in the state. Bear Lake strain of Bonneville cutthroat trout *O. clarkii utah*, has been stocked since 2009, also as an additional control measure.

Consequently, three top predators with the potential for considerable competition for food and/or space occur in the reservoir. Further, despite its historic and contemporary popularity, angler use of Scofield Reservoir has declined since 1986. During 2011 and 2012, I collected the necessary information to address the

following questions in regard to the management of the reservoir: 1) How does the food web operate and what are the abiotic and biotic constraints on fish performance? 2) What is the size and condition of the predator population in the reservoir? 3) What are the preferred prey species, degree of diet overlap, and consumption rates of the three predators on Utah Chub? 4) Can the predator population limit the prey population through top-down control? And 5) Are the three predators limited by interspecific competition for resources?

In chapter 2, I quantify the relative potential for biological control of the expanding prey fish by three different trout predators in Scofield Reservoir. In chapter 3, I evaluate the food web impacts of introduced piscivores in the Scofield Reservoir fish assemblage. A summary of the results is provided in chapter 4.

CHAPTER 2
UNWELCOME INVADERS AND TROUT PREDATORS: EFFECTIVE BIOLOGICAL
CONTROL IN A WESTERN RESERVOIR?

Introduction

Biological agents are becoming increasingly common as a method of natural control to remove invasive species and maintain native biodiversity worldwide (Freeman et al. 2010). Biological control, an environmentally sound and effective means of reducing or mitigating nuisance species and their impacts through the use of natural enemies, depends upon parasites, pathogens, or predators to lower population densities of the nuisance species (Debach 1964; Freeman et al. 2010; USDA 2013a). The United States alone has employed almost 200 biological control agents towards nuisance weeds in agriculture (USDA 2013b). Since 2002, the Emerald Ash Borer *Agrilus planipennis*, from northeastern Asia has been a poster-child of destructive pest and threat to the United States economy (USDA 2013b). Nevertheless, despite seemingly prolific use of biological control agents, vertebrate species represent a small portion of biological control targets (Saunders et al. 2010). Only in the past few decades has the biomanipulation of fishes become a common technique to prevent over-expanding prey bases from negatively affecting sport fish (Stewart et al. 1981; Hartman and Margraf 1993; Irwin et al. 2003) or to improve water quality (Shapiro et al. 1975; Carpenter et al. 1985; Ireland 2010). Many such techniques are employed within artificial systems, which commonly contain

intentionally introduced and intensively managed species (Anderson and Neumann 1996).

Reservoir systems exhibit characteristics intermediate to lotic and lentic habitat and thus incorporate an atypical community of fish (Wetzel 1990; Anderson and Neumann 1996; Wetzel 2001). These artificial systems, manipulated through stocking, may have unpredictable food webs with decoupled predator and prey dynamics (Kitchell and Crowder 1986; Ruzycki et al. 2001). In addition, reservoirs are usually relatively young, such that assemblage community members have not co-evolved (Havel et al. 2005; Raborn et al. 2007). Finally, predominant uses of reservoirs, such as for water storage and flood control, may dramatically change water levels, leading to fluctuations in fish habitat and population dynamics (Gasinth and Gafny 1990; Rose and Mesa 2013).

Similarly, the balance of interactions within reservoir food webs may be unstable due to their simplicity, where the entire assemblage can be affected by random fluctuations in a single species (Stein et al. 1995; Raborn et al. 2007). In the west, non-native Lake Trout *Salvelinus namaycush*, have had a substantial impact on native, and federally threatened, Bull Trout *S. confluentus*, populations due to predation, competition for food, and varying life history traits of these two top predators (Guy et al. 2011). Burbot *Iota Iota*, rapidly invading Flaming Gorge Reservoir, Utah-Wyoming, threaten to be a detriment to native fishes through predation or competitive interactions for shared prey resources (Gardunio et al. 2011). The strength of interactions within reservoir food webs may change with the introduction of other non-native fishes; however, establishment of a species is not always successful (Kohler et al.

1986; Williamson and Fitter 1996). Successful introductions to artificial assemblages may result in a lengthened food chain (Walsworth et al. 2013), alter energy flow through the system (Sousa et al. 2008), initiate novel predator-prey interactions (Kitchell et al. 1997; Romare and Hansson 2003; Schoen et al. 2012), or alter trophic structure (Reissig et al. 2006; Skov et al. 2010; Ellis et al. 2011). The addition of species also increases potential for competition (Tyus and Saunders 2000; Tronstad 2008). Consequently, unwelcome invaders may disrupt certain linkages and alter the strength of interactions within a complex and not well understood reservoir food web.

Our understanding of the use of top predators as a tool for biological control in aquatic systems is of utmost importance, as there has been a surge of invasive fish species in recent years (Sorenson and Stacey 2004). Piscivorous fishes represent a commonly introduced species, intentionally stocked as a management tool in an attempt to control undesired species (Courtenay and Kohler 1986), as well as to enhance angling opportunities (Martinez et al. 2009). In the Laurentian Great Lakes, a salmonid stocking program was launched to trigger top down control of an invasive and nuisance Alewife *Alosa pseudoharengus*, population, which resulted in a valuable sport fishery and a reduction in Alewife abundance (Bunnell et al. 2006). After Largemouth Bass *Micropterus salmoides*, were stocked in ponds to control Gizzard Shad *D. cepedianum*, Shad populations plummeted, suggesting Largemouth Bass consumed enough Shad to limit their overall abundance (Irwin et al. 2003). However, as with many introductions, there can be adverse effects on non-target organisms as a result (Wittenberg and Cock 2001; Simberloff 2009). A notable example of a successful

biological control with unintended results is the Mosquito-fish *Gambusia affinis*, introduced to prey on mosquito larvae, thus, successfully controlling adult mosquito populations (Kumar and Hwang 2006); however, these fish have decreased native fish populations through predation (Simberloff and Stiling 1996). Nonetheless, when introduced as potential biological controls, top predators present a potentially powerful tool for invasive species management, where a carefully-selected, upper-trophic level species theoretically uses the undesired organism as a primary food resource to reduce the population size (Hoddle 2004).

Predator growth and survival depends on the availability of prey resources. This dependence is described by the classic supply-demand relationship; prey abundance and accessibility (i.e., supply) is directly related to biomass and production of predators in the system (i.e., demand; Ney 1990). This link to prey availability, however, is not always apparent in manipulated, artificial assemblages (Vatland et al. 2008). Predator size relative to prey size often limit (or influence) predator ability to capture, handle, and consume prey (Hambright 1991; Magnhagen and Heibo 2001; Juanes et al. 2002). Gape size limitations, where a larger gape increases the potential size of prey captured, is exemplified by Yellow Perch *Perca flavescens*, where size selection of Round Goby *Neogobius melanostomus*, prey increased with predator size (Truemper and Lauer 2005). Further, young fish with rapid growth rates may quickly exceed the gape of piscivores, thereby allowing them to become less vulnerable to predation and attain high survival rates, such as Gizzard Shad throughout the southeast (Noble 1981; Michaletz 2013). With few predators and abundant resources, the prey species may

dominant the assemblage (Stein et al. 1995). Additionally, based on optimal foraging theory, foraging behavior should maximize fitness (the ultimate measure of performance), through choices relating to foraging time, diet selection, and handling time (Werner and Hall 1974; Mittlebach 2002; Gill 2003). These behaviors and feeding choices are based on a theoretical goal of expending the least amount of energy while still obtaining the most calories, and may result in different interactions between predator and prey than those predicted by supply and demand alone. Thus, the strength of complex food web interactions depends on prey life-history traits and subsequent predator foraging decisions. Given these complexities, understanding the mechanisms driving predator-prey relationships in cold water impoundments can be challenging, but is also therefore critical for making informed management decisions (Johnson and Goettle 1999).

Bioenergetics-based modeling, coupled with comprehensive field sampling, provides a quantitative and predictive tool for managers to estimate current and future predator impacts on prey populations (Rice and Cochran 1984; Hanson et al. 1997). This approach, based on a balanced energy budget, uses physiological and allometric relationships driven by food, temperature, and fish size to predict consumption, growth, or production of fish (Brandt and Hartman 1993; Chipps and Wahl 2008). More specifically, the model can compute the consumption, in terms of biomass and associated prey energy, necessary to satisfy the annual growth of a fish, given the body mass, thermal experience, and diet of the modeled fish (Beauchamp et al. 2007). The results can be used to effectively evaluate complex interactions within reservoir food

webs and the mechanisms that operate to structure these webs (Baldwin et al. 2000; Beauchamp and Van Tassell 2001; Irwin et al. 2003). In Bear Lake, Utah, Bonneville Cutthroat Trout *Oncorhynchus clarkii utah*, and introduced Lake Trout prey heavily on endemic prey fish; as a result, model simulations estimated strong predation impacts from Lake Trout with consumption exceeding prey fish production (Ruzycki et al. 2001). Similarly, Strawberry Reservoir, Utah, stocked with a unique assemblage of salmonids, quantified monthly sport fish consumption to highlight a bottleneck in *Daphnia* prey supply which was limiting to fish production (Baldwin et al. 2000). In sum, this approach has been effectively used to 1) assess water quality constraints on fish growth (Budy et al. 2011); 2) estimate management effects, such as slot limits and angler harvest (Luecke et al. 1994); 3) investigate species invasion success (Budy et al. 2013); and 4) predict predation pressure due to climate effects (Peterson and Kitchell 2001; Mesa et al. 2013), among many other uses.

In Scofield Reservoir, Utah, the fast-reproducing non-game fish, Utah Chub *Gila atraria*, was unintentionally introduced in the reservoir, and subsequently the population exploded in 2005. Utah Chub are native to the nearby Snake River and Lake Bonneville basins, though not native to the Colorado River drainage, where Scofield Reservoir is located. Within the past decade, populations of sport fish, Bear Lake strain Bonneville Cutthroat Trout, Rainbow Trout *O. mykiss*, and Tiger Trout *Salmo trutta*, female x *Salvelinus fontinalis*, male, have been stocked in relatively high numbers as an effort to suppress the Utah Chub population. Since the majority of the lake-wide fish abundance consisted of Utah Chub, there was concern the expanding Utah Chub

population would adversely affect the popular blue-ribbon sport fishery. Maintaining balanced predator and prey populations can thus be an ongoing management challenge for fisheries managers. Accordingly, the Scofield Reservoir food web poses a unique opportunity to investigate the use of salmonids as biological control agents to control an unwelcome non-game fish population.

One of my project goals was to identify the best single, or combination of species for suppressing Utah Chub abundance, as well as to assess the relative performance of three popular sport fish (Cutthroat Trout, Rainbow Trout, and Tiger Trout). Specifically, my objectives were to 1) estimate the abundance, biomass, and population growth trajectory of the principal prey fish, Utah Chub; 2) quantify trout consumptive demand relative to production of Utah Chub; and 3) compare the relative abundance and condition of the three predator species. To achieve these objectives, I estimated catch-per-unit-effort and collected fish for measurements of growth and diet using a combination of common fisheries field techniques, conducted hydroacoustics surveys of fish density, and lastly, assembled this information into bioenergetic simulations of predator population consumption, compared with prey abundance and production. This study, and the results presented herein, is also one of the first documented rigorous studies of tiger trout ecology.

Study Site

Scofield Reservoir is a high elevation (2,322 m) impoundment on the Price River, eventually flowing to the Colorado River, located within the Manti-La Sal National Forest in Utah (Figure 2.1). The reservoir was created by Scofield Dam in 1926 and is

predominantly used for irrigation water storage, with recreation and flood control as additional benefits (Bureau of Reclamation 2011). The current reservoir has a capacity of 73,600 acre-ft (90,800,000 m³) at full pool, mean surface area of 1,139 ha, and a mean depth of eight meters (Bureau of Reclamation 2009). Scofield Reservoir is characterized as eutrophic, with 'excessive' total phosphorous enrichment (Department of Environmental Quality 2010). Blue-green algae dominate the phytoplankton community, indicative of poorer water quality, with blooms typically occurring in summer. The reservoir stratifies thermally in summer, and hypolimnetic oxygen deficits historically lead to fish kills of varying degrees (Hart and Birdsey 2008). Zooplankton composition is typically dominated by the cladocera, *Daphnia*, at densities of .09 #/L and a biomass of 1.5 ug/L in the summer.

Scofield Reservoir is managed as an extremely popular family fishery. Historically, around 600,000 150-250 mm age-1 Rainbow Trout were stocked every year. However, the fish stocking program has been adjusted nearly every year since 2005 in response to the re-appearance of Utah Chub in gill nets, with the goal to reduce the population before an expansion of a magnitude similar to Utah's Strawberry Reservoir (Hart and Birdsey 2008). Tiger Trout and Bear Lake strain Bonneville Cutthroat Trout have been stocked in the fishery as potential biological controls for Utah Chub, as well as an alternative sport fish. These populations demonstrate little to no natural reproduction, and are artificially maintained with approximately 80,000 of each species stocked yearly at 200 mm (Table 2.1). Other species present in the reservoir include the

Redside Shiner *Richardsonius balteatus*, and Mountain Sucker *Catostomus platyrhynchus*.

Methods

Predator Abundance

I sampled fishes intensively from summer 2011 through autumn 2012 in Scofield Reservoir. In this type of fixed-station sampling, index sites were selected to be representative of the reservoirs' longitudinal axis from the upper riverine zone to the lower lacustrine zone (McMahon et al. 1996), while maintaining consistency with long-term Utah Division of Wildlife Resources (UDWR) monitoring, in order to monopolize on previously collected data.

I used gill netting to collect data to evaluate the size structure, growth rate, body condition, and diet of trout in the reservoir. I set two horizontal sinking gill nets at each of eight index sites within the reservoir (Figure 2.1). I set these experimental gill nets (1.8 m tall x 24 m long with eight monofilament panels of 38-, 57-, 25-, 44-, 19-, 64-, 32-, and 51- mm bar mesh) according to standard gill-net methods to capture a representative size distribution of all fish in the reservoir (Beauchamp et al. 2009; Lester et al. 2009). I placed gill nets in littoral areas offshore at depths fish were predicted to be most abundant; set before dusk and pulled after dawn, spanning two crepuscular periods. I calculated catch-per-unit-effort (CPUE; fish/net/hour) at each sample site for each trout species and Utah Chub. Within each season, catches from all gill nets were summed and divided by total effort in order to estimate seasonal reservoir-wide CPUE.

Relative abundance of each species was expressed as a percentage of CPUE. An analysis of variance (ANOVA) was run to compare the catch-per-unit-effort between each trout species and by season. All statistical analyses were completed using SAS and a proc glimmix statement, with an *a priori* α of 0.05 (SAS Institute Inc., Cary, NC, USA).

Predator Diet Composition

I collected Cutthroat Trout, Rainbow Trout, and Tiger Trout diets primarily from fish captured in gill nets from July 2011 through October 2012. I placed all fish captured on ice and removed and preserved their stomachs whole for later analysis. All organisms sampled from stomach contents were identified to the lowest taxonomic level possible (Brooks 1957; Edmonson 1959; Merritt and Cummins 1996). I grouped fish stomach contents by prey fish (identified to species when possible), zooplankton, organic matter, aquatic invertebrates (classified to order), and terrestrial invertebrates (classified to order). I counted and weighed (blot-dry wet weight to nearest 0.001 g) prey fish, and weighed invertebrate prey en masse by classification. I measured intact prey fish to nearest mm (backbone and standard length). For model simulations, diet composition was required as proportion by wet weight, and was calculated as seasonally aggregated percentages. Seasons were delimited as follows: spring (April – May), summer (June – August), and autumn (September – October). I applied these seasonal diet data to the appropriate size-class bioenergetic simulations, which interpolates changes in diet composition between seasonal inputs.

Predator Growth

I estimated annual mean size at age from a combination of otolith-aging data, analysis of length-frequency modes, and mark-recapture data (from dye-marked fish). All otoliths were aged whole, independently by at least two laboratory personnel who were experienced in otolith aging. Otoliths were viewed under a microscope and were aged by counting the opaque bands (annuli) from the center to the anterior edge. Size-at-age datasets were then used to estimate annual growth (g/year) from July 2011 to July 2012. I used the resulting growth estimates for size-specific growth inputs in bioenergetics simulations.

Thermal History

I estimated the thermal history of the modeled cohorts of trout from a combination of monthly vertical temperature profiles and remote temperature data loggers placed at depths of 3, 6, and 9m attached to a stationary buoy on the reservoir for a full year. Since the depth distribution of catches in gill nets were varied throughout the water column, and the reservoir is shallow, I used the average of the three temperature loggers as the representative thermal history. I modeled all sizes and species of trout with the same temperature regime. To identify temperature sensitivity of model estimates of consumption, I also ran a set of simulations using the species consumption thermal optimum assigned for each day the temperature was available in the reservoir. This scenario assumes trout will behaviorally thermoregulate when possible (Budy et al. 2013).

Prey Biomass and Production

I conducted hydroacoustic surveys to provide density and abundance information of fishes > 100 mm TL in Scofield Reservoir. I conducted surveys during the new moon event when fish are most likely dispersed and to reduce the likelihood of fish associating with the lake bottom, where they could not be detected by the acoustic transducer. I conducted night-time cross-reservoir transects on Scofield Reservoir covering a representative area of the reservoir. In August 2011, twelve acoustic transect distances ranged from 436 – 2,279 m with mean depths ranging from 4.0 – 10.5 m. In June 2013, due to lower water levels, eleven acoustic transect distances ranged from 417 – 2,250 m with mean depths ranging from 4.4 – 7.6 m. I collected data using a Biosonics Model DE6000 scientific echosounder with 420 kHz dual-beam transducer (6 X 15°) and towed the transducer on a fin at 1-m depth while recording data using Biosonics Visual Acquisition processing software. I sampled at a rate of two pings per second traveling at a boat speed of 1 – 2 m/s (2 – 5 kph). Pulse width of the signal was 0.4 ms. I processed acoustic target and density data using Biosonics Visual Analyzer software, using single fish targets with dual-beam target strengths ranging from -48 to -32 decibels (dB), representing fish 100 mm and larger (Dahm et al. 1985). I selected only echoes that met the single-target shape criteria used by the analysis software to calculate target strengths and densities. Transects were treated as replicates in the analysis to produce mean fish per cubic meter with 1 standard error, and I then extrapolated density of fish (fish/m³) to lake-wide abundance using lake volume.

To verify and apportion acoustic targets, I used gill-net catch information collected near the time of acoustic surveys (August 2011 and May 2013; trawling is not possible in this shallow reservoir). I summarized gill-net catch by species and size classes (100 – 150 mm, 151 – 250 mm, 251 – 350 mm, and fish larger than 350 mm) and determined percentage of species by size class to delineate the acoustic-derived abundance estimates by species by size class.

I estimated the production of Utah Chub for the 2011-2012 period for four size-age classes (< 100 mm, 100- 150 mm, 151- 250 mm, and 250- 350 mm) using mean body size from each size class and biomass from June 2013 hydroacoustic estimates.

Production (P, kg/year) was estimated as:

$$P = G \times B$$

where G is the instantaneous rate of growth (natural log of the ratio of final to initial weight), and B is the mean biomass (kg; Ney 1993). Abundance estimates for < 100 mm Utah Chub were extrapolated from literature values of survival and fecundity (Olson 1959; Jackson et al. 2004).

Bioenergetics Modeling

I used the Wisconsin bioenergetics program (Hanson et al. 1997) to estimate individual predator consumption of Utah Chub prey (g/g/year) and developed models for each species of predator trout in the reservoir. For Rainbow Trout, I used physiological parameters for Steelhead *Oncorhynchus mykiss* (Rand et al. 1993). For Cutthroat Trout, I used their closest published taxonomic surrogates (Steelhead) for

most parameters. I based lower consumption thermal optimum (CTO) and upper consumption thermal maximum (CTM) temperature values on models of Dwyer and Kramer (1975; Beauchamp 1995; Ruzycki et al. 2001). For Tiger Trout, the closest published taxonomic surrogate was the Brown Trout *Salmo trutta*, which I modeled similarly with parameters from Dieterman et al. (2004; see also Whitley et al. 2010).

Models were run over a time period of 1 year, initiated on July 26 and continued through July 25 of the following year. I accounted for an ontogenetic shift in diet preferences based on fish size in model simulations; at approximately 350 mm trout switch from a predominantly invertebrate-fueled diet to becoming increasingly piscivorous. Limited diet information by ages also necessitated the use of size-classes; I used age-3 and age-5 cohort growth of each species to be representative of small and large size classes, respectively, so annual growth could be most accurately estimated given available data. Additionally, I accounted for seasonal variation in feeding habits, incorporating diet proportions for six sampling periods throughout the year: 26 July 2011, 5 October 2011, 22 April 2012, 6 May 2012, 6 June 2012, and 25 July 2012. Predator and prey energy densities were derived from the literature, and/or taxonomically-close surrogates (Table 2.2). The percentage of indigestible prey biomass was set at 10% for all invertebrate prey, 3.3% for prey fish (Stewart et al. 1983), and 25% for crayfish (Stein and Murphy 1976). I scaled individual consumption estimates to the population level using size class-based abundance for each trout species (g of prey fish/year) derived from hydroacoustics surveys.

Additionally, I used bioenergetic efficiency (*BioEff*) as a scalar representation of the realized percentage of maximum possible consumption (g/g/day; 0-100%) for each of the size-class models based on fish growth observed in the field (Budy et al. 2013). This *BioEff* value is a proxy for overall fish performance, where a *BioEff* near 100% indicates a fish feeding near their maximum possible consumption rate (based on temperature, diet, and body size), whereas a *BioEff* value near 0% indicates a fish performing poorly, feeding at a rate much lower than theoretically possible.

Predator Performance

I calculated condition of all predators using two indices, Fulton's K (K_{TL}) and relative weight (W_r), since body condition is related to the availability of prey:

$$\text{Fulton's } K_{TL} = \frac{W}{L^3} * 100,000$$

$$\text{Relative Weight } W_r = 100 * \left(\frac{W}{W_s} \right)$$

where W is the weight of the fish (g), L is the total length (mm) of the fish, and W_s is the standard weight of a fish of the same length. The K_{TL} index assumes larger ratios reflect a healthier physiological state (Pope and Kruse 2007). Equations and values for W_s were obtained from the literature for lentic Cutthroat Trout and lentic Rainbow Trout (Kruse and Hubert 1997; Simpkins and Hubert 1996). Parameters for lentic Tiger Trout were estimated using a length-weight regression of summer 2011 Tiger Trout data ($r^2=0.97$, $a = -6.2159$ and $b = 3.4608$). A W_r of 100 is generally accepted as the national standard

(Anderson and Neumann 1996). Analysis of variance (ANOVA) was run to compare Fulton's K_{TL} between each trout species and by season.

Additionally, the Utah Division of Wildlife Resources has marked all stocked Cutthroat Trout and Rainbow Trout since 2009 with unique fluorescent dyes, where each year corresponds to a different color dye. I examined all Rainbow Trout and Cutthroat Trout caught for fluorescent dye marks by using an ultraviolet lamp set up in a dark room. I then calculated the relative return rate as the number of marked fish recaptured, divided by the initial number stocked by Utah Division of Wildlife Resources.

I determined the proportional stock density (PSD) for each trout species following procedures outlined in Anderson and Neumann (1996):

$$PSD = \frac{(\text{number of fish} \geq \text{minimum quality length})}{(\text{number of fish} \geq \text{minimum stock length})} * 100$$

Values of PSD range from 1 to 100, and are a descriptor value of length-frequency data which may identify potential for "imbalances" in predator-prey population dynamics.

For most fish, 40-70 is a typical objective range for "balanced" populations. Values less than the objective range indicate a population dominated by small fish, whereas values greater than the objective range indicate a population comprised mainly of large fish.

Stock and quality lengths vary by species, and are based on percentages of world-record lengths (Gabelhouse 1984; Kruse and Hubert 1997; Simpkins and Hubert 1996; Hyatt and Hubert 2001). Stock length (20-26% of world-record length) refers to the minimum size fish with recreation value, while quality length (36-41% of world-record length) refers to the minimum size fish most anglers want to catch.

I also evaluated the relative stock density (RSD) using values reported in Table 2.3. “Preferred length” (45-55% of world-record length) refers to the minimum size fish anglers prefer to catch when given a choice. “Memorable length” (59-64% of world-record length) refers to the minimum size fish most anglers remember catching, whereas “trophy length” (74-80% of world-record length) refers to the minimum size fish considered worthy of acknowledgement. Like PSD, RSD can provide useful information regarding population dynamics, but is more sensitive to changes in year-class strength. I calculated RSD as

$$\text{RSD} = \frac{(\text{number of fish} \geq \text{specified length})}{(\text{number of fish} \geq \text{minimum stock length})} * 100$$

For example, RSD-Preferred (RSD-P) was the percentage of stock length fish that were also longer than the preferred length.

Results

Predator Population Estimation

From July 2011 to October 2012 I captured and processed 699 Cutthroat Trout, 111 Rainbow Trout, 398 Tiger Trout, and 8,489 Utah Chub. Fish were captured at a variety of locations throughout the lake, with equal effort applied at each site. Utah Chub dominated the Scofield Reservoir fish community and were the most abundant, regardless of season. I collected approximately 5 Utah Chub per gill net-hour in 2012 (CPUE = 3.3 ± 0.5 in spring, 6.8 ± 0.6 in summer, and 5.2 ± 0.3 in autumn [mean \pm 1 SE];

Figure 2.2), lower catch rates than previously recorded from Utah Division of Wildlife Resource sampling in 2008 and 2009.

The trout community catch rates varied by season and by species. By season in 2012, trout were caught more frequently in fall (CPUE = 0.737 ± 0.053 fish per hour [mean ± 1.96 SE]), than either the summer (CPUE = 0.242 ± 0.053 fish per hour) or spring (CPUE = 0.216 ± 0.053 fish per hour; ANOVA; $F=34.39$; $df=2, 14$; $P < 0.001$). By species, Cutthroat Trout were numerically dominant from Rainbow Trout, which were significantly less than Tiger Trout. There were no significant differences in Cutthroat Trout and Tiger Trout catch.

Estimates of abundance for Cutthroat Trout, Rainbow Trout, and Tiger Trout fluctuated based on season. Notably, Cutthroat Trout abundance ranged from low in August 2011 to high abundance in June of 2013 (Table 2.5; Figure 2.3), and made up 7% of the total catch in 2013. Tiger Trout were caught less frequently in gill nets than Cutthroat Trout, but still increased in abundance in early 2013, making up 4% of the total catch. Regardless of season, Rainbow Trout had extremely low catch rates ($< 1\%$), with the population appearing to consist of only a small fraction of individuals compared to Cutthroat Trout and Tiger Trout. Proportionally, the Cutthroat Trout population was dominated by large fish (81%) and the Tiger Trout population varied by year (47% and 80% large, respectively); however, the population of all sizes of Rainbow Trout remained low. Notably, species relative catch rates have shifted considerably with Utah Chub establishment, as Rainbow Trout exhibited peak returns in 2005 when Utah Chub were first discovered and have since declined to make up $< 1\%$ of the total catch (Figure 2.4).

Predator Diet Composition, Growth, and Thermal History

Utah Chub were the predominant prey item for large Cutthroat Trout and large Tiger Trout throughout the year (Figure 2.5). The percentage of piscivory for large Cutthroat Trout ranged from 35% in autumn 2011 to 69% in summer 2012. For large Tiger Trout, prey fish represented 19-79% of their total diet depending on season. I found only one Redside Shiner and no trout in diets, therefore, for simplicity of this study I assumed all prey fish were Utah Chub. The relative importance of secondary food sources varied; large Cutthroat Trout relied heavily on chironomids and terrestrial invertebrates, whereas large Tiger Trout consumed significant portions of crayfish. Aquatic invertebrates, supplemented by lesser proportions of terrestrial invertebrates and organic matter, represented the largest proportion of prey in diets of small and large Rainbow Trout, during most of the year. Similarly, small Cutthroat Trout and small Tiger Trout relied heavily on aquatic invertebrates, terrestrial invertebrates, and crayfish.

I determined annual growth estimates for a representative small and large size class for each trout species. For Cutthroat Trout, starting and ending weight used in bioenergetics simulations were conservative estimates, determined from cohort length and weight information (mean size) for two size classes (small: 274 - 333 g, large: 420 - 617 g; Figures 2.6 and 2.9). Rainbow Trout collected during both 2011 and 2012 ranged from age-2 to age-7 according to otoliths, with weight estimates based on otolith aging (small: 114 - 186 g, large: 495 - 614 g; Figures 2.7 and 2.9). There were no marked cohorts of Tiger Trout in Scofield Reservoir, therefore mean weight at size was

determined from otolith size-at-age data (small: 134 – 327 g, large: 761 – 1901 g; Figures 2.8-2.9).

Temperature was recorded at 1- hour intervals from 19 July 2011 – 7 September 2011 and 23 April 2012 to 7 June 2013, for depths of 3, 6, and 9m from the surface (Figure 2.10). These data were combined with monthly temperature profiles taken by hand using a data logger to obtain a representative simulation year. Maximum average daily temperature during the simulation period was 18.5°C. The consumption thermal optimum (CTO) for Rainbow Trout, 20°C, was higher than Rainbow Trout experienced in the reservoir, whereas CTO for Tiger Trout, 17.5°C, was available in Scofield Reservoir during the summer months, and near-CTO of Cutthroat Trout, 14°C, were available through much of the time series. The consumption thermal optimum of a fish represents the optimum water temperature of a fish needed for maximum achieved consumption, based on laboratory studies (Hartman and Hayward 2007).

Prey Biomass and Production

I estimated biomass and production of Utah Chub to quantify the amount of prey available in Scofield Reservoir. The biomass of Utah Chub (as estimated from hydroacoustic surveys) varied from a low of 318,900 kg of Utah Chub (11,678,000 chub) in August 2011 to a high of 627,600 kg of Utah Chub (23,281,000 chub) in June 2013. Age -1 chub, or those < 100 mm TL, were estimated as 9,027,000 fish in the population in 2011 and 17,970,000 fish in 2013. Using biomass and mass gain by size class, Utah Chub production was estimated at 433,960 kg/year (8,272,600 chub/year) during the

end of the summer growth season in 2011. In comparison, Utah Chub production at the start of the season in 2013 was 649,630 kg/year (9,989,700 chub/year; Figure 2.11).

Bioenergetics Simulations of Consumption

Of all predator species, an individual large Tiger Trout consumed the largest proportion of prey fish, primarily Utah Chub. The average large *individual* Tiger Trout consumed over 2,660 g of prey fish in a given year (63 chub per year; Table 2.6). The average large Cutthroat Trout consumed 1,820 g Utah Chub annually (49 chub per year). The mean total length of Utah Chub eaten by Cutthroat Trout was 131 mm (37 g), while the mean total length of Utah Chub eaten by Tiger Trout was 139 mm (42 g); these sizes were used to scale consumption estimates (g) to number of chub. Rainbow Trout did not display an affinity for prey fish; an individual large Rainbow Trout consumed only 400 g of Utah Chub in a year. The smaller sizes of trout (< 350 mm TL) had only a minor contribution towards the overall consumption of Utah Chub prey.

When the estimated consumption of an individual predator of each species was scaled to the overall reservoir-wide population of each species, proportional contributions to total piscivory changed accordingly. The population of large Cutthroat Trout in the reservoir consumed over 615,000 kg of Utah Chub in a year (16.6 million chub), about 65% of the overall reservoir-wide consumption of Utah Chub. The smaller population of Tiger Trout contributed 33% of the overall consumption, consuming about 359,000 kg (8.5 million chub) yearly. The Rainbow Trout population contributed less than 1% of the total piscivory in Scofield Reservoir. Using consumption thermal optimum temperatures for each species when available in the reservoir did not strongly

influence consumption estimates of Utah Chub; Cutthroat Trout consumption (kg) at optimal temperature was <1% lower, and Tiger Trout consumption was <2% lower. Therefore, although individual consumption of prey fish was less for Cutthroat Trout, due to their higher lake-wide abundance, Cutthroat Trout currently exert the strongest predation pressure on the Utah Chub population.

The combined consumption by Cutthroat Trout and Tiger Trout exceeds the annual production estimate of Utah Chub. Large Cutthroat Trout and large Tiger Trout alone consumed over 22 million chub scaling with end of summer hydroacoustic abundance estimates. When consumption was calculated based on early summer predator abundance, large Cutthroat Trout and large Tiger Trout consumed over 26 million chub in a year, approaching the combined estimate of 33 million Utah Chub abundance and annual (Figure 2.11).

Salmonid Performance

Bioenergetics simulations indicated that *BioEff* values for all predator species were much lower than 100%, suggesting fish were not feeding near their maximum possible consumption rate (Table 2.7). Cutthroat Trout fed at approximately 39% of maximum consumption rate, whereas Rainbow Trout fed more efficiently at 47% of their maximum, and Tiger Trout were the most efficient, feeding at 56% of their maximum rate during the 2011-2012 simulation year. Additionally, Cutthroat Trout and Tiger Trout both exhibit lower bioenergetic efficiency with larger size.

The condition metric, K_{TL} , additionally supported BioEff results. There were no significant differences in K_{TL} by season (ANOVA; $F=0.89$; $df=2, 14$; $P > 0.05$); however,

there were strong condition differences by species (ANOVA; $F=14.27$; $df=2, 14$; $P < 0.001$). Cutthroat Trout exhibited the significantly lowest overall performance, with decreasing values as seasons progressed ($K_{TL} = 0.89 - 0.82$; Table 2.8). Rainbow Trout performance was substantially higher than that of Cutthroat Trout, but also decreased seasonally ($0.97 - 0.90$). Tiger Trout performed best in the summer (0.96), with lower condition in the spring and autumn.

All three species of trout exhibited W_r values significantly lower than standard performance in the summer of 2012 (all t-test $P < 0.001$; Figure 2.12). The average relative weight values for Cutthroat Trout and Rainbow Trout were both 79, where a relative weight less than 80 is considered severely thin. The average relative weight of Tiger Trout was much higher (96), describing a fish in relatively good condition. When standard values for lotic Brown Trout (Milewski and Brown 1994) were substituted in Tiger Trout calculations, the average relative weight decreased to 90, indicating feeding conditions may be lacking or fish are competing. While this assessment of fish condition was highlighted for the summer 2011 season, studies show seasonal trends of W_r may be present in some systems, with the highest values occurring October- May (Quist et al 2002); therefore, these estimates are conservative.

Based on limited mark-recapture data, Cutthroat Trout and Rainbow Trout both exhibit relative return rates of $< 0.01\%$ (Table 2.9). Notably, I caught marked Rainbow Trout very infrequently (Table 2.10), and as return rates are extremely low for both species of fish, there are potential issues related to mark retention of the fluorescent

dye utilized in marking. Thus these data could not be incorporated into management recommendations.

Stock density values of trout in Scofield Reservoir fluctuated widely, despite initial stockings at similar numbers and sizes. In Scofield Reservoir, Rainbow Trout exhibited extremely low PSD and RSD-P values, with few fish above the “preferred” length of 500 mm and no proportion of fish above the “memorable” length of 650 mm (Table 2.11). Cutthroat Trout exhibited relatively high values of proportional stock density, with a substantial proportion of fish above the “preferred” length of 450 mm. Nearly all Tiger Trout in Scofield Reservoir were of “preferred” length (450 mm), and there was a significant portion of fish of “memorable” length (525 mm), indicating the population was dominated by large fish.

Discussion

In response to the exponential increase of the unwelcome Utah Chub in Scofield Reservoir in recent years, I used a combination of field sampling, hydroacoustic surveys, and bioenergetics simulations for three top predators in the system to quantitatively assess the relative potential of these species to act as biological control agents. Comparison of trout consumption of Utah Chub revealed striking differences among the species with important management implications. I found that the population of large (≥ 350 mm) Cutthroat Trout consumed the largest proportion of Utah Chub in Scofield Reservoir. These trout are voracious predators, consuming 615,000 kg of Utah Chub in a single year. Furthermore, based on model simulations, the average large Tiger Trout rely

heavily on Utah Chub as well, which as a population, equals almost 359,000 kg more Utah Chub consumed annually. However, Rainbow Trout, known to exhibit variable rates of piscivory, do not consume a significant number of Utah Chub in Scofield Reservoir. Not only does the average large Rainbow Trout consume few chub in a year, but the population of Rainbow Trout is so small, their collective impact on Utah Chub is insignificant. In sum, comparisons between bioenergetic estimates of predator consumption versus chub production demonstrated that Tiger Trout and Cutthroat Trout both appear to have significant potential to act as effective biological control agents on Utah Chub, whereas Rainbow Trout currently contribute little to Utah Chub control.

Utah Chub were caught in extremely high densities throughout the time period of this study, confirming that the population of Utah Chub has increased to very high levels. Abundance estimates from June 2013 suggest there are over 23 million chub (1,277,000 kg) in the reservoir. This estimate is substantially lower when using acoustic data from late August, perhaps because trout consumed large quantities of chub throughout the summer growing season. Nonetheless, I estimated production of Utah Chub in 2013 at a rate of 2.5 million chub per year. Utah Chub are a non-game fish that are not targeted by harvest and that exhibit high reproductive potential (Neuhold 1957). As such, the high production rates of Utah Chub in Scofield Reservoir are not surprising, and are most likely due to favorable littoral habitat and abundant food supply (Olson 1959). In Scofield Reservoir, summer *Daphnia* densities (0.1 /L) were low compared to a

nearby Utah reservoir (7.4 /L), possibly indicating Utah Chub feed heavily on these available aquatic zooplankton (Baldwin et al. 2000).

Abundance and production estimates for Utah Chub are based on a few important assumptions. Our acoustic surveys were only able to clearly account for fish 100 mm and larger, as such, the age-0 and age-1 Utah Chub fell outside target acceptance guidelines; these values were necessarily back-calculated based on literature estimates of fecundity and survival values for Tui Chub *Gila bicolor* (Jackson et al. 2004). Nonetheless, our results are logical and consistent with expected values from similar prey-dominated systems. Eilers et al. (2011) estimated up to 23 million Tui Chub present in Diamond Lake, Oregon before a prescribed rotenone treatment, with a density of “catchable” Tui Chub equal to 0.09 fish/m³. Comparatively, I estimated densities of 0.04 fish /m³ - 0.13 fish /m³ of Utah Chub at Scofield Reservoir. Additionally, historical evidence demonstrates that Utah Chub coexisting with Cutthroat Trout display higher juvenile growth rates, delayed age at maturity, and larger size at maturity, as chub that reach adult sizes are less vulnerable to predation (Johnson and Belk 1999). Utah Chub in Scofield Reservoir display similar life-history traits; there are a substantial proportion of Utah Chub larger than gape-limited predators are able to consume. Consequently, the reproductively-mature portion of this population of chub must senesce before trout predators will be fully capable of controlling the population.

The full impacts of Cutthroat Trout and Tiger Trout on Utah Chub in Scofield reservoir are likely even greater, as this study did not consider non-consumptive effects of predators on chub. Predators may affect Utah Chub survival and production through

behavioral changes, such as predator avoidance. Understanding density dependent responses of the Utah Chub population, stunting and potentially restraining Utah Chub within the size range at which predators are not gape limited, is important for predicting long term effects of trout predation on chub (Freckleton et al. 2003; Irwin et al. 2003). Effective biological control will be more difficult if the chub population growth rate increases at low densities (Hein et al. 2006).

My bioenergetics model predictions demonstrated the large Cutthroat Trout population annually could consume more than half the standing prey biomass in Scofield Reservoir, highlighting their potential as an efficient biological control agent. The disparity between consumption and production suggests strong predation pressure from Cutthroat Trout on Utah Chub, but could also indicate we are unsurprisingly underestimating one or more components of chub production (Jackson et al. 2004). Regardless, Bear Lake Cutthroat Trout, the strain stocked in Scofield Reservoir, are known to exhibit traits of top-level predators and attain large sizes using fishes as forage (Neilson and Lentsch 1988; Hepworth et al. 1999; Hepworth et al. 2009). In Lake Chelan, Washington, Lake Trout consumption on Kokanee Salmon *O. nerka*, exceeded Kokanee Salmon production rates, leading to an almost 90% decline in the Kokanee population over 5 years (Schoen et al. 2012). Additionally, at Flaming Gorge Reservoir, UT-WY, researchers postulated the slower-growing Utah Chub were more vulnerable to predation by Lake Trout than fast-growing Kokanee (Yule and Luecke 1993). Prey size is an important factor determining consumption (Scharf et al. 2000), and Cutthroat Trout in Scofield Reservoir are consuming prey at and above their theoretical gape limit,

demonstrating consumption of chub up to 60% of their own total length. Collectively, these observations and those of others support the argument that these piscivorous trout may effectively control Utah Chub in Scofield Reservoir.

Similar to Cutthroat Trout, Tiger Trout appear to have potential as an effective biological control agent. Despite a paucity of literature on Tiger Trout ecology, Tiger Trout in Scofield Reservoir demonstrate the aggressive and piscivorous nature suggested of this new hybrid species. Tiger Trout displayed strong predation impacts on Utah Chub prey, relatively high catch rates, high condition factors, and modest *BioEff* values in Scofield Reservoir. Furthermore, Tiger Trout have high proportional stock density (and relative stock density) values, indicating the importance of this species to the Scofield Reservoir fishery. Tiger Trout are currently being stocked in over 30 bodies of water throughout the state of Utah to potentially enhance fisheries and consume undesired prey species. In addition to their contribution to the fishery and ability to control undesired prey species, Tiger trout have the added benefit that they are a sterile hybrid (Brown Trout x Brook Trout) and unable to permanently expand beyond where they are stocked, an important conservation consideration for native species and ecosystems downstream (Zelasko et al. 2010).

My study indicated Rainbow Trout, a ubiquitous species stocked throughout the western U.S. and potential top predator, does not contribute substantially to predation pressure on Utah Chub in Scofield Reservoir. There are at least a dozen strains of Rainbow Trout stocked worldwide, which display a range of piscivory (Hudy and Berry 1983; Swales 2006). Rainbow Trout have demonstrated piscivory at sizes greater than

250 mm TL (Beauchamp 1990), sizes as small as 100 mm TL for age-1 fish (Juncos et al. 2013), and broadly feed on this more energetically-favorable prey at least seasonally (Galbraith 1967; Taylor and Gerking 1980; Juncos et al. 2011). However, Rainbow Trout in Flaming Gorge, UT-WY, consume primarily aquatic invertebrates and zooplankton and rarely demonstrate an ontogenetic shift to piscivory at larger sizes (Haddix and Budy 2005). Hatchery personnel stock Fish Lake/DeSmet or Erwin/Sand Creek Rainbow Trout into Scofield Reservoir, likely originating from the Eagle Creek, California strain, where their diet has been documented to not contain fish prey (Hubert et al. 1994; Wagner 1996).

Rainbow Trout recreational fisheries and subsequent stocking programs are common throughout North America (Baird et al. 2006; Swales 2006; Josephson et al. 2012), however, performance varies widely across lentic systems (Hepworth et al. 1999). The success of stocking programs may be attributed to strain (Babey and Berry 1989), age and size at stocking (Baird et al. 2006), lack of predation (Matkowski 1989), abundant food supplies (Hubert and Chamberlain 1996; Haddix and Budy 2005), or productivity of waters (Gipson and Hubert 1991; Budy et al. 2011; Blair et al. 2013). Specifically, Rainbow Trout in Scofield Reservoir exhibit poor returns and low survival, despite seemingly high prey availability, contributing to a declining fishery. However, the few Rainbow Trout survivors display relatively high body condition indices. It is possible that Fulton's K and relative weight are not sufficient indices to detect a decline in energy reserves, as water content will increase with food limitation (Josephson et al. 2012). Nonetheless, the few Rainbow Trout that persist are of size that parallel Rainbow

Trout in other systems. Mean total lengths of Rainbow Trout populations stocked in Utah reservoirs at similar sizes to those of Scofield Reservoir were around 300 mm one year after stocking (Hepworth et al. 1999), similar to the 290 – 310 mm TL range of Rainbow Trout in Scofield Reservoir a year after being stocked. Low proportions of fish in the diet of Rainbow Trout may limit maximum growth potential (Hubert et al. 1994; Luecke et al. 1999; Haddix and Budy 2005).

Furthermore, reduced Rainbow Trout performance may be due to competition for resources or predator avoidance behaviors with other sport or non game species. Rainbow Trout in Fish Lake, Utah, have exhibited substantially lower catch and harvest rates in recent years, as the community composed of Yellow Perch, Splake, Lake Trout, and Utah Chub led to a shift to predation on Rainbow Trout by Lake Trout, as well as other potential food limitations (Hepworth et al. 2011). Thus, while Rainbow Trout in Scofield Reservoir are stocked at relatively large sizes and in large quantities, presence of other top predators in the system may influence feeding and behavior of Rainbow Trout, leading to low apparent survival and also possibly realized growth potential.

In contrast, Cutthroat Trout in Scofield Reservoir switch to a more piscivorous diet at smaller sizes than observed elsewhere. In Scofield Reservoir, Cutthroat Trout switch to a Utah Chub-based diet around 300 mm TL, whereas Cutthroat Trout in Bear Lake, UT-WY, a very unproductive reservoir, did not become more piscivorous until 380 mm TL with very high mortality of these adult age-classes (Ruzycki et al. 2001). In Strawberry Reservoir, Utah, the diet of stocked Bear Lake Cutthroat Trout is dominated by *Daphnia* prey, and fish only represent a small fraction of their diet (Baldwin et al.

2000). Bioenergetic efficiency values for Cutthroat Trout in Scofield Reservoir indicate they are feeding at less than half of their maximum possible consumption rate, suggesting this species may be food-limited and/or experiencing inter or intraspecific competitive exclusion effects (Budy et al. 2013).

The superior performance of the Tiger Trout stock in Scofield Reservoir contradicts observations in other Utah reservoirs. Tiger trout stocked in Panguitch Reservoir after a rotenone treatment in 2006 demonstrated poor survival and were found in limited numbers during annual gill-net surveys (Hepworth et al. 2009). However, Tiger Trout in Panguitch were stocked in lower quantities and at smaller sizes, with 20,000 fish at 75 mm yearly, as opposed to 120,000 fish at 150 mm TL in Scofield Reservoir. Predation risk due to a smaller size at stocking and lack of fish prey-base due to chemical treatment may have contributed to the poor performance of Tiger Trout elsewhere. Additionally, piscivores may interact strongly with prey populations in one system, but interact very weakly if at all with the same prey in other systems (Rudolf 2012). Tiger Trout in lakes of eastern Washington rarely became piscivorous, even in the presence of a dense Redside Shiner population (Miller 2010). In contrast, Tiger Trout within our study exhibited strong preferences for fish prey (Utah Chub). The high performance of Scofield Reservoir Tiger Trout is similar to High Savery Reservoir, Wyoming, where state record Tiger Trout has become an annual occurrence (Carrico 2012). This proven strong performance of Tiger Trout reflects on their potential to support a valuable sport fishery.

Although I observed several different lines of evidence that consistently demonstrated trout exert a strong predatory effect on Utah Chub, there are some notable uncertainties associated with my bioenergetics estimates. Borrowing parameters from other species could produce unreliable or biased results, especially when the physiology of the species varies. These discrepancies may explain low *BioEff* values (Ney 1993; Chipps and Wahl 2008; Hartman and Kitchell 2008) and lead to under- or overestimates of consumption. While it is not uncommon to borrow parameters (e.g., Beauchamp et al. 1995; Ruzycki et al. 2001; Beauchamp and Van Tassel 2001) improved parameter estimates may be needed, specifically for Tiger Trout, a new species. Nevertheless, I borrowed metabolic costs of activity, respiration, and thermal habit parameters for Tiger Trout from studies of Brown Trout (Ney 1990; Dieterman et al. 2004; Whitley et al. 2010). Nonetheless, Tiger Trout have been generally accepted to behave similarly to Brown Trout, their close relative, and no studies to-date has quantified consumption potential of this unique species.

Predator control of nuisance prey has been variable with other organisms. Despite citing typical failure to control target species (Williamson and Fitter 1996), Simberloff (2009) argues many species have been successfully eradicated and other species maintained at low densities for long periods of time. Consequently, pessimism surrounding the potential to eradicate invasive species or manage at very low densities may be unwarranted. The species-specific models presented herein were based on wild fish, natural prey, and ecologically-realistic temperature ranges, which typically results in models with reasonable predictive capability (Mesa et al 2013). Others have used a

similar approach to predict consumption of Brook Trout *S. fontinalis* (Hartman and Cox 2008), Bull Trout *S. confluentus* (Mesa et al. 2013), Chinook Salmon *O. tshawytscha* (Madenjian et al. 2004), hybrid Sunfish *Lepomis cyanellus x L. macrochirus* (Whitledge et al. 1998), and Burbot (Paakkonen et al. 2003). Thus, I believe these results represent a plausible reflection of the consumption occurring in Scofield Reservoir and indicate strong potential for Cutthroat Trout and Tiger Trout to act as effective biological control agents of undesired prey fish.

Management Implications

The findings of this study contribute to our understanding of the potential for stocked trout to act as biological control agents on unwelcome forage fishes. My results suggest that the high rates of piscivory of Cutthroat Trout and Tiger Trout in artificial lentic ecosystems are likely sufficient to effectively reduce the overall abundance of Utah Chub and control their ability to dominate fish assemblages. Further, since 2009, there has been a dramatic reduction in Utah Chub catch rates and the population no longer appears to be increasing. Additionally, Tiger Trout caught in the reservoir have been of state record status, an exciting aspect of this new fishery for anglers. Management regulations that protect large Cutthroat Trout and Tiger Trout and increase predator densities may provide the predation pressure necessary to suppress overabundant Utah Chub populations, whereas Rainbow Trout have little potential for responsive management manipulations. A stocking shift from Rainbow Trout to Tiger Trout may be beneficial, if chub reduction is the overall management goal. Careful

scrutiny of the current system as well as management goals and objectives, must continue to be taken into consideration when determining management actions.

References

- Anderson, R.O., and R.M. Neumann. 1996. Length, weight, and associated structural indices. Pages 447-482 in B.R. Murphy and D.W. Willis, editors. *Fisheries Techniques*, 2nd edition. American Fisheries Society, Bethesda, Maryland.
- Babey, G.J., and C.R. Berry. 1989. Post-stocking performance of three strains of Rainbow Trout in a reservoir. *North American Journal of Fisheries Management* 9:309-315.
- Baird, O.E., C.C. Krueger, and D.C. Josephson. 2006. Growth, movement, and catch of Brook, Rainbow, and Brown Trout after stocking into a large, marginally suitable Adirondack river. *North American Journal of Fisheries Management* 26:180-189.
- Baldwin, C. M., D.A. Beauchamp, and J.J. Van Tassell. 2000. Bioenergetic assessment of temporal food supply and consumption demand by salmonids in the Strawberry Reservoir food web. *Transactions of the American Fisheries Society* 129(2):429-450.
- Beauchamp, D. A. 1990. Seasonal and diel food habits of Rainbow Trout stocked as juveniles in Lake Washington. *Transactions of the American Fisheries Society* 119:475-482.
- Beauchamp, D. A., A.D. Cross, J.L. Armstrong, K.W. Myers, J.H. Moss, J.L. Boldt, and L.J. Haldorson. 2007. Bioenergetic responses by Pacific Salmon to climate and ecosystem variation. *North Pacific Anadromous Fish Commission Bulletin No. 4*: 257-269.
- Beauchamp, D. A., M.G. LaRiviere, and G.L. Thomas. 1995. Evaluation of competition and predation as limits to juvenile Kokanee and Sockeye Salmon production in Lake Ozette, Washington. *North American Journal of Fisheries Management* 15:193-207.
- Beauchamp, D. A., and J.J. Van Tassell. 2001. Modeling trophic interactions of Bull Trout in Lake Billy Chinook, Oregon. *Transactions of the American Fisheries Society* 130:204-216.

Beauchamp, D. A., D.L. Parrish, and R.A. Whaley. 2009. Coldwater fish in large standing waters. Pages 97-118 in S.A. Bonar, W.A. Hubert, and D.W. Willis, editors. Standard methods for sampling North American freshwater fishes. American Fisheries Society, Bethesda, Maryland.

Blair, J.M., I. Ostrovsky, B.J. Hicks, R.J. Pitkethley, and P. Scholes. 2013. Growth of Rainbow Trout (*Oncorhynchus mykiss*) in warm-temperate lakes: implications for environmental change. Canadian Journal of Fisheries and Aquatic Sciences 70:815-823.

Brandt, S. B., and K.J. Hartman. 1993. Innovative approaches with bioenergetics models: future applications to fish ecology and management. Transactions of the American Fisheries Society 122:731–735.

Brooks, J.L. 1957. Identifications and nomenclature of Cladocera, Calanoida, and Cyclopoida. Memoirs of the Connecticut Academy of the Arts and Science 13(1).

Budy, P., M. Baker, and S. K. Dahle. 2011. Predicting fish growth potential and identifying water quality constraints: a spatially-explicit bioenergetics approach. Environmental Management 48(4):691–709.

Budy, P., G.P. Thiede, J. Lobon-Cervia, G. Gonzalez Fernandez, P. McHugh, A. McIntosh, L. Asbjorn Vollestad, E. Becares, and P. Jellyman. 2013. Limitation and facilitation of one of the world 's most invasive fish: an intercontinental comparison. Ecology 94(2):356–367.

Bunnell, D. B., C.P. Madenjian, and R.M. Claramunt. 2006. Long-term changes of the Lake Michigan fish community following the reduction of exotic Alewife (*Alosa pseudoharengus*). Canadian Journal of Fisheries and Aquatic Sciences 63:2434-2446.

Bureau of Reclamation. 2009. Scofield Dam. U.S. Department of the Interior. Available: https://www.usbr.gov/projects/Facility.jsp?fac_Name=Scofield+Dam. (August 2013).

Bureau of Reclamation. 2011. Scofield Project. U.S. Department of the Interior. Available: https://www.usbr.gov/projects/Project.jsp?proj_Name=Scofield%20Project. (August 2013).

Carpenter, S.R., J.F. Kitchell, and J.R. Hodgson. 1985. Cascading trophic interactions and lake productivity. BioScience 35(10):634-639.

- Carrico, M. 2012. High Savery Reservoir, Wyoming. Available: www.highsavery.com. (November 2013).
- Cauffope, G., and S.J.J. Heymans. 2005. Energy contents and conversion factors for sea lion's prey. Pages 225-237 *in* S. Guenette and V. Christensen, editors. Food web models and data for studying fisheries and environmental impacts on Eastern Pacific Ecosystems. Fisheries. Centre Research Reports 13(1).
- Chipps, S.R., and D.H. Wahl. 2008. Bioenergetics modeling in the 21st century: reviewing new insights and revisiting old constraints. *Transactions of the American Fisheries Society* 137:298-313.
- Ciancio, J. E., M.A. Pascual, and D.A. Beauchamp. 2007. Energy density of Patagonian aquatic organisms and empirical predictions based on water content. *Transactions of the American Fisheries Society* 136:1415–1422.
- Courtenay, W. R., and C.C. Kohler. 1986. Regulating introduced aquatic species: a review of past initiatives. *Fisheries* 11(2):34-38.
- Cummins, K. W., and J.C. Wuycheck. 1971. Caloric equivalents for investigations in ecological energetics. *International Association for Theoretical and Applied Limnology Proceedings No. 18*.
- Dahm, E., J. Hartmann, T. Lindem, and H. Loffler. 1985. ELFAC experiments on pelagic fish stock assessment by acoustic methods in Lake Constance. *European Inland Fisheries Advisory Commission Occasional Paper No. 15*. FAO, Rome, Italy.
- Debach, P.D. 1964. *Biological control of insect pests and weeds*. Chapman and Hall Ltd., London.
- Department of Environmental Quality. 2010. Scofield Reservoir TMDL. Division of Water Quality, Salt Lake City, UT.
- Dieterman, D. J., W.C. Thorn, and C.S. Anderson. 2004. Application of a bioenergetics model for Brown Trout to evaluate growth in Southeast Minnesota streams. Minnesota Department of Natural Resources, St. Paul, MN.

Dwyer, W. P., and R.H. Kramer. 1975. The influence of temperature on scope for activity in Cutthroat Trout, *Salmo clarki*. Transactions of the American Fisheries Society 104(3):552–554.

Edmonson, W.T. 1959. The rotifera. Pages 420-494 in G.C. Whipple and H.B. Ward, editors. Freshwater Biology, 2nd edition. Wiley, New York.

Eilers, J. M., H.A. Truemper, L.S. Jackson, B.J. Eilers, and D.W. Loomis. 2011. Eradication of an invasive cyprinid (*Gila bicolor*) to achieve water quality goals in Diamond Lake, Oregon (USA). Lake and Reservoir Management 27(3):194–204.

Ellis, B.K., J.A. Stanford, D. Goodman, C.P. Stafford, D.L. Gustafson, D.A. Beauchamp, D.W. Chess, J.A. Craft, M.A. Deleray, and B.S. Hansen. 2011. Long-term effects of a trophic cascade in a large lake ecosystem. Proceedings of the National Academy of Sciences 108:1070-1075.

Freckleton, R.P., D.M. Silva Matos, M.L.A. Bovi, and A.R. Watkinson. 2003. Predicting the impacts of harvesting using structured population models: the importance of density-dependence and timing of harvest from a tropical palm tree. Journal of Applied Ecology 40:846-858.

Freeman, M.A., J.F. Turnbull, W.E. Yeomans, and C.W. Bean. 2010. Prospects for management strategies of invasive crayfish populations with an emphasis on biological control. Aquatic Conservation: Marine and Freshwater Ecosystems 20(2):211-223.

Gabelhouse, D.W. 1984. A length-categorization system to assess fish stocks. North American Journal of Fisheries Management 4:273-285.

Galbraith, M. G. 1967. Size-selective predation on *Daphnia* by Rainbow Trout and Yellow Perch. Transactions of the American Fisheries Society 96:1–10.

Gardunio, E.I., C.A. Myrick, R.A. Ridenour, R.M. Keith, and C.J. Amadio. 2011. Invasion of illegally introduced Burbot to the upper Colorado River Basin, USA. Journal of Applied Ichthyology 27:36-42.

Gasith, A., and S. Gafny. 1990. Effects of water level fluctuation on the structure and function of the littoral zone. Pages 156-171 in M.M. Tilzer and C. Serruya, editors. Large Lakes. Springer, Berlin Heidelberg.

- Gill, A.B. 2003. The dynamics of prey choice in fish: the importance of prey size and satiation. *Journal of Fish Biology* 63(1):105-116.
- Gipson, R.D., and W.A. Hubert. 1991. Factors influencing the body condition of Rainbow Trout in small Wyoming reservoirs. *Journal of Freshwater Ecology* 6:327-334.
- Guy, C.S., T.E. McMahon, C.J. Smith, B.S. Cox, W.A. Fedenberg, and D.W. Garfield. 2011. Diet overlap of top-level predators in recent sympatry: Bull Trout and nonnative Lake Trout. *Journal of Fish and Wildlife Management* 2(2):183-189.
- Haddix, T., and P. Budy. 2005. Factors that limit growth and abundance of Rainbow Trout across ecologically distinct areas of Flaming Gorge Reservoir, Utah–Wyoming. *North American Journal of Fisheries Management* 25(3):1082–1094.
- Hambright, K. D. 1991. Experimental analysis of prey selection by Largemouth Bass: role of predator mouth width and prey body depth. *Transactions of the American Fisheries Society* 120:500–508.
- Hanson, M. J., D. Boisclair, S.B. Brandt, and S.W. Hewett. 1993. Applications of bioenergetics models to fish ecology and management: where do we go from here. *Transactions of the American Fisheries Society* 122:1019–1030.
- Hanson, P.C., T.B. Johnson, D.E. Schindler, and J.F. Kitchell. 1997. Bioenergetics model 3.0 for Windows. University of Wisconsin, Sea Grant Institute, Technical Report WISCU-T-97-001. Madison, Wisconsin.
- Hart, J., and P.W. Birdsey. 2008. Scofield Research Proposal. Price, UT: Utah Division of Wildlife Resources, Southeastern Regional Office.
- Hartman, K.J., and M.K. Cox. 2008. Refinement and testing of a Brook Trout bioenergetics model. *Transactions of the American Fisheries Society* 137:357-363.
- Hartman, K.J., and R.S. Hayward. 2007. Bioenergetics. Pages 515-560 *in* C.S. Guy and M.L. Brown, editors. *Analysis and interpretation of freshwater fisheries data*. American Fisheries Society, Bethesda, Maryland.
- Hartman, K.J., and J.F. Kitchell. 2008. Bioenergetics modeling: progress since the 1992 symposium. *Transactions of the American Fisheries Society* 137:216-223.

Hartman, K.J., and F.J. Margraf. 1993. Evidence of predatory control of Yellow Perch (*Perca flavescens*) recruitment in Lake Erie, USA. *Journal of Fish Biology* 43(1):109-119.

Havel, J.E., C.E. Lee, and J. VanderZanden. 2005. Do reservoirs facilitate invasions into landscapes? *BioScience* 55(6):518-525.

Hein, C.L., B.M. Roth, A.R. Ives, and J.M. Vander Zanden. 2006. Fish predation and trapping for Rusty Crayfish (*Orconectes rusticus*) control: a whole-lake experiment. *Canadian Journal of Fisheries and Aquatic Sciences* 63:383-393.

Hepworth, D. K., C.B. Chamberlain, and M.J. Ottenbacher. 1999. Comparative sport fish performance of Bonneville Cutthroat Trout in three small put-grow-and-take reservoirs. *North American Journal of Fisheries Management* 19(1):774–785.

Hepworth, R.D., J. Warner, M.J. Ottenbacher, and M.J. Hadley. 2009. Panguitch Lake: an evaluation of the sport fishery management plan. Utah Department of Natural Resources, Division of Wildlife Resources, Salt Lake City.

Hepworth, R.D., M. Ottenbacher, and M.J. Hadley. 2011. Angler survey and monitoring results, Fish Lake Utah 2010. Utah Department of Natural Resources, Division of Wildlife Resources, Salt Lake City.

Hodde, M.S. 2004. Restoring balance: using exotic species to control invasive exotic species. *Conservation Biology* 18(1):38-49.

Hubert, W.A., and C.B. Chamberlain. 1996. Environmental gradients affect Rainbow Trout populations among lakes and reservoirs in Wyoming. *Transactions of the American Fisheries Society* 125:925-932.

Hubert, W.A., D. Gipson, R.A. McDowell, and A.C. Stewart. 1994. Diet of Eagle Lake Rainbow Trout in Lake DeSmet, Wyoming. *North American Journal of Fisheries Management* 14:457-459.

Hudy, M., and C.R. Berry Jr. 1983. Performance of three strains of Rainbow Trout in a Utah reservoir. *North American Journal of Fisheries Management* 3(2):136-141.

Hyatt, M.W., and W.A. Hubert. 2001. Proposed standard-weight (Ws) equation and length-categorization standards for Brown Trout (*Salmo trutta*) in lentic habitats. *Journal of Freshwater Ecology* 16(1):53-56.

Ireland, P.A. 2010. Changes in native aquatic vegetation, associated fish assemblages, and food habits of Largemouth Bass (*Micropterus salmoides*) following the addition of triploid Grass Carp to manage Hydrilla (*Hydrilla verticillata*) in Lake Conroe, TX. Master's Thesis, Texas A&M University, College Station.

Irwin, B. J., D.R. Devries, and R.A. Wright. 2003. Evaluating the potential for predatory control of gizzard shad by Bargemouth bass in small impoundments: a bioenergetics approach. *Transactions of the American Fisheries Society* 132(5):913–924.

Jackson, L.S., D.H. Jackson, and D.W. Loomis. 2004. Analysis of Tui Chub data collected at Diamond Lake by the Oregon Department of Fish and Wildlife, 1992-2003. Oregon Department of Fish and Wildlife, Roseburg.

Johnson, B.M., and J.P. Goettle. 1999. Food web changes over fourteen years following introduction of Rainbow Smelt into a Colorado reservoir. *North American Journal of Fisheries Management* 19:629–642.

Johnson, J.B., and M.C. Belk. 1999. Effects of predation on life-history evolution in Utah Chub (*Gila atraria*). *Copeia* 4:948–957.

Josephson, D.C., J.M. Robinson, J.M. Lepak, and C.E. Kraft. 2012. Rainbow Trout performance in food-limited environments: implications for future assessment and management. *Journal of Freshwater Ecology* 27(2):159-170.

Juanes, F., J.A. Buckel, and F.S. Scharf. 2002. Feeding ecology of piscivorous fishes. Pages 267-283 in P. J. B. Hart and J. D. Reynolds, editors. *Handbook of Fish Biology and Fisheries*, 1st edition. Blackwell Publishing Ltd., Oxford, UK.

Juncos, R., D.A. Beauchamp, and P.H. Vigliano. 2013. Modeling prey consumption by native and nonnative piscivorous fishes: implications for competition and impacts on shared prey in an ultraoligotrophic lake in Patagonia. *Transactions of the American Fisheries Society* 142:268–281.

Juncos, R., D. Milano, P.J. Macchi, M.F. Alonso, and P.H. Vigliano. 2011. Response of Rainbow Trout to different food web structures in northern Patagonia: implications for growth, bioenergetics, and invasiveness. *Transactions of the American Fisheries Society* 140:415–428.

- Kitchell, J.F., and L.B. Crowder. 1986. Predator-prey interactions in Lake Michigan: model predictions and recent dynamics. *Environmental Biology of Fishes* 16:205-211.
- Kitchell, J. F., D.E. Schindler, R. Ogutu-Ohwayo, and P.N. Reinhart. 1997. The Nile Perch in Lake Victoria: interactions between predation and fisheries. *Ecological Applications* 7(2):653–664.
- Kohler, C.C., J.J. Ney, and W.E. Kelso. 1986. Filling the void: development of a pelagic fishery and its consequences to littoral fishes in a Virginia mainstem reservoir. Pages 166-177 in G.E. Hall and M. J. Van Den Avyle, editors. *Reservoir fisheries management: strategies for the 80's*. Southern Division, American Fisheries Society, Bethesda, Maryland.
- Kruse, C.G., and W.A. Hubert. 1997. Proposed standard weight (W_s) equations for Interior Cutthroat Trout. *North American Journal of Fisheries Management*, 17(3):784-790.
- Kumar, R., and J.S. Hwang. 2006. Larvicidal efficiency of aquatic predators: a perspective for mosquito biocontrol. *Zoological Studies* 45(4):447–466.
- Lester, N.P., P.E. Bailey, and W.A. Hubert. 2009. Coldwater fish in small standing waters. Pages 85-96 in S.A. Bonar, W.A. Hubert, & D.W. Willis, editors. *Standard methods for sampling North American freshwater fishes*. American Fisheries Society, Bethesda, Maryland.
- Luecke, C., T.C. Edwards, M.W. Wengert, S. Brayton, and R. Schneidervin. 1994. Simulated changes in Lake Trout yield, trophies, and forage consumption under various slot limits. *North American Journal of Fisheries Management* 14(1):14–21.
- Luecke, C.M., W. Wengert, and R.W. Schneidervin. 1999. Comparing results of a spatially explicit growth model with changes in the length-weight relationship of Lake Trout (*Salvelinus namaycush*) in Flaming Gorge Reservoir. *Canadian Journal of Fisheries and Aquatic Sciences* 56:162-169.
- Madenjian, C.P., D.V. O'Connor, S.M. Chernyak, R.R. Rediske, and J.P. O'Keefe. 2004. Evaluation of a Chinook Salmon (*Oncorhynchus tshawytscha*) bioenergetics model. *Canadian Journal of Fisheries and Aquatic Sciences* 61:627-635.

- Magnhagen, C., and E. Heibo. 2001. Gape size allometry in Pike reflects variation between lakes in prey availability and relative body depth. *Functional Ecology* 15:754–762.
- Martinez, P.J., P.E. Bigelow, M.A. Deleray, W.A. Fredenberg, B.S. Hansen, N.J. Horner, S.K. Lehr, R.W. Schneidervin, S.A. Tolentino, and A.E. Viola. 2009. Western Lake Trout woes. *Fisheries* 34:424-442.
- Matkowski, S.M.D. 1989. Differential susceptibility of three species of stocked trout to bird predation. *North American Journal of Fisheries Management* 9:184-187.
- McMahon, T. E., A.V. Zale, and D.J. Orth. 1996. Aquatic habitat measurements. Pages 83 -120 in B.R. Murphy & D.W. Willis, editors. *Fisheries techniques*. American Fisheries Society, Bethesda, Maryland.
- Merritt, R.W., and K.W. Cummins, editors. 1996. *An introduction to the aquatic insects of North America*. Kendall & Hunt, Dubuque, Iowa.
- Mesa, M.G., L.K. Weiland, H.E. Christiansen, S.T. Sauter, and D.A. Beauchamp. 2013. Development and evaluation of a bioenergetics model for bull trout. *Transactions of the American Fisheries Society* 142(1):41-49.
- Michaletz, P.H. 2013. Temperature, plankton and conspecific density influence dynamics of age-0 Gizzard Shad: implications for a gape-limited piscivore. *Ecology of Freshwater Fish* DOI: 10.1111/eff.12083.
- Milewski, C.L., and M.L. Brown. 1994. Proposed standard weight (W_s) equation and length-categorization standards for stream-dwelling Brown Trout (*Salmo trutta*). *Journal of Freshwater Ecology* 9(2):111-116.
- Miller, A.L. 2010. Diet, growth, and age analysis of Tiger Trout from ten lakes in Eastern Washington. Master's Thesis. Eastern Washington University, Cheney.
- Mittlebach, G.G. 2002. Fish foraging and habitat choice: a theoretical perspective. *Handbook of Fish Biology and Fisheries* 1:251–266.
- Neilson, B.R. and L. Lentsch. 1988. Bonneville Cutthroat Trout in Bear Lake: status and management. *American Fisheries Society Symposium* 4:128-133.

- Neuhold, J. M. 1957. Age and growth of the Utah Chub, *Gila atraria* (Girard), in Panguitch Lake and Navajo Lake, Utah, from scales and opercular bones. *Transactions of the American Fisheries Society* 85(1):217–233.
- Ney, J. J. 1990. Trophic economics in fisheries: assessment of demand-supply relationships between predators and prey. *Reviews in Aquatic Sciences* 2(1):55–81.
- Ney, J. J. 1993. Bioenergetics modeling today: growing pains on the cutting edge. *Transactions of the American Fisheries Society* 122:736–748.
- Noble, R. L. 1981. Management of forage fishes in impoundments of the Southern United States. *Transactions of the American Fisheries Society* 110(6):738–750.
- Olson, H. F. 1959. Biology of the Utah Chub, *Gila atraria*, of Scofield Reservoir, Utah. Master's Thesis. Utah State University, Logan.
- Paakkonen, J.P.J., O. Tikkanen, and J. Karjalainen. 2003. Development and validation of a bioenergetics model for juvenile and adult Burbot. *Journal of Fish Biology* 63:956–969.
- Penczak, T., A.A. Agostinho, N.S. Hahn, R. Fugi, and L.C. Gomes. 1999. Energy budgets of fish populations in two tributaries of the Parana River, Parana, Brazil. *Journal of Tropical Ecology* 15:159–177.
- Peterson, J. H., and J.F. Kitchell. 2001. Climate regimes and water temperature changes in the Columbia River: bioenergetic implications for predators of juvenile sSalmon. *Canadian Journal of Fisheries and Aquatic Sciences* 58:1831–1841.
- Pope, K.L., and C.G. Kruse. 2007. Condition. Pages 423–472 in C.S. Guy and M.L. Brown, editors. *Analysis and interpretation of freshwater fisheries data*. American Fisheries Society, Bethesda, Maryland.
- Quist, M.C., C.S. Guy, R.J. Bernot, and J.L. Stephen. 2002. Seasonal variation in condition, growth and food habits of walleye in a Great Plains reservoir and simulated effects of an altered thermal regime. *Journal of Fish Biology* 61(6):1329–1344.
- Raborn, S. W., L.E. Miranda, and M.T. Driscoll. 2007. Prey supply and predator demand in a reservoir of the Southeastern United States. *Transactions of the American Fisheries Society* 136(1):12–23.

Rand, P.S., D.J. Stewart, P.W. Seelbach, M.L. Jones, and L.R. Wedge. 1993. Modeling steelhead population energetics in lakes Michigan and Ontario. *Transactions of the American Fisheries Society* 122:977–1001.

Raymond, A.W., and E. Sobel. 1990. The use of Tui Chub as food by Indians of the Western Great Basin. *Journal of California and Great Basin anthropology* 12(1):2-18.

Reissig, M., C. Trochine, C. Quelimalinos, E. Balseiro, and B. Modenutti. 2006. Impact of fish introduction on planktonic food webs in lakes of the Patagonian Plateau. *Biological Conservation* 132:437–447.

Rice, J.A., and P.A. Cochran. 1984. Independent evaluation of a bioenergetics model for Largemouth Bass. *Ecology* 65(3):732-739.

Romare, P., and L.A. Hansson. 2003. A behavioral cascade: top-predator induced behavioral shifts in planktivorous fish and zooplankton. *Limnology and Oceanography* 48(5):1956–1964.

Rose, B.P., and M.G. Mesa. 2013. Effects of summer drawdown on the fishes and larval chironomids in Beulah Reservoir, Oregon. *Northwest Scientific Association* 87(3):207-218.

Rudolf, V.H.W. 2012. Seasonal shifts in predator body size diversity and trophic interactions in size-structured predator-prey systems. *Journal of Animal Ecology* 81:524-532.

Ruzycki, J. R., W.A. Wurtsbaugh, and C. Luecke. 2001. Salmonine consumption and competition for endemic prey fishes in Bear Lake, Utah–Idaho. *Transactions of the American Fisheries Society* 130(6):1175–1189.

SAS Institute Inc. 2009. SAS Web Report Studio 4.2: Users guide. SAS Institute Inc., Cary, North Carolina.

Saunders, G., B. Cooke, K. McColl, R. Shine, and T. Peacock. 2010. Modern approaches for the biological control of vertebrate pests: an Australian perspective. *Biological Control* 52(3):288-295.

- Scharf, F.S., F.J. Juanes, and R.A. Rountree. 2000. Predator size - prey size relationships of marine fish predators: interspecific variation and effects of ontogeny and body size on trophic-niche breadth. *Marine Ecology Progress Series* 208:229-248.
- Schoen, E.R., D.A. Beauchamp, and N.C. Overman. 2012. Quantifying latent impacts of an introduced piscivore: pulsed predatory inertia of Lake Trout and decline of Kokanee. *Transactions of the American Fisheries Society* 141(5):1191–1206.
- Shapiro, J., V. Lamarra, and M. Lynch. 1975. Biomanipulation: an ecosystem approach to lake restoration. Pages 85-96 *in* P.L. Brezonik and J.L. Fox, editors. *Water quality management through biological control*. University of Florida.
- Simberloff, D. 2009. We can eliminate invasions or live with them. Successful management projects. *Biological Invasions* 11:149-157.
- Simberloff, D., and P. Stiling. 1996. Risks of species introduced for biological control. *Biological Conservation* 78:185–192.
- Simpkins, D.G., and W.A. Hubert. 1996. Proposed revision of the standard-weight equation for Rainbow Trout. *Journal of Freshwater Ecology* 11(3):319-325.
- Skov, T., T. Buchaca, S.L. Amsinck, F. Landkildehus, B.V. Odgaard, J. Azevedo, V. Goncalves, P.M. Raposeiro, T.J. Anderson, and E. Jeppesen. 2010. Using invertebrate remains and pigments in the sediment to infer changes in trophic structure after fish introduction in Lake Fogo: a crater lake in the Azores. *Hydrobiologia* 654(1):13–25.
- Sorenson, P.W., and N.E. Stacey. 2004. Brief review of fish pheromones and discussion of their possible uses in the control of non-indigenous teleost fishes. *New Zealand Journal of Marine and Freshwater Research* 38(3):399-417.
- Sousa, R., A.J.A. Nogueira, M.B. Gaspar, C. Antunes, and L. Guilhermino. 2008. Growth and extremely high production of non-indigenous invasive species *Corbicula fluminea*: possible implications for ecosystem functioning. *Estuarine, Coastal, and Shelf Science* 2:289–295.
- Stein, R.A., D.R. Devries, and J.M. Dettmers. 1995. Food-web regulation by a planktivore: exploring the generality of the trophic cascade hypothesis. *Canadian Journal of Fisheries and Aquatic Sciences* 52:2518–2526.

- Stein, R.A., and M.L. Murphy. 1976. Changes in the proximate composition of crayfish with size, sex, and life stage. *Journal of Fisheries Research Board of Canada* 33:2450-2458.
- Stewart, D.J., D. Weininger, D.V. Rottiers, and T.A. Edsall. 1983. An energetics model for Lake Trout, *Salvelinus namaycush*: application to the Lake Michigan population. *Canadian Journal of Fisheries and Aquatic Sciences* 40:681–698.
- Stewart, D.J., J.F. Kitchell, and L.B. Crowder. 1981. Forage fishes and their salmonid predators in Lake Michigan. *Transactions of the American Fisheries Society* 110:751-763.
- Swales, S. 2006. A review of factors affecting the distribution and abundance of rainbow trout (*Oncorhynchus mykiss* Walbaum) in lake and reservoir systems. *Lake and Reservoir Management* 22:167-178.
- Taylor, W.W., and S.D. Gerking. 1980. Population dynamics of *Daphnia pulex* and utilization by the Rainbow Trout (*Salmo gairdneri*). *Hydrobiologia* 71:277–287.
- Tronstad, L. 2008. Ecosystem consequences of declining Yellowstone Cutthroat Trout in Yellowstone Lake and spawning streams. Doctoral dissertation. University of Wyoming, Laramie.
- Truemper, H.A., and Lauer, T.E. 2005. Gape limitation and piscine prey size-selection by Yellow Perch in the extreme southern area of Lake Michigan , with emphasis on two exotic prey items. *Journal of Fish Biology* 66:135–149.
- Tyus, H.M., and J.F. Saunders. 2000. Nonnative fish control and endangered fish recovery: lessons from the Colorado River. *Fisheries* 25:17–24.
- U.S. Department of Agriculture, Animal and Plant Health Inspection Service. 2013a. Biological Control, Center for Plant Health Science and Technology. Last modified April 4, 2013. http://www.aphis.usda.gov/plant_health/cphst/projects/biological-control.shtml
- U.S. Department of Agriculture. 2013b. Weeds and biological control agents. Technical Advisory Group, Biological Control Agents of Weeds. DRAFT. May 9, 2013. Available: http://www.aphis.usda.gov/plant_health/permits/tag/downloads/Weeds%20and%20Biological%20Control%20Agents%20Released%20in%20US%20and%20Canada.pdf

- Vatland, S., P. Budy, and G.P. Thiede. 2008. A bioenergetics approach to modeling striped bass and threadfin shad predator-prey dynamics in Lake Powell, Utah-Arizona. *Transactions of the American Fisheries Society* 137(1):262-277.
- Wagner, E.J. 1996. History and fluctuating asymmetry of Utah salmonid broodstocks. *The Progressive Fish-Culturist* 58:92-103.
- Walsworth, T.E., P. Budy, and G.P. Thiede. 2013. Longer food chains and crowded niche space: effects of multiple invaders on desert stream food web structure. *Ecology of Freshwater Fish* 22(3):439–452.
- Werner, E.E., and D.J. Hall. 1974. Optimal foraging and the size selection of prey by the Bluegill Sunfish (*Lepomis macrochirus*). *Ecology* 55(5):1042–1052.
- Wetzel, R.G. 1990. Reservoir ecosystems: conclusions and speculations. Pages 227-238 in K.W. Thorton, B.I. Kimmel, and F.E. Payne, editors. *Reservoir limnology: ecological perspectives*. John Wiley and Sons, New York.
- Wetzel, R.G. 2001. *Limnology: lake and river ecosystems*, third edition. Academic Press, San Diego, California.
- Whitledge, G.W., R.S. Hayward, D.B. Noltie, and N. Wang. 1998. Testing bioenergetics models under feeding regimes that elicit compensatory growth. *Transactions of the American Fisheries Society* 127:740-746.
- Whitledge, G.W., P.G. Bajer, and R.S. Hayward. 2010. Laboratory evaluation of two bioenergetics models for Brown Trout. *Transactions of the American Fisheries Society* 139(4):929–936.
- Williamson, M., and A. Fitter. 1996. The varying success of invaders. *Ecology* 77(6):1661-1668.
- Wittenberg, R., and M.J.W. Cock, editors. 2001. *Invasive alien species: a toolkit of best prevention and management practices*. Wallingford, Oxon, UK: CAB International.
- Yule, D.L., and C. Luecke. 1993. Lake Trout consumption and recent changes in the fish assemblage of Flaming Gorge Reservoir. *Transactions of the American Fisheries Society* 122(6):1058–1069.

Zelasko, K.A., K.R. Bestgen, and C. White. 2010. Survival rates and movement of hatchery-reared Razorback Suckers in the Upper Colorado River Basin, Utah and Colorado. *Transactions of the American Fisheries Society* 139(5):1478-1499.

Table 2.1. Summary of trout stocking from 2005-2012. The number stocked and mean total length (TL) was estimated by state fish hatcheries.

Month	Cutthroat Trout		Rainbow Trout		Tiger Trout	
	Number stocked	Mean TL (mm)	Number stocked	Mean TL (mm)	Number stocked	Mean TL (mm)
2005						
July	----	----	478,484	83	----	----
September	----	----	----	----	103,716	122
October	----	----	100,003	169	----	----
2006						
June	----	----	399,214	78	----	----
October	----	----	134,880	151	46,800	135
2007						
May	----	----	467,365	74	----	----
October	----	----	100,960	135	129,941	150
2008						
October	----	----	----	----	139,375	152
2009						
May	86,052	207	24,320	217	----	----
October	----	----	58,533	201	122,500	148
November	----	----	162,544	170	----	----
2010						
May	90,132	193	----	----	----	----
October	----	----	----	----	108,560	160
November	----	----	80,100	183	----	----
2011						
May	80,143	203	----	----	----	----
October	----	----	74,523	183	119,635	149
2012						
April	81,152	199	----	----	----	----
October	----	----	91,702	187	116,681	182

Table 2.2. Wet weight energy density estimates of individual predators and prey items used for bioenergetics simulations. All estimates are from literature sources; where noted, a similar prey surrogate was substituted.

Prey	Energy Density	
	(J/g)	Source
Amphipoda	4429	Cummins and Wuycheck 1971
Chironomidae	3304	Cummins and Wuycheck 1971
Coleoptera	2448	Cummins and Wuycheck 1971
Decapoda	4507	Cummins and Wuycheck 1971
Ephemeroptera	3715	Cummins and Wuycheck 1971
Hemiptera	2621	Ciancio et al. 2007; Penczak et al. 1999
Isopoda	2624	Cummins and Wuycheck 1971
Mollusca	2007	Cauffope & Heymans 2005
Zooplankton	2445	Cladoceran, Cummins and Wuycheck 1971
Tricoptera	3342	Cummins and Wuycheck 1971
Fish	5230	Tui Chub (<i>Gila bicolor</i>), Raymond and Sobel 1990
Other Aquatic		
Invertebrates	3351	Cummins and Wuycheck 1971
Terrestrial Invertebrates	2742	Cummins and Wuycheck 1971
Organic Matter	2116	Penczak et al. 1999
Cutthroat trout	5764	Steelhead, Hanson et al. 1997 Cummins and Wuycheck 1971, Hanson et al.
Rainbow trout	5921	1997
Tiger trout	5591	Brown Trout (<i>S. trutta</i>), Dieterman et al. 2004

Table 2.3. Length categories (mm TL) proposed for trout species found in Scofield Reservoir. No Tiger Trout values were found in literature, so lotic Brown Trout values were substituted for reference. Tiger Trout values were calculated based on upper percent of world record length, using the 2012 Utah Tiger Trout state record (820 mm).

Species	Stock (S)	Quality (Q)	Preferred (P)	Memorable (M)	Trophy (T)	Source
Cutthroat trout	200	350	450	600	750	Kruse and Hubert 1997
Rainbow trout	250	400	500	650	800	Simpkins and Hubert 1996
Brown trout (lotic)	150	230	300	380	460	Hyatt and Hubert 2001
Tiger trout	213	336	451	525	656	

Table 2.4. Seasonal catch rate (CPUE), an index of relative abundance, calculated as the number of fish, per net, per hour, for Cutthroat Trout, Rainbow Trout, Tiger Trout, and Utah Chub in Scofield Reservoir, Utah. One standard error shown in parentheses.

Species	Season	CPUE	
		2011	2012
Cutthroat Trout			
	Spring	--	0.45 (0.1)
	Summer	0.18 (0.022)	0.45 (0.08)
	Autumn	0.20 (0.048)	0.68 (0.03)
Rainbow Trout			
	Spring	--	0.03 (0.01)
	Summer	0.060 (0.015)	0.068 (0.02)
	Autumn	0.014 (0.010)	0.037 (0.005)
Tiger Trout			
	Spring	--	0.18 (0.08)
	Summer	0.19 (0.03)	0.20 (0.03)
	Autumn	0.16 (0.04)	0.32 (0.01)
Utah Chub			
	Spring	--	3.3 (0.5)
	Summer	3.7 (0.4)	6.8 (0.6)
	Autumn	4.5 (1.4)	5.2 (0.3)

Table 2.5. Predator abundance and density (fish/ha) estimates based on hydroacoustics surveys in August 2011 and June 2013. The 'small' size class refers to fish < 350 mm TL and the 'large' size class refers to fish \geq 350 mm TL.

Species	2011			2013		
	Small	Large	Density	Small	Large	Density
Cutthroat						
trout	39,800	174,200	188	81,400	337,700	368
Rainbow						
trout	39,800	15,100	48	0	9,650	8
Tiger trout	48,600	189,500	209	153,800	135,100	254

Table 2.6. Annual Utah Chub consumption (g) estimates per individual predator for two representative size classes of Cutthroat Trout, Rainbow Trout, and Tiger Trout for the 2011 – 2012 simulation year. Abundance values used are those estimated from hydroacoustics surveys in June 2013. Population-level estimates are annual consumption (kg).

	Individual			Population	
	Consumption (g)	Number of chub consumed	Abundance	Consumption (kg)	Number of chub consumed
Cutthroat Trout					
Small	110	3	81,400	8,900	252,000
Large	1820	49	337,700	615,000	16,619,000
		Total:	419,100	625,000	16,870,000
Rainbow Trout					
Small	90	3	0	0	0
Large	400	11	9,700	3,900	105,000
		Total:	9,700	3,900	105,000
Tiger Trout					
Small	60	2	153,800	9,200	231,000
Large	2660	63	135,100	359,000	8,565,000
		Total:	288,900	368,000	8,796,000

Table 2.7. Bioenergetic efficiency expressed as a percentage of the realized maximum possible consumption rate, determined with the Fish Bioenergetics 3.0 model (Hanson et al. 1997).

Species	Size Class	BioEff (%)
Cutthroat Trout	Small	41.6
	Large	36.0
Rainbow Trout	Small	43.4
	Large	50.2
Tiger Trout	Small	57.7
	Large	54.0

Table 2.8. Condition (K_{TL}) of Cutthroat Trout, Rainbow Trout, and Tiger Trout captured in Scofield Reservoir during 2012. One standard error shown in parentheses, “----” indicates no data available.

	Cutthroat Trout		Rainbow Trout		Tiger Trout	
	Small	Large	Small	Large	Small	Large
Spring	0.83 (0.02)	0.93 (0.01)	0.97 (0.05)	----	0.84 (0.04)	0.89 (0.02)
Summer	0.79 (0.01)	0.88 (0.01)	0.91 (0.02)	1.03 (0.06)	0.84 (0.02)	0.98 (0.02)
Autumn	0.76 (0.01)	0.88 (0.02)	0.87 (0.04)	0.96 (0.2)	0.87 (0.02)	0.94 (0.03)

Table 2.9. Relative return rates of Cutthroat Trout stocked in Scofield Reservoir and recaptured from summer 2011- autumn 2012.

Season and Year	Total Caught	Number Marked	Percent Marked	Mark Type	Cohort	Total Length (mm)	Weight (g)
Summer							
2011	81	7	8.6	Ad Clip	2009	358.0	420.2
		3	3.7	Red Dye	2010	309.0	273.7
		2	2.5	Green Dye	2011	290.0	209.4
		69	85.2	Unmarked		406.1	655.6
Fall 2011	42	12	28.6	Ad Clip	2009	362.3	466.6
		1	2.4	Red Dye	2010	323.0	291.5
		8	19.0	Green Dye	2011	289.1	202.5
		21	50.0	Unmarked		320.1	329.1
Spring 2012	197	101	51.3	Ad Clip	2009	399.7	661.3
		10	5.1	Red	2010	339.4	324.4
		11	5.6	Green	2011	308.7	237.5
		10	5.1	Orange	2012	214.7	93.4
		65	33.0	Unmarked		349.4	421.6
Summer							
2012	179	55	30.7	Ad Clip	2009	409.4	658.4
		1	0.6	Red	2010	346.0	311.4
		26	14.5	Green	2011	318.1	248.4
		8	4.5	Orange	2012	247.3	127.7
		89	49.7	Unmarked		361.6	484.2
Autumn							
2012	109	47	43.1	Ad Clip	2009	447.1	827.8
		8	7.3	Red	2010	343.3	309.4
		5	4.6	Green	2011	326.4	252.0
		22	20.2	Orange	2012	275.9	164.0
		27	24.8	Unmarked		353.9	510.5

Table 2.10. Relative return rates of Rainbow Trout stocked in Scofield Reservoir and recaptured from summer 2011 – autumn 2012. The “-” indicates data was not available.

Season and Year	Total Caught	Number Marked	Percent Marked	Mark Type	Cohort	Total Length (mm)	Weight (g)
Summer							
2011	27	2	7.4	Ad Clip	2009	334.0	357.9
		4	14.8	Red Dye	2010	287.0	449.1
		21	77.78	Unmarked		342.81	459.82
Fall 2011	3	1	33.3	Ad Clip	2009	320	334.5
		1	33.3	Red Dye	2010	316	333.9
		0	0.0	Green Dye	2011	-	-
		1	33.3	Unmarked		340	426.3
Spring 2012	13	1	7.7	Ad Clip	2009	344	374.1
		2	15.4	Red	2010	330.5	443.0
		4	30.8	Green	2011	297.0	250.5
		6	46.2	Unmarked		273.2	224.5
Summer							
2012	27	2	7.4	Ad Clip	2009	357.5	457.15
		1	3.7	Red	2010	332.0	382.1
		2	7.4	Green	2011	307.0	295.1
		22	81.5	Unmarked		291.2	264.3
Autumn							
2012	6	1	16.7	Ad Clip	2009	251.0	134.9
		1	16.7	Red	2010	326.0	285.4
		0	0.0	Green	2011	-	-
		1	16.7	Orange	2012	256.0	140.5
		3	50.0	Unmarked		323.7	363.4

Table 2.11. Stock density index ranges for Scofield Reservoir trout species. Proportional stock density (PSD), relative stock density of preferred length fish (RSD-P) and relative stock density of memorable length fish (RSD-M) given. Values were calculated based on summer (1 June – 31 August) data for both 2011 and 2012.

Species	2011			2012		
	PSD	RSD-P	RSD-M	PSD	RSD-P	RSD-M
Cutthroat Trout	78.5	22.8	0.0	52.0	14.1	0.6
Rainbow Trout	8.0	4.0	0.0	5.0	0.0	0.0
Tiger Trout (Brown)	99.0	90.0	60.0	98.8	91.3	81.3
Tiger Trout (state record)	86.9	33.3	13.1	91.1	49.4	24.1

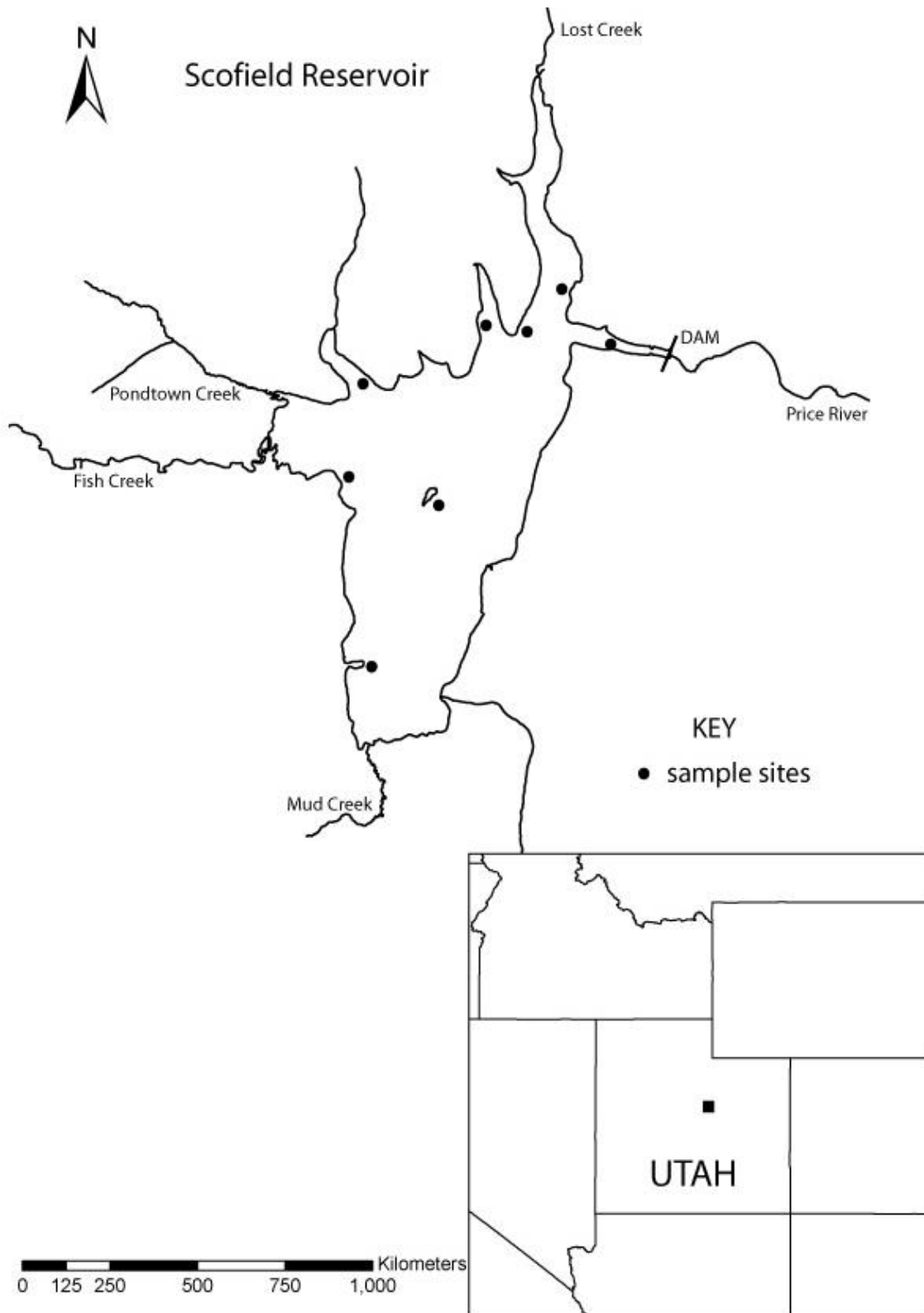


Figure 2.1. Map of Scofield Reservoir, Utah showing the eight locations during which fish were sampled in 2011 and 2012.

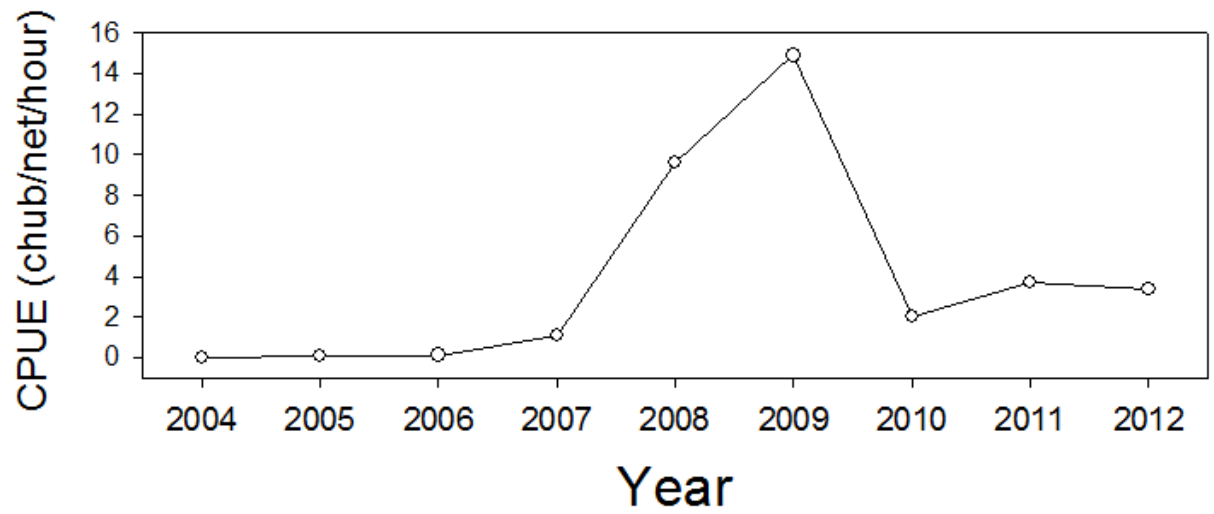


Figure 2.2. Utah Chub catch-per-unit-effort from 2004 until 2012. Catch data 2004-2010 courtesy of Utah Division of Wildlife Resources.

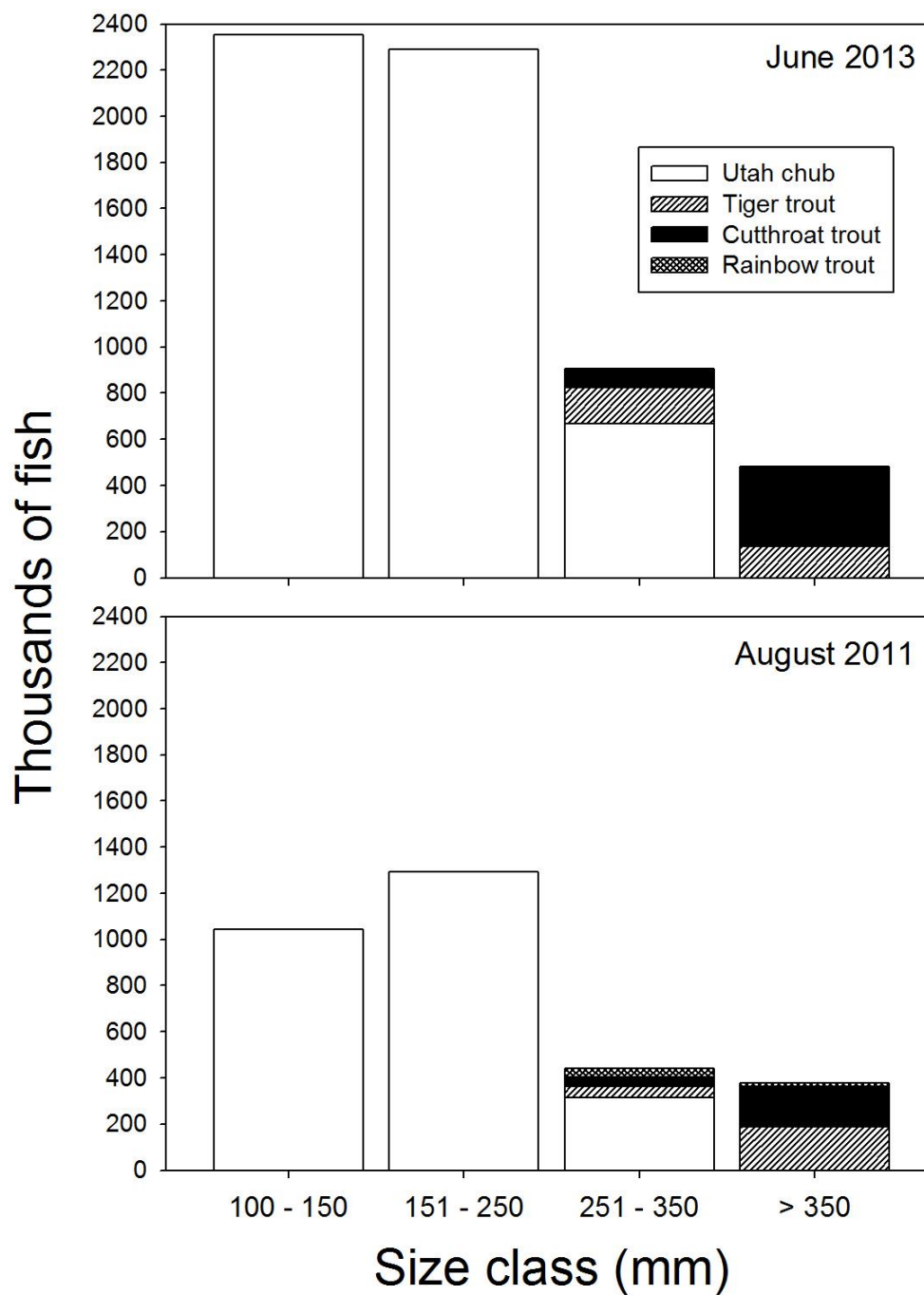


Figure 2.3. Abundance estimates by size class of Utah Chub and three trout species derived from hydroacoustic surveys in Scofield Reservoir on 6 June 2013 and 31 August 2011.

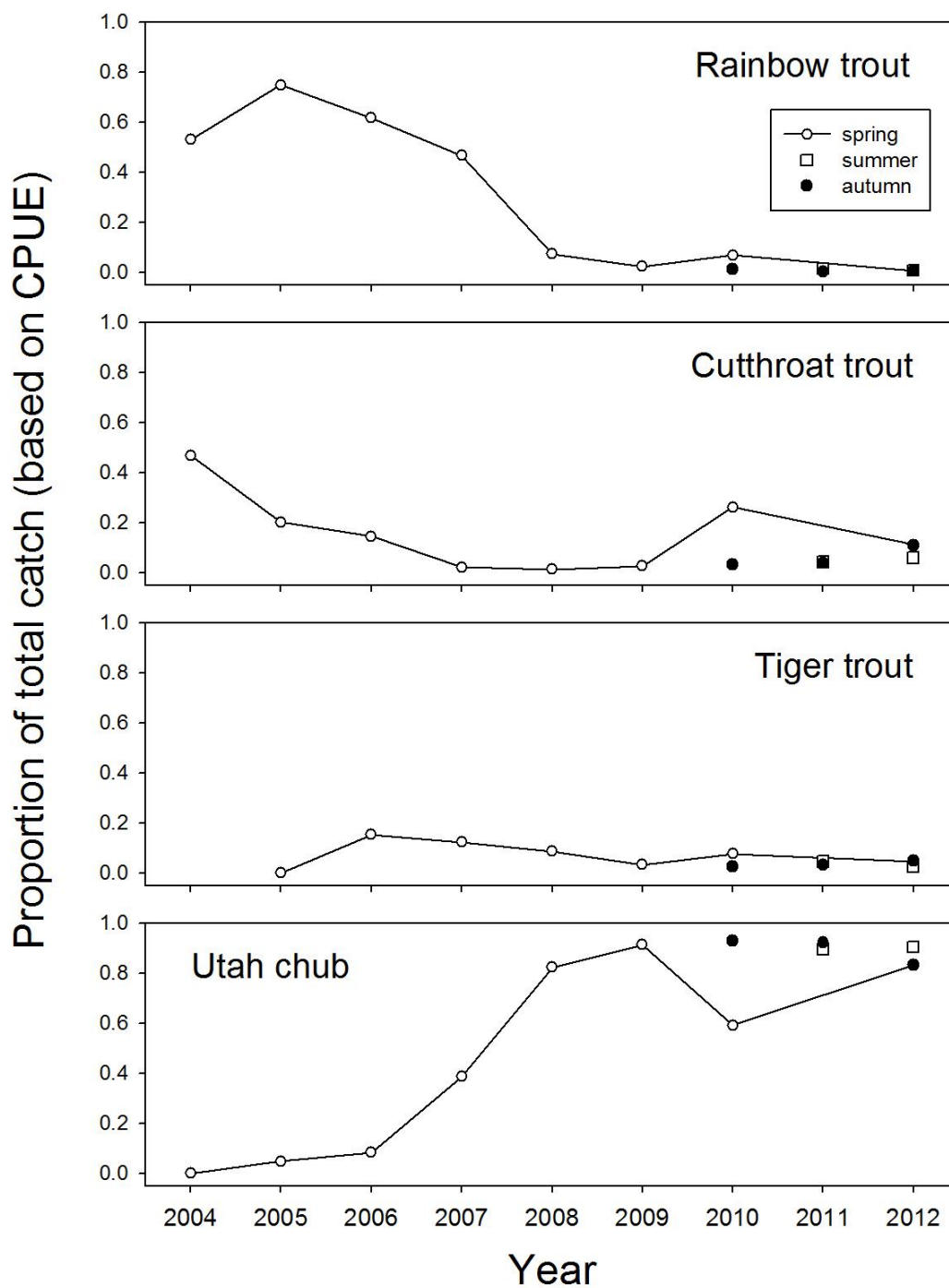


Figure 2.4. Proportion of total catch, based on CPUE, for each of the trout species and Utah Chub in Scofield Reservoir. Solid lines represent data from Utah Division of Wildlife Resources yearly spring sampling, with additional summer and fall representing data collected for this study (metrics calculated similarly).

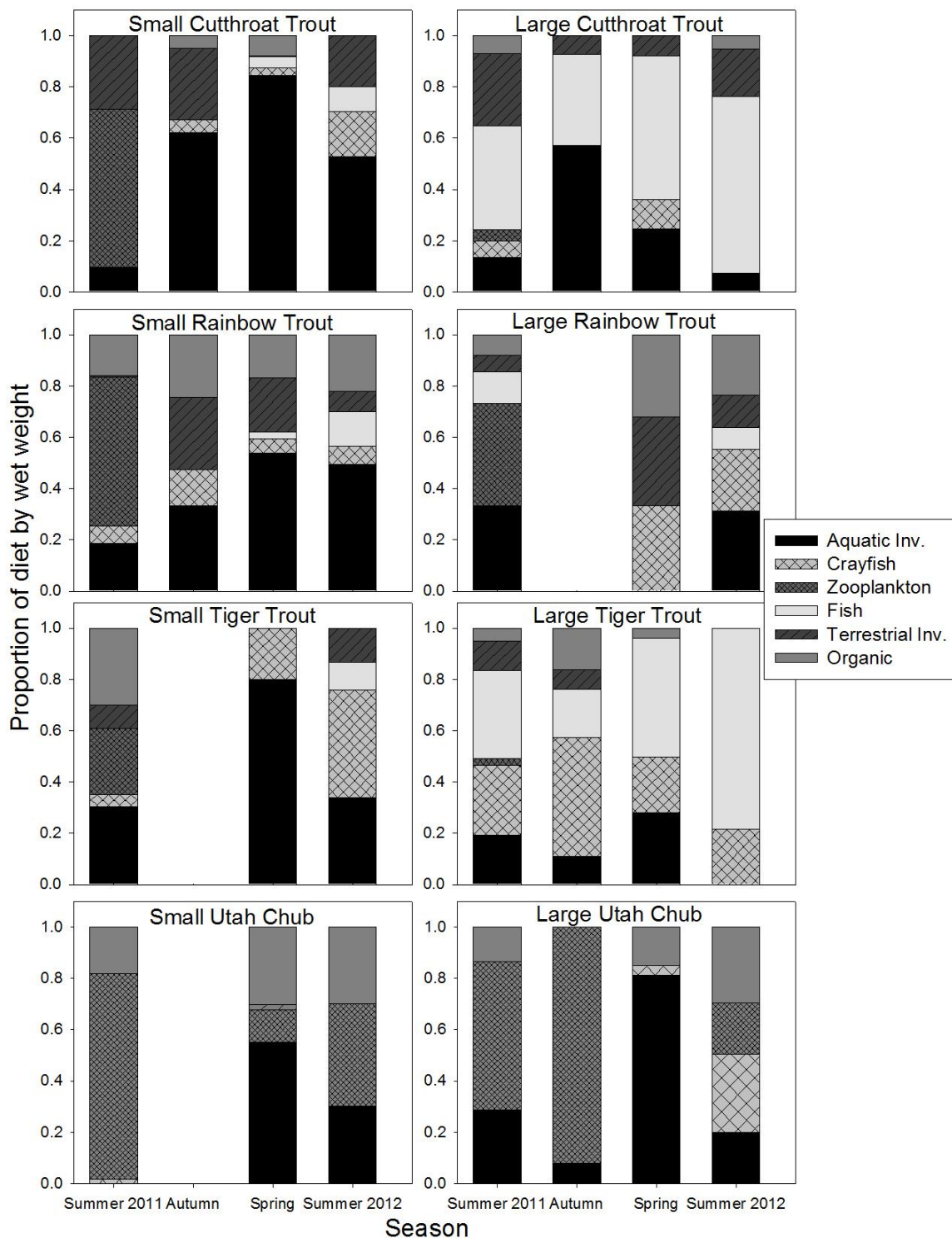


Figure 2.5. Seasonal diet composition of small (< 350 mm TL) and large (≥ 350 mm TL) Cutthroat Trout, Rainbow Trout, and Tiger Trout, as well as small (< 250 mm TL) and large (≥ 250 mm TL) Utah Chub captured in Scofield Reservoir. Diet composition was calculated as the proportion of diet by wet weight (g).

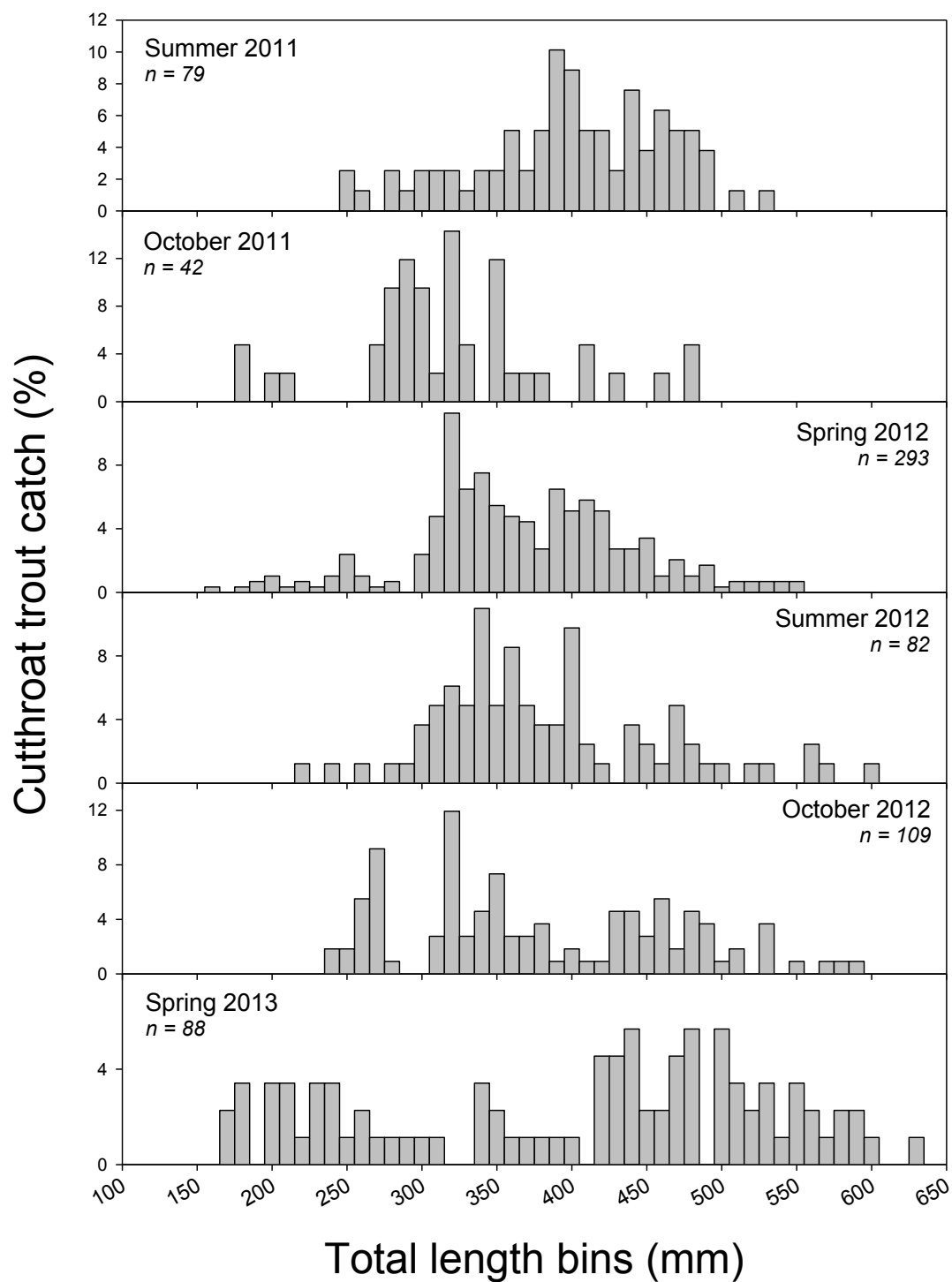


Figure 2.6. Length-frequency (%) distributions of Bear Lake Cutthroat Trout captured in gill nets during seasonal sampling events from July 2011 – May 2013 in Scofield Reservoir. Number (n) captured in nets is given.

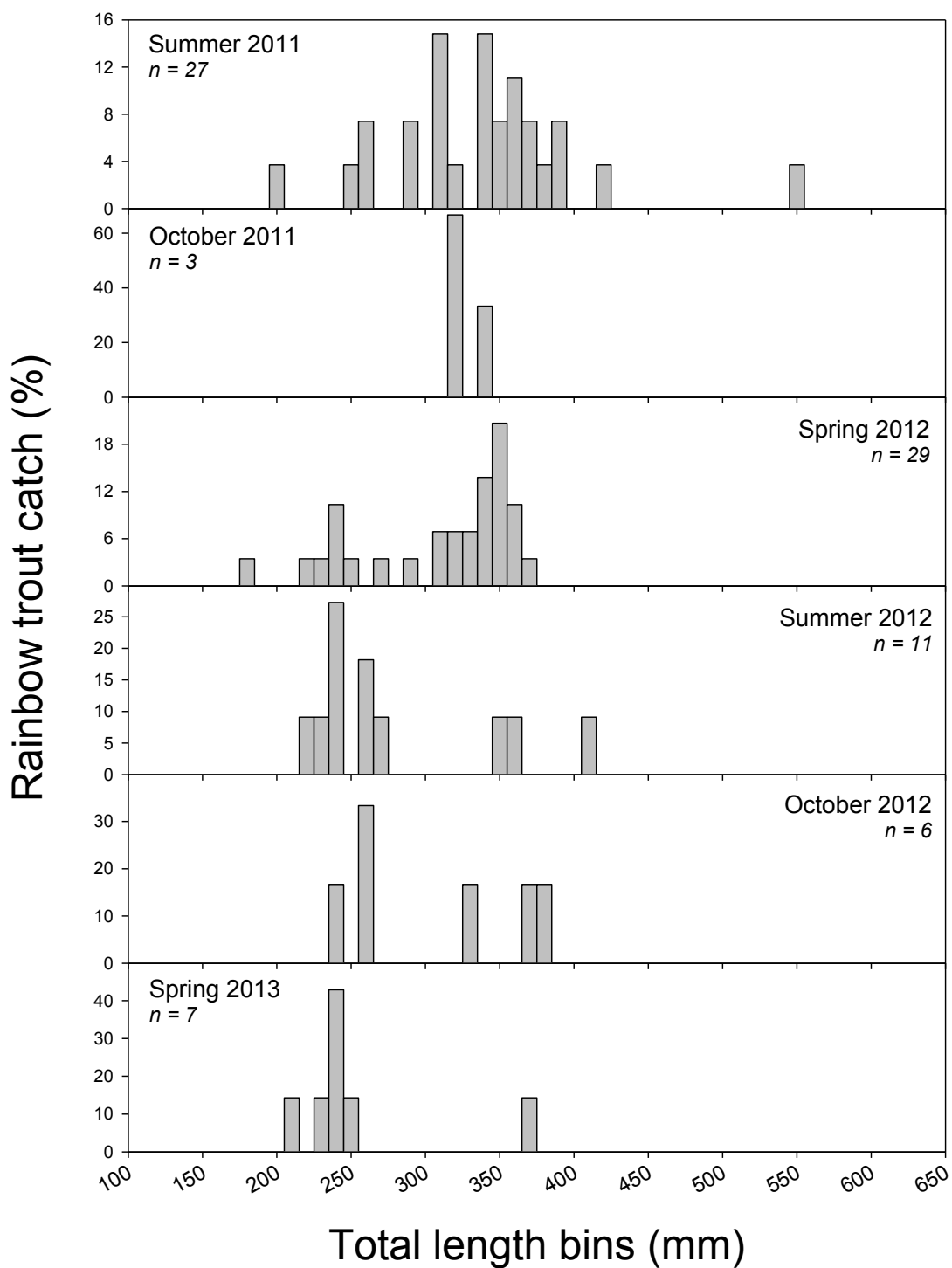


Figure 2.7. Length-frequency (%) distributions of Rainbow Trout captured in gill nets during seasonal sampling events from July 2011 – May 2013 in Scofield Reservoir. Number (n) captured in nets is given.

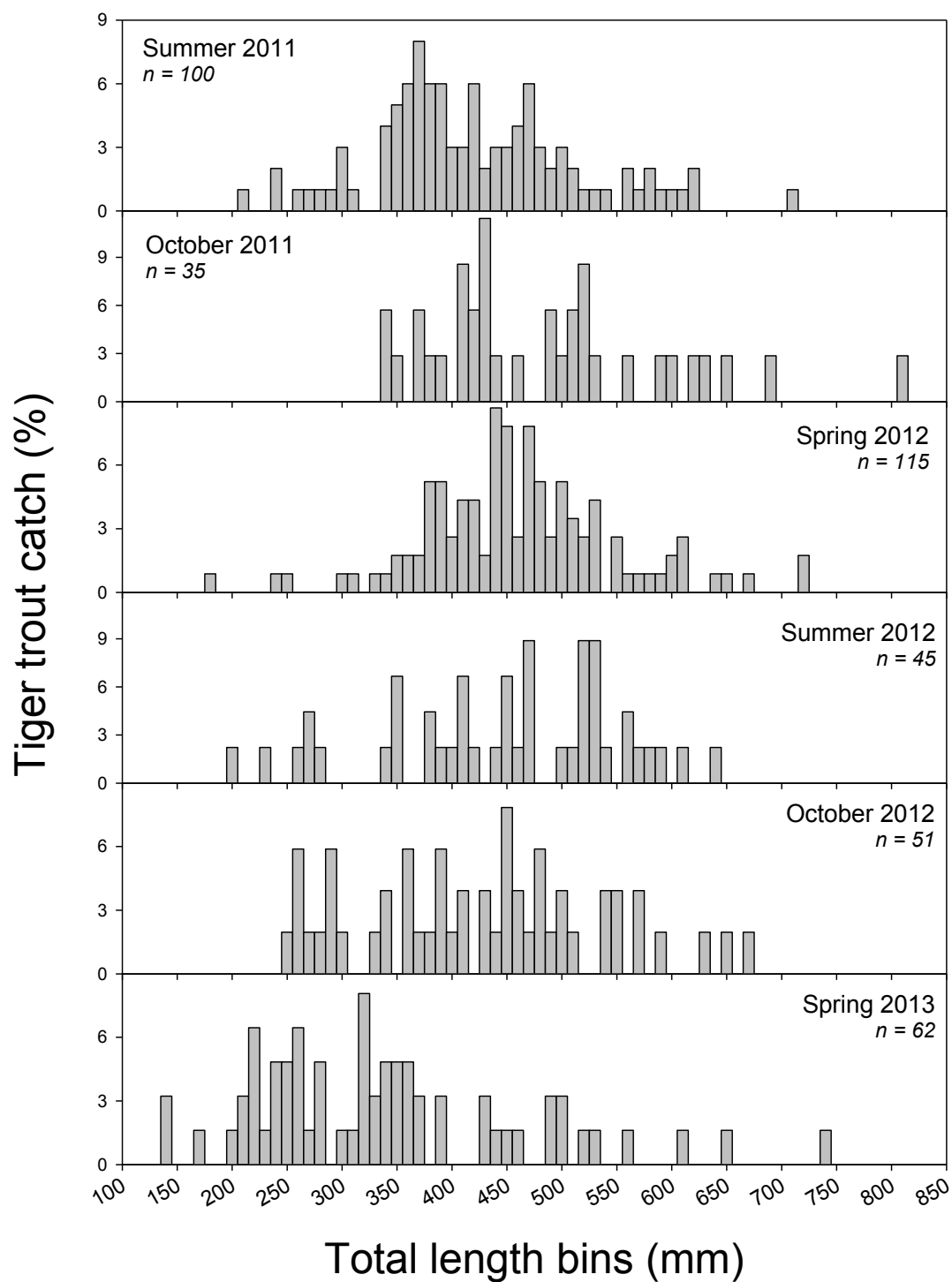


Figure 2.8. Length-frequency (%) distributions of Tiger Trout captured in gill nets during seasonal sampling events from July 2011 – May 2013 in Scofield Reservoir. Number (n) captured in nets is given.

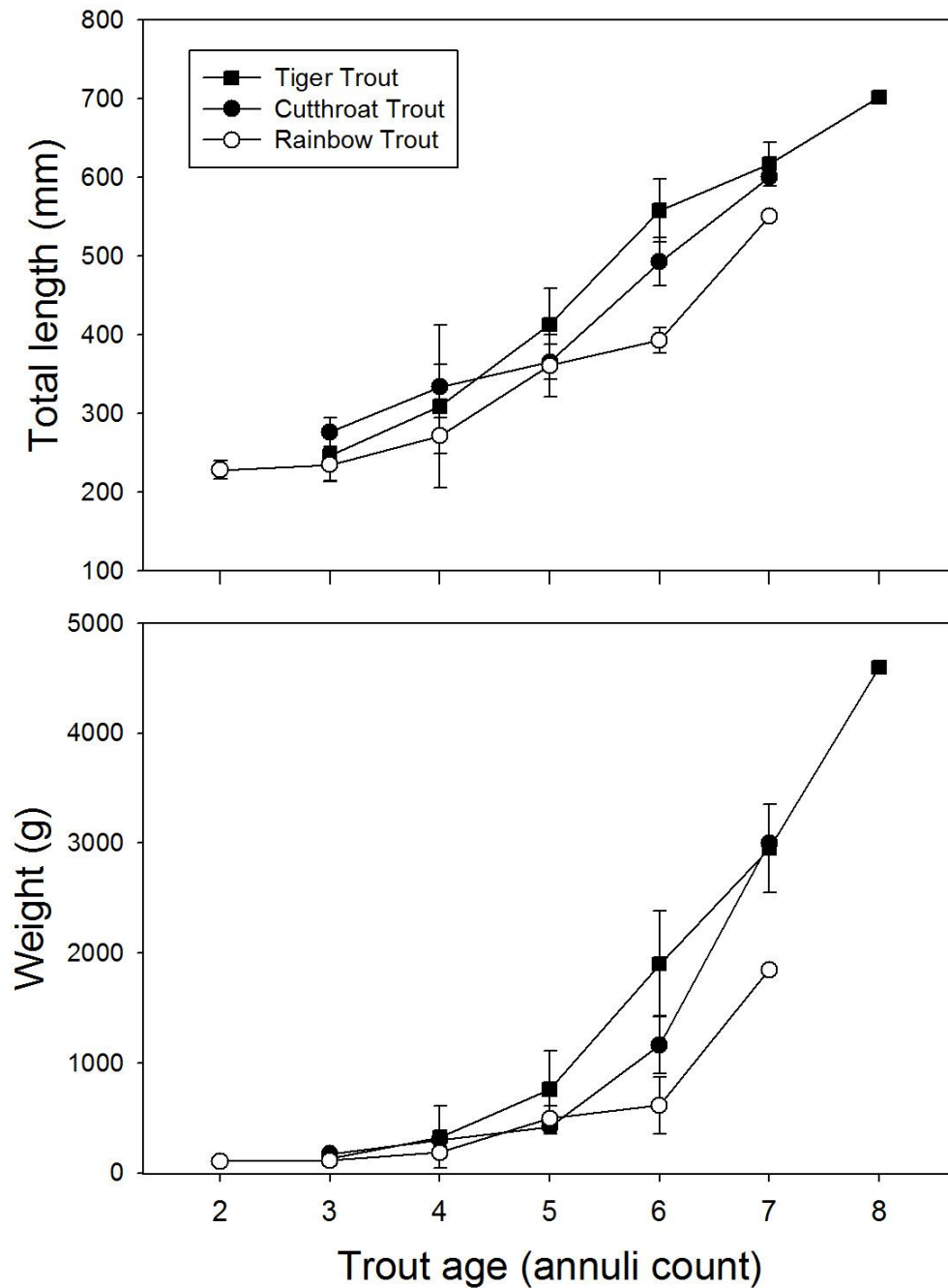


Figure 2.9. Mean ($\pm 2SE$) total length (top panel) and weight (bottom panel) at age of each trout species in Scofield Reservoir. Ages were determined as annuli counts from 30 of each species captured in 2012.

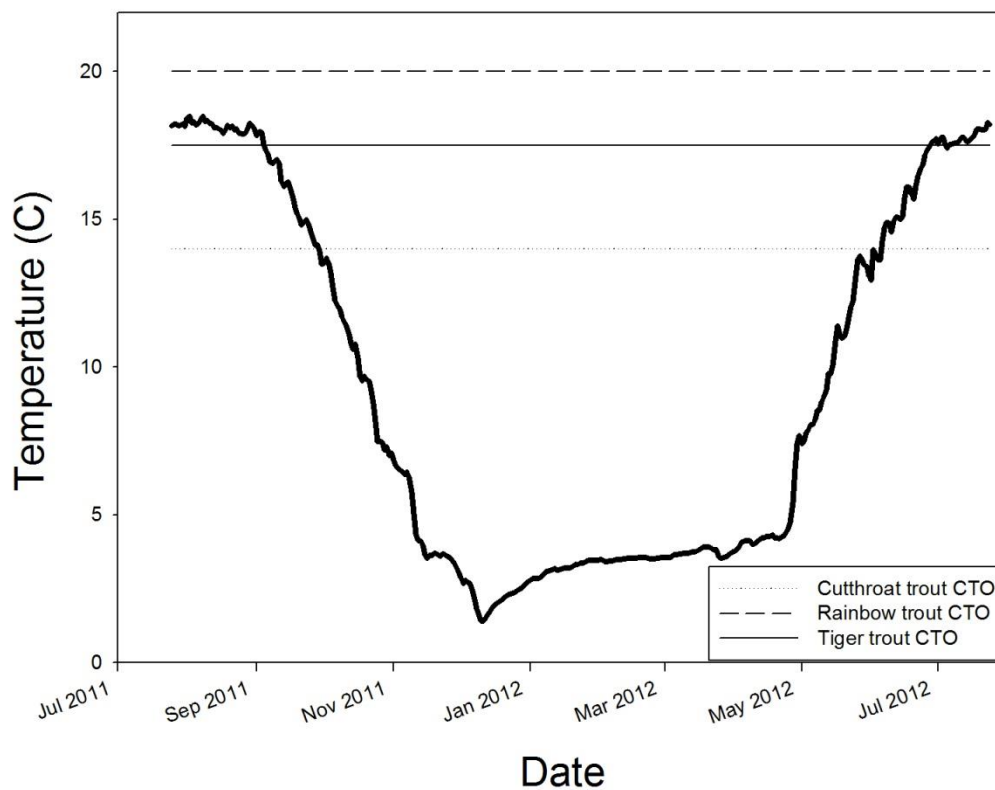


Figure 2.10. Daily mean temperatures experienced by fish in Scofield Reservoir during 2011 and 2012. Horizontal lines show consumption thermal optimum (CTO) for each species, which varied around the average temperature encountered throughout the year; Cutthroat Trout CTO is 14°C, Rainbow Trout CTO is 20°C, and Tiger Trout CTO (assumed similar to brown trout) is 17.5°C.

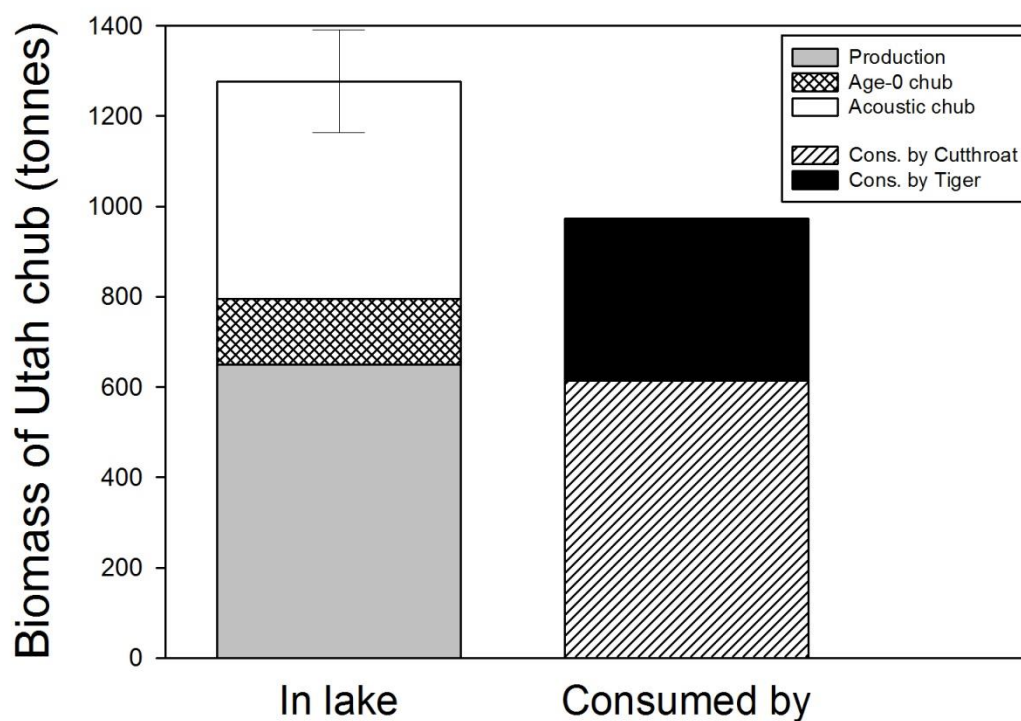


Figure 2.11. Comparison of Utah Chub abundance and annual production (In lake) versus estimates of annual Cutthroat Trout and Tiger Trout consumption of chub (Consumed by) in Scofield Reservoir, using June 2013 hydroacoustic estimates of abundance. The error bar consists of 1 SE derived from hydroacoustic estimates of 100-350 mm abundance of Utah Chub.

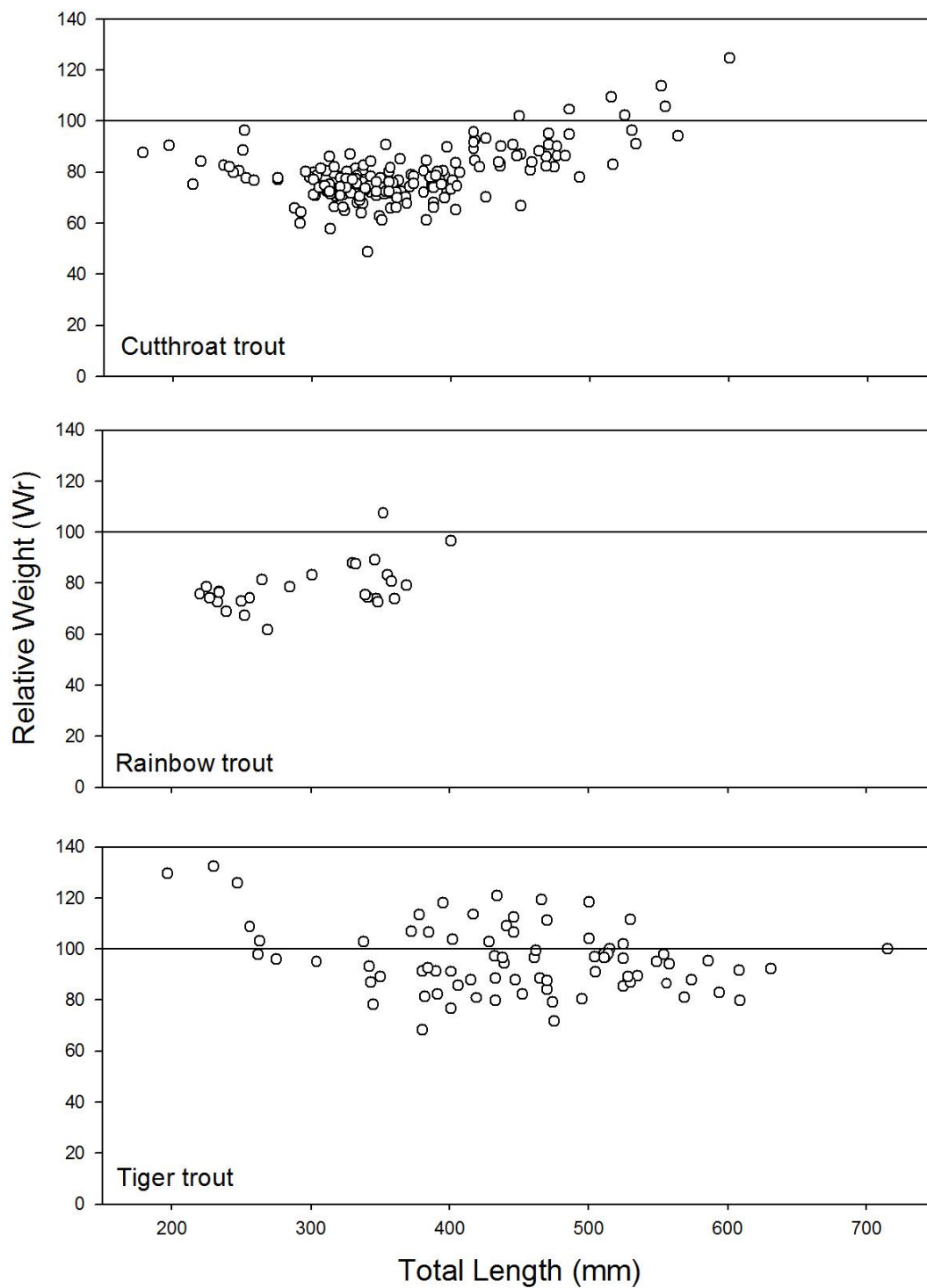


Figure 2.12. Relationship between total length and relative weight (W_r) of Cutthroat Trout (top), Rainbow Trout (middle), and Tiger Trout (bottom) from Scofield Reservoir in summer of 2012. Reference line at $W_r = 100$.

CHAPTER 3
QUANTIFYING FOOD WEB INTERACTIONS AND THE IMPACTS OF INTRODUCED
PISCIVORES ON RESERVOIR FISH ASSEMBLAGES

Introduction

Ecologists are continually challenged with describing and quantifying the interactions that define food webs and community structure of aquatic systems (Paine 1980; Polis 1991; Polis and Strong 1996). Food webs are dynamic, as linkages between organisms rely on the movement of nutrients, prey, and consumers (Polis et al. 1997). Human manipulations, such as the widespread construction of reservoirs, present uncertainties in our understanding of aquatic food web structure. Reservoirs in particular differ from the “typical” structure and functioning of aquatic ecosystems, making them an interesting study system to inform freshwater ecology (Miranda and DeVries 1996; Havel et al. 2005). Fish populations and subsequent food web interactions in impounded riverine systems likely differ from those in lakes, as the highly-manipulated and recently-stocked fish communities in reservoirs are often unstable (Stein et al. 1995; Havel et al. 2005).

Reservoirs are thus novel, dynamic ecosystems that often demonstrate complex trophic interactions among resident species. Not only do species roles change with ontogenetic shifts, but species composition in reservoirs may vary from natural rivers and lakes in the region and may consist of an assemblage of species that did not co-evolve. This assemblage may include both native stream species that persist in the

reservoir, and non-native species either intentionally or accidentally introduced (Olson et al. 1995; Matthews et al. 2004; Clavero et al. 2013). These artificial assemblages may have an increased number of trophic positions relative to a prior state (Walsworth et al. 2013), decoupled or novel predator-prey interactions (Noble 1986), or may result in increased potential for competition of nutrients and resources amongst species (Ney 1996; Wuellner et al. 2010). Reservoirs are often managed similarly to natural lakes because they are assumed to be functionally comparable; however, direct comparisons of fish assemblages has demonstrated dissimilarity between systems (Terra and Araujo 2011). These unnatural lentic habitats may be unsuitable for stream fishes, but favorable for introduced piscivorous fishes. (Gido et al. 2009; Kashiwagi and Miranda 2009; Franssen and Tobler 2013). Understanding the biotic interactions of artificial assemblages of fish will expand our knowledge of novel food web interactions, as well as assist towards developing and implementing suitable management strategies for these highly manipulated fisheries.

Top predators in reservoir systems that are highly managed (i.e., stocked) for fishing may exhibit strong competition between species. Competition amongst coexisting species can structure community dynamics and limit predator performance, in addition to, or in combination with predation (Kitchell and Crowder 1986; Ney 1990; Wuellner et al. 2010). Additionally, exploitative competition may be a strong driver of decreasing angler success (Marrin and Erman 1982; Wuellner et al. 2010), or the poor relative return rates of stocked sport fish. In Patagonian lakes, invasive rainbow trout *Oncorhynchus mykiss* and brown trout *Salmo trutta* cause a niche shift in a native

galaxiid, leading to reduced growth and survival (Correa et al. 2012). Overlapping food habits may also lead to limited supplies of prey resources for the predator community (Bacheler et al. 2004). In Flaming Gorge, Utah-Wyoming, kokanee *Oncorhynchus nerka* and Utah chub *Gila atraria* fed extensively and similarly on zooplankton; subsequently, zooplankton biomass declined, and the decline in kokanee growth was correlated with increased chub densities (Teuscher and Luecke 1996). Similarly, the introduction of lake trout *Salvelinus namaycush* into Bear Lake, Utah reduced survival of Bear Lake strain Bonneville cutthroat trout *O. clarki utah* due to shared competition for Bear Lake sculpin *Cottus extensus* prey (Ruzycki et al. 2001). Competition among top predators may therefore result in reduced growth and survival, or affect behavior such as changes in habitat use (Werner and Hall 1977) or variable recruitment success (Marrin and Erman 1982).

Piscivores are commonly introduced as a management tool in an attempt to control undesired species (Courtenay and Kohler 1986), as well as to enhance or provide new angling opportunities (Wuellner et al. 2010). The growth and survival of these piscivores depends on prey fish availability (Ney and Orth 1986), subsequently, the size of prey consumed and the frequency of piscivory both generally increase with predator size (Juanes et al. 2002). Accordingly, body morphology is a major factor affecting foraging performance of fish; for example, mouth gape size affects the size of prey species that can be eaten by piscivores (Mittelbach and Persson 1998). While the selection of prey fish of larger sizes increases proportionally with predator size, sizes of prey consumed often appear to be smaller than what is thought possible based on gape

size measurements (Truemper and Lauer 2005). Further, the range of prey sizes eaten typically increases in larger predators, as maximum prey size often increases rapidly while minimum prey size may change only modestly over a broad range of predator sizes (Juanes et al. 2002). The overall impact of these introduced piscivores on complex food web interactions thus depends, in part, on prey life-history traits relating to size and predator avoidance, and subsequent predator foraging decisions (Lundvall et al. 1999).

Predator feeding is not solely based on predator and prey size, but also on a suite of characteristics related to the search, pursuit, attack, and handling of prey by predators (Werner and Gilliam 1984; Bronmark and Hansson 1998). According to optimal foraging theory, fish will forage in such a way as to maximize fitness, typically taking into consideration food quality, quantity, and spatial distribution (Werner and Hall 1974; Svanback and Bolnick 2007). The amount of food consumed relative to the prey density is a functional response, where the amount of predation generally increases with prey density, up until a saturation point (Abrams and Fung 2010). High spatiotemporal overlap between the predator and prey is necessary for encounter, and strategies vary from the sit-and-wait predation of pike *Esox* to the sensing of prey electrical activity by paddlefish *Polyodon spathula* (Dodds and Whiles 2010).

On the other hand, defenses against predation, such as habitat and behavior choices or mechanical and chemical protections by prey, act in concert with predator behavior to influence predator diet (Romare and Hansson 2003; Sih et al. 2010; Dodds and Whiles 2010). If prey detect predators before they are detected by predators, they

have the potential to actively avoid them. Increased refuge efficiency by prey species was shown to cause a decrease in piscivorous perch *Perca* growth rates, likely due to a necessary shift in predator diet (Persson and Eklov 1995). The use of these structurally-complex habitats may therefore reduce predation rates because of a decrease in predator-prey encounters (Tabor and Wurtsbaugh 1991; Christensen and Persson 1993; Carey and Wahl 2010). Encounter rates also depend on the spatiotemporal patterns of prey. Zooplankton exhibit diel vertical migrations, foraging at night to avoid visual predators (Hays 2003). A high cost of handling time for low energy returns is unfavorable for predators; prey may employ behaviors (e.g., schooling), protective spines (e.g., spiny water flea *Bythotrephes*), armor (e.g., mollusks), or toxins (e.g., *Coleoptera*) to deter predators (Dodds and Whiles 2010). Finally, abiotic factors such as water clarity may impact food web structure, as many fish are visual predators.

Introductions of a novel predator or prey into a system may cause unintended or unanticipated impacts. Trout introduced into alpine lakes have had unintended effects on their amphibian and invertebrate prey, as naïve prey are poorly adapted to novel predators (Knapp 2005; Sih et al. 2010). In contrast, spiny water fleas make up a large part of salmonid diets in their native Norway but function as a serious threat in North America, as top predators in North America may be incapable of recognizing or capturing the newly introduced species (Yan et al. 2011). Additionally, galaxioid fishes have been identified as in serious conservation crisis partially due to negative competitive interactions with introduced brown trout and rainbow trout from the northern hemisphere (McDowall 2006).

Rainbow trout are one of the most widely stocked and highly valuable sport fish world-wide (FAO Inland Water Resources and Aquaculture 2003 in Fausch 2008). Located in the western United States, Scofield Reservoir is a high-elevation Utah reservoir with an historic blue-ribbon rainbow trout fishery. This reservoir now contains an assemblage of top predators including rainbow trout, Bear Lake strain Bonneville cutthroat trout, and tiger trout *Salmo trutta*, female x *Salvelinus fontinalis*, male. These additional species have been stocked into the reservoir in an effort to suppress Utah chub, an unwelcome and rapid invader that re-appeared in 2005. Though each species is known for their individual piscivorous nature, this combination of multiple potential top predators is unique, with relatively little knowledge of the likely interspecific interactions between cutthroat trout, rainbow trout, and tiger trout. Subsequent to the timing of chub invasion, rainbow trout have experienced apparent reductions in abundance and survival.

Scofield Reservoir is typical of many systems in the intermountain west, where a nuisance species may threaten the existence of a popular and artificial sport fishery. Therefore, Scofield Reservoir presents an opportunity to better understand how multiple top predators in a food web may interact in reservoirs throughout the West. In this study, I examined the interspecific interactions among Scofield Reservoir piscivores using stable isotope analysis and gut content analysis. Specifically, the objectives of this study were to (1) explore the food habits and use gut content to calculate indices of diet overlap between top predators or top predators and the principal prey fish, to identify potential for competition, and (2) evaluate niche overlap using stable isotope

techniques, by collecting tissue samples of fish and aquatic organisms throughout the food web, to further characterize potential predation and competition linkages of the three top predators in the system.

Study Site

Scofield Reservoir is a high elevation (2,322 m) impoundment on the Price River, a tributary of the Green River, located in southeast Utah. The reservoir was created by Scofield Dam in 1926 and is predominantly used for irrigation water storage, with recreation and flood control as additional benefits (Bureau of Reclamation 2011). The current reservoir has a capacity of 73,600 acre-ft at full pool, mean surface area of 2,815 acres (1,139 ha), and a mean depth of 8 m (Bureau of Reclamation 2009). Scofield Reservoir is classified as eutrophic, with “excessive” total phosphorous enrichment (Department of Environmental Quality 2010), typical of reservoirs, as high loads of organic materials and nutrients correspond to a proportionally large watershed area relative to volume (Wetzel 1990). Carlson Trophic State Index calculated for 1981-2007, a general measure of eutrophication based on Secchi depth, chlorophyll a, and phosphorous indicated a mesotrophic system (Bureau of Reclamation 2012). Blue-green algae dominate the phytoplankton community, indicative of poorer water quality, with blooms typically occurring in summer. The reservoir stratifies thermally in summer, and hypolimnetic oxygen deficits historically lead to fish kills of varying degrees (Hart and Birdsey 2008).

Scofield Reservoir is managed as a put-grow-and take sport fishery. Historically, around 600,000 150-250 mm long rainbow trout were stocked every year. However, the

fish stocking program has been adjusted nearly every year since 2005 in response to the appearance of Utah chub in gill nets and fear of a population expansion, with potential for negative impacts to the trout fishery (Hart and Birdsey 2008). Tiger trout and Bear Lake strain Bonneville cutthroat trout have been stocked in the fishery as a potential biological control for the Utah chub as well as alternative sport fishes. These populations demonstrate little to no natural reproduction, and are artificially maintained with approximately 80,000 of each stocked yearly at 200 mm long (see Table 2.1). Non-game species also present include the redbside shiner *Richardsonius balteatus* and mountain sucker *Catostomus platyrhynchus*.

Methods

Field sampling

I sampled fishes in spring, summer, and autumn of 2012 in Scofield Reservoir. In this type of fixed-station sampling, index sites were selected to be representative of the reservoirs' longitudinal axis from the upper riverine zone to the lower lacustrine zone (McMahon et al. 1996), while maintaining consistency with long-term Utah Division of Wildlife Resources monitoring (Figure 3.1). I set horizontal sinking gill nets (24 m long x 1.8 m tall with eight monofilament panels of 38-, 57-, 25-, 44-, 19-, 64-, 32-, and 51-mm bar mesh) according to standard gill net methods to capture a representative size distribution of all fish in the reservoir (Beauchamp et al. 2009). I placed two nets at each of eight sample sites within the reservoir in littoral areas offshore at depths that fish

were predicted to be most abundant; set before dusk and pulled at dawn, spanning two crepuscular periods.

Diet analysis

I collected cutthroat trout, rainbow trout, tiger trout, and Utah chub diets from each gill-netting survey. I immediately preserved trout and chub stomachs in 95% ethanol for later analysis. I identified all organisms from stomach contents to the lowest taxonomic level possible (Brooks 1957; Edmonson 1959; Merrit and Cummins 1996) to determine abundance of species and composition. I grouped stomach contents by prey fish (identified to species when possible), zooplankton, organic matter, aquatic invertebrates (classified to order), and terrestrial invertebrates (classified to order). I counted and weighed (blot-dry wet weight to nearest 0.001 g) individual prey fish, and weighed invertebrate prey *en masse* by classification. I measured intact prey fish to the nearest mm (backbone and standard length). I then calculated the contribution of each prey category to the diet of each predator species as the mean proportion by weight (g) for each stomach individually, and then averaged across all nonempty stomachs (Chippis and Garvey 2007):

$$MW_i = 1/N \sum_{j=1}^N (W_{ij} / \sum_{i=1}^Q W_{ij})$$

where N is the total number of fish with nonempty stomachs, W_{ij} is the weight of prey i in the stomach of predator j , and Q is the total number of prey categories.

I used Schoener's index of diet overlap to calculate the percent diet overlap between species. The index is determined using the formula:

$$\alpha = 1 - 0.5 \left(\sum_{i=1}^n |p_{xi} - p_{yi}| \right)$$

where α is the degree of overlap, n is the number of food categories, p_{xi} is the proportion of food category i in the diet of species x , and p_{yi} is the proportion of food category i in the diet of species y (Schoener 1970). Index values range from 0 to 1, where a value approaching 0 means the species share no prey resources and a value closer to 1 means the species have identical prey utilizations. Values exceeding 0.6 are considered "biologically significant" in terms of overlap in resource use (Wallace 1981). All of the fish from each species were pooled into representative 'small' (fish < 350 mm TL) and 'large' (\geq 350 mm TL) size classes with diet overlap values calculated for each season of the study period.

Trophic position analysis

From all gill-netted trout and chub, I removed a small dorsal muscle tissue sample for isotopic diet analysis. I quantified longer-term dietary habits of a subset of cutthroat trout ($n = 15$), rainbow trout ($n = 11$), tiger trout ($n = 8$), and Utah chub ($n = 10$) using stable isotope analysis. Specifically, I assessed fish trophic position and dietary carbon source based on the respective $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ signatures of dorsal muscle tissue (Post 2002). Tissue samples were dried in an oven for 48 hours at 70°C, ground to a powder, encapsulated in 8.5 mm tin capsules, and analyzed at the Washington State

University Stable Isotope CORE for a mass spectrometry-based determination of isotopic signatures. Signatures are an expressed ratio ($^{15}\text{N}:^{14}\text{N}$ and $^{13}\text{C}:^{12}\text{C}$), per mille (‰) values relative to ratios of the standard atmospheric N_2 and Pee Dee Belemnite, respectively.

I then plotted isotopic signature values as coordinates in niche space to determine both resource and habitat use of each species (Newsome et al. 2007). I used the program SIBER (Stable Isotope Bayesian Ellipses in R) to fit standard ellipses based on multivariate normal distributions and maximum likelihood estimators. I then calculated standard ellipse area and overlap, corrected for small sample size (Jackson et al. 2011). Additionally, I used stable isotope data to estimate the relative contribution of Utah chub prey to predator diets using the program SIAR (Stable Isotope Analysis in R), a linear mass balance mixing model (Philips and Gregg 2001; Clarke et al. 2005).

Gape Limit

To determine the gape size of predators, which indicates the size of fish prey available, I measured several morphometric features of each predator, including total body length (nearest mm TL) and length of the lower (L_L) and upper (L_U) jaw, using a digital caliper (to nearest 0.1 mm). I then calculated gape size (G) trigonometrically assuming a maximum mouth opening of 60° during food uptake, using the equation as per Jensen et al. (2004):

$$G_{\text{pred}} = [(L_L \sin 60) + (L_U - L_L \cos 60)]^{0.5}$$

where G_{pred} is the gape size of the predator, L_L is the length of the predators lower jaw (mm), and L_U is the length of the predators upper jaw (mm). Second, I also measured

the stretched width (laterally left to right) of the predator's mouth using a digital caliper (to nearest 0.1 mm; Truemper and Lauer 2005).

To determine actual sizes of prey consumed by piscivores, I examined diet contents of predators. From fish prey found in diets, when possible, I obtained prey: backbone lengths, standard lengths, and total length measurements. To determine the size of prey "vulnerable" to predators based on their gape, I also measured body depth and total length of prey (i.e., Utah chub) found in the reservoir, and created a relationship relating body depth to total length.

Results

Diet

Food habits varied substantially among trout species and Utah chub in Scofield Reservoir. Utah chub were found in the diets of large (≥ 350 mm TL) cutthroat trout (n=53) throughout every season in 2012 (Figure 3.2). Large cutthroat trout stomachs contained from 50-100% Utah chub prey. Aquatic invertebrates (primarily chironomids) and terrestrial invertebrates made up the remainder of large cutthroat trout diets. However, considerable differences in individuals based on size were evident. Aquatic invertebrates composed 25-85% of small (< 350 mm TL) cutthroat trout diets (n=65). Small cutthroat trout relied heavily on zooplankton as well (up to 53%).

Tiger trout displayed similar food habits to cutthroat trout. Large tiger trout (n=57) were distinguished by their piscivorous diet, containing 44-80% Utah chub by season. Small tiger trout (n=39) displayed a similar affinity for aquatic invertebrates, but

additionally, tiger trout consumed a substantial proportion of crayfish at all sizes throughout all seasons (upwards of 20%). Small tiger trout demonstrated a varied diet of not only aquatic invertebrates (primarily Ephemeroptera, Isopoda, and Mollusca) and crayfish, but included prey fish and terrestrial invertebrates.

Rainbow trout differed considerably from these trends. Diets of small (n=67) and large rainbow trout (n=13) were similar, characterized by low proportions of prey fish (Figure 3.3). Approximately half of the rainbow trout diet was composed of aquatic invertebrates (primarily Chironomids, with some Isopoda). These rainbow trout also included crayfish, terrestrial invertebrates, and organic matter as a substantial proportion of their diet.

Utah chub diets consisted substantially of aquatic invertebrates at both smaller (n=30) and larger (n=20) sizes (ranging from 20-81%). Smaller Utah chub also relied more heavily on zooplankton and organic matter, whereas large Utah chub were found to have a sizable proportion of crayfish in their diet.

Trout and chub also displayed substantial changes in food habits across seasons. The proportion of Utah chub in large cutthroat trout diets in the fall was twice that in spring. Small cutthroat trout relied heavily on aquatic invertebrates regardless of season, but consumed a greater diversity of invertebrates in spring than in summer and fall. Small cutthroat trout exhibited a strong affinity for zooplankton in the fall, much more than the remainder of the year.

Large tiger trout consumed 30% more prey fish in summer than during spring or fall of 2012. Small tiger trout consumed a hefty 80% of aquatic invertebrates in the

spring, whereas only 34% in summer and 56% in fall. Overall, tiger trout incorporated crayfish as 20% of their diet annually, whereas small tiger trout relied more heavily on crayfish for about 42% of their diet in summer. Furthermore, both small and large rainbow trout had a high proportion of aquatic invertebrates, terrestrial invertebrates, and organic matter in their diet regardless of season.

Finally, Utah chub consumed less aquatic invertebrates in summer than in the spring (20-30% compared with 50-80%), but made up the difference with substantial zooplankton consumption at both small (40%) and large (20%) size classes in the summer. Small and large Utah chub also exhibited an exceptionally strong affinity for zooplankton (72% and 100%) in the fall of 2012.

Diet overlap amongst Scofield Reservoir trout and Utah chub was lowest in spring of 2012. Based on Schoener's index, there was significant diet overlap between small cutthroat trout ($\alpha = 0.63$) and small rainbow trout ($\alpha=0.64$) with Utah chub, as well as large cutthroat trout with large tiger trout ($\alpha =0.66$) in the spring of 2012. There is also evidence of diet overlap between small and large tiger trout ($\alpha =0.68$). Similarly, there is significant diet overlap between small cutthroat trout with large rainbow trout ($\alpha=0.68$) and small tiger trout ($\alpha=0.61$), as well as overlap between large cutthroat ($\alpha = 0.69$) with large tiger trout during the summer season. In autumn, there were many instances of significant diet overlap, the strongest involving: small cutthroat trout with small Utah chub ($\alpha=0.76$), large cutthroat trout with large tiger trout ($\alpha=0.77$), and large rainbow trout with both small and large tiger trout ($\alpha= 0.66$). Similar patterns of extensive overlap were observed with summer and autumn of 2011 food habits.

Trophic position

Organisms collected displayed carbon and nitrogen signatures indicative of their habitat use and feeding position. Tiger trout (n=10) had the highest carbon isotopic signature, indicative of their use of more littoral primary carbon sources. Utah chub (n=10), however, had the most negative carbon isotopic signature, reflecting usage of pelagic habitat at all sizes. Large Utah chub were significantly more depleted in carbon than tiger trout, as well as cutthroat trout (both Student's t-tests $P = 0.02$). In comparison, there were no statistical differences between carbon signatures of any large trout species, they all utilized similar carbon sources (Figure 3.4).

Based on $\delta^{15}\text{N}$ results, large cutthroat trout (n=13) and large tiger trout share a similar position as top predators in this system, feeding at trophic positions corresponding to high $\delta^{15}\text{N}$ values (Student's t-test $P > 0.05$). The nitrogen signature of large rainbow trout was also statistically similar to tiger, although less similar to cutthroat trout (both Student's t-tests $P > 0.05$). Large Utah chub occupy trophic positions similar to rainbow trout and tiger trout, but have a trophic position lower than large cutthroat trout (Student's t-test $P < 0.001$).

Small Utah chub fed more littorally, and additionally fed at lower trophic positions, with $^{15}\delta\text{N}$ signatures similar to small rainbow trout and small tiger trout. Small cutthroat trout fed at nearly the same position as both small and large Utah chub. All three trout species varied in niche space with respect to size class, demonstrating an ontogenetic shift around 350 mm in length, to higher trophic positions. These results suggest that for tiger trout and rainbow trout, small individuals fed in littoral areas

whereas the diet of larger individuals originated in more pelagic areas. Cutthroat trout sampled for stable isotope analysis shifted to feed more littorally with an increase in size.

When the isotopic niche of these species was plotted in 2-dimensional niche space, large tiger trout had a very broad niche (ellipse area, EA=10.4); they consumed food at a wide range of trophic positions and vary with respect to their basal resources (Figure 3.5). Large cutthroat trout (EA=2.2) and large rainbow trout (EA=2.7) both had smaller more focused isotopic niche areas which overlapped significantly with the tiger trout niche (78% and 64%, respectively), and with each other (31% and 26%, respectively). The isotopic niche of tiger trout only overlapped 17% with both cutthroat trout and rainbow trout.

Small rainbow trout (EA=3.2) and small tiger trout (EA=2.8) overlap significantly with respect to their isotopic niches (45% of the rainbow trout niche and 52% of the tiger trout niche), sharing similar prey resources at an intermediate trophic position. Small cutthroat trout (EA=6.6), closely share a feeding niche space with all sizes of Utah chub, as demonstrated by their similar isotopic signatures, with 19% of their niche overlapping with the entirety of the small chub niche. Small Utah chub may consume more pelagic prey than do small rainbow trout, however, adult rainbow trout may share a large proportion of niche space with small Utah chub.

Gape limit

Utah chub found in cutthroat trout diets ranged from 80 to 272-mm in total length. Cutthroat trout became piscivorous at approximately 320-mm TL, and consumed

Utah chub near and well above both their horizontal and vertical gape size (Figure 3.6).

In several instances, cutthroat trout consumed Utah chub that were greater than 50% of their body size. One 425-mm cutthroat trout consumed a 272-mm Utah chub (64% of the trout's body size). However, on average, cutthroat trout consumed fish prey 30% of their body size. Gape-width limit was very similar to gape-size limit calculated using vertical gape measurements.

Utah chub found in tiger trout diets ranged from 37 to 234-mm in total length. Tiger trout switched to piscivory at approximately 340-mm TL and consumed fish very close to or just exceeding their horizontal and vertical gape sizes. On average, tiger trout consumed prey fish approximately 28% of their body size. One 418-mm tiger trout consumed a 202-mm Utah chub (48% of the trout's body size). Comparable to cutthroat trout, gape-width limit was very similar to gape-size limit calculated using vertical gape measurements. Rainbow trout, however, demonstrated limited piscivory in Scofield Reservoir, and we found no measureable fish prey in diets.

Discussion

In this study, I present new information on diet among a unique assemblage of trout in a lentic environment, and quantified species interactions and diet overlap of three top trout predators. I also described the feeding niches of three top predators and Utah chub using stable isotope analyses. Overall, the fish composition in Scofield Reservoir was dominated by Utah chub, a species which consumed large quantities of a suite of aquatic invertebrates and zooplankton throughout the growing season. Isotopic

signatures of Utah chub, indicative of its feeding position and primary food source, compared similarly to small cutthroat trout. I observed consistently low numbers of rainbow trout, which consumed few prey fish, and relied substantially on aquatic and terrestrial invertebrates for food resources. High overlap was demonstrated amongst rainbow trout with all other species, strength of overlap varying based on season. Additionally, I found cutthroat trout and tiger trout share a top trophic position in the food web, relying on an ontogenetic shift to piscivory to consume Utah chub as a substantial proportion of their adult diet. Both cutthroat trout and tiger trout consumed Utah chub at and above theoretical predictions of gape limit, demonstrating they were not food-limited based on gape morphology or prey size.

Throughout the study period, all large trout relied extensively on shared resources. I found evidence that large cutthroat trout and large tiger trout exhibited high diet overlap, with both species feeding primarily on Utah chub. There was no evidence of predation by one species on the other; Utah chub dominated the diets of both. The diets of cutthroat trout reported in this study differed substantially from diets reported from other lentic systems. At least 50% of cutthroat trout diet in Scofield Reservoir consisted of Utah chub throughout the year. Small cutthroat trout displayed an expansive diet throughout all seasons and fed on many different aquatic and terrestrial invertebrates, crayfish, and zooplankton. Within Strawberry Reservoir, Utah, *Daphnia* were important prey for juvenile cutthroat trout and were seasonally important to adult fish; additionally, fish was a minor contributor to adult diet (Baldwin et al. 2000). However, in Bear Lake, Utah-Idaho, Bonneville cutthroat trout are a

dominant piscivore, predominantly consuming cisco *Prosopium gemmifer* and sculpin *Cottus extensus* (Ruzycki et al. 2001). The similar piscivorous behavior of cutthroat trout in Scofield Reservoir is likely influenced by the abundant fish prey.

The potential for competition between top predators is indicated by similar trophic habits among cutthroat trout and tiger trout. Small tiger trout consumed a wide variety of aquatic invertebrates, whereas large tiger trout switched to a diet primarily of prey fish and crayfish. Tiger trout have been described as a “predator trout” capable of utilizing nuisance prey fish, and as such, added to stocking programs for this purpose (Hepworth et al. 2009; Hepworth et al. 2011). In contrast, tiger trout in eastern Washington appeared to rely substantially on *Daphnia*, and were intermittently piscivorous (to pumpkinseed *Lepomis gibbosus* and redbreast shiners), but only in the summer months (Miller 2010). The same study postulated that kokanee were outcompeting tiger trout for zooplankton, and thus tiger trout had adapted a more benthic diet. While I observed tiger trout consuming a significant proportion of crayfish, a benthic prey item, fish still were the favored prey of tiger trout in this study.

The shared chub diet of cutthroat trout and tiger trout alone does not necessarily indicate competition for prey resources (Matthews et al. 1982). Resources must be limited and fitness or performance-related factors such as growth, condition, and fecundity must be negatively affected in order for competition to occur. Consequently, there is likely minimal potential for competition between these trout species as Utah chub are abundant and as cutthroat trout and tiger trout are caught at large sizes and in high numbers throughout the reservoir (see chapter 2). However, if

the Utah chub population collapsed under high predation, or if the trout population continued to expand via increased stocking rates, then con-specific competition and predation rates may increase.

Both predator size and prey size strongly influence predation (Hambright 1991; Fritts and Pearsons 2006). Cutthroat trout and tiger trout displayed an ontogenetic shift to piscivory around 330 mm TL, and consumed prey fish at 30% of their own size. Additionally, the mouth size and morphometry of these top piscivores does not appear to be limiting prey consumption, as both species also consumed prey at and above their theoretical gape limits. Piscivorous mouth gape size restricts the size of prey based on the body depth of that prey; however, food can be attacked and then manipulated in such a way as to consume larger than expected sizes (Nilsson and Bronmark 2000). In contrast, Hambright (1991) and Hill et al. (2004) both suggest the vulnerability of prey larger than predator gape size is reduced to zero. Subsequently, predation may also depend on prey morphology and predator behavior. Northern pike *E. lucius* prefer shallow bodied roach *Rutilus rutilus* before deep-bodied bream *Abramis brama* in Swedish lakes, experiments that also highlighted pike may swallow larger prey than suggested by gape measurements (Nilsson and Bronmark 2000). Convincingly, our study also demonstrates the ability of cutthroat trout and tiger trout to consume prey up to 50% of their own size, much larger than gape limit alone would predict.

Unlike the piscivorous cutthroat trout and tiger trout, rainbow trout behaved mostly as invertivores in Scofield Reservoir and occupied a more pelagic habitat than the other trout species. Large rainbow trout displayed a similar propensity for aquatic

invertebrates as small rainbow trout. Although our sample size of rainbow trout diets was low, the results agreed with previous studies, demonstrating that rainbow trout relied heavily on aquatic invertebrates, zooplankton, and a small percentage of prey fish (Tabor et al. 1996; Baldwin et al. 2000; Haddix and Budy 2005). In contrast however, there are many studies which depict rainbow trout as aggressive piscivores (Beauchamp 1990; McDowell 2003; Yard et al. 2011; Juncos et al. 2011). Consequently, the suite of top predators in Scofield Reservoir may have indirect effects on rainbow trout through exploitative competition or behavioral interactions (Duffy et al. 2007; Sih et al. 2010). For example, the presence of cutthroat trout and tiger trout could cause rainbow trout to decrease activity, exhibit predator avoidance, or change feeding strategies (Romare and Hansson 2003). Catch rates of rainbow trout throughout our study were low, and the blue-ribbon rainbow trout fishery has abated from this western reservoir.

I observed no biologically-significant diet overlap between large rainbow trout and Utah chub, contradicting expectation that rainbow trout were performing poorly due to shared food resources, and thereby limited food resources, with Utah chub. The small sample size of rainbow trout, which inflated average contributions of prey towards diet composition, may have substantially and unrealistically altered diet proportions. Marrin and Erman (1982) found minimal diet overlap between brown trout and rainbow trout with tui chub *Gila bicolor*, and Tahoe sucker *Catostomus tahoensis*, demonstrating these trout and nongame fish partition resources sufficiently, and contradicting the common belief in that system that competition for food resources was the cause for the decrease in trout performance. However, apparent survival of rainbow trout, a relevant

measure of interaction strength (Keeley 2001), is extremely low in Scofield Reservoir, and we may not have captured changes in competitive abilities with size and environmental conditions (Hayes 1989).

Our analyses of stable isotope data corroborate with overall diet contributions, and reaffirm evidence of potential for competition amongst this unique assemblage of species. High nitrogen signatures of large cutthroat trout and large tiger trout confirm these top predators are piscivorous share a top trophic position in the food web, relying heavily on prey fish. Carbon signatures from tiger trout suggest they utilize more littoral resources, a pattern corresponding with the high percentage of crayfish in diets.

The trophic positions of small cutthroat trout, rainbow trout, and tiger trout all shifted to higher nitrogen values at larger sizes, indicating a strong ontogenetic shift in diet preferences with size. Rainbow trout also shifted to a more negative $\delta^{13}\text{C}$ value as they became larger. Vander Zanden et al. (1999) documented a similar carbon shift of lake trout in bass-invaded Canadian lakes, reflecting a diet shift towards zooplankton and reduced dependence on littoral prey fish. This diet shift from the littoral to the pelagia for rainbow trout in Scofield Reservoir may indicate rainbow trout are altering their trophic niche in response to direct or indirect competition with the new predators recently stocked into this system (Correa et al. 2012). Despite low sample size, my results indicate rainbow trout are now performing poorly in Scofield Reservoir as suggested, in part, by very low rates of apparent survival and return to the creel, a pattern that could very likely be due to feeding constraints or other limitations associated with the other predators.

Our dietary findings are particularly important given the recent interest in tiger trout and managers' desire to expand their use in stocking regimes. Several lines of evidence suggest that tiger trout are performing very well and are not limited by strong food web interactions such as competition or predation. Utah chub make up at least 30% of the diet of tiger trout seasonally, suggesting encounter rates are high and prey fish are energetically favorable (Wallace 1981). Large tiger trout also have a wide breadth of diet preferences, relying on a diversity of prey. In addition, this hybrid species feeds more littorally than other trout, thus potentially allowing them to minimize competition for food and space (Petchey 2000; Helland et al. 2011). Accordingly, tiger trout hold a high trophic position in the ecosystem. Tiger trout are also ideal predators to stock into reservoirs as sport fishes, because they are sterile hybrids, and energy normally allocated for gamete production should be allocated into growth (Budy et al. 2012). In addition, sterile trout are easier to control over the long-term (Scheerer and Thorgaard 1987), a consideration that has important conservation implications.

The combination of gut content and stable isotope analysis performed in this study provided a more complete understanding of potential limitations due to competitive or predatory interactions among a suite of novel predators. Competition for food resources between sport and nongame fishes is commonly cited as a reason for decreased salmonid angling success, and competition is often assumed to exist between desired sport fish and undesired invasive prey species (Marking 1992). Nevertheless, competition does not always occur, and, my data suggests two of the top trout

predators are not competing, likely because food is not limiting. Both tiger trout and cutthroat trout are monopolizing upon the abundant prey fish, Utah chub, and their growth and survival rates are high. However, prey availability may change spatially, as well as on a seasonal or annual basis, and increased growth rates of prey may result in chub outgrowing predator gape quickly, causing a shift in predator-prey dynamics. This novel fish community should be monitored carefully, as large-scale recent changes in the food web as well as annual changes in reservoir volume may result in an extremely dynamic predator-prey system.

References

- Abrams, P.A. & Fung, S.R. 2010. Prey persistence and abundance in systems with intraguild predation and type-2 functional responses. *Journal of Theoretical Biology* 264: 1033-1042.
- Bacheler, N.M., Neal, J.W. & Noble, R.L. 2004. Diet overlap between native bigmouth sleepers (*Gobiomorus dormitor*) and introduced predatory fishes in a Puerto Rico reservoir. *Ecology of Freshwater Fish* 13: 111–118.
- Baldwin, C.M., Beauchamp, D.A. & Van Tassell, J.J. 2000. Bioenergetic assessment of temporal food supply and consumption demand by salmonids in the Strawberry Reservoir food web. *Transactions of the American Fisheries Society* 129: 429-450.
- Beauchamp, D.A. 1990. Seasonal and diel food habits of rainbow trout stocked as juveniles in Lake Washington. *Transactions of the American Fisheries Society* 119: 475-482.
- Beauchamp, D.A., Parrish, D.L. & Whaley, R.A. 2009. Coldwater fish in large standing waters. In: Bonar, S.A., Hubert, W.A. & Willis, D.W., eds. *Standard Methods for Sampling North American Freshwater Fishes*. American Fisheries Society: Bethesda, Maryland, pp 97-118.
- Brooks, J.L. 1957. Identifications and nomenclature of Cladocera, Calanoida, and Cyclopoida. *Memoirs of the Connecticut Academy of the Arts and Science* 13(1).

- Bronmark, C. & Hansson, L.A. 1998. Consumption patterns, complexity and enrichment in aquatic food chains. *Proceedings of the Royal Society* 265: 901-906.
- Budy, P., Thiede, G.P., Dean, A., Olsen, D. & Rowley, G. 2012. A comparative and experimental evaluation of performance of stocked diploid and triploid brook trout. *North American Journal of Fisheries Management* 32: 1211-1224.
- Bureau of Reclamation. 2009. Scofield Dam. U.S. Department of the Interior.
- Bureau of Reclamation. 2011. Scofield Project. U.S. Department of the Interior.
- Bureau of Reclamation. 2012. Scofield Reservoir. U.S. Department of the Interior.
- Carey, M.P. & Wahl, D.H. 2010. Interactions of multiple predators with different foraging modes in an aquatic food web. *Oecologia* 162: 443-452.
- Chipps, S. R., & Garvey, J.E. 2007. Assessment of diets and feeding patterns. In: Guy, C.S. & Brown, M.L., eds. *Analysis and Interpretation of Freshwater Fisheries Data*. American Fisheries Society: Bethesda, Maryland, pp 473-514.
- Christensen, B., & Persson, L. 1993. Species-specific antipredator behaviours: effects on prey choice in different habitats. *Behavioral Ecology and Sociobiology* 32: 1-9.
- Clarke, L.R., Vidergar, D.T., & Bennett, D.H. 2005. Stable isotopes and gut content show diet overlap among native and introduced piscivores in a large oligotrophic lake. *Ecology of Freshwater Fish* 14: 267-277.
- Clavero, M., Hermoso, V., Aparicio, E. & Godinho, F.N. 2013. Biodiversity in heavily modified waterbodies: native and introduced fish in Iberian reservoirs. *Freshwater Biology* 58: 1190-1201.
- Correa, C., Bravo, A.P. & Hendry, A.P. 2012. Reciprocal trophic niche shifts in native and invasive fish: salmonids and galaxiids in Patagonian lakes. *Freshwater Biology* 57: 1769-1781.
- Courtenay, W.R. & Kohler, C.C. 1986. Regulating introduced aquatic species- a review of past initiatives. *Fisheries* 11: 34-38.
- Department of Environmental Quality. 2010. Scofield Reservoir TMDL. Division of Water Quality. Salt Lake City, Utah.
- Dodds, W.K. & Whiles, M.R. 2010. *Freshwater Ecology: Concepts and Environmental Applications of Limnology*, second edition. Burlington: Elsevier Inc., pp 545-568.

- Duffy, J.E., Cardinale, B.J., France, K.E., McIntyre, P.B., Thebault, E. & Loreau, M. 2007. The functional role of biodiversity in ecosystems: incorporating trophic complexity. *Ecology Letters* 10: 522-538.
- Edmonson, W.T. 1959. The rotifera. In: Whipple, G.C. & Ward, H.B., eds. *Freshwater Biology*, 2nd edition. New York: Wiley, pp 420-494.
- FAO Inland Water Resources and Aquaculture Service. 2003. *Fishery Record Collections. FIGIS Data Collection*. FAO - Rome. Food and Agriculture Organization.
- Fausch, K.D. 2008. A paradox of trout invasions in North America. *Biological Invasions* 10: 685-701.
- Franssen, N.R. & Tobler, M. 2013. Upstream effects of a reservoir on fish assemblages 45 years following impoundment. *Journal of Fish Biology* 82: 1659-1670.
- Fritts, A.L. & Pearsons, T.N. 2006. Effects of predation by nonnative smallmouth bass on native salmonid prey: the role of predator and prey size. *Transactions of the American Fisheries Society* 135: 853-860.
- Gido, K.B., Schaefer, J. & Falke, J.A. 2009. Convergence of littoral zone fish communities in reservoirs. *Freshwater Biology* 54: 1163-1177.
- Haddix, T. & Budy, P. 2005. Factors that limit growth and abundance of rainbow trout across ecologically distinct areas of Flaming Gorge Reservoir, Utah-Wyoming. *North American Journal of Fisheries Management* 25: 1082-1094.
- Hambright, K.D. 1991. Experimental analysis of prey selection by largemouth bass: role of predator mouth width and prey body depth. *Transactions of the American Fisheries Society* 120: 500-508.
- Hart, J. & Birdsey, P.W. 2008. *Scofield Research Proposal*. Price, UT: Utah Division of Wildlife Resources, Southeastern Regional Office.
- Havel, J.E., Lee, C.E. & VanderZanden, J. 2005. Do reservoirs facilitate invasions into landscapes? *BioScience* 55: 518-525.
- Hayes, J.W. 1989. Social interaction between 0+ brown and rainbow trout in an experimental stream design. *New Zealand Journal of Marine Freshwater Resources* 23: 163-170.
- Hays, G.C. 2003. A review of the adaptive significance and ecosystem consequences of zooplankton diel vertical migrations. *Hydrobiologia* 503: 163-170.

- Helland, I.P., Finstad, A.G., Forseth, T., Hesthagen, T. & Ugedal, O. 2011. Ice-cover effects on competitive interactions between two fish species. *Journal of Animal Ecology* 80: 539-547.
- Hepworth, R.D., Warner, J., Ottenbacher, M.J. & Hadley, M.J. 2009. Panguitch Lake: an evaluation of the sport fishery management plan. Division of Wildlife Resources. Salt Lake City: Utah Department of Natural Resources.
- Hepworth, R.D., Ottenbacher, M. & Hadley, M.J. 2011. Angler survey and monitoring results, Fish Lake Utah 2010. Division of Wildlife Resources. Salt Lake City: Utah Department of Natural Resources.
- Hill, J.E., Nico, L.G., Cichra, C.E. & Gilbert, C.R. 2004. Prey vulnerability to peacock cichlids and largemouth bass based on predator gape and prey body depth. *Proceedings of the Annual Conference, Southeast Association for Fish and Wildlife Agencies* 58: 47-56.
- Jackson, A.L., Inger, R., Parnell, A.C. & Bearhop, S. 2011. Comparing isotopic niche widths among and within communities: SIBER - Stable Isotope Bayesian Ellipses in R. *The Journal of Animal Ecology* 80: 595–602.
- Jensen, H., Bohn, T., Amundsen, P. & Aspholm, P.E. 2004. Feeding ecology of piscivorous brown trout (*Salmo trutta* L.) in a subarctic watercourse. *Annales Zoologici Fennici* 41: 319-328.
- Juanes, F., Buckel, J.A. & Scharf, F.S. 2002. Feeding ecology of piscivorous fishes. In: Hart, P.J.B & Reynolds, J.D., eds. *Handbook of Fish Biology and Fisheries*, first edition. Oxford, UK: Blackwell Publishing Ltd., pp 267-283.
- Juncos, R., Milano, D., Macchi, P.J., Alonso, M.F. & Vigliano, P.H. 2011. Response of rainbow trout to different food web structures in Northern Patagonia: implications for growth, bioenergetics, and invasiveness. *Transactions of the American Fisheries Society* 140: 415-428.
- Kashiwagi, M.T. & Miranda, L.E. 2009. Influence of small impoundments on habitat and fish communities in headwater streams. *Southeastern Naturalist* 8: 23-36.
- Keeley, E.R. 2001. Demographic responses to food and space competition by juvenile steelhead trout. *Ecology* 85: 1247-1259.
- Kitchell, J.F., & Crowder, L.B. 1986. Predator-prey interactions in Lake Michigan: model predictions and recent dynamics. *Environmental Biology of Fishes* 16: 205-211.

- Knapp, R.A., Hawkins, C.P., Ladau, J. & McClory, J.G. 2005. Fauna of Yosemite National Park lakes has low resistance but high resilience to fish introductions. *Ecological Applications* 15: 835-847.
- Layman, C.A., Araujo, M.S., Boucek, R., Hammerschlag-Peyer, C.M., Harrison, E., Jud, Z.R., Matich, P., Rosenblatt, A.E., Vaudo, J.J., Yeager, L.A., Post, D.M. & Bearhop, S. 2012. Applying stable isotopes to examine food-web structure: an overview of analytical tools. *Biological Reviews* 87: 545-562.
- Lundvall, D., Svanback, R., Persson, L. & Bystrom, P. 1999. Size-dependent predation in piscivores: interactions between predator foraging and prey avoidance abilities. *Canadian Journal of Fisheries and Aquatic Sciences* 56: 1285-1292.
- Marking, L.L. 1992. Evaluation of the toxicants for the control of carp and other nuisance species. *Fisheries* 17: 6-13.
- Marrin, D.L. & Erman, D.C. 1982. Evidence against competition between trout and nongame fishes in Stampede Reservoir, California. *North American Journal of Fisheries Management* 2: 262-269.
- Matthews, W.J., Gido, K.B. & Gelwick, F.P. 2004. Fish assemblages of reservoirs, illustrated by Lake Texoma (Oklahoma-Texas, USA) as a representative system. *Lake and Reservoir Management* 20: 219-239.
- Matthews, W.J., Bek, J. & Surat, E. 1982. Comparative ecology of the darters *Etheostoma podostemone*, *E. flabellare*, and *Percina roanoka* in the upper Roanoke River drainage, Virginia. *Copeia* 805-814.
- McDowall, R.M. 2003. Impacts of introduced salmonids on native galaxiids in New Zealand upland streams: a new look at an old problem. *Transactions of the American Fisheries Society* 132: 229-238.
- McDowall, R.M. 2006. Crying wolf, crying foul, or crying shame: alien salmonids and a biodiversity crisis in the southern cool-temperate galaxioid fishes? Review in *Fish Biology and Fisheries* 16: 233-422.
- McMahon, T.E., Zale, A.V. & Orth, D.J. 1996. Aquatic habitat measurements. In: Murphy, B.R. & Willis, D.W., eds. *Fisheries Techniques*. Bethesda, Maryland: American Fisheries Society, pp 83-120.
- Merritt, R.W. & Cummins, K.W., eds. 1996. *An introduction to the aquatic insects of North America*. Dubuque, Iowa: Kendall & Hunt.

- Miller, A.L. 2010. Diet, growth, and age analysis of tiger trout from ten lakes in Eastern Washington. Master's Thesis. Cheney: Eastern Washington University.
- Miranda, L.E. & DeVries, D.R., eds. 1996. Multidimensional approaches to reservoir fisheries management. American Fisheries Society Symposium 16, Bethesda, Maryland.
- Mittelbach, G.G. & Persson, L. 1998. The ontogeny of piscivory and its ecological consequences. *Canadian Journal of Fisheries and Aquatic Sciences* 55: 1454–1465.
- Newsome, S.D., del Rio, C.M. & Bearhop, S. 2007. A niche for isotopic ecology. *Frontiers in Ecology and the Environment* 5: 429-436.
- Ney, J.J. 1990. Trophic economics in fisheries: assessment of demand-supply relationships between predators and prey. *Reviews in Aquatic Sciences* 2: 55-81.
- Ney, J.J. 1996. Oligotrophication and its discontents: effects of reduced nutrient loading on reservoir fisheries. In: Miranda, L.E. & DeVries, D.R., eds. *Multidimensional Approaches to Reservoir Fisheries Management*. Bethesda, Maryland: American Fisheries Society Symposium 16, pp 285-295.
- Ney, J.J., & Orth, D.J. 1986. Coping with future shock: the challenge of matching predator stocking programs to prey abundance. In: Stoud, R.H., ed. *Fish culture in fisheries management*. American Fisheries Society: Bethesda, Maryland, pp 81-92.
- Nilsson, P.A. & Bronmark, C. 2000. Prey vulnerability to a gape-size limited predator: behavioural and morphological impacts on northern pike piscivory. *Oikos* 88: 539-546.
- Noble, R.L. 1986. Management of reservoir fish communities by influencing species interactions: predator-prey interactions in reservoir communities. In: Hall, G.E. & Van Den Avyle, M.J., eds. *Reservoir Fisheries Management Strategies for the 80's*. Bethesda, Maryland: American Fisheries Society, pp 137-143.
- Olson, M.H., Mittelbach, G.G. & Osenberg, C.W. 1995. Competition between predator and prey: resource-based mechanisms and implications for stage-structured dynamics. *Ecology* 76: 1758–1771.
- Paine, R.T. 1980. Food webs: linkage, interaction strength and community structure. *Journal of Animal Ecology* 49: 667–685.

Persson, L. & Eklov, P. 1995. Prey refuges affecting interactions between piscivorous perch and juvenile perch and roach. *Ecology* 76: 70-81.

Petchey, O.L. 2000. Prey diversity, prey composition, and predator population dynamics in experimental microcosms. *Journal of Animal Ecology* 69: 874-882.

Phillips, D.L. & Gregg, J.W. 2001. Uncertainty in source partitioning using stable isotopes. *Oecologia* 127: 171-179.

Polis, G.A. 1991. Complex trophic interactions in deserts: an empirical critique of food web theory. *The American Naturalist* 138: 123-155.

Polis, G.A. & Strong, D.R. 1996. Food web complexity and community dynamics. *The American Naturalist* 147(5): 813-846.

Polis, G.A., Anderson, W.B. & Holt, R.D. 1997. Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. *Annual Review of Ecological Systems* 28: 289-316.

Post, D.M. 2002. Using stable isotopes to estimate trophic position: models, methods, and assumptions. *Ecology* 83: 703-718.

Romare, P. & Hansson, L. 2003. A behavioral cascade: top-predator induced behavioral shifts in planktivorous fish and zooplankton. *Limnology and Oceanography* 48: 1956-1964.

Ruzycki, J.R., Wurtsbaugh, W.A. & Luecke, C. 2001. Salmonine consumption and competition for endemic prey fishes in Bear Lake, Utah-Idaho. *Transactions of the American Fisheries Society* 130: 1175-1189.

Scheerer, P.D. & Thorgaard, G.H. 1987. Performance and developmental stability of triploid tiger trout (brown trout x brook trout). *Transactions of the American Fisheries Society* 116: 92-97.

Schoener, T.W. 1970. Non-synchronous spatial overlap of lizards in patchy habitats. *Ecology* 51: 408-418.

Sih, A., Bolnick, D.I., Luttbeg, B., Orrock, J.L., Peacor, S.D., Pintor, L.M., Preisser, E., Rehage, J.S. & Vonesh, J.R. 2010. Predator-prey naiveté, antipredator behavior, and the ecology of predator invasions. *Oikos* 119: 610-621.

- Stein, R.A., DeVries, D.R. & Dettmers, J.M. 1995. Food-web regulation by a planktivore: exploring the generality of the trophic cascade hypothesis. *Canadian Journal of Fisheries and Aquatic Sciences* 52: 2518-2526.
- Svanback, R. & Bolnick, D.I. 2007. Intraspecific competition drives increased resource use diversity within a natural population. *Proceedings of the Royal Society* 274: 839-844.
- Tabor, R.A. & Wurtsbaugh, W.A. 1991. Predation risk and the importance of cover for juvenile rainbow trout in lentic systems. *Transactions of the American Fisheries Society* 120: 728-738.
- Tabor, R.A., Luecke, C. & W. Wurtsbaugh. 1996. Effects of daphnia availability on growth and food consumption of rainbow trout in two Utah reservoirs. *North American Journal of Fisheries Management* 16: 591-599.
- Terra, B.F. & Araujo, F.G. 2011. A preliminary fish assemblage index for a transitional river-reservoir system in southeastern Brazil. *Ecological Indicators* 11: 874-881.
- Teuscher, D. & Luecke, C. 1996. Competition between kokanees and Utah chub in Flaming Gorge Reservoir, Utah-Wyoming. *Transactions of the American Fisheries Society* 125: 505-511.
- Truemper, H.A. & Lauer, T.E. 2005. Gape limitation and piscine prey size-selection by Yellow Perch in the extreme southern area of Lake Michigan , with emphasis on two exotic prey items. *Journal of Fish Biology* 66: 135-149.
- Vander Zanden, M.J., Casselman, J.M. & Rasmussen, J.B. 1999. Stable isotope evidence for the food web consequences of species invasions in lakes. *Nature* 401: 464-467.
- Wallace, R.K. 1981. An assessment of diet-overlap indexes. *Transactions of the American Fisheries Society* 110: 72-76.
- Walsworth, T., Budy, P. & Thiede, G.P. 2013. Longer food chains and crowded niche space: effects of multiple invaders on desert stream food web structure. *Ecology of Freshwater Fish* 22: 439-452.
- Werner, E.E. & Gilliam, J.F. 1984. The ontogenetic niche and species interactions in size-structured populations. *Annual Review of Ecology and Systematics* 15: 393-425.
- Werner, E.E. & Hall, D.J. 1974. Optimal foraging and size selection of prey by the bluegill sunfish (*Lepomis macrochirus*). *Ecology* 55: 1042-1052.

- Werner, E.E. & Hall, D.J. 1977. Competition and habitat shift in two sunfishes (Centrarchidae). *Ecology* 58: 869-876.
- Wetzel, R.G. 1990. Land-water interfaces: metabolic and limnological regulators. *Verhandlungen des Internationalen Verein Limnologie* 24: 6–24.
- Wuellner, M.R., Chipps, S.R, Willis, D.W. & Adams Jr, W.E. 2010. Interactions between walleyes and smallmouth bass in a Missouri river reservoir with consideration of the influence of temperature and prey. *North American Journal of Fisheries Management* 30: 445-463.
- Yan, N.D., Lueng, B., Lewis, M.A. & Peacor, S.D. 2011. The spread, establishment and impacts of the spiny water flea, *Bythotrephes longimanus*, in temperate North America: a synopsis of the special issue. *Biological Invasions* 13: 2423-2432.
- Yard, M.D., Coggins Jr., L.G., Baxter, C.V., Bennett, G.E. & Korman, J. 2011. Trout piscivory in the Colorado River, Grand Canyon: effects of turbidity, temperature, and fish prey availability. *Transactions of the American Fisheries Society* 140: 471-486.

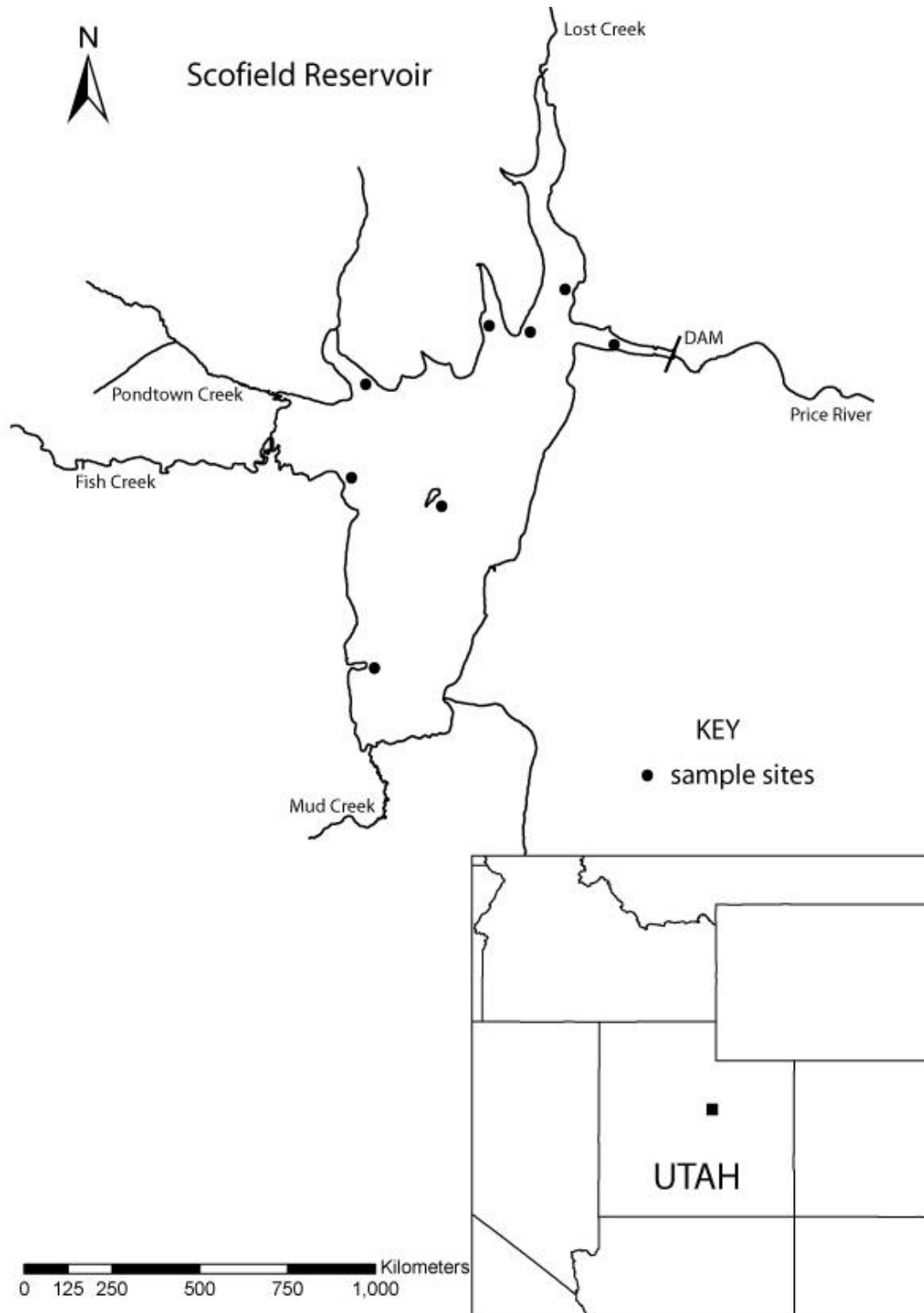


Figure 3.1. Map of Scofield Reservoir, Utah showing the eight locations during which fish were sampled in 2011 and 2012, denoted as black circles.

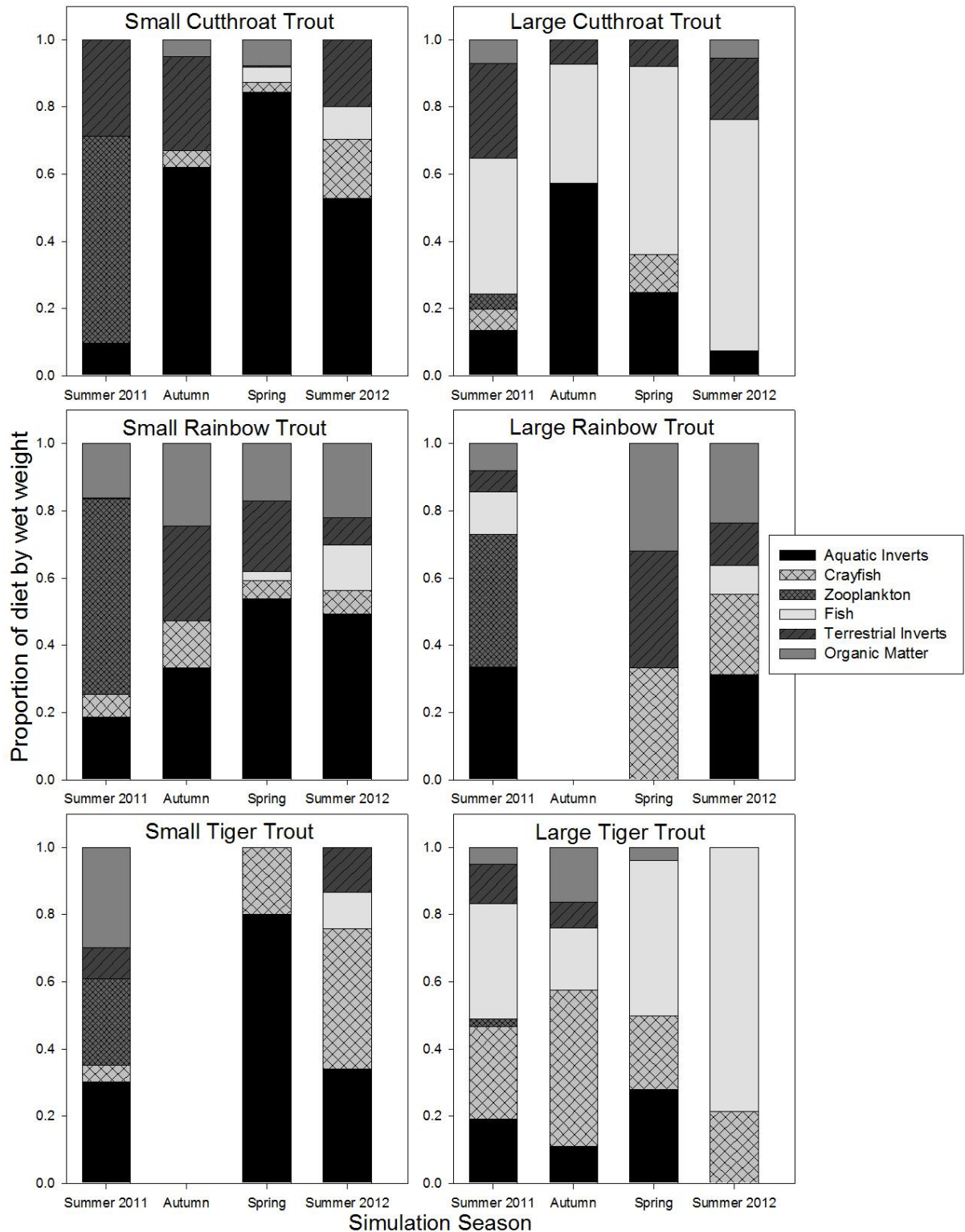


Figure 3.2. Seasonal diet composition of small (<350 mm TL) and large (≥ 350 mm TL) cutthroat trout, rainbow trout, and tiger trout captured in Scofield Reservoir. Diet composition was calculated as the proportion of diet by wet weight (g).

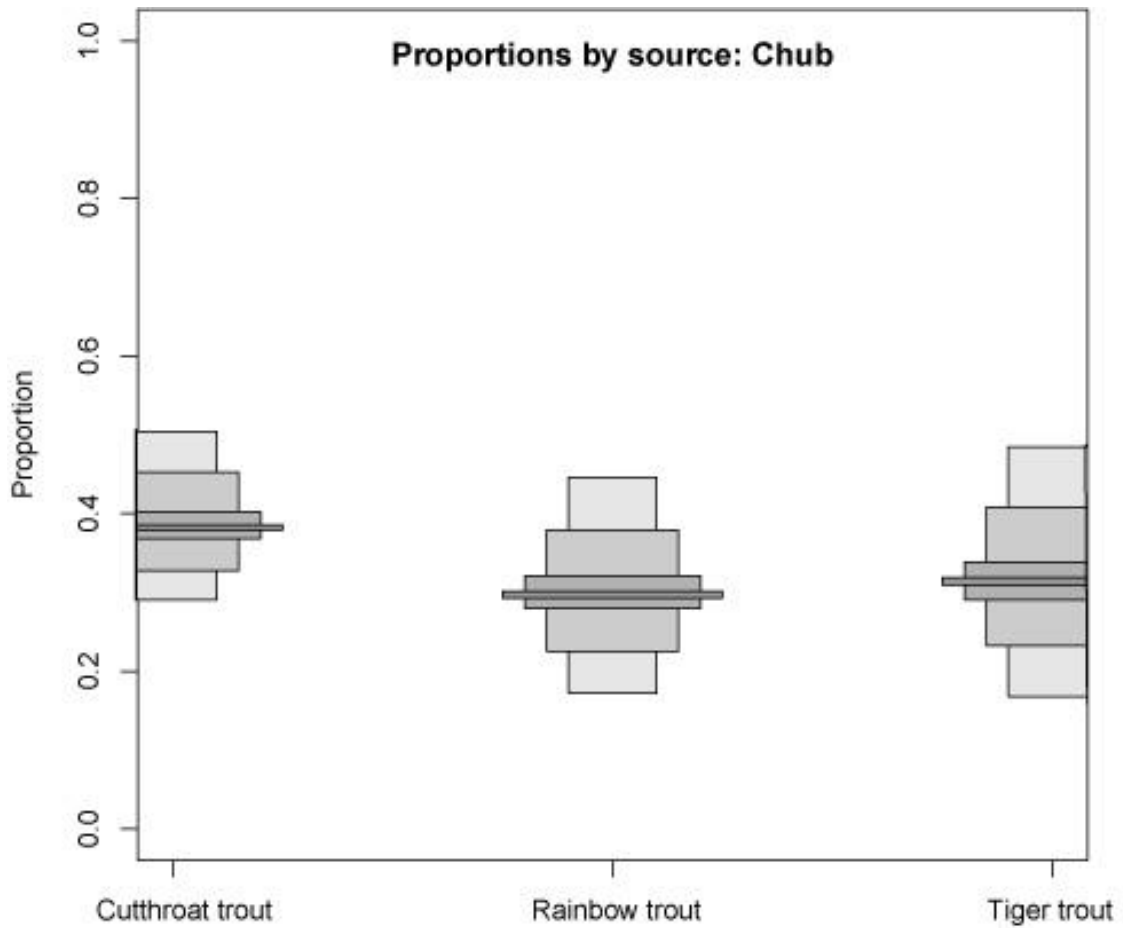


Figure 3.3. Proportion of Utah chub diet contribution for each predator species in Scofield Reservoir. Proportions are displayed with 95% confidence intervals in dark gray, then 75%, 25%, to 5% credibility intervals in light gray.

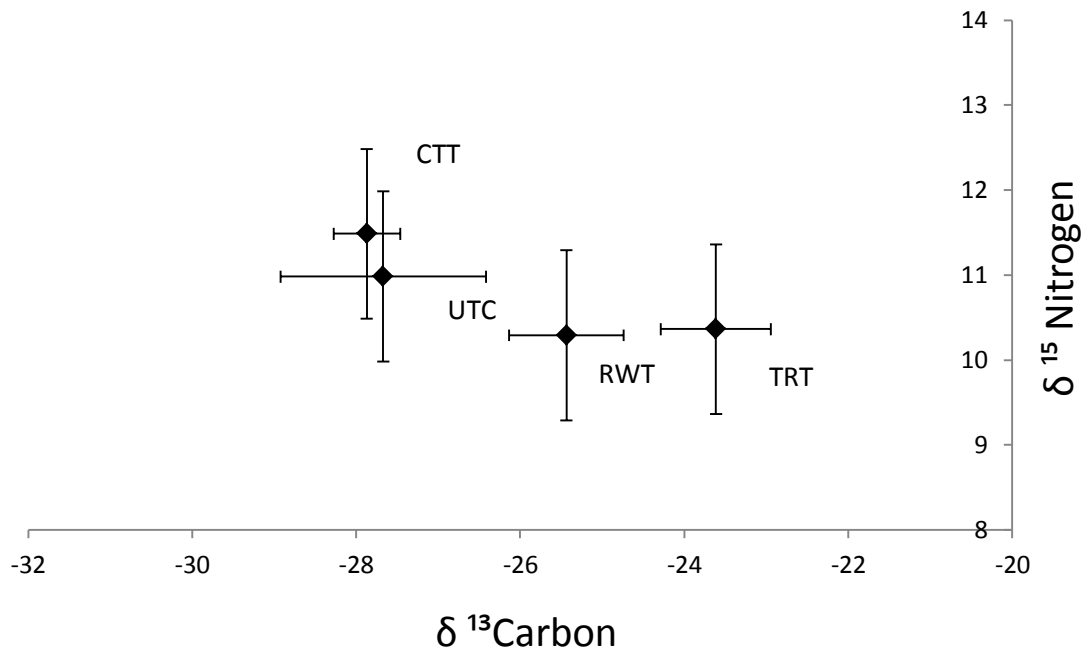
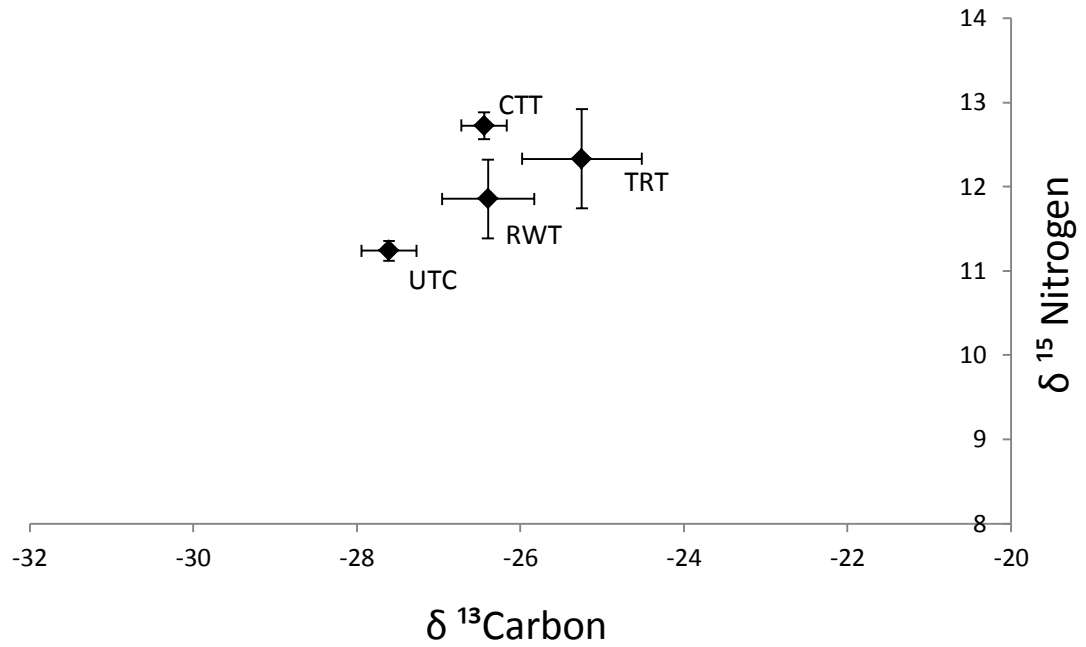


Figure 3.4. Stable isotope bi-plots for ^{13}C and ^{15}N of (top) large trout (≥ 350 mm TL) and large chub (≥ 250 mm TL), and (bottom) small trout (< 350 mm TL) and small chub (< 250 mm TL). Error bars are 1 standard error.

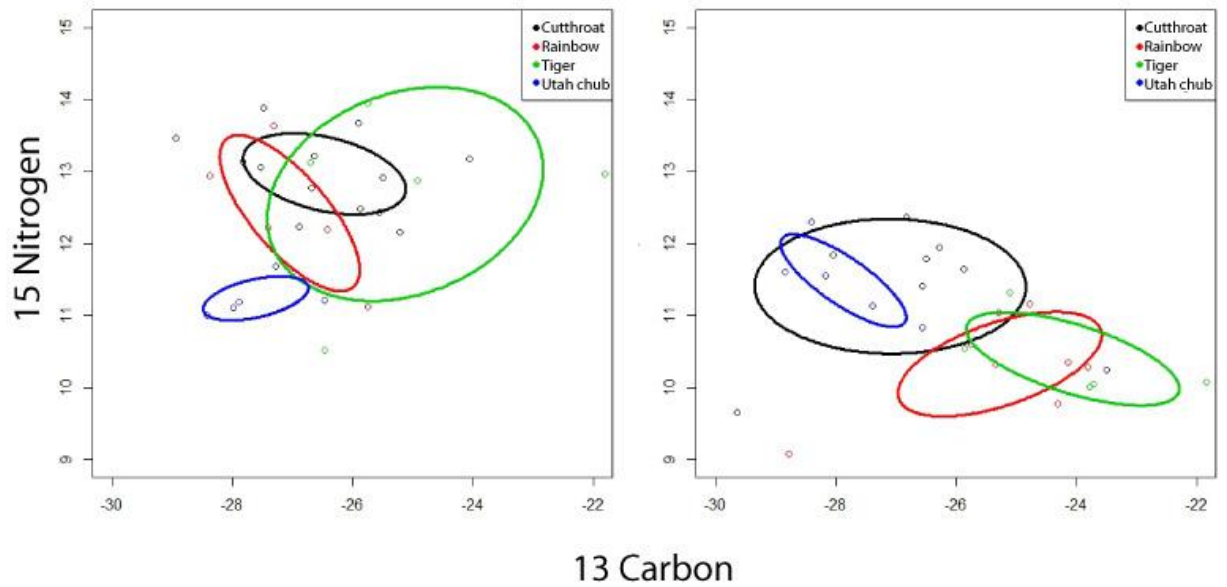


Figure 3.5. Two-dimensional isotopic ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) niche plots of (left) large (≥ 350 mm) cutthroat trout, rainbow trout, tiger trout, and Utah chub (≥ 250 mm) from Scofield Reservoir, and (right) small (< 350 mm) cutthroat trout, rainbow trout, tiger trout, and Utah chub (< 250 mm).

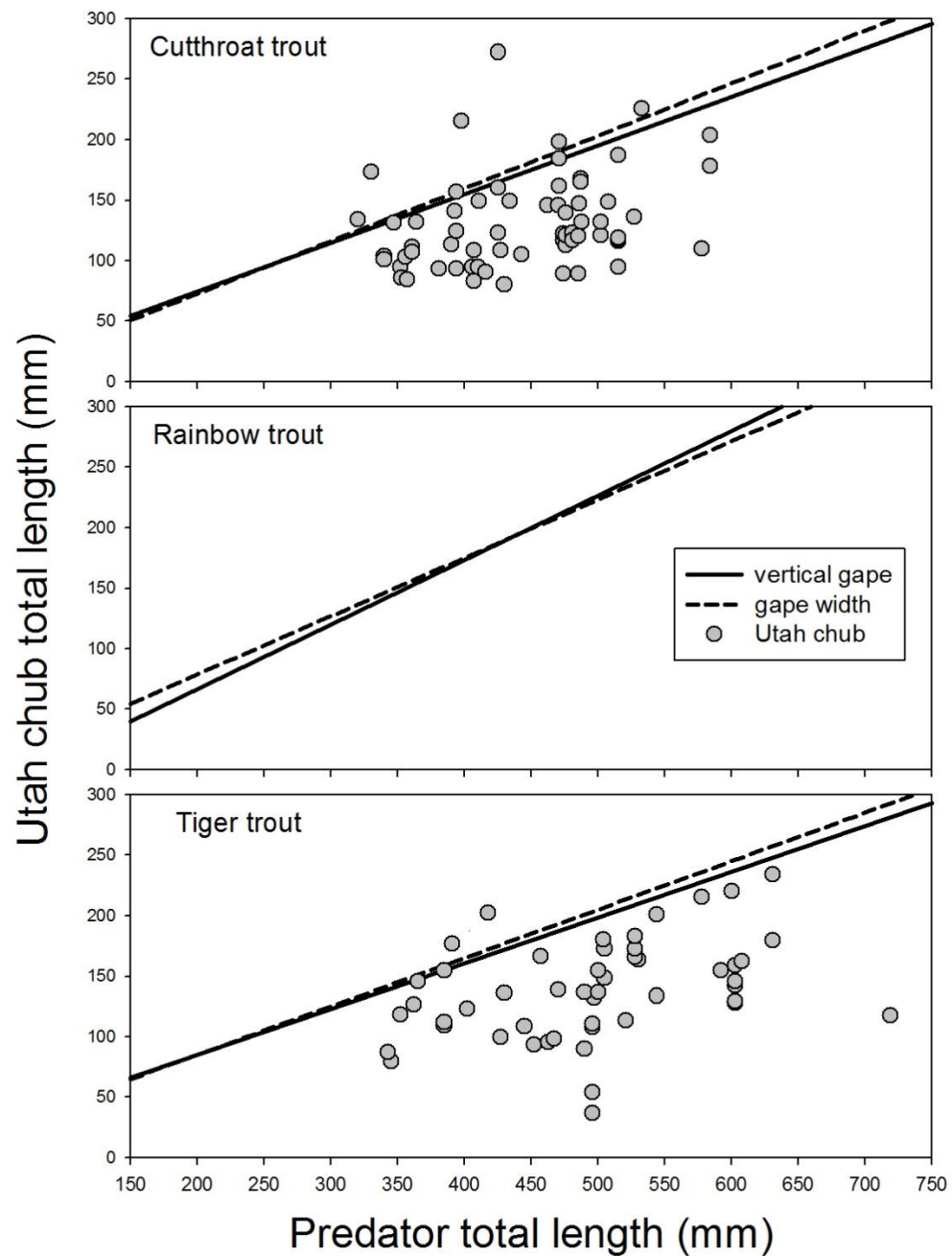


Figure 3.6. Relationship between cutthroat trout (top), rainbow trout (middle), and tiger trout (bottom) length with Utah chub length in Scofield Reservoir, Utah. Gray circles represent actual sizes of prey found in trout diets. Lines show the calculated gape limit for trout based on two gape measurements. Although rainbow trout did consume fish prey, we found no measureable fish prey in diets.

CHAPTER 4

SUMMARY

In this thesis, I presented the findings of a two year intensive survey on the Scofield Reservoir fish community. Scofield Reservoir is typical of many systems in the Intermountain West, where an unwelcome species may threaten the existence of a popular and artificial sport fishery. Therefore, Scofield Reservoir presented an opportunity to better understand how multiple top predators of a species assemblage may interact in artificial systems. My overall goal was to assess the relative performance of three popular sport fish, as well as to identify the best single, or combination of species for suppressing Utah chub abundance. Additionally, I intended to quantify the food web impacts of these introduced piscivores to reservoir fish assemblages.

To achieve those objectives, I collected fish for measurements of growth and diet using a combination of common fisheries field techniques, and assembled the information into bioenergetic simulations of predator population consumption to compare with prey abundance and production. I found cutthroat trout to be the largest consumer of Utah chub prey, and when combined with the tiger trout population, estimated these top predators consume vastly more chub than produced on a yearly basis. On the other hand, rainbow trout consume few Utah chub prey. Rainbow trout condition and bioenergetic values were not exceptionally low, however, return rates and stock density values were extremely low, suggesting poor survival.

I also employed stable isotope analysis and gut content analysis to investigate the potential interactions amongst top predators and Utah chub. Specifically, I

documented the food habits and used gut content to calculate indices of diet overlap to identify potential for competition, and used stable isotope techniques, by collecting tissue samples of fish and aquatic organisms throughout the food web, to further characterize potential predation and competition linkages of the three top predators in the system. In general, I found that large cutthroat trout and tiger trout share a top trophic position within the food web. Both species consume large amounts of prey fish after an ontogenetic switch in diet around 350 mm TL. In comparison, rainbow trout do not exhibit diet ontogeny. I calculated significant diet overlap between rainbow trout with each other focal species depending on season. Stable isotope values corroborate with these observations, showing rainbow trout may have similar isotopic niches to Utah chub and small cutthroat trout.

Consequently, rainbow trout performance may be affected by a wide range of factors. Biological factors that may influence their persistence in Scofield Reservoir may include food availability or competition between others in the fish community. The control or removal of Utah chub may highlight their strong interactions and force on the community.

Although I recognize my study is only a single version of many prevalent artificial assemblages, this work expanded on our knowledge of the use of piscivorous fish as biological control agents, and additionally is one of the first known studies of tiger trout ecology. Most importantly, this study highlighted the impacts of both intentionally and unintentionally introduced species on reservoir food webs, and will inform fisheries management.