Trophic relations and seasonal effects of predation on Pacific salmon by fluvial bull trout in a riverine food web

Erin Douglas Lowery

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

Master of Science

University of Washington

2009

Program Authorized to Offer Degree:
School of Aquatic and Fishery Sciences

University of Washington

Graduate School

This is to certify that I have examined this copy of a master's thesis by

Erin Douglas Lowery

and have found that it is complete and satisfactory in all respects, and that any and all revisions required by the final examining committee have been made.

Committee Members:

____

David A. Beauchamp

____

Timothy E. Essington

____

Edward Connor

Date:_______________

University of Washington

Abstract

Trophic relations and seasonal effects of predation on Pacific salmon by fluvial bull trout in a riverine food web

Erin Douglas Lowery

Chair of the Supervisory Committee:
Professor David A. Beauchamp
School of Aquatic and Fishery Sciences

Bull trout *Salvelinus confluentus* occupy upper trophic positions in most ecosystems where they occur. Since federal listing, natural resource managers are frequently challenged to manage bull trout and their prey which can often include federally listed Pacific salmon *Oncorhynchus* spp. The Skagit River in Northwest Washington State contains one of the largest populations of bull trout *Salvelinus confluentus* and Chinook salmon *O. tshawytscha* in the Puget Sound region, and a regionally large population of steelhead *O. mykiss*; all three species are listed as threatened under the Endangered Species Act (ESA). The objective of this investigation was to determine the trophic ecology of bull trout, especially their role as predators and consumers in the river food web. I sampled distribution, diets, and growth of bull trout in mainstem and tributary habitats during 2007 and winter and spring 2008. Consumption rates were estimated with a bioenergetics model to determine annual and seasonal energy budgets of bull trout and to estimate their potential predation impacts on juvenile Pacific salmon populations. Salmon carcasses and eggs contributed approximately 50% of the annual energy budget for large bull trout in mainstem habitats but were largely inaccessible in tributary habitats. The remaining 50% was acquired from juvenile salmon, resident fishes, and immature aquatic insects. Predation on listed Chinook salmon and steelhead/rainbow trout was highest during winter and spring (January-June). Predation on juvenile salmon differed between 2007 and 2008, and was likely due to the

dominant odd-year spawning cycle for pink salmon *O. gorbuscha*. The population impact on ocean- and stream-type Chinook salmon was negligible while the impact on steelhead/rainbow trout was potentially very high. Due to the ESA-listed status of bull trout, steelhead, and Chinook salmon, the complex trophic interactions in this drainage create both challenges and opportunities for creative adaptive management strategies.

Table of Contents

List of Figures

List of Tables

Acknowledgements

This project was fully funded by Seattle City Light and the Puget Sound Anglers Fidalgo Chapter and I thank both organizations very much.

I would like to extend a very special thank you to Matt Smith, Jamie Thompson (and his raft), Mike Mazur, Dave Pflug, Ed Connor, and Steve Stout. All of whom had a strong hand in the technical development of this project and provided invaluable logistical and scientific support. Anna Buettner, Mike Shepard, Nathanael Overman, Cathy Ekblad, and Jim Matilla gave great effort in the field or laboratory during different phases of this project, and I thank them. I would also like to acknowledge Eric Schoen, Liz Duffy, Jen McIntyre, and Verna Blackhurst in the Washington Cooperrative Fish and Wildlife Research Unit who helped out in a variety of ways, usually giving sound advice and help beyond my expertise. I especially want to extend a huge thanks to all the field volunteers they are the reason this project succeeded at all.

The staff of the State salmon hatchery in Marblemount, especially Steve Stout, provided logistical support, samples, and access to resources integral to this project. Dave Pflug gave countless hours on the City Light jet sled and many days on the river allowing for sampling opportunities beyond the constraints of the Coop Unit drift boat. Janet Aldridge and the crew of the Diablo cookhouse worked tirelessly providing housing and meals for my crew and myself allowing me to concentrate on my work, knowing that my team was taken care of.

Dave Beauchamp, my advisor, provided irreplaceable help and insight into this project. He allowed me to develop my ideas and explore investigative routes without applying too much control on this project. His approach, allowing me to make mistakes and guiding me through difficult logic, and his insight are largely reflected in this document. John Skalski provided much support and inspiration for the snorkel survey and was instrumental in its initial development and final analysis. Ed Connor, Tim Essington, and Dave Pflug provided excellent suggestions to make this paper ready for publication and their input is appreciated more than they will know.

I want to thank my family who gave encouragement, razzing, and support throughout this process. Finally, I want to thank my wife Robynn. This was a trying chapter in our lives and her understanding and support allowed this project to succeed.

Introduction

Currently bull trout *Salvelinus confluentus* is listed as "Threatened" under the United States Endangered Species Act (1973) (ESA). Some of the major factors contributing to their decline are cited as: high temperature, population fragmentation, habitat degradation, and non-native species interactions. Recent declines in other western salmonid populations have resulted in the listing of many populations under the Endangered Species Act (E.S.A). Due to the sensitive nature of these animals and ecosystems that support them it is often difficult to conduct research on listed species. Because of this restriction, ecological modeling to analyze the function of biological systems containing listed species is desirable. To facilitate analysis, healthy populations of listed species can be used for data collection to "feed" models, minimizing impacts to depressed populations.

The Skagit River in Northwest Washington State contains the largest population of Chinook salmon *Oncorhynchus. tshawytscha*, bull trout in the Puget Sound region and a regionally large population of steelhead *O. mykiss* all listed species. Furthermore the Skagit River contains the largest population of pink *O. gorbuscha* and chum *O. keta* salmon in the lower 48 states (Connor and Pflug 2004). The Skagit is also the location of a three-project hydroelectric facility owned and operated by the publicly owned utility Seattle City Light. This project is built at a historical anadromous barrier and the free flowing reach directly below the third dam, extending approximately 40 km, is the location of the largest spawning populations of these salmon in the Skagit River system (Connor and Pflug 2004). Although the bull trout are only known to spawn in tributary streams, large fluvial adults are very abundant in this reach. A population assessment of bull trout and other resident fish has not been implemented and the health of the population is based largely on the professional opinion of local biologists and managers. While there is no in stream assessment of the bull trout population, migrating bull trout captured during smolt trapping operations in the Lower Skagit, conducted by the Washington Department of Fish and Wildlife, produce estimates of 14,000 to 49,000 anadromous age-1and age-2 bull trout smolts out migrating per year. The high numbers of bull trout make the Skagit River ideal for the study of a relatively healthy bull trout population. The results of which can potentially be applied to more depressed and recovering populations of these fish.

In the study reach, altered stream flow to prevent salmon fry stranding and redd dewatering, implemented by Seattle City Light, resulted in higher local salmon production (Connor and Pflug 2004). This increased production is believed responsible for an increase in resident fish in the reach. The resulting lower winter flows and higher summer flows are believed to make prey fish in this reach less susceptible to the effects of seasonal water flow fluctuations present in the rest of the Skagit River system but also increase the presence of piscivorous fishes such as cutthroat and bull trout. Concerns of predation on juvenile Chinook and steelhead by bull trout make this river reach an excellent opportunity to study a healthy, bull trout dominated, food web. The stability and health of fish species present in the river is vitally important to researchers and managers trying to improve declining populations of these species in other regions of Western North America. All salmonid species in the Skagit River are the targets of tribal, commercial, and/or sport fisheries. In fact the Skagit River is one of very few rivers in Washington where retention of bull trout is legal in the sport fishery. With this in mind the Skagit can provide the data necessary for a comprehensive food web study, utilizing a bioenergetics model, without the concerns raised in other river systems with less robust salmonid populations. Food web analysis of the Skagit will allow researchers and managers insight into the structure and function of this socially, culturally, and economically important river system.

The aim of this project is to answer fishery resource management questions by describing the structure and function of the Skagit River food web and the role of bull trout in that food web by: (1) using diet analysis to determine size and stage specific trophic interactions between food web members; (2) use stable isotope analysis to identify energy sources and transfer within the food web; (3) collect physical data from the river; and (4) utilize these data in a bioenergetics modeling capacity.

Bull trout (*Salvelinus confluentus*) are native to Western North America and range form Northern Nevada north to Southern Northwest territories, and from the Pacific Coast to the Rocky Mountains (Cavender 1978, Haas and McPhail 1991, Reist et al. 2002) in high mountains, desert streams, and coastal drainages (Cavender 1978, Wissmar and Craig 2004, Brenkman and Corbett 2005, Mogen and Kaeding 2005). The greatest limiting factor of bull trout distribution appears to be temperature. In fact, in the most southern bull trout populations, temperature was found to be the most influential factor in predicting the presence or absence of bull trout (Dunham et al. 2003). Its wide distribution within disparate habitats is due in part to a variety of displayed life histories in bull trout. Populations are composed of fluvial, adfluvial, stream resident, and/or anadromous sub-populations (Beauchamp and Van Tassel 2001, Brenkman et al. 2001, Brenkman and Corbett 2005, and Mogen and Kaeding 2005). Although, not all observed morphological types are necessarily representative of different life histories (Bahr and Shrimpton 2004). Bull trout dietary habits range from benthivory and ovivory to piscivory with the largest individuals exhibiting an almost complete piscivorous habit (Beauchamp and Van Tassell 2001, Clarke et al. 2005). Individuals within these populations exhibit gradients within each of these life history and feeding strategies resulting in displayed life history complexity. For example some stream residents will reside for 1-5 years in streams spawning at least once then undergo an ontogenetic shift to a fluvial or adfluvial life history. In addition, anadromous individuals can remain in fresh water for 1-3 years between migrations and potentially spawn during that time prior to subsequent marine migration (Brenkman et al. 2001, Bahr and Shrimpton 2004, Brenkman and Corbett 2005, and Mogen and Kaeding 2005). Life history plasticity in fish buffers populations against environmental change (Hilborn et al. 2003). Other biological factors can result in the isolation and extirpation of fish that have plastic life history strategies (Wissmar and Craig 2004, Mogen and Kaeding 2005). This diversity in life histories creates a challenge for managers and also makes bull trout vulnerable to isolation caused by alterations to their habitat, particularly changes in temperature.

Bull trout have some of the lowest temperature tolerances of any western salmonid. They only spawn in very cold tributaries where the water temperature rarely rises above 8°C during the egg incubation period (McPhail and Baxter 1996). At temperatures above 8°C egg mortality is high and results in low egg to juvenile survivor rates. The most efficient temperature for feeding in bull trout is higher than their incubation tolerances but is still lower than most other salmonids, around 10-13°C (Selong et al. 2001). This temperature range makes bull trout vulnerable to seasonal and anthropogenic temperature changes. Within impoundments and during warmer months of the year, bull trout distributions can become restricted in response to rising temperatures (Nelson et al. 2002, Wissmar and Craig 2004). This allows other fish species to occupy the expanding warmer water habitat and utilize resources seasonally unavailable to bull trout and can result in the isolation of previously migratory populations (Nelson et al. 2002, Mogen and Kaeding 2005).

This project is part of a larger system wide research program initiated by Seattle City Light and other Government agencies responsible for management of Skagit River resources. Understanding the food web structure using a bioenergetics model necessitates the inclusion of other inputs currently being collected by other researchers. Researchers from state, federal, and tribal agencies are collaborating with Seattle City Light within the Skagit system and areas of Puget Sound where Skagit River bull trout occur. Currently a project is proposed to identify habitat use by resident fish in the Skagit River system. This will allow us to identify relative abundance of stream resident fishes in the Skagit River giving more precision to annual consumption estimates. The Washington Department of Fish and Wildlife (WDFW) is compiling data and preparing a report from a 4 yr bull trout spawning and habitat assessment study (Dave Pflug Seattle City Light personal communication). Prior to this, there was only one regularly monitored spawning reach for bull trout in the Skagit system, located on the South

Fork Sauk River. WDFW identified many additional index streams useful in enumerating bull trout spawner abundance. Furthermore, work by WDFW produced new information on spawn migration timing, and migration and habitat selection within the Skagit system.

Understanding the consumption demands of bull trout allows researchers to estimate carrying capacity and the effect of this species on the ecology of the river system and conversely how physical conditions affect the ecology of bull trout. Further research can continue this investigation to study survival by different age classes and identify population bottlenecks for bull trout. Identification of bottlenecks can direct managers when implementing enhancement programs and recovery strategies. Work on inland bull trout populations has commenced for many years and research on coastal populations is only now starting to move beyond the agency investigations necessary for management. The listing of this species as threatened under the ESA demonstrates the need for practical applications of current techniques and the development of new methods to research this species. This project will provide insight into ecosystem processes where bull trout occur. It is anticipated that investigations into the migratory habits of bull trout will continue because of its use of the near shore, and habit of migrating to other river systems (Goetz et al. 2004, Brenkman and Corbett 2005). Critical habitat for bull trout was designated in 2005 and included 2,444 km of stream, 1,585 km of marine shoreline, and 13,500 ha of lakes and reservoirs in Washington State. Implications for this designation are very complex since bull trout may utilize areas of the near shore that are necessary for the operation of the major ports of Everett, Seattle, Tacoma, Port Angeles, and Grays Harbor.

Anadromy in bull trout is little documented, currently there are only a handful of published papers and technical reports that describe the presence of bull trout in marine waters (Brenkman and Corbett 2005, Baker et al. 2003). WDFW has operated a smolt trap that catches out-migrating bull trout at the mouth of the Skagit River. The data from smolt trapping operations indicate that out migrating smolts range from 14,000 to 49,000 annually (WDFW 2004). In addition, an ongoing biotelemetry study tracking bull trout in the nearshore Puget Sound and other major Puget Sound tributaries has documented anadromy in Skagit River bull trout (Goetz et al. 2004). This project will build on these datasets by adding receivers in the river to track bull trout movement within and out of the system. Our ability to characterize residency time in the study reach will allow researchers to characterize the migratory habits of bull trout in the Skagit River. Data are down loaded from in river receivers approximately every 6 mo. Preliminary data from existing receivers suggest that the majority of anadromous bull trout in the Skagit are returning to the Sauk River rather than other known spawning areas (Connor per. Com.). WDFW and the marine biotelemetry study has a long-term data set of lengths and scales, for aging, of caught and released bull trout from the Skagit River and Puget Sound which will allow general characterization of the population as a whole.

Interactions with commercial and sport fisheries are of concern since bull trout migrate during times of fishery activity. Understanding the ecological role of bull trout in all the habitats it occupies is essential for the recovery of the species. This research can provide a template for inland populations, where temperature is considered the most important limiting factor. The current project provides a baseline for the status of bull trout in the Skagit that will allow accurate comparisons for future research. Investigations of future dam operations, the effect of drought and climate change, and other environmental changes will all be part of the recovery for this species. Additionally, it is important to recognize that most anadromous bull trout populations utilize many river systems during their migrations and are not simply associated with their natal rivers and streams. For all of the above reasons, work to classify bull trout populations and behavior will be the focus of research and continue to play a crucial role in the recovery of the species.

Trophic relations and seasonal effects of predation on Pacific salmon by fluvial bull trout in a riverine food web

Introduction

Predator-prey dynamics are important ecosystem processes. These interactions can mediate energy transfer, regulate populations, alter prey behavior, and generally delineate the structure and function of food webs (Woodward et al. 2008). The relationship between predators and prey is complex, comprising a combination of direct (consumptive) and indirect (non-consumptive) interactions and in many cases it is difficult to ascribe which process has the most influence on food web dynamics (Peckarsky et al. 2008). Indirect effects can operate in the same direction as consumptive effects by changing the demography or behavior of prey populations (He and Kitchell 1990, Lima 1998), but might be masked by the direct effect of predatory behavior.

Bull trout (*Salvelinus confluentus*), a top fish predator in many systems, are listed as threatened under the United States Endangered Species Act and are native to coldwater habitats in western North America ranging from northern Nevada to the southern Northwest territories, and from the Pacific Coast to the Rocky Mountains (Cavender 1978, Haas and McPhail 1991, Reist et al. 2002) in mountains, high desert streams, and coastal drainages (Cavender 1978, Wissmar and Craig 2004, Brenkman and Corbett 2005, Mogen and Kaeding 2005).

The Skagit River in northwest Washington State contains one of the largest populations of bull trout *Salvelinus confluentus* and Chinook salmon *Oncorhynchus tshawytscha* in the Puget Sound region and a regionally large population of steelhead *O. mykiss*; all three species are listed as threatened under the Endangered Species Act (ESA). The Skagit River also contains the largest population of pink *O. gorbuscha* and chum *O. keta* salmon in the lower 48 states (Connor and Pflug 2004). Located on the river are three dams in a hydroelectric project owned and operated by the publicly owned utility Seattle City Light. The most downstream dam was built at a historical anadromous barrier and the free flowing reach directly below the hydroelectric project, extending approximately 40 km, is the location of the largest spawning populations of these salmon species in the Skagit River system (Connor and Pflug 2004). Large fluvial adult bull trout are also very abundant in this reach supporting sport harvest regulations that allow a catch limit of two fish per day 50 cm (20 inches) or larger.

In this 40 km reach, Seattle City Light implemented altered dam operations to prevent salmon fry stranding and redd dewatering. The new dam operations resulted in higher localized production of Pacific salmon species that migrate to sea as under-yearling, or ocean-type, migrants of pink, chum, and Chinook salmon (Connor and Pflug 2004). However, species with prolonged stream residence, termed stream-type migrants, like yearling migrant Chinook or coho salmon *O. kisutch,* and two-year old migrant steelhead declined over the same period (Beamer et al. 2005b; D. Pflug Seattle City Light personal communication unpublished data). The resulting lower spring flows and higher winter and summer flows were hypothesized to reduce the susceptibility of juvenile and small-bodied fishes in this reach to the effects of seasonal water flow fluctuations, but might have also increased the abundance of piscivorous fishes such as cutthroat trout and bull trout. This decline in life history types of anadromous salmonids with prolonged stream residence was unexpected, because Pacific salmon production and escapement had been stable or increasing in this reach.

There is no comprehensive assessment of this observed change in life history expression, but local resource managers are concerned that the alteration of habitat, density dependence, and environmental conditions could limit production of the yearling life history, particularly in Chinook salmon (Beamer et al. 2005b). This evaluation did not consider the effects of biological factors such as predation by numerous potential consumers in the system including, but not limited to: belted kingfisher *Ceryle alcyon*, osprey *Pandion haliaetus*, merganser *Mergus* spp., cormorant *Phalacrocorax* spp., river otter *Lontra canadensis*, American mink

Mustela vision, cutthroat trout *O. clarki*, yearling coho salmon, steelhead/rainbow trout adults, juveniles and presmolts, and bull trout. It is difficult to determine definitively if direct or indirect predation effects are driving a change in life histories without considering the expression of these life histories under different flow regimes in the absence of predators. However, the use of diet and stable isotope analysis in conjunction with bioenergetics modeling can estimate the potential impact of predation on prey. Since bull trout are the predominant fish predator in this reach of the Skagit River it is likely that they could affect stream-type salmonids if the bull trout population was large enough and if they fed on those fish.

Research on dietary patterns for bull trout is limited, with most studies focusing on adfluvial populations. Reported diet patterns include benthivory and ovivory, but bull trout usually occupy upper trophic levels, with many individuals exhibiting almost complete piscivory in adfluvial populations (Beauchamp and Van Tassell 2001, Hagen and Taylor 2001, Clarke et al. 2005). Currently, no comprehensive analysis of bull trout feeding habits exists for a river system. Therefore, the objective of this investigation was to first determine the trophic ecology of bull trout, especially their role as predators and consumers in the river food web. To accomplish this, year-round feeding habits of bull trout were measured within the anadromous zone of the Skagit River. This analysis of fluvial bull trout trophic ecology was focused on utilization of food sources that vary seasonally and inter-annually with particular attention on identifying major seasonal energy sources and estimating the magnitude of predation on juvenile Pacific salmon.

I hypothesized that fish prey contributed a major portion of the energy budget for bull trout and that predation by bull trout could regulate stream type anadromous and resident salmonid populations in the study reach. I will describe the role of bull trout in the upper Skagit River food web using diet analysis, stable isotopes, and bioenergetics modeling to determine size and stage specific trophic interactions between food web members particularly bull trout and other salmonids.

Since energy sources in the river vary annually and inter-annually, I predict a seasonality to diet composition. Based on energy content, I expect the following key contributors to seasonal diets: salmon eggs in fall, stream type salmonids, resident fishes and presmolts in winter, migrating smolts in spring, and stream type salmonids and resident fishes in summer.

Study Area

The mainstem Skagit River was sampled from the Gorge Powerhouse to approximately 40 km downstream at the confluence of the Sauk River (Figure 1). All sampling was conducted in the Skagit River and two tributary streams, Bacon Creek and Illabot Creek, in Skagit and Whatcom Counties, in northwestern Washington State during winter, spring, summer, and fall 2007 and winter and spring of 2008. Major components of the Skagit River fish assemblage in this section of river and tributaries included: dace *Rhinichthys* spp., three-spine stickleback *Gasterosteus aculeateus*, sucker *Catostomus* spp., lamprey *Lampetra* spp., sculpin *Cottus* spp., mountain whitefish *Prosopium williamsoni*, Pacific salmon and trout: Chinook salmon, coho salmon, chum salmon, pink salmon, sockeye salmon *O. nerka*, rainbow trout and anadromous steelhead, resident and anadromous cutthroat trout, and resident, fluvial, and anadromous bull trout.

Methods

I used bioenergetics model simulations, combined with directed field data, to quantify seasonal and stage-specific consumption rates by bull trout on juvenile salmonids and other key prey species in the Skagit River main stem and tributary habitats. Field sampling provided data inputs for the model including age-specific growth, size-specific diet, spatial distribution, thermal experience, abundance, and energy density of bull trout and key prey. These bioenergetic simulations quantified the magnitude of predation on key prey species in terms of monthly or seasonal consumption, gross energy uptake, and numbers of prey consumed over a range of bull trout population levels, and estimated the importance of different prey for the seasonal, annual, and lifetime energy budget of bull trout. The annual and lifetime energy budgets of bull trout were compared with stable isotope ratios of carbon ($\delta^{13}C$) and nitrogen ($\delta^{14}N$) because both lifetime energy budgets calculated from bioenergetics modeling and stable isotope analysis produce time integrated measures of consumption (Harvey et al. 2002).

Sample Collection

I used a stratified sampling regime to examine seasonal patterns in relative abundance, size structure, and diet of bull trout in main stem, side channel, and tributary habitats. Sampling and subsequent data analyses were stratified by seasons, size classes of bull trout, and mainstem versus tributary habitats. Multi-day sampling trips were conducted every other week throughout the year from February 2007 to June 2008. Mainstem sampling was conducted from a drift boat or jet sled. Tributary streams were accessed by foot after driving to entry points and sampled seasonally within the logistical constraints imposed by snow access and avalanche danger. River and tributary habitats were sampled with traps, hook and line, short set gill nets, and electroshocking for fish, and kick nets were used for invertebrates. All predatory fishes, non-predatory fishes, prey fishes, and invertebrates that were kept for processing in the lab were placed on ice or frozen in the field. It is possible that some anadromous bull trout were included in the study but, determining which individuals were anadromous was beyond the scope of this study and all fish present in the river were considered fluvial since they were interacting in the main stem food web.

Seasons were determined by water temperature and defined temporally as fall during October – December (mean 8.1°C SD = 0.37°C), winter during January – March (mean 4.6°C SD = 1.61°C), spring during April – June (mean 7.7°C SD = 1.34°C), and summer during July – September (mean 11.7°C SD = 0.64°C). In order to understand critical trophic interactions among different ages and size classes within the food web, all fishes and important invertebrates of the aquatic food web were sampled during sampling events. Mammals and birds, while important components of the food web, were not sampled due to logistic constraints.

Bull trout of most size classes were caught during all seasons, but in different habitats (*N* = 767). Fish from the side channel habitats (*n* = 13 in 2007 and *n* = 3 in 2008) were caught in low numbers, but their diets and other biological characteristics were similar to bull trout captured in main stem habitats. Side channels and braided channels were directly connected to the main stem and represented a small proportion of the river as a whole. Due to the mobile nature of bull trout and the aforementioned similarities in diet, I combined main stem and side channel data.

Growth and Spawning Losses

Bull trout were classified into ecologically relevant size classes based on ontogenetic habitat usage patterns and fork length (FL): 30-95 mm, 96-300 mm, 301-450 mm, and >450 mm. Age 0-2 bull trout were 30-95 mm FL and occupied their natal tributaries. Fish in the 96-300 mm class were presumptive age 3 sub-adults transitioning from the tributaries to the main stem. This life stage was captured in low numbers in both the tributaries and main stem either from ineffectiveness of the gear or low abundance in the river. Fish of the 301-450 size class represented 4-5 year olds that were fully recruited to the main stem and the sport fishery. The final size class, >450mm, were primarily age 6-8 and older individuals.

Mean length at age was determined by annular checks on scales and was used to characterize annual growth (Figure 2). Scales were read by a single observer three times with at least 4 days between readings. Only scales sampled during fall and winter with consistent repeatable ages were used to characterize age (n = 212). The calculated lengths at age were converted to weight using the least squares regression of $\log_{10}$ transformed length and weight measurements derived for all bull trout captured in the study during 2006-2008 (r^2 = 0.99; FL range 34 – 687 mm; N = 853):

$$W\ (g) = 0.0000135 * FL^{2.96}$$

to estimate the average initial and final weight for each age class in September (Table 1).

Bull trout are iteroparous and can potentially spawn annually. Spawning occurred September-November in the Skagit system (Downen 2006). I assumed that both male and female bull trout matured at age 5 (Dowenen 2006). To estimate the energy loss due to spawning, the change in length-specific body mass of mature fish was compared using length-weight regressions computed separately for each month prior to and after spawning (August-November). These analyses revealed that the greatest loss occurred between September and October and the percentage loss increased with the size of the fish.

Stable Isotope Analysis

Stable isotope ratios of carbon and nitrogen in the tissues of fish and invertebrates are useful for describing trophic structure and feeding habitats of aquatic organisms (Peterson and Fry 1987). In general, $\delta^{13}C$ isotope values are similar between prey and consumer and can be used to identify the flow of energy through the ecosystem after a correction of ≈1‰ per trophic level (DeNiro and Epstein 1976; Vander Zanden and Rasmussen 2001). Stable isotopes of nitrogen concentrate in tissues and are good indicators of trophic level. Trophic levels in the ecosystem are generally indicated by an increase of approximately 3.4‰ for $\delta^{15}N$ (Minagawa and Wada 1984; Vander Zanden and Rasmussen 2001). These stable isotope ratios allow researchers to determine the trophic position and energy pathways utilized by different members of a food web (Johnson et al. 2002; Post 2002, McIntyre et al. 2006).

Stable isotopes were measured via continuous flow using a Carlo Erba 2100 elemental analyzer interfaced with a Thermo-Finnigan Deltaplus isotope ratio mass spectrometer at the Colorado Plateau Stable Isotope Laboratory at Northern Arizona University, Flagstaff. Stable isotope values, in δ notation, were reported as a ratio (*R*) of the heavy isotope to the light isotope ($^{13}C/^{12}C$ or $^{15}N/^{14}N$) normalized by internationally recognized reference standards:

$$\delta = \left[\left(R_{sample}/R_{standard} - 1\right)\right] \cdot 100$$

The reference material for carbon was Vienna Pee Dee belemnite limestone and nitrogen was atmospheric N_2.

Isotope values from identified prey items were used to calculate the percentage contribution to bull trout diets using the free IsoSource program available at: www.epa.gov/wed/pages/models/stableIsotopes/isosource/isosource.htm. Mean $\delta^{13}C$ and $\delta^{15}N$ of prey were corrected for fractionation, 3.4‰ for $\delta^{15}N$ and 1‰ for $\delta^{13}C$. Then the percentage contribution of Pacific salmon products (carcass and eggs), salmonid fry and resident fishes, and aquatic invertebrates was compared to lifetime energy budgets of bull trout >300mm calculated from bioenergetics modeling as a complimentary method of characterizing bull trout diets.

Diet Analysis

I examined the variability in diet composition of bull trout among size classes and seasons between tributary and main stem river habitats. All diets from bull trout were removed by non-lethal gastric lavage and stored frozen in individual containers. All stomach contents were blotted dry and weighed to the nearest 0.001g wet weight. Prey items were identified under a dissecting microscope. Fish prey were identified to species and standard lengths (SL, mm) were measured for relatively intact prey whenever possible. Additional prey categories included salmon eggs, salmon carcass flesh, aquatic invertebrates, terrestrial and adult aquatic invertebrates, and other miscellaneous prey. Prey items were classified into these groups based on energetic content and similarities in ecological function or the foraging modes used by bull trout to obtain them (i.e., benthic, drift, surface, and piscivory) rather than their taxonomic status. For example, the energy density of immature aquatic invertebrates was lower than for adult aquatics or terrestrial invertebrates, so the latter two were grouped for more accurate determination of energy densities. Vertebrate prey items were usually more variable in energy density, and were identified to species whenever possible. After all items in the diet were identified, the contents were preserved in a solution of 95% ethanol and archived.

I used a mean weighted proportion by weight to characterize bull trout diets:

$$\overline{W_{mi}} = \frac{\sum_{s=1}^{n} W_i \cdot m_s}{\sum_{s=1}^{n} m_s}$$

where, i is a diet category in non-empty stomach s, n is the number of non-empty stomachs, m is the mass of all food in stomach s, and W_i (Chipps and Garvey 2007) is defined as:

$$W_i = \frac{M_i}{\sum_{i=1}^{Q} M_i}$$

where, Q is the number of diet categories, and M_i is the weight (g wet mass) of prey type i.

W_i is an estimate of average diet proportions by weight when all gut contents are pooled within each combination of time, consumer size, and habitat strata. The $\overline{W_{mi}}$ index produces the same diet proportions as W_i but allows for statistical analyses of the resulting proportions such as calculating variance. For a discussion of alternate methods for calculating diet proportions see Appendix.

Population and Size Structure Assessment

I used a strip-transect method to estimate the standing stock of predatory bull trout (>300 mm) in the main stem Skagit River by combining visual counts from geo-referenced snorkeling surveys, aerial photos, and geographic information system (GIS) software (ESRI ArcView 9.2 2006). Most previous snorkel surveys for bull trout focus on fish <300mm in low order streams (Thurow and Schill 1996) which do not target or detect bull trout >300mm, but similar surveys for salmonids in moderate sized rivers have been successful in detecting and enumerating fish >300mm in Finland (Orell and Erikinaro 2007) and New Zealand (Young and Hayes 2001). A simple random sampling regime utilizing strip transects was used for the survey. Starting points for transects were chosen by projecting random points on an image of the river using GIS software. Points in areas that were logistically difficult to reach or that compromised snorkler safety were not used in the survey, and adjacent starting points were substituted. Fish counts were performed along 5-m wide transects of variable lengths by a snorkler passively transported by the river current. All bull trout >300mm within each transect were counted. Lateral visibility of approximately 6 m was estimated by using a flat, oblong, black plastic plate held below the surface of the water. The starting and ending points of each transect were recorded in a handheld global positioning system (GPS) unit. Starting and ending points of each transect were projected on an image of the Skagit River in GIS software and traced to determine transect length. The total wetted area of the river (m^2) and the area of each transect was determined using GIS software.

To estimate the number of bull trout in the study reach I used a ratio estimator (eq. 6.1 in Cochran 1977):

$$\hat{N} = \frac{A}{w}\left(\frac{\sum_{j=1}^{n} f_j}{\sum_{j=1}^{n} l_j}\right)$$

Where: $\hat{N}$ is the estimated number of bull trout in the population, *A* is the total area of the river in the survey, *w* is the constant width of the transect, *j* is the *jth* transect, f_j is the number of fish counted in the j_{th} transect, and l_j is the length of the *jth* transect.

Variance of the population total is estimated using (eq 2.46 in Cochran 1977):

$$Var\left(\hat{N}\right) = \left(\frac{A}{w}\right)^2 \left[\frac{(1-F)^2}{n\,(\bar{l})^2}\,\frac{\sum_{j=1}^{n}\left(f_j - \hat{R}\, l_j\right)^2}{(n-1)}\right]$$

Where $\bar{l}$ is the mean transect length, *F* is the fraction of the total area sampled in this survey and is defined as:

$$F = \frac{w\sum l_j}{A}$$

and $\hat{R}$ is the ratio estimator:

$$\left(\frac{\sum_{j=1}^{n} f_j}{\sum_{j=1}^{n} l_j}\right)$$

Since the size structure of the population was unknown I used assumed survival rates of 10% for ages 0-3 bull trout in tributaries (Al-Chokhachy and Budy 2008) and 47-50% (Beauchamp and Van Tassell 2001) in the main stem to estimate size structure. I also used information on the total catch of 650 bull trout > 300 mm FL and oldest age of bull trout (age 9) encountered while sampling the main stem during 2006-2008 to evaluate whether the assumed 50% survival rates were reasonable for the age 4 and older bull trout in the main stem of the Skagit River. Assuming constant annual survival rates among age 4 and older and a stable age distribution, I iteratively fit different survival rates and initial abundances for age-4 bull trout recruiting to the main stem to determine the survival rates wherein in bull trout ≥10 years old would fall below detection in a sample of 650 bull trout ≥ 4 years old. Since the resulting survival curve is asymptotic, an arbitrary threshold value of ≤ 10 out of a sample of 650 fish, or ≤ 1.5%, was considered below detection limits. The range of survival rates that satisfied the criteria above while maintaining younger age classes above the detection limit was 50-57% with age-10 representing less than 1% of the population at an annual survival rate of 50%. Annual mortality rates were converted into daily instantaneous mortality by dividing the natural log of annual survival by 365 days. The resulting population estimate of bull trout >300mm was distributed within fish age 4-9 such that the sum of individual fish from age 4-9 structured by a 50% mortality rate equaled the estimated population total from the snorkel survey. To structure fish age 1-3 I assumed a 10% survival rate back calculated from the estimated number of age 4 fish.

Bioenergetics Modeling

Bull trout consumption was estimated using the Wisconsin bioenergetics model (Hansen et al. 1997). The most common application of the model estimates consumption by an average representative from each age class based on growth achieved over some specified time interval (e.g., season or year). I used the model to estimate daily consumption by the average individual for each age/size class of bull trout, based on annual growth increments, monthly changes in size specific diet composition, and daily changes in the thermal experience. Predation (consumption) estimates were extrapolated to a unit population of 1,000 individuals that reflected the assumed size structure of the population (i.e., size-structured predation rate per 1000 bull trout FL > 300 mm) so that estimates of predation per unit population could inform management decisions without relying on estimates of absolute population abundance (Beauchamp et al. 2007). If consumer abundance can be estimated, then absolute population-level predation rates can be easily computed. In that way managers and researchers can use the outputs of the model to understand how the ecosystem functions with or without knowing the exact size of the population (Hanson et al. 1997).

A parameter set for bull trout was not available in the Wisconsin model, and past applications of the model to adfluvial bull trout in a reservoir used the lake trout (*S. namaycush*) model (Stewart et al. 1983) due to the ecological and taxonomic similarities between the two species (Beauchamp and Van Tassell 2001). Ideally species specific parameters would be used to increase the precision of the model estimates (Ney 1993).

This study utilized a parameter set for brook trout *Salvelinus fontinalis* (Table 2), based on taxonomic, behavioral, and habitat similarities to fluvial bull trout, developed by Hartman and Cox (2008) for all parameters except for the temperature dependent consumption function (Thornton and Lessem 1978, Equation 3 Hansen et al. 1997) which was generated using published data specific to bull trout (Selong et al. 2001).

Temperatures used in model simulations were the mean daily temperatures from USGS Gauge #12181000 in Marblemount, WA. This gauge is near the center of the study reach and likely represents the thermal experience of most fluvial fish (Table 3).

Annual simulations were performed on nine age cohorts for 2007 starting on September 1 (simulation day 1) and ended on August 31 (simulation day 365). For winter and spring 2008 simulations ran from January 1 (simulation day 1) to

June 30 (simulation day 181). Growth for 2008 was estimated by using the outputs of bioenergetics simulations from winter and spring 2007. Mean length at age for age 4 and 5 bull trout in winter 2007 and 2008, and age 4, 5, and 6 in spring of 2007 and 2008 showed no statistical difference; Winter: age 4 ($t = 1.13$, $p = 0.27$), age 5 ($t = -0.22$, $p = 0.81$), and spring age 4 ($t = -1.63$, $p = 0.12$), age 5 ($t = -1.67$, $p = 0.09$), and age 6 ($t = 0.61$, $p = 0.54$). This allowed me to use the modeled growth trajectories from 2007 to estimate growth for 2008.

Diet inputs to the model varied between tributary and mainstem habitats and among size classes and seasons (Table 4). Diets for age 3 sub-adults that were transitioning from tributary to main stem habitats were partitioned at the midpoint of the simulation to reflect a shift from tributary to main stem habitats on April 1 (simulation days 184 in 2007 and 92 in 2008) to correspond with the increased catch of this cohort in the mainstem observed during that season. Since diet data can vary considerably due to low sample sizes and random error, I calculated seasonal standard error estimates for important diet items found in bull trout >300mm stomachs. I focused on prey of conservation or fishery concern like Chinook salmon, steelhead/rainbow trout, and coho salmon, plus other major energy contributors like eggs, salmon carcass flesh, and resident fishes, to provide bounds on consumption estimates for predatory bull trout in all seasons.

The energy densities (J/g wet weight) of bull trout and prey used as inputs for the bioenergetics model were either measured directly or obtained from values in the literature (Table 5). Seasonal values were measured whenever possible. Samples of bull trout (450-530mm and 465-2600g), prey fishes (35-260mm and 0.3-66g), and invertebrates were weighed, dried, reweighed, ground, homogenized, and pressed into pellets (0.0048-0.2236g). The pellets were burned in pure O_2 in a Parr semi-micro bomb calorimeter, and the energy density per unit dry mass was recorded. Energy per unit wet mass was calculated by using the ratio of wet to dry mass for each sample.

Energy budgets were calculated over various time scales to determine the energetic importance of different food sources for bull trout during different life stages, seasons, and throughout a life cycle completed within the study reach. The estimated biomass of each prey consumed during each season and life stage in the model simulations was multiplied by the corresponding energy density of prey to calculate the total energy contributed by each prey during the different seasons and life stages for bull trout.

Predation Impact Scenarios

To better inform natural resource management, the estimated predation rates were placed in a population level context. The above total predation rates were calculated for a population level of 1,600 bull trout based on expanding the unit population-level predation by a size-structured population of 1,000 bull trout >300mm. Since the total basin-wide population level was unknown it was useful to consider predation rates on key species by different population sizes of bull trout. Proportions of the total age-0 and age-1 steelhead, age-0 and age-1 Chinook, and coho salmon populations consumed by bull trout were calculated by combining the total estimated smolt production and the estimated predation by bull trout. For 0+ Chinook and 1+ coho salmon I used the mean out-migration reported in Kinsel et al (2007). For age-1 Chinook salmon I used the estimated out-migration from the study reach reported in Beamer et al (2005a).

The relative abundance of resident rainbow trout and steelhead fry in the mainstem and tributaries in the anadromous zone is unknown and difficult to measure therefore steelhead predation effects assumed that all *O. mykiss* detected in bull trout guts were steelhead. This provides a measure of maximum population level effect from predation mortality. To estimate the total number of steelhead present in the study reach I first assumed that eggs were fertilized on 15 May, with emergence 8 weeks later (Pauly et al. 1986), out-migration takes place on 15 May after 2+ full years in freshwater (34 months) based on smolt trap catches (Kinsel et al 2007). I took the mean annual redd count of 148 (Ed Connor and Dave Pflug Seattle City Light Personal Communication unpublished data), and (assuming a sex ratio of 1:1 for the Skagit River Brett Barkhdul WDFW personal communication) multiplied each redd by the estimated female fecundity 4,923 (Quinn 2005), this results in 727,784 eggs deposited annually. I then took the estimated egg to fry survival rate, 0.293, and fry to smolt survival, 0.135, (Quinn 2005) to estimate the total number of age-0 fry, 213, 241, and age-2 smolts, 28,787, produced during that time. To estimate the number of age-1 parr I took an instantaneous monthly mortality rate based on an assumed stream residency of 34 months resulting in an estimated 99,163 1+ steelhead/rainbow trout available for consumption.

I used bull trout populations ranging from 1,000 to 30,000 for the scenarios to encompass the breadth of possible population sizes present in the river. Smolt production was reported at a downstream smolt trap; therefore, the smolts had been subjected to additional sources of mortality beyond bull trout predation in the study reach. This method produces estimates of predation by bull trout only, and fails to incorporate other sources of natural mortality incurred during out-migration.

Results

Stable Isotope Analysis

Isotopic signals for both $\delta^{15}N$ and $\delta^{13}C$ in the main stem river became increasingly enriched from aquatic invertebrates to large bull trout (Figure 3). The $\delta^{15}N$ values in the main stem ranged from 4.0‰ for aquatic invertebrates to 15.3‰ for bull trout >300 mm representing three trophic levels at an assumed fractionation rate of 3.4‰ per trophic level. Salmon carcasses and adult steelhead showed $\delta^{15}N$ values of 13.3‰, 2‰ lower than bull trout. Juvenile steelhead/rainbow trout, cutthroat trout, whitefish, and sculpin spp. were positioned about 1.5 trophic levels below large bull trout with $\delta^{15}N$ averaging 10.1‰. Age-0 Chinook salmon occupied the next trophic level with an average $\delta^{15}N$ of 7.6‰, aquatic invertebrates were below juvenile salmon at 4.5‰ and at nearly the same level as two different samples of periphyton, with lamprey ammocetes occupying the lowest trophic level at 1.3‰.

General trends in main stem $\delta^{13}C$ values showed aquatic invertebrates as the most depleted ($\delta^{13}C$ = -28.7) and salmon carcasses as the most enriched ($\delta^{13}C$ = -17.2). The mean value for large bull trout was $\delta^{13}C$ = -18.2 placing them closest to, but 1.0‰ lower than salmon carcasses. All other potential aquatic prey showed considerably more depleted $\delta^{13}C$ values than large bull trout with mountain whitefish ($\delta^{13}C$ = -19.91) and juvenile steelhead/rainbow trout ($\delta^{13}C$ = -19.47) offering the next closest values.

These results suggest that bull trout occupy the uppermost trophic level in the mainstem, primarily utilizing marine derived food sources. Stable isotope values for $\delta^{15}N$ and $\delta^{13}C$ generally became more enriched with an increase in bull trout length suggesting an ontogenetic shift in diet and habitat at approximately 300mm (FL) **(**Figure 4**)**. The foraging pattern suggested in the stable isotope values was also observed in the diet data.

Diet

Of the 767 bull trout sampled in mainstem and tributary habitats, 32% of the stomachs were empty, resulting in *N* = 525 non empty stomachs that were available for diet composition determination. High catch rates of larger predatory bull trout (FL > 300mm; *N* = 672) with 66% non-empty stomachs allowed comprehensive characterization of their diets. The percentage of non-empty stomachs was generally higher for smaller size classes (FL ≤ 300 mm) in tributaries (85% non-empty) than for larger fluvial fish (68%) in the main stem.

Diets varied by size class, season, and year depending on available prey. In 2007, the 30-95 mm size class in the tributaries contained mostly aquatic insects during all seasons. Bull trout became piscivorous at approximately 100 mm FL (Figure 5) with bull trout primarily consuming prey fish with SL < 30% of their FL (Figure 6**)**. Diets from the 96-300 mm size class in the tributaries contained primarily age-0 rainbow trout/steelhead (SL = 26-47 mm) and some aquatic insects in autumn, then primarily coho salmon (FL = 40-46 mm) and some aquatic insects during the other seasons (Table 4**)**. In main stem habitats, diets of the smallest fluvial size class (301-450 mm FL) contained predominantly salmon eggs during autumn, salmon carcass flesh and fry during winter, salmon and rainbow trout/steelhead fry in spring, and resident fishes (almost exclusively sculpin spp.) during summer. The largest bull trout >450 mm also consumed primarily salmon eggs during autumn, salmon carcass flesh and eggs, resident fish (sculpin spp.), and smaller proportions of juvenile bull trout, juvenile salmon, and steelhead/rainbow trout during winter, salmon and steelhead/rainbow trout fry and resident fishes (mountain whitefish, sculpin spp., and dace spp.) during spring, and primarily resident fishes (dace spp. and sculpin spp.), invertebrates, and salmon eggs, followed by smaller proportions of juvenile coho salmon (FL ≈ 70mm) and steelhead/rainbow trout (FL ≈ 60mm) during summer (Tables 4 and 6). Despite an estimated 300,000 pink salmon spawning in the fall of 2007, no pink salmon eggs were detected in the stomach samples of bull trout.

During 2008 (Table 4), bull trout from the 30-95 mm size class were not collected in tributaries during winter, but contained mostly aquatic insects during spring. Diets from the 96-300 mm size class in tributaries contained primarily salmon eggs during winter and juvenile coho salmon (FL = 45 mm) with some aquatic insects during spring**.** In the main stem, diets of the smallest fluvial size class, 301-450 mm contained predominantly salmon carcass flesh, aquatic invertebrates, unidentified salmon fry, and Chinook salmon fry during winter. During spring, the diets shifted to immature aquatic insects, unidentified salmon fry, and pink salmon fry. The largest bull trout >450 mm also consumed primarily salmon carcass flesh, Chinook salmon fry, and fish eggs during winter, and immature aquatic insects, pink salmon fry, and resident fishes (mountain whitefish, and dace spp.) during spring.

Energy Density

Energy densities of all fish and invertebrates in tributaries and the main stem varied seasonally (Table 5). The energy density for bull trout was highest during summer and fall and lowest in winter and spring. The mean annual energy density for bull trout was 6570 J/g which was 2000 J/g higher than the average for fish prey (mean 4513 J/g). Salmon eggs were the only diet items consistently higher than bull trout with an energy density of 12,000 J/g.

Population Survey and Size Structure

Counts were performed on February 9, 10, and 23 and March 15-17, and 26-28 2008 resulting in 9 snorkeling days. A total of 178 bull trout were observed in 155 5-m wide transects covering 65,134 linear meters (mean (SD) = 420 m (SD m) long transects), which represented sampling coverage of 11% of the total 2,931,863 m^2 wetted channel of the river from Newhalem, WA to Rockport, WA. The survey estimated 1,602 bull trout >300 mm with 13% CV and 95% confidence interval of 1,191-2,014.

Other fish observed but not quantified were; sucker spp. (>400 mm), adult and jack coho salmon (>300 mm), adult steelhead (>500 mm), sub-yearling Chinook salmon (≈45 mm), sub-yearling steelhead/rainbow trout (≈50 mm), large mountain whitefish (>400 mm), and small mountain whitefish (<300 mm). No resident rainbow trout or cutthroat trout were seen during the nine snorkeling days.

The estimated size structure of the population was based on the snorkel survey estimates where 1,602 (1,600 for simplicity) bull trout ≥300mm were distributed among age 4-9. Individuals <300mm were distributed among age 1-3 resulting in a total of 179,265 age 1-3 bull trout in tributary habitats (Table 7).

Modeling Consumption

The age 3 (96-300mm) transitional size class was caught in low numbers and an accurate growth rate was not measurable, therefore estimated growth and consumption for this size class should be considered a maximum estimate. More accurate growth and diet data are needed to increase the precision of consumption estimates for this age/size class.

The use of a model not fully parameterized or corroborated for bull trout did not allow me to fully interpret the resulting p-values from model simulations.

Nonetheless the estimated p-values suggest that the model simulations resulted in reasonable feeding rates well within the expected range for this type of population. Model simulations for 2007 indicated that juvenile bull trout in tributary habitats were feeding at 28-35% of their theoretical C_{max} with growth efficiencies (GE) of 7-10% (Table 1). The age-3 bull trout transitioning from tributary to main stem habitats exhibited a high feeding rate at 54% of C_{max} and GE of 24%. Sub-adults and adult bull trout in the main stem fed at 20-25% of C_{max}. Growth efficiencies for the sub-adults and first time spawners (age 5) were 13-15%, whereas GE for the larger mature fish ranged 3%-11% (Table 1).

During winter and spring 2008, juvenile bull trout in the tributaries were feeding at 28%-35% C_{max} with GE = 13%-18%. The transitionary age-3 bull trout fed at 28% C_{max} with GE = 43%, while the sub-adult and adult fish fed at 16%-22% C_{max} with GE of 5%-14% for the two seasons (Table 1).

Simulations for 2007 predicted that a unit population of 1,000 bull trout >300 mm consumed 1,739 kg of food annually, including 976 kg of fish (Figure 7). The top five contributors to annual bull trout diets were: 451kg of resident fishes (primarily sculpin spp. and dace spp.), 440 kg of fish eggs (primarily Pacific salmon), 327 kg of steelhead/rainbow trout, 144 kg of Pacific salmon carcass, and 93 kg of aquatic insects (Figure 7). In winter and spring, 1,000 bull trout consumed 735 kg of food, 531 kg of which were fish. Major contributors to the diets of bull trout were 268 kg of steelhead/rainbow trout, 144 kg of salmon carcass, 70 kg of resident fishes, 65 kg of coho salmon, and 48 kg of Chinook salmon fry and parr. During winter and spring 2008, the simulations predicted that 1,000 bull trout consumed 640 kg of food of which 407 kg were fish. Top contributors to the diets were 140 kg of steelhead/rainbow trout, 91 kg of resident fishes, 77 kg of pink salmon fry, 69 kg of aquatic insects, and 63 kg of other food, but only 5 kg of Chinook salmon fry and parr were consumed (**Figure 7**).

Variability in Consumption Estimates

The variation in diet proportions for key prey and energy contributors was calculated and presented as the proportion of the $\overline{W_{mi}}$ estimate using the following formula:

$$\frac{\overline{W}_{mi} \pm SE}{\overline{W_{mi}}}$$

where: $\overline{W_{mi}}$ is defined above and *SE* is the standard error of the weighted average proportion. This gave me a measure of the sensitivity for the predation estimates. For example, in spring 2007 the >450 mm size class ate both coho salmon and steelhead/rainbow trout (Table 8). The estimated range of coho salmon biomass consumed by bull trout (0kg-1,286kg) included zero suggesting that the vulnerability of coho salmon was low. Compare this to the estimated range in steelhead/rainbow trout biomass consumed during that same season (468kg-3,146kg) which did not contain zero suggesting an elevated vulnerability for steelhead/rainbow trout during that season. That, and the considerably lower overall range in consumption estimates for coho vs. steelhead is suggestive of higher vulnerability by steelhead.

In general the diet data were highly variable within size-class and seasonal strata, with the major contributors to the diets of bull trout >300 mm being the least variable. Those items on a seasonal basis for 2007 were: eggs in fall, resident fish and salmon carcass in winter, steelhead/rainbow trout, Chinook salmon, and resident fishes in spring, and resident fishes and carcass in summer. In 2008 resident fishes, fish eggs, and carcass were less variable in winter and steelhead/rainbow trout and coho in spring (Table 8).

Estimated Energy Budgets

The contributions of various prey to the annual energy budget of bull trout varied by size class (Figure 8). Aquatic invertebrates represented 95-96% of the estimated energy budget for ages 1-2 in tributary habitats. The energy budget for age 3 bull trout was more varied with aquatic invertebrates contributing 34%, terrestrial invertebrates 29%, and resident fishes 18% (unidentified non-salmonid fishes). Age 4 and older fish were supported mostly by eggs (38-43%), resident fishes (20-27%; primarily sculpin and dace spp., and mountain whitefish), and steelhead/rainbow trout (15-18%), with lower contributions from juvenile salmon and salmon carcasses. The total seasonal energy budget was similar for fish <300mm in tributaries, but varied from that of fish >300 mm in the mainstem. Model simulations indicated that the majority of energy intake occurred during fall and summer, due largely to the energetic contribution of salmon eggs. This differed from the seasonal pattern for consumption (Figure 7) wherein total consumption for all size classes was heaviest during summer followed by spring. The proportion of annual consumption in fall always ranked 3rd after summer and spring while the majority of energy intake always occurred during fall in fish >300mm. Consumption and energy intake during winter consistently ranked last for all size classes.

Predation Estimates

Total predation by an estimated 1,600 bull trout >300mm on key salmonids ranged seasonally in the Skagit River with the majority of predation occurring in the main stem in the winter during fry emergence and in the spring during smolt out-migration. Total estimated predation by bull trout on stream-type (yearling) Chinook salmon was 876 in 2007 with none detected during winter-spring 2008. Yearling steelhead/rainbow trout were consumed in higher numbers, 42,022 throughout 2007 and 30,058 during winter-spring 2008, than yearling Chinook salmon. Predation on age-0 Chinook salmon was estimated at 68,325 in 2007 and 22,786 during 2008. Predation on age-0 steelhead/rainbow trout saw a loss of 14,426 in 2007 and 905 during winter-spring 2008. Coho predation was estimated at 20,515 yearlings and no sub-yearlings in 2007 compared to 295,206 sub-yearlings and no yearlings consumed in during winter-spring 2008. Chum salmon were consumed in high numbers with 249,772 consumed in 2007 and none detected in 2008, but chum salmon were difficult to distinguish when heavily digested in stomach samples, so I assumed pink and chum fry both contributed to bull trout diets and therefore unidentified pacific salmon fry should include chum salmon. Pink salmon experienced high predation rates in 2008 with a loss of 937,549 individuals. Unidentified Pacific salmon fry, parr, and alevin showed the highest number of individuals consumed, 451,340, in 2007 and 735,747, in 2008 **(**Table 9**)**.

Predation Impact Scenarios

The percentage of the yearling Chinook salmon population consumed in the study reach in 2007 ranged from 3-19%, based on an average of 29,129 yearling smolts produced in the study reach annually (Beamer et al. 2005b), indicating a possible negative effect at higher bull trout population levels but a negligible effect at current levels. Predation on ocean-type Chinook salmon ranged from 2%-11% in 2007 and 1%-4% in 2008, from a mean annual production of 3.3 million (Kinsel et al. 2007), suggesting a minor effect on the ocean-type life history (Table 10).

In 2007 bull trout consumed an estimated 18%-87% of age-0 fry and 31%-74% of the age-1 steelhead parr population. In 2008 only 0%-3% of the age-0 fry were consumed while an estimated 24%-67% of the age-1 population was consumed. This suggests a highly negative effect on steelhead yearlings during both years (Table 10).

Discussion

Fluvial bull trout were apex predators in the Skagit River and exploited seasonally-available food resources. Bull trout became piscivorous in tributaries after age 2 and initially consumed coho salmon or steelhead/rainbow trout fry. After shifting to main stem habitats, age 4 and older bull trout benefited from large contributions of salmon eggs and carcasses to their annual energy budgets.

Although bull trout >300mm utilize these transient energy sources, juvenile salmonids, resident fishes, and immature aquatic insects were also seasonally important contributors to annual energy budgets. Steelhead fry and parr were present in the river year-round and very vulnerable to bull trout predation. Only the age-0 and age-1 steelhead were detected in bull trout diets and the resulting model simulations predict a highly negative effect on the pre-smolt steelhead population in the study reach. The short term population level effects of predation on steelhead appear to be manifested in the low returns of steelhead adults returning to this section of the Skagit River. The impact of bull trout predation on the Chinook salmon population was estimated to be relatively low during the course of this study despite the fact that stream-type Chinook salmon are present year round. The impact on the ocean-type fry was also predicted to be low at the current bull trout population size. This result gives support to the life-history shifts assumed to be occurring in the Skagit River Pacific salmon populations.

Scheuerell et al. (2007) described similar feeding behaviors in resident rainbow trout and Arctic grayling (*Thymallus arcticus*) in a southwest Alaskan stream. Bioenergetics models predicted an increase in ration size and energy ingestion for both species during Pacific salmon spawning with rainbow trout utilizing direct energetic contributions from Pacific salmon and grayling capitalizing primarily on benthic insects dislodged by the action of redd construction by Pacific salmon (Scheuerell et al. 2007).

Predation on juvenile salmonids was detected in the Skagit River primarily in winter and spring (January-June) indicating a potential predation bottleneck for migrating smolts. Analysis of prey lengths found in bull trout diets indicated that age-0 and age-1 fry were more vulnerable to bull trout predation than larger salmonid parr and age-2 smolts. Duffy and Beauchamp (2008) found that salmonid smolts were important prey for sea-run coastal cutthroat trout in near-shore marine waters of Puget Sound during spring (April-June), but that this predation was a minor source of mortality for juvenile salmon due to the high numbers of salmon smolts in Puget Sound and the narrow time window that salmonid predation was detected. This study expands the scope of juvenile predation mortality to include in-river predation patterns on the earliest life stages which may help direct adaptive management approaches in the future.

Past population level effects of bull trout predation are difficult to evaluate with this study, but the current level of predation detected on juvenile steelhead/rainbow trout during spring and summer suggests that some main stem rearing salmonids are vulnerable to high levels of predation that were capable of regulating smolt production. It is important to note that mountain whitefish, typically an important and abundant prey species for fluvial bull trout, were rarely encountered during sampling and were found in low numbers in bull trout stomachs most seasons and very few were seen during snorkeling surveys. Anecdotal reports from longtime anglers and biologists with extensive experience on the Skagit River also reported alarmingly low levels of mountain whitefish and fluvial rainbow trout compared to years in the recent past and extending back to at least 30 years. On the other hand, cryptic species such as sculpin spp. and dace spp. were consumed in large numbers by bull trout. This may be indicative of a population decline in mountain whitefish. If that was indeed the case, a generalist visual predator such as bull trout would likely switch to the next most abundant and visible prey, salmonids, in addition to the cryptic species. The currently low abundance of mountain whitefish in the main stem Skagit River could have shifted more predation onto juvenile steelhead/rainbow trout, and other salmonids utilizing open water habitats.

The high predation mortality estimated for steelhead/rainbow trout, combined with the current low abundance of fluvial rainbow trout in the main stem, suggests that future investigations should focus on juvenile steelhead life-history and increasing the capability to discriminate between resident rainbow trout and steelhead juveniles. A focus on the tributary habitats to determine the size structure and behavior of resident rainbow trout populations and tributary spawning steelhead would also be prudent. Shifts in migratory behavior due to predation are not uncommon and the trade off between freshwater mortality and marine growth is often cited as a key factor influencing ocean migration in anadromous salmonids (Quinn 2005). Gross et al. (1988) suggested that the productivity of marine and freshwaters could be a driving factor in the evolution of anadromous life histories in salmonid populations, where we should see the marine environment favored over freshwater environments in the temperate latitudes. McDowell (1997) also concluded that the anadromous life history in salmonids was a likely mechanism for increased growth and fecundity but disagreed that ocean productivity was a causal factor in the evolution and phenotypic expression of anadromy although it may be a factor on shorter time scales. Indeed residualization of many Pacific salmon and steelhead/rainbow trout occurs in lakes throughout their native and introduced range (Quinn 2005). Rather, McDowell (1997, 2008a,b) suggested that a hypothesis for the evolution of anadromy was primarily a dispersal mechanism that allowed fishes expressing that life history trait to follow the retreat of glaciers. This permitted anadromous fishes to remain in thermally favorable environments in higher latitudes where egg incubation and juvenile rearing was not negatively affected by gradual lower latitude warming. Since steelhead/rainbow trout are not obligatory adfluvial or anadromous migrants like Pacific salmon they could potentially cease anadromous migrations to reduce in-river predation mortality in exchange for reduced growth and fecundity in tributary streams. The mainstem bull trout population is large and current reductions in the mountain whitefish population could cause predation-mediated selection for a non-migratory life history strategy in steelhead/rainbow trout resulting in a decline in steelhead with a higher population of rainbow trout in tributary streams. Alternatively the low number of age-2 steelhead smolts that do migrate may suffer from increased ocean mortality due to their low relative abundance. The low abundance of steelhead in the Skagit River may be a result of other factors such as poor ocean conditions, degraded habitat, and hatchery fish interactions reflecting the declining regional trend in steelhead productivity (Federal Register 2007). Predators altering the behavior, distribution, and demography of prey populations are well documented (He and Kitchell 1990; Biro et al. 2003a,b; Biro et al. 2005; Peckarsky et al. 2008) and often the distribution of prey is influenced by the behavior of predators and foraging opportunities (Werner and Gilliam 1984; Werner and Hall 1988; Lima 1998) reflecting the mortality/growth tradeoff in fresh/marine water hypothesized for salmonids (Quinn 2005).

Chinook salmon may also be favoring one migratory strategy over the more diverse array of historically expressed life histories in the Skagit River. Unlike steelhead/rainbow trout, Chinook salmon are obligate ocean migrants. High levels of in-river predation mortality could select for an earlier seaward migration resulting in the demographic shift to ocean type Chinook salmon observed in annual smolt migrations. Other important factors influencing smoltification could be the effect of thermal regulation through dam operations in the river and food availability. Zydlewski et al. (2005) found cumulative thermal experience rather than a temperature threshold to be the key factor determining the initiation and cessation of smolt out-migrations in Atlantic salmon. This suggests that the relatively constant annual thermal regime in the mainstem verses that of the more variable tributary streams could be a selective force on some mainstem salmonids. Additionally, Beamer et al. (2005b) determined that density dependence was driving the size of the stream type Chinook population suggesting that the growth potential of stream type salmonids in the mainstem Skagit River could be too low to support that life history type, thus favoring the ocean type life history.

For many species, growth is a common measure of success (Kennedy et al. 2008). For Pacific salmon the ability to out grow predators and achieve a certain size by a certain time, critical size/period, is often cited as a measure of individual success (Beamish and Mahnken 2001; Cross et al. 2008). On a population level the presence of a predator can determine the size of feeding aggregations and the success of individuals in those aggregations (Cardinale et al. 2006). As success declines, a tradeoff of migrating to achieve higher growth can occur regardless of predation risk (Lewis 2001). In the case of Pacific salmon the majority of somatic growth occurs in marine environments. While marine waters present fishes with many potential predators, anadromy has proven a successful strategy for a variety of fish species (McDowell 1997). The observed dynamics in the Skagit River suggest that the current regime favors avoiding main stem habitats in favor of either tributaries for steelhead/rainbow trout or marine waters for Chinook salmon.

The ecology of fear has recently been discussed as a driving factor in shaping ecosystem processes (Ripple and Beschta 2004). For higher vertebrates, stress responses in prey species can alter reproduction and foraging behavior (Fraser and Gilliam 1992, Ylönen and Ronkainen 1994). In lower vertebrates and invertebrates, the effects of density and predation are key factors in shaping the demography and distribution of prey species (Peacor et al. 2007; Ferrari et al. 2008). In an ecosystem perspective, the success of prey and predators are dependent on factors associated with resource utilization (Orrock et al. 2008). Many prey species make ontogenetic shifts where they too become predators either in natal systems or in new habitats where they can realize a positive growth and survival trajectory (Olson et al. 1995). These processes can vary due to large scale forcing wherein one species may realize benefits under one regime and not another (Schiesari et al. 2006). It is within this framework of stochastic processes that drive the evolution of the predator-prey relationship and creates challenges for natural resource managers attempting to facilitate human utilization of those resources.

This study is unique in that it gives a comprehensive analysis of bull trout trophic ecology in a major river system with a relatively intact native fish assemblage. The findings in the present study can guide monitoring and reintroduction strategies for the restoration of anadromous salmonids in areas occupied by bull trout or bull trout reintroductions where anadromous salmonids are present. For instance, heavy predation was detected on steelhead/rainbow trout, sculpin spp., and dace spp. in the Skagit River. These fishes usually occupy open water or rocky habitat which can make them more vulnerable to predation by bull trout compared to fishes that are associated with complex woody debris.

A focus on habitat use by prey and predator in the recovery process is one key step in population recovery. This study identified predator behavior and available prey as another important component of the recovery process. As prey populations fluctuate, targeted diet analysis may be necessary to determine if predation pressure will remain a key factor limiting steelhead and stream-type Chinook production. While predator control by removal or culling can reduce mortality for prey populations, it may also have unintended negative effects by altering the structure of the food web. Modifying the behavior of the predator population may also be equally effective as culling and could reduce the impacts on food web structure. Meka and Margraf (2007) found that rainbow trout foraging could be reduced due to stressors associated with hooking during a catch and release event. Young and Hayes (2004) found an increase in hiding behavior and reduced feeding by large brown trout (*Salmo trutta*) between streams with high angler pressure compared to streams with low angler pressure. Methods that reduce the effectiveness of predators during times of high prey vulnerability, which do not negatively impact the growth of that predator, could be important tools for effective recovery. In the case of bull trout, an expanded catch and release or harvest season during spring could reduce the foraging efficiency of listed bull trout, and might release steelhead smolts from some predation pressure. Since the majority of bull trout growth and energy intake occurs during the fall, impacts on bull trout should be minimized by this strategy. Other adaptive management techniques such as hatchery smolt release timing, structured to avoid attracting predators and reducing predator density, could also be employed. In the management of threatened and endangered species, ecological interplay within ecosystems must be considered when making prudent decisions for effective recovery (Good et al. 2007). In the recovery of Chinook salmon, steelhead, and bull trout it is important to consider regulation, and predation when developing sound management strategies.

`

References

Al-Chokachy, R. and P. Budy (2008) Demographic characteristics, population structure, and vital rates of a fluvial population of bull trout in Oregon. Transactions of the American Fisheries Society 137:1709-1722

Bahr, M.A. and J.M. Shrimpton (2004) Spatial and quantitative patterns of movement in large bull trout (*Salvelinus confluentus*) from a watershed in north-western British Columbia, Canada, are due to habitat selection and not differences in life history Ecology of Freshwater Fishes13:294-304

Baker, J.D., P. Moran and R. Ladley (2003) Nuclear DNA identification of migrating bull trout captured at the Puget Sound Energy diversion dam on the White River, Washington State. Molecular Ecology 12:2:557-561

Beauchamp, D.A. and J.J. Van Tassell (2001) Modeling seasonal trophic interactions of adfluvial bull trout in Lake Billy Chinook, Oregon. Transactions of the American Fisheries Society 130: 204-216.

Beauchamp, D. A., D. Wahl, and B. M. Johnson. (2007). Predator-Prey Interactions. Pages 765-842. *In* C.S. Guy and M.J. Brown , editors, Analysis and interpretation of inland fisheries data. American Fisheries Society. Bethesda, Maryland.

Beamer, E., R. Bernard, B. Hyman, B. Hebner, S. Hinton, G. Hood, C. Kraemer, A. McBride, J. Musslewhite, D. Smith, L. Wasserman, K. Wyman (2005a) Skagit Chinook Recovery Plan Skagit River System Cooperative and Washington Department of Fish And Wildlife.

Beamer, E.M., B. Hayman, D. Smith (2005b) Linking freshwater rearing habitat to Skagit Chinook salmon recovery. Appendix C of the Skagit Chinook recovery plan.

Brenkman, S.J., G.L. Larson, and R.E. Gresswell (2001) Spawning migration of lacustrine-adfluvial bull trout in a natural area. Transactions of the American Fisheries Society 130:981-987

Brenkman, S.J. and S.C. Corbett (2005) Extent of Anadromy in bull trout and implications for conservation of a threatened species. North American Journal of Fisheries Management 25:1073-1081.

Brio, P.A., J.R. Post, and E.A. Parkinson (2003a) Population consequences of a predator-induced habitat shift by trout in whole-lake experiments. Ecology 84:3:691-700

Brio, P.A., J.R. Post, and E.A. Parkinson (2003b) From individuals to populations: prey fish risk-taking mediates mortality in whole-system experiments. Ecology 84:9:2419-2431

Brio, P.A., J.R. Post, and M.V. Abrahams (2005) Ontogeny of energy allocation reveals selective pressure promoting risk-taking behavior in young fish cohorts. Proceedings of the Royal Society B 272:1443:1448

Cardinale, B.J., J.J. Weis, A.E. Forbes, K.J. Tilmon, and A.R. Ives (2006) Biodiversity as both a cause and consequence of resource availability: a study of reciprocal causality in a predator-prey system. Journal of Animal Ecology 75:497-505

Cavender, T.M. (1978) Taxonomy and distribution of the bull trout, *Salvelinus confluentus* (Suckley), from the American Northwest. California Fish and Game 64(3):139-174.

Chipps, S. R., and J. E. Garvey. 2007. Assessment of diet and feeding patterns. Pages 473-514. *In* C.S. Guy and M.J. Brown , editors, Analysis and interpretation of inland fisheries data. American Fisheries Society. Bethesda, Maryland.

Clarke, L.R., D.T. Vidergar, and D.H. Bennett (2005) Stable isotopes and gut content show diet overlap among native and introduced piscivores in a large oligotrophic lake. Ecology of Freshwater Fish 14:3:267-277.

Connor, E.J. and Pflug, D.E. (2004) Changes in the distribution and density of pink, chum, and Chinook salmon spawning in the upper Skagit River in response to flow management measures. North American Journal of Fisheries Management 24:3:835-852.

Cochran, W.G. (1977) Sampling techniques. Wiley and Sons

Cross, A.D., D.A. Beauchamp, K.W. Myers, and J.H. Moss (2008) Early marine growth of pink salmon in Prince William Sound and the coastal Gulf of Alaska during years of low and high survival. Transactions of the American Society 137:927-939

Dunham, J., B. Rieman and G. Chandler (2003) Influences of temperature and environmental variables on the distribution of bull trout within streams at the southern margin of its range. North American Journal of Fisheries Management. 23:3:894-904

Downen, M. (2006) Skagit bull trout monitoring program 2002-2005 report (draft) Washington department of fish and wildlife

DeNiro, M.J. and S. Epstein (1981) Influence of diet on the distribution of carbon isotopes in animals. Geochimica et Cosmochimica Acta 42:5:495-506

Duffy, E.J. and D.A. Beauchamp (2008) Seasonal patterns of predation on juvenile Pacific salmon by anadromous cutthroat trout in Puget Sound. Transactions of the American Fisheries Society 137:165-181

Federal Register (2007) Endangered and threatened species: final listing determination for Puget Sound steelhead. Federal Register 72:91:26722-26735

Ferrari, M.C.O., F. Messier, D.P. Chivers (2008) Larval amphibians learn to match antipredator response intensity to temporal patterns of risk. Behavioral Ecology 19:5:980-983

Fraser, D.F., and J.F. Gilliam (1992) Nonlethal impacts of predator invasion: Facultative suppression of growth and reproduction. Ecology 73:3:959-970

Goetz, F.A., E. Jeanes and E. Beamer (2004) Bull trout in the nearshore. U.S. Army Corps of Engineers, Preliminary Draft, Seattle

Good, T.P., T.J. Beechie, P McElhany, M.M. McClure, and M.H. Ruckelshaus Recovery planning for endangered species act-listed Pacific salmon: using science to inform goals and strategies Fisheries 32:9426-440

Gross, M.R., R.M. Coleman, and R.M. McDowall (1988) Aquatic productivity and the evolution of diadromous fish migration. Science 239:4845:1291-1293

Haas, G.R. and J.D. McPhail (1991) Systematics and distribution of Dolly Varden (*Salvelinus malma*) and bull trout (*Salvelinus confluentus*) in North America. Canadian Journal of Fisheries and Aquatic Science 48:2191-2211.

Hagen, J. and E.B. Taylor (2001) Resource partitioning as a factor limiting gene flow in hybridizing populations of Dolly Varden char (*Salvelinus malma*) and bull trout (*Salvelinus confluentus*). Canadian Journal of Fisheries and Aquatic Science 58:2037-2047

Hansen, M.J., D. Boisclair, S.B. Brandt, S.W. Hewett, J.F. Kitchell, M.C. Lucas and J.J. Ney (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) Fish Bioenergetics 3.0 University of Wisconson-Madison Center for Limnology and University of Wisconsin Sea Grant.

Hartman, K.J. and M.K. Cox (2008) Refinement and testing of a brook trout bioenergetics model. Transactions of the American Fisheries Society 137:1:357-363

He, X., J.F. Kitchell (1990) Direct and indirect effects of predation on a fish community: a whole lake experiment. Transactions of the American Fisheries Society 119:825-835

Hilborn, R., T.P. Quinn, D.E. Schindler, and D.E. Rogers (2003) Biocomplexity and fisheries sustainability. Proceedings of the National Academy of Science 100:11:6564-6568

Johnson, B.M., P.J. Martinez and J.D. Stockwell (2002) Tracking trophic interactions in coldwater reservoirs using naturally occurring stable isotopes. Transactions of the American Fisheries Society 131:1-13.

Kennedy, B.P., K.H. Nislow, and C.L. Folt (2008) Habitat mediated foraging limitations drive survival bottlenecks for juvenile salmon. Ecology 89:9:2529-2541

Kinsel, C., G. Volkhardt, L. Kishimoto, and P. Topping (2007) 2006 Skagit River wild salmon production evaluation annual report. Washington Department of Fish and Wildlife

Lewis, D.B. (2001) Trade-offs between growth and survival: responses of freshwater snails to predacious crayfish. Ecology 82:3:758-765

Lima, S.L. (1998) Nonlethal effects in the ecology of predator-prey interactions what are the ecological effects of anti-predator decision-making? Bioscience 48(1):25-34

McDowall, R.M. (1997) The evolution of diadromy in fishes (revisited) and its place in phylogenetic analysis. Reviews in fish biology and Fisheries 7:443-462

McDowall, R.M. (2008a) Why are so many boreal freshwater fishes anadromous? Confronting conventional ‘wisdom’. Fish and Fisheries 9:208-213

McDowell R.M. (2008b) Diadromy, history and ecology: a question of scale. Hydrobiologia 602:5-14

McIntyre, J.K., D.A. Beauchamp, M.M. Mazur, N.C. Overman (2006) Ontogenetic trophic interactions and benthopelagic coupling in Lake Washington: evidence from stable isotopes and diet analysis. Transactions of the American Fisheries Society 135:1312-1328.

McPhail, J.D. and J.S. Baxter (1996) A review of bull trout (*Salvelinus confluentus*) life-history and habitat use in relation to compensation and improvement opportunities.British Columbia Ministry of Environment Fisheries Management Report ISSN 0705-5390 no. 104

Meka, J.M. and F.J. Margraf (2007) Using a bioenergetic model to assess growth reduction from catch-and –release fishing and hooking injury in rainbow trout, *Oncorhynchus mykiss* Fisheries Management and Ecology 14:131-139

Minagawa, M., and E. Wada (1984) Stepwise enrichment of ^{15}N along food chains: Further evidence and the relation between delta ^{15}N and animal age. Geochimica Et Cosmochimica Acta 48:1135:1140.

Mogen, J.T. and L.R. Kaeding (2005) Identification and characterization of migratory and nonmigratory bull trout populations in the St. Mary River drainage, Montana. Transactions of the American Fisheries Society 134:841-852.

Nelson, J.S., T.E. McMahon, and R.F. Thurow (2002) Decline of the migratory form in bull charr, *Salvelinus confluentus*, and implications for conservation. Environmental Biology of Fishes 64:321-332

Ney, J.J. (1993) Bioenergetics modeling today: growing pains on the cutting edge. Transactions of the American Fisheries Society 122:736-748

Olson, M.H., G.G. Mittelbach, C.W. Osengerg (1995) Competition between predator and prey: resource-based mechanisms and implications for stage structured dynamics. Ecology 76:6:1758-1771

Orell, P. and J. Erikinaro (2007) Snorkelling as a method for assessing spawning stock of Atlantic salmon, *Salmo salar*. Fisheries Management and Ecology 14:199-208

Orrock, J.L., J.H. Grabowski, J.H. Pantel, S.D. Peacor, B.L. Peckarsky, A. Sih, and E.E. Werner (2008) Consumptive and nonconsumptive effects of predators on metacommunities of competing prey. Ecology 89:9:2426-2435

Peacor, S.D., L. Schiesari, E.E. Werner (2007) Mechanisms of nonlethal predator effect on cohort size variation: Ecological and evolutionary implications. Ecology 88:6:2007

Peterson, B.J., B. Fry (1987) Stable isotopes in ecosystem studies. Annual Review of Ecology and Systematics 18:293-320.

Petersen, J.H., D.L. Ward (1999) Development and corroboration of a bioenergetics model for northern pikeminnow feeding on juvenile salmonids in the Columbia River. Transactions of the American Fisheries Society 128:784-801.

Peckarsky, B.L., P.A. Abrams, D.I. Bolnick, L.M. Dill, J.H. Grabowski, B. Luttberg, J.L. Orrock, S.D. Peacor, E.L. Preisser, O.J. Schmitz, G.C. Trussell (2008) Revisiting the classics: considering nonconsumptive effects in textbook examples of predator-prey interactions. Ecology 98(9):2416-2425

Post, D.M. (2002) Using stable isotopes to estimate trophic position: models, methods, and assumptions. Ecology 83:3:703-718

Quinn, T.P. (2005) The behavior and ecology of Pacific salmon and trout. American Fisheries Society, Bethesda, Maryland

Reist, J.D., G. Low, J.D. Johnson, and D. McDowell (2002) Range extension of bull trout, *Salvelinus confluentus*, to the Central Northwest Territories, with notes on identification and distribution of Dolly Varden, *Salvelinus malma*, in the Western Canadian Arctic. Arctic 55:1:70-76.

Ripple, W.J., and R.L. Beschta (2004) Wolves and the ecology of fear: can predation risk structure ecosystems? BioScience 54:8:755-766

Scheuerell, M.D., J.W. Moore, D.E. Schindler, and C.J. Harvey (2007) Varying effects of anadromous sockeye salmon on the trophic ecology of two species of resident salmonids in southwest Alaska. Freshwater Biology 52:1944-1956

Schiesari, L., S.D. Peacor, E.E. Werner (2006) The growth-mortality tradeoff: evidence from anuran larvae and consequences for species distributions. Oecologia 149:194-202

Selong, J. H., T.E. McMahon, A.V. Zale, and F.T. Barrows (2001) Effect of temperature on growth and survival of bull trout, with application of an improved method for determining thermal tolerances in fishes Transactions of the American Fisheries Society 130:1206-1307.

Stewart, D.J., D. Weininger, D.V. Rottiers, and T.A. Edsall (1983) An energetics model for lake trout (*Salvelinus namaycush*) Canadian Journal of Fisheries and Aquatic Sciences 40:6:681-698

Thurrow, R.F. and D.J. Schill (1996) Comparison of day snorkeling, night snorkeling, and electrofishing, to estimate bull trout abundance and size structure in a second-order Idaho stream. North American Journal of Fisheries Management 16:314-323

Thornton, K.W. and A.S. Lessem (1978) Temperature algorithm for modifying biological rates. Transactions of the American Fisheries Society 107:2:284-287

Vander Zanden and J.B. Rasmussen (2001) Variation in δ^{15}N and δ^{13}C trophic fractionation: implications for aquatic food web studies Limnology and Oceanography 46(8) 2061-2066

Wissmar, R.C. and S.D. Craig (2004) Factors affecting habitat selection by a small spawning charr population, bull trout, *Salvelinus confluentus*: implications for recovery of an endangered species. Fisheries Management and Ecology 11:23-31.

Woodward, G., G. Papantoniou, F. Edwards, R. B. Lauridsen (2008) Trophic trickles and cascades in a complex food web: impacts of a keystone predator on stream community structure and ecosystem processes. Oikos 117:683-692

Ylönen, H. and H. Ronkainen (1994) Breeding suppression in the bank vole as antipredatory adaptation in a predictable environment. Evolutionary Ecology 8:658-666

Young, R.G. and J.W. Hayes (2001) Assessing the accuracy of drift-dive estimates of brown trout (*Salmo trutta*) abundance in two New Zealand rivers: a mark-resighting study. 35:269-275

Young, R.G. and J.W. Hayes (2004) Angling pressure and trout catchability: behavioral observations of brown trout in two New Zealand backcountry rivers. North American Journal of Fisheries Management 24:1203-1213

Zydlewski, G.B., Alex Haro, and S.D. Mcormick (2005) Evidence for cumulative temperature as an initiating and terminating factor in downstream migratory behavior of Atlantic salmon (*Salmo salar*) smolts. 62:68-78

Tables and Figures

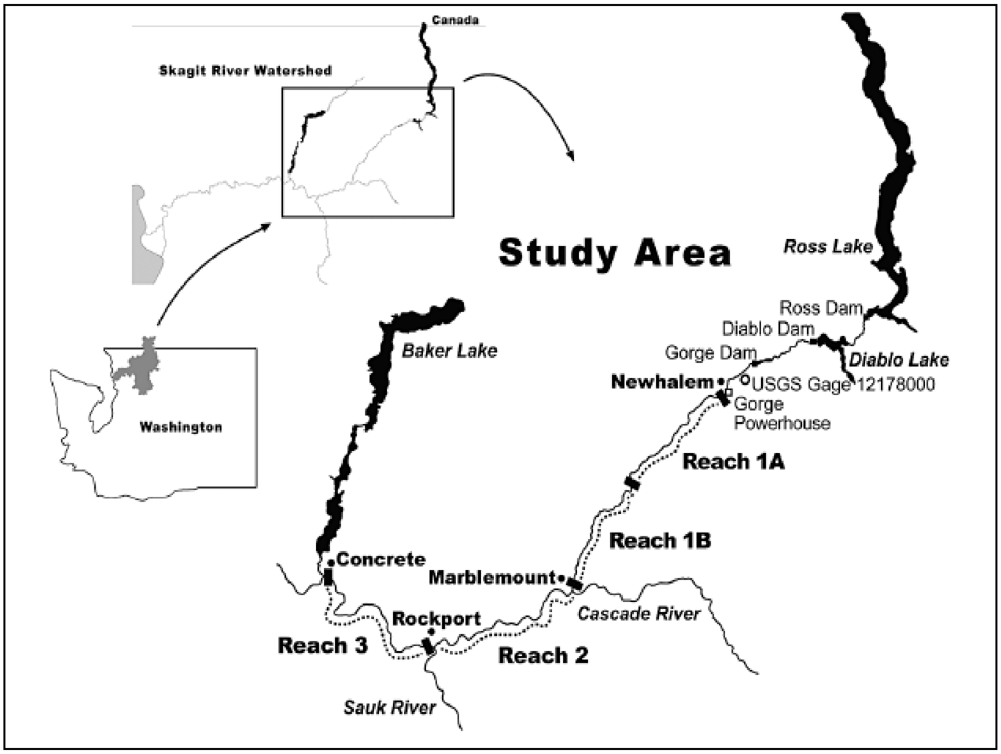

Figure 1. Map showing the location of the Skagit River in relation to Washington State and the location of the study area in relation to the Skagit River. The study area extended from the Gorge Powerhouse in Newhalem to the confluence of the Sauk River near Rockport.

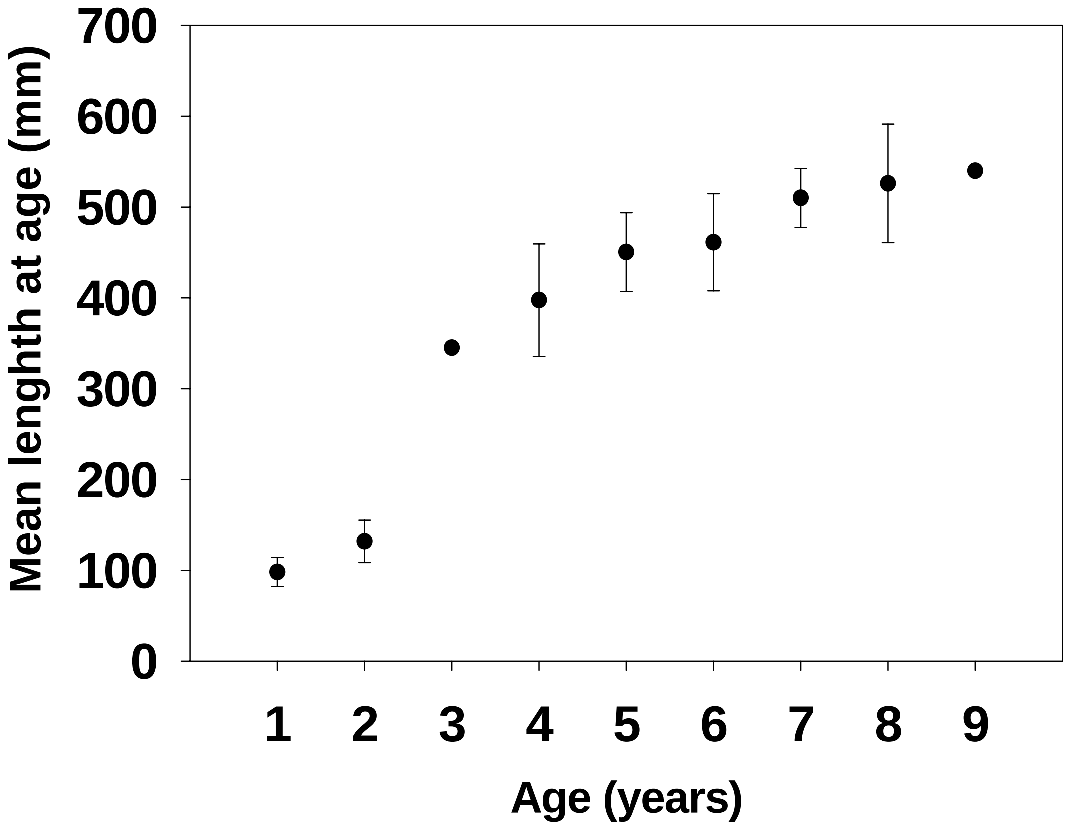

Figure 2. Mean length at age (error bars represent 1 standard deviation) of bull trout captured in the tributaries and main stem of the Skagit River in 2007 and winter and spring 2008.

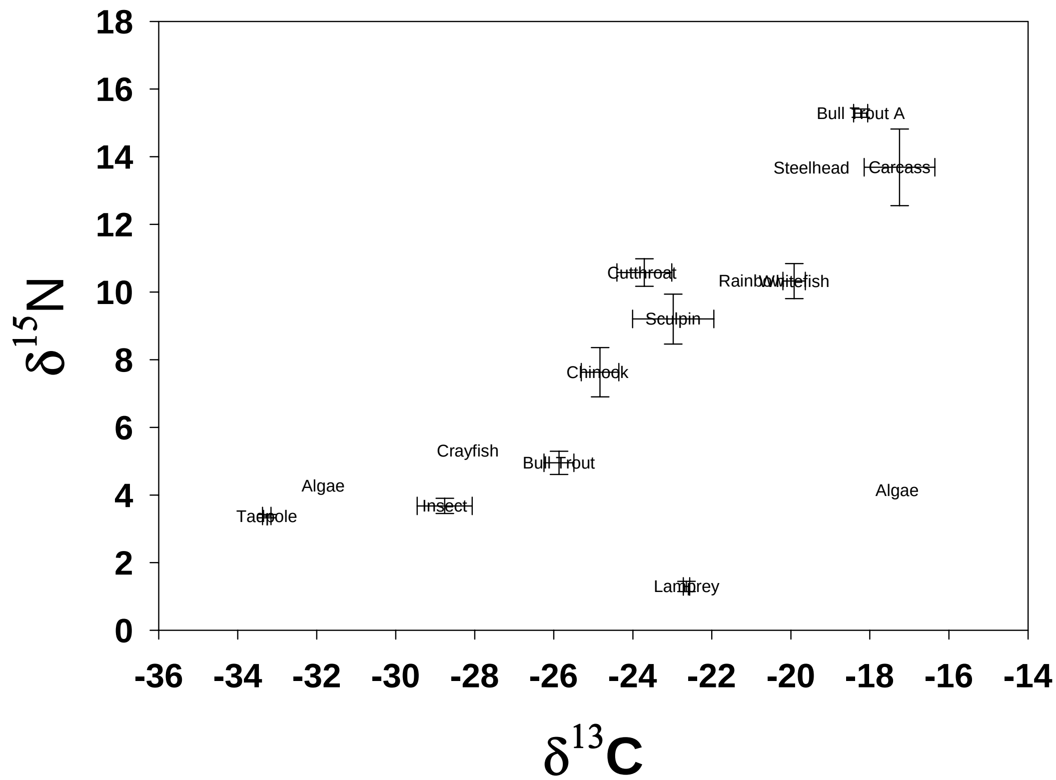

Figure 3. Mean carbon and nitrogen stable isotope values for components of the Skagit River food web (error bars represent one standard error). Symbols were defined as follows: Lamprey were *Lampetra* spp., Tadpole was tadpoles of unknown species found in flood plain ponds, Algae was periphyton collected in the mainstem, Insect was the average of all immature aquatic insects, crayfish was signal crayfish *Pacifastacus leniusculus*, Bull Trout were juvenile bull trout from tributaries, Chinook were juvenile Chinook salmon, Sculpin were *Cottus* spp., Cutthroat were cutthroat trout, Rainbow were rainbow trout or steelhead juveniles, Whitefish were mountain whitefish, Steelhead were returning adult steelhead, Carcass was pink, Chinook, and coho Pacific salmon carcass, Bull Trout A was mainstem fluvial bull trout.

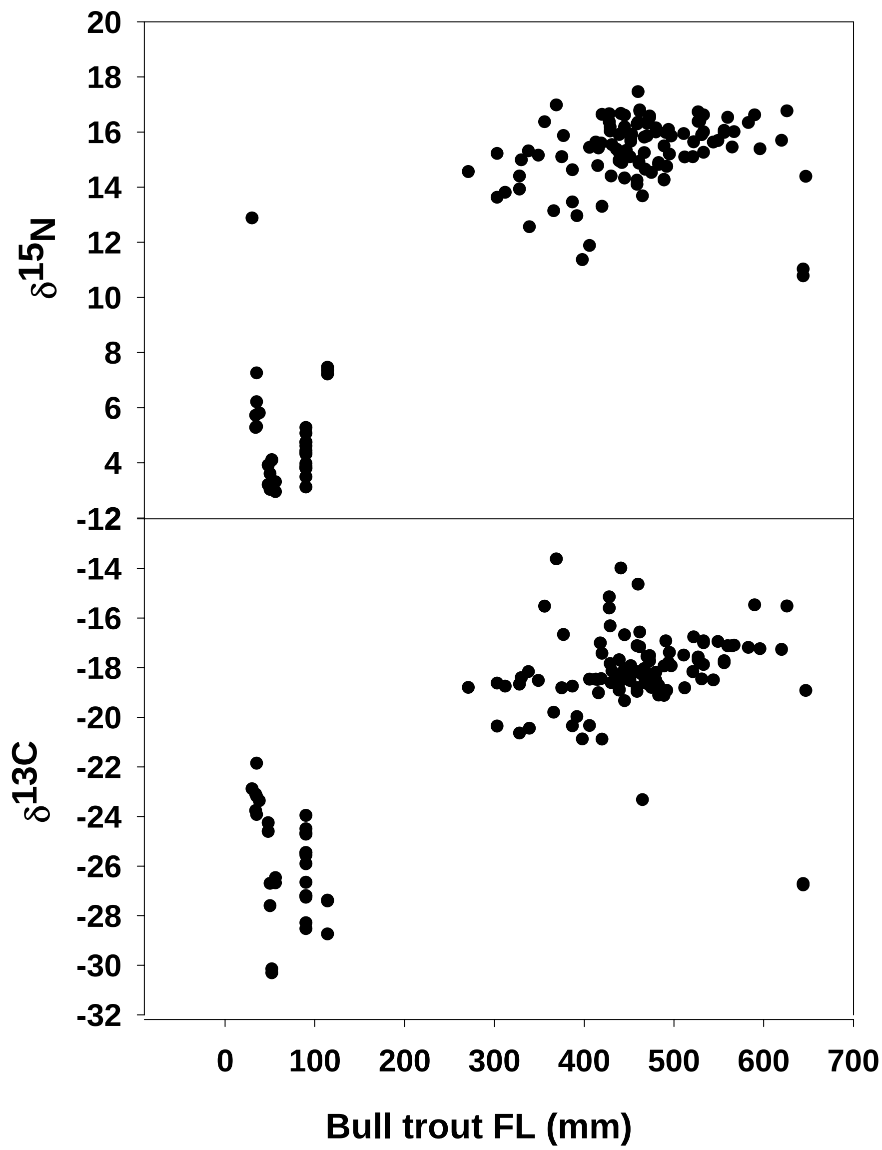

Figure 4. Plots comparing the ontogeny of $\delta^{13}C$ and $\delta^{14}N$ values to fork length of bull trout in the Skagit River tributaries and mainstem.

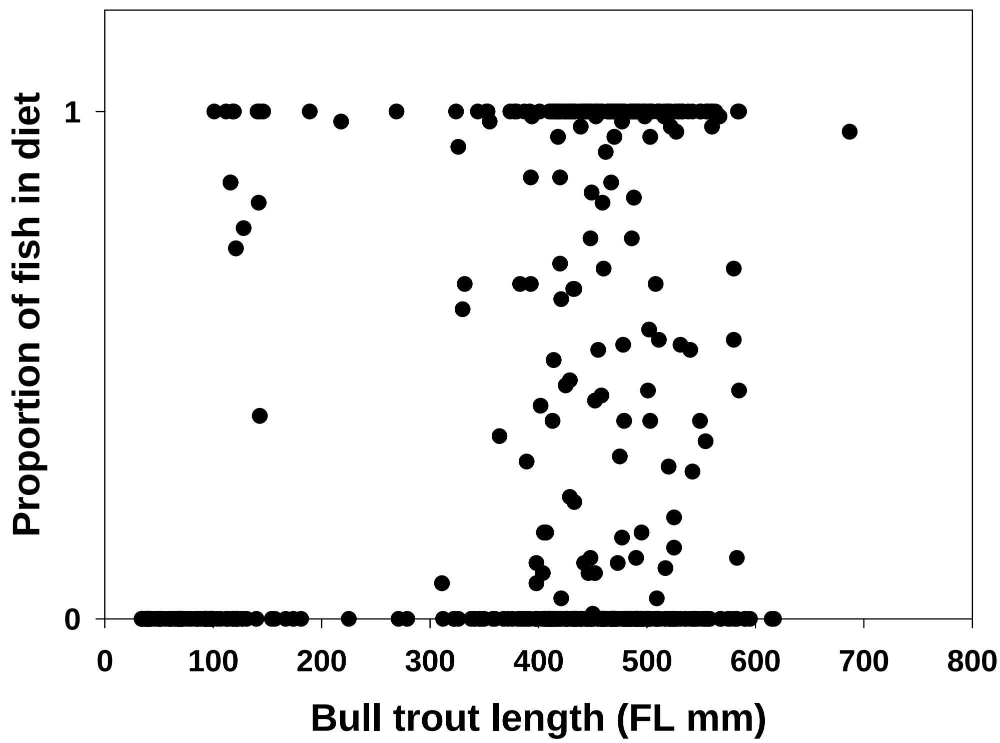

Figure 5. Bull trout FL (n = 525) verses the proportion of fish (ww) found in the diet of Skagit river bull trout caught in 2007 and winter and spring 2008. A size threshold for piscivory of approximately 110mm was detected.

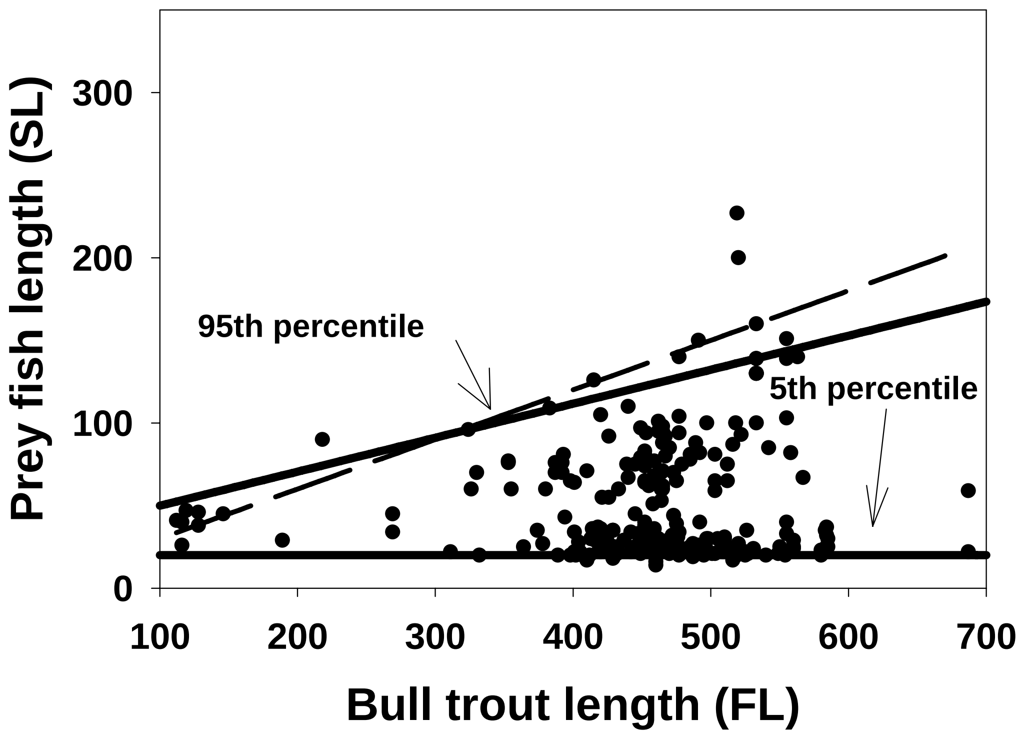

Figure 6. Bull trout FL verses prey fish SL. Data represent bull trout diet items collected from the Skagit River and tributaries in 2007 and winter and spring 2008. Dashed line indicates 30% bull trout FL. Solid lines represent the 95th ($\beta_0 = 29.34$, $\beta_1 = 0.205$, $P < 0.0001$) and 5th ($\beta_0 = 20$, $\beta_1 = 0$, $P = 0$) percentile regressions.

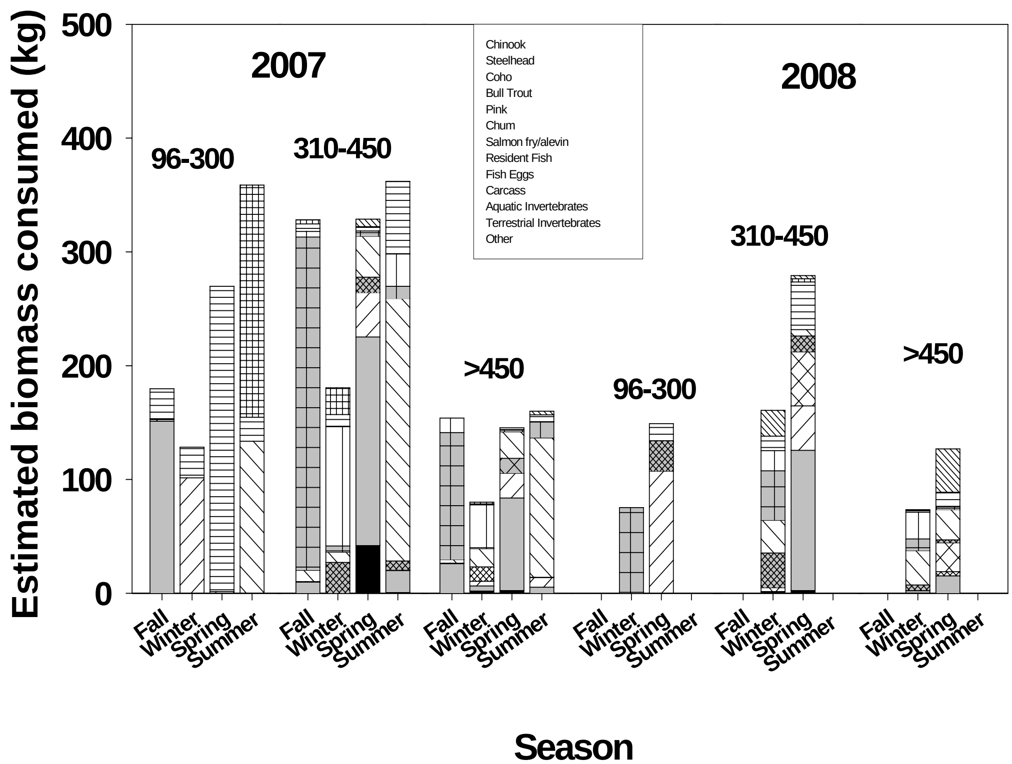

Figure 7. Population-level consumption estimates for a unit population of n = 100 Skagit River bull trout >300mm caught in 2007 and winter and spring 2008.

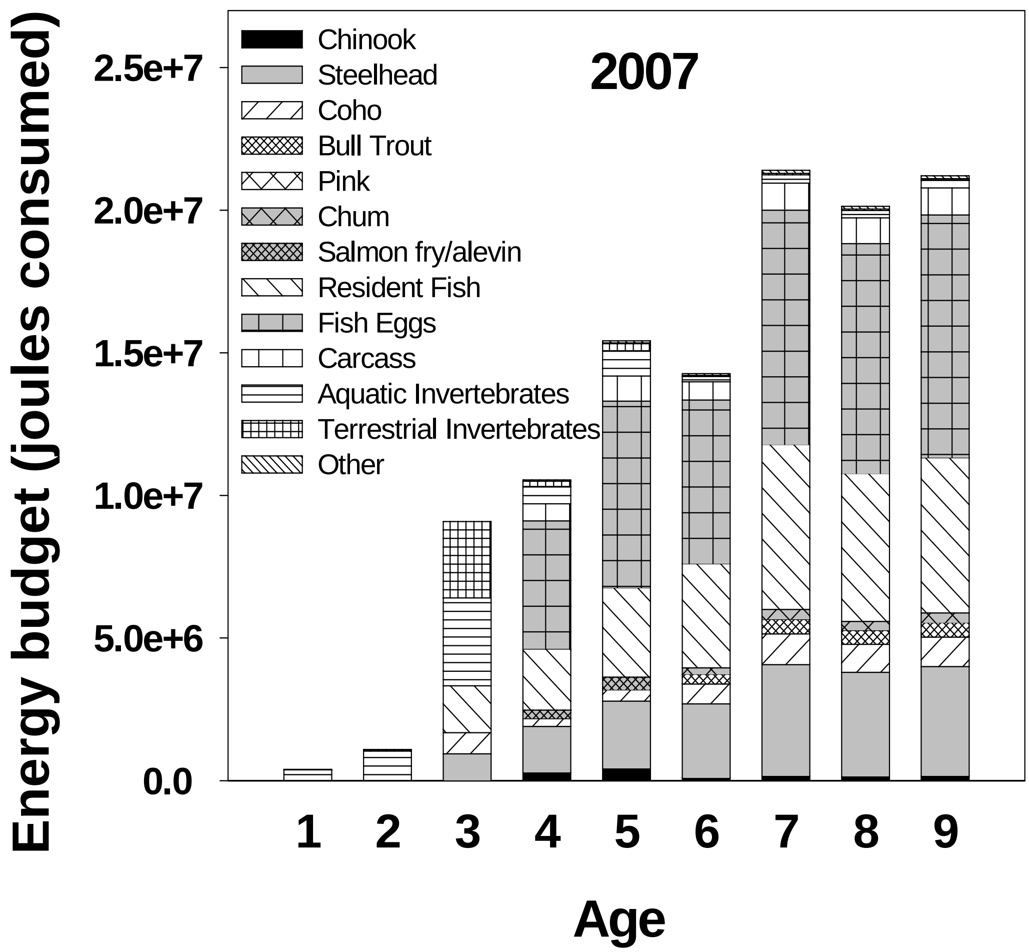

Figure 8. Contributions of major prey categories to the annual energy budget for each age class of bull trout in the Skagit River. In these simulations, ages 0-2 fed exclusively in tributaries, whereas age-3 bull trout fed in tributaries during fall-winter then transitioned into the mainstem during spring summer.

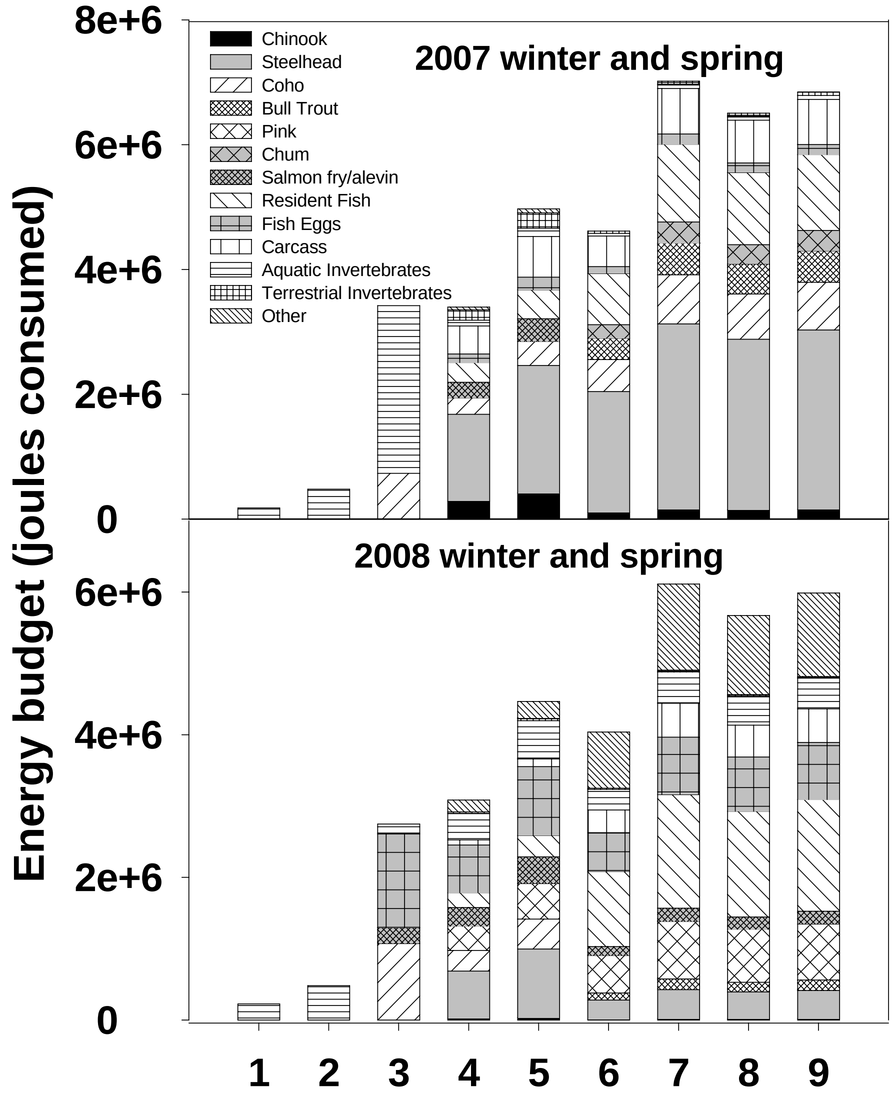

Figure 9. The estimated contribution of each prey category to the annual energy budget by age of bull trout during winter-spring 2007 when juvenile pink salmon were absent and 2008 when juvenile pink salmon were abundant

Table 1. Individual age structured consumption estimates of bull trout in the Skagit River fitted to initial and final mass, and spawning losses.

2007

Age	Size Classes	Initial/Final Mass (g)	Spawning Loss (% body weight)	Total Growth (g)	p-Value	Total Consumption (g)	Growth Efficiency
1	30-95	0.3-11	0	10	0.35	107	10%
2	30-95	11-26	0	15	0.28	219	7%
3	96-300	26-442	0	417	0.54	1744	24%
4	301-450	442-676	0	233	0.20	1607	15%
5	301-450	676-972	9.8%	296	0.22	2350	13%
6	>450	972-1044	11.6%	72	0.23	2171	3%
7	>450	1044-1408	13.7%	364	0.25	3297	11%
8	>450	1408-1543	13.7%	135	0.20	3067	4%
9	>450	1543-1668	13.7%	125	0.20	3229	4%
2008							
1	30-95	2.3-8.4	0	8	0.35	47	18%
2	30-95	19-23	0	13	0.28	100	13%
3	96-300	90-316	0	170	0.28	399	43%
4	301-450	695-707	0	85	0.17	607	14%
5	301-450	1024-1041	9.8%	150	0.19	880	17%
6	>450	1274-1138	11.6%	45	0.16	831	5%
7	>450	1500-1495	13.7%	182	0.22	1259	14%
8	>450	1830-1683	13.7%	100	0.18	1167	9%
9	>450	1990-1823	13.7%	95	0.18	1232	8%

Table 2. Wisconsin bioenergetics model parameter set used in this project following the notation of Hansen et al. 1997. The following equations were used during simulations; consumption equation (3) (CA and CB Hartman and Cox (2008), and the remainder derived from Selong et al. 2001), respiration equation (2) Hartman and Cox (2008), egestion and excretion equation (3) Stewart et al. 1983.

Parameter	Value	Description
Consumption		
CA	0.3013	Intercept of the mass dependent consumption function
CB	-0.3055	Exponent of the mass dependent consumption function
CQ	8	Temperature at which consumption is a small fraction (CK1) of the maximum
CTO	10.9	Temperature at 98% on the ascending limb of the temperature dependent consumption curve
CTM	15.4	Temperature at 98% on the descending limb of the temperature dependent consumption curve
CTL	20	Temperature at which consumption is a large fraction (CK4) of the maximum
CK1	0.8	Consumption fraction at water temperature CQ
CK4	0.2	Consumption fraction at water temperature CTL
Respiration		
RA	0.0132	Intercept of the mass dependence function for respiration
RB	-0.265	Exponent of the mass dependence function for respiration
RQ	4.5	Approximation of the slope of the respiration function at lower temperatures
RTO	20.2	Optimal temperature for respiration
RTM	25	Maximum lethal temperature for respiration
ACT	2.89	Activity rate multiplier
SDA	0.172	Specific dynamic action
Egestion and excretion		
FA	0.212	Intercept of the temperature dependence function for egestion
FB	-0.222	Exponent of the temperature dependence function for egestion
FG	0.631	Coefficient for the feeding level dependence of egestion
UA	0.0314	Intercept of the temperature dependence for excretion
UB	0.58	Exponent of the temperature dependence function for excretion
UG	-0.299	Coefficient for the feeding level dependence of excretion

Table 3. Mean, maximum and minimum monthly temperatures (C°) for the Skagit River 2007. All data were taken from USGS Gauge #12181000 in Marblemount, WA

Month	Mean	Maximum	Minimum
September	11.7	12.6	11.0
October	9.8	10.2	9.4
November	8.4	8.7	8.1
December	6.2	6.4	5.9
January	4.6	4.8	4.4
February	4.5	4.7	4.3
March	4.8	5.2	4.6
April	6.0	6.6	5.6
May	8.0	9.1	7.1
June	9.0	9.7	8.5
July	11.1	11.9	10.5
August	12.2	13.3	11.2

Table 4. Seasonal and size structured diet proportions of bull trout captured in 2007 and winter and spring 2008 (“M” and “T” indicate main stem and tributary habitats. Where n = 0 diet composition was not estimated.

	Wi		n	Chinook salmon	Steelhead / rainbow trout	Coho Salmon	Bull Trout	Pink Salmon	Chum Salmon	Pacific Salmon fry/alevin	Resident Fish	Fish Eggs	Pacific Salmon Carcass	Aquatic Invertebrates	Terrestrial Invertebrates	Other
2007	Autumn	30-95 T	19	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.78	0.22	0.00
	Winter	30-95 T	0	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Spring	30-95 T	7	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00
	Summer	30-95 T	25	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.98	0.02	0.00
	Autumn	96-300 T	16	0.00	0.85	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.15	0.00	0.00
	Winter	96-300 T	0	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Spring	96-300 T	2	0.00	0.00	0.79	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.21	0.00	0.00
	Summer	96-300 T	16	0.00	0.00	0.83	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.17	0.00	0.00
	Autumn	96-300 M	1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00
	Winter	96-300 M	1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00
	Spring	96-300 M	2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00
	Summer	96-300 M	5	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.38	0.00	0.00	0.04	0.58	0.00
	Autumn	301-450	46	0.00	0.03	0.00	0.00	0.00	0.00	0.00	0.03	0.90	0.01	0.02	0.01	0.00
	Winter	301-450	18	0.00	0.00	0.00	0.00	0.00	0.00	0.15	0.05	0.03	0.58	0.06	0.13	0.00
	Spring	301-450	16	0.13	0.56	0.12	0.00	0.00	0.00	0.04	0.11	0.01	0.00	0.01	0.00	0.02
	Summer	301-450	18	0.00	0.04	0.00	0.00	0.00	0.00	0.02	0.65	0.03	0.08	0.18	0.00	0.00
	Autumn	>450	41	0.00	0.17	0.00	0.00	0.00	0.00	0.00	0.02	0.73	0.08	0.00	0.00	0.00
	Winter	>450	27	0.03	0.05	0.05	0.16	0.00	0.00	0.00	0.20	0.01	0.47	0.01	0.02	0.00
	Spring	>450	40	0.02	0.56	0.15	0.00	0.00	0.09	0.00	0.16	0.01	0.00	0.01	0.00	0.00
	Summer	>450	12	0.00	0.02	0.05	0.00	0.00	0.00	0.00	0.78	0.09	0.00	0.04	0.00	0.02
2008	Winter	30-95	0	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Spring	30-95	10	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00
	Winter	96-300 T	1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00
	Spring	96-300 T	2	0.00	0.00	0.99	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00
	Winter	96-300 M	2	0.00	0.00	0.00	0.00	0.63	0.00	0.00	0.00	0.00	0.00	0.32	0.05	0.00
	Spring	96-300 M	2	0.00	0.00	0.72	0.00	0.00	0.00	0.18	0.00	0.00	0.00	0.10	0.00	0.00
	Winter	301-450	32	0.01	0.00	0.00	0.00	0.02	0.00	0.18	0.18	0.28	0.11	0.08	0.00	0.14
	Spring	301-450	34	0.01	0.44	0.14	0.00	0.17	0.00	0.05	0.02	0.00	0.00	0.15	0.01	0.01
	Winter	>450	56	0.01	0.02	0.00	0.00	0.01	0.00	0.06	0.41	0.14	0.32	0.02	0.01	0.00
	Spring	>450	74	0.00	0.12	0.00	0.03	0.20	0.00	0.02	0.21	0.01	0.01	0.10	0.00	0.30

Table 5. Seasonal energy densities (ED) and expected indigestible fraction for bull trout and prey items used in bioenergetics simulations. Numbers in parentheses indicate sample sizes.

Taxa	Winter	Spring	Summer	Fall	Wet weight : Dry weight Ratio	Indigestible Fraction	Comments
Bull Trout	6167 (8)	6091 (20)	7272 (4)	6752 (4)	3.6	9%	
Chinook salmon	3859 (9)	3997 (6)	4878 (2)	4878	5.2	9%	
Rainbow trout/Steelhead	3906 (9)	3900 (9)	3806 (2)	5535 (3)	5.0	9%	
Coho salmon	5359 (4)	4414 (5)	3494 (5)	4898 (3)	4.9	9%	
Pink salmon	4902 (9)	4000 (3)	4000	4000	5.0	9%	
Chum salmon	4110	4110 (5)	4110	4110	5.5	9%	
Unidentified Pacific salmon fry/alevin	4427	4084	4058	4684		9%	Average seasonal ED for all Pacific salmon was used
Mountain whitefish	4800	4800	4800	4800		9%	
Sculpin spp.	4500	4500 (6)	5552 (1)	5552	4.3	9%	Average seasonal ED for mountain whitefish and sculpin was used
Resident Fishes	4650	4650	5176	5176		9%	
Fish Eggs	12000	12000 (7)	12000	12000 (6)	2.1	2%	Eggs from spring Chinook salmon in spring and coho salmon in fall
Pacific salmon carcass	3300	3300 (2)	3300 (10)	3300	4.4	9%	The average of Spring and fall Chinook, pink, and coho Pacific salmon carcasses
Immature aquatic invertebrates	4978 (8)	3419 (13)	3419	4978	4.3	15%	
Adult aquatic/terrestrial invertebrates	5500	5500	5500	5500		15%	
Other	5000	5000	5000	5000		9%	

Table 6. Mean (SD) length (mm) of fish prey found in Skagit River bull trout diets captured in 2007 and winter and spring 2008

	Fall 2007	Winter 2007	Spring 2007	Summer 2007	Winter 2007	Spring 2007
Chinook Salmon Fry		57.5 (31.8)	65.8 (9.1)		35.3 (4.7)	33.5 (0.7)
Steelhead/rainbow trout	85.5 (52.9)	84.5 (14.8)	103.7 (35.1)	60	59	80.7 (33.9)
Pink Salmon					25.8 (3)	25.8 (2.9)
Chum			27.4 (7.6)			
Coho Salmon Fry		73 (12.2)	83.1 (12.2)	70		57 (30.8)
Unidentified Pacific Salmon Fry		27.6 (3.8)	30		37	27
Pacific Salmon Alevin	19.5 (3.5)	27 (4.2)			21.3 (2.1)	22.4 (3.1)
Unidentified Salmonid				55 (28.3)		
Bull Trout		140				140
Unidentified Salmonid	46.5 (12)		32 (2.4)			44.5 (14.8)
Dace spp.	67.5 (3.5)		98 (3.5)	78		65
Sculpin spp.	81.5 (10.6)	89 (9.4)	68 (12.5)	80.3 (18.7)	55 (23.4)	
Mountain Whitefish	60		130		125 (144.2)	
Unidentified Fish	60			90	62	

Table 7. Estimated size structured unit populations of bull trout from the Skagit River based on winter snorkel counts. Assumed mortality for age 1-3 was 90% and age 4-9 was 50%.

Age	>300 = 1000	>300 = 1600
1	101550	162480
2	10155	16248
3	1016	1625
4	508	812
5	254	406
6	127	203
7	63	102
8	32	51
9	16	25
Total	25720	16064

Table 8. Variability in bull trout >300mm diet data from the Skagit River for key prey species and major energy contributors. The top panel presents variability as a range of values around the estimated individual seasonal size structured consumption (kg) from bioenergetics modeling (details in the text). The bottom panel presents variability as one standard error of the mean weighted proportion of that diet item. .

301-450	Season	n	Chinook	Range	Steelhead	Range	Coho	Range	Resident Fish	Range	Fish Eggs	Range	Carcass	Range
2007	Fall	46	-	-	28	0-251	-	-	29	0-193	851	540-1,163	14	0-164
	Winter	18	-	-	-	-	-	-	28	18-39	17	0-111	329	249-409
	Spring	16	144	28-261	621	414-827	133	16-250	122	36-208	11	0-523	-	-
	Summer	18	-	-	68	0-150	-	-	842	630-1,053	39	0-223	103	30-176
2008	Winter	32	5	0-14	-	-	-	-	91	42-140	136	54-218	55	26-85
	Spring	34	9	0-46	416	246-586	132	19-246	19	0-66	-	-	-	-
>450														
2007	Fall	41	-	-	503	0-1,650	-	-	64	0-327	2,153	878-3,428	248	0-1,047
	Winter	27	50	0-141	83	0-225	83	0-227	333	32-635	17	0-419	783	303-1,264
	Spring	40	66	0-335	1,816	486-3,146	487	0-1,286	523	0-1,325	33	0-2,226	11	-
	Summer	12	-	-	123	0-519	201	0-459	2,957	2,056-3,858	340	0-1,107	-	-
2008	Winter	56	15	0-143	31	0-461	-	-	626	0-1,345	214	0-1,080	489	0-1,085
	Spring	74	-	-	342	0-887	-	-	598	0-1,433	28	0-1,646	28	0-259

301-450	Season	n	Chinook	SE	Steelhead	SE	Coho	SE	Resident Fish	SE	Fish Eggs	SE	Carcass	SE
2007	Fall	46	-	-	0.03	0.22	-	-	0.03	0.15	0.91	0.33	0.01	0.12
	Winter	18	-	-	-	-	-	-	0.05	0.02	0.03	0.16	0.58	0.14
	Spring	16	0.13	0.11	0.56	0.19	0.12	0.11	0.11	0.08	0.01	0.23	-	-
	Summer	18	-	-	0.04	0.05	-	-	0.65	0.16	0.03	0.15	0.08	0.06
2008	Winter	32	0.01	0.02	-	-	-	-	0.18	0.10	0.27	0.16	0.11	0.06
	Spring	34	0.01	0.03	0.45	0.18	0.14	0.12	0.02	0.04	-	-	-	-
>450														
2007	Fall	41	-	-	0.17	0.38	-	-	0.02	0.08	0.73	0.43	0.08	0.25
	Winter	27	0.03	0.05	0.05	0.08	0.05	0.08	0.20	0.18	0.01	0.34	0.47	0.29
	Spring	40	0.02	0.10	0.56	0.41	0.15	0.24	0.16	0.25	0.01	0.47	-	-
	Summer	12	-	-	0.02	0.05	0.05	0.06	0.79	0.24	0.09	0.19	-	-
2008	Winter	56	0.01	0.07	0.02	0.24	-	-	0.42	0.48	0.14	0.56	0.32	0.39
	Spring	74	-	-	0.12	0.19	-	-	0.21	0.29	0.01	0.47	0.01	0.08

Table 9. Estimated individual prey fish consumed by a unit population of n=1000 bull trout >300mm in the Skagit River Tributaries and mainstem in 2007 and winter/spring 2008. Numbers for tributary feeding represent bull trout <300 mm.

	Winter		Spring		Summer		Fall		
Tributary	# Consumed	FL (mm)	# Consumed	FL (mm)	# Consumed	FL (mm)	# Consumed	FL (mm)	Total 2007
Steelhead/rainbow trout	-	-	-	-	-	-	108,628	49	108,628
Coho Salmon	19,520	73	247	76	-	70	322	70	20,089
Resident Fishes	-	90	-	98	9,503	55	-	66	9,503
Mainstem									
Chinook Salmon	2,252	35	30,741	35	-	-	-	-	43,250
	213	80	9,710	65	334	65	-	-	-
Steelhead/rainbow trout	-	-	11,640	78	-	-	-	-	35,280
	676	78	12,588	106	9,016	60	1,359	126	-
Coho Salmon	771	73	9,964	76	2,087	70	-	-	12,822
Chum Salmon	-	-	152,251	27	3,857	27	-	-	156,108
Pacific Salmon Fry/Alevin	203,896	27	63,205	27	3,876	55	11,111	20	282,087
Resident Fishes	2,867	90	7,934	98	57,340	82	3,000	66	71,141

Table 9. (Continued) Estimated individual prey fish consumed by a unit population of n=1000 bull trout >300mm in the Skagit River Tributaries and mainstem in 2007 and winter/spring 2008. Numbers for tributary feeding represent bull trout <300 mm

	Winter		Spring		
Tributary	# Consumed	FL (mm)	# Consumed	FL (mm)	Total 2008
Coho Salmon	-	-	181,189	40	181,189
Pacific Salmon Fry/Alevin	-	-	283,320	25	283,320
Mainstem					
Chinook Salmon	5,601	36	8,640	34	14,241
Steelhead/rainbow trout	565	59	18,786	83	19,352
Coho Salmon	-	-	3,315	40	3,315
Pink Salmon	44,986	24	540,983	27	585,968
Pacific Salmon Fry/Alevin	275,143	27	65,167	25	459,842
	-	-	119,531	45	-
Resident Fishes	186,682	23	-	-	-
	1,645	115	10,352	65	198,678

Table 10. Consumption scenarios based on bioenergetics model simulations for various population sizes of bull trout in the Skagit River, WA.

		Bull trout Population size						
2007	Age Class (length range (mm))	n = 1,000	n = 1,600	n = 2,000	n = 4,000	n = 10,000	n = 15,000	n = 30,000
Tributary								
Steelhead/rainbow trout	0+ (25-65)	108,628	173,805	217,257	434,513	1,086,284	1,629,426	3,258,851
Coho	1+ (60-90)	12,822	20,515	25,644	51,289	128,222	192,332	384,665
Mainstem								
Chinook	0+ (30-90)	42,703	68,325	85,406	170,813	427,032	640,548	1,281,096
	1+ (>90)	547	876	1,094	2,189	5,472	8,208	16,416
Steelhead/rainbow trout	0+ (25-65)	9,016	14,426	18,032	36,065	90,162	135,243	270,486
	1+ (65-150)	26,264	42,022	52,528	105,056	262,640	393,960	787,920
Coho	1+ (60-90)	12,822	20,515	25,644	51,289	128,222	192,332	384,665
2008								
Tributary								
Coho	0+ (30-60)	181,189	289,903	362,378	724,756	1,811,891	2,717,836	5,435,672
Mainstem								
Chinook	0+ (30-40)	14,241	22,786	28,482	56,964	142,409	213,614	427,228
Steelhead/rainbow trout	0+ (25-65)	565	905	1,131	2,261	5,653	8,480	16,960
	1+ (65-150)	18,786	30,058	37,573	75,146	187,865	281,797	563,594
Coho	0+ (30-60)	184,504	295,206	369,008	738,015	1,845,038	2,767,558	5,535,115

Appendix

Two indices were used to characterize bull trout diets; mean proportion by weight MW_i and proportion by weight W_i (Chipps and Garvey 2007):

$$MW_i = \frac{1}{P}\sum_{j=1}^{P}\left(\frac{M_{ij}}{\sum_{i=1}^{Q} M_{ij}}\right)$$

$$W_i = \frac{M_i}{\sum_{i=1}^{Q} M_i}$$

where, i is a diet item, j is the number of fish, Q is the number of diet categories, P is the number of non-empty stomachs, and M_i is the weight (g wet mass) of prey type i.

MW_i estimates the diet proportions for individual stomachs first, then these proportions are averaged across all non-empty stomach samples within a combination of time, consumer size, and habitat strata. In contrast, W_i is an estimate of average diet proportions by weight when all gut contents are pooled across samples within any time-size-habitat stratum.

MW_i, is generally used to track energy flow through the ecosystem (Chipps and Garvey 2007) suggesting that this is a more representative measure of diet and produces less volatile estimates of diet composition (Beauchamp et al. 2007). This method allows researchers to identify the regular feeding habits of the population and reduces bias from rare large prey items found in the stomach due to opportunistic feeding events. Since this method reduces the influence of large novel diet items, it seems appropriate for characterization of a generalist consumer diet. Chipps and Garvey (2007) state that W_i has been used to describe the potential impacts of predator-prey interactions, but give no specific rationale for that statement, whereas Beauchamp et al. (2007) advocated using MW_i for predation studies. Other experiences have noted that the W_i method generally yields higher predation estimates than MW_i, but can overestimate the contribution of rare large diet items. Due to the uncertainty associated with potential differences in predation estimates generated by these two methods, I compared diet and consumption resulting from the MW_i *and* W_i methods to quantify the sensitivity of predation estimates to these different diet computations. Once the diet proportions were calculated they were compared to frequency of occurrence, O_i, where $O_i = J_i/P$, to determine whether differences between MW_i and W_i, for key prey, could be explained by large, rare prey items consumed by a small fraction of predators.

Diet Composition Differences Between MW_i *and* W_i

The diet proportions calculated using MW_i (Table A1) and W_i (Table A2) were markedly different. When comparing MW_i and W_i to the frequency of occurrence O_i of key prey categories, WM_i detected 99% of the diet items targeted by bull trout while missing occurrences of terrestrial insects in two season-size class strata and other food in one stratum. In contrast, *Wi* detected 95% of the diet items consumed by bull trout and failed to detect terrestrial insects in six strata, carcass (three strata), salmon fry (three strata), other food (four strata), and one stratum each for steelhead/rainbow trout, chum salmon, and fish eggs.

In general W_i estimated higher proportions of steelhead/rainbow trout, coho salmon, bull trout, pink salmon, resident fishes, fish eggs, and other food compared to MW_i, whereas MW_i estimated higher proportions of Chinook salmon, chum salmon, salmon fry/alevin, salmon carcass, immature aquatic invertebrates, and adult or terrestrial invertebrates. These results followed the expected trend of the W_i index estimating greater proportions of larger bodied prey and MW_i calculating higher proportions of smaller bodied prey with pink salmon being the only exception. One notable comparison was an incidence of anthropogenic allochthonous input, food scraps (chicken) found in one bull trout, weighing 83g resulted in W_i of the other food category contributing 30% to bull trout diets. However, when the chicken was removed from the calculation, the other food category only represented 3.6% of the diets.

Modeling Consumption

The age 3 (96-300mm) transitional size class was caught in low numbers and an accurate growth rate was not measurable, therefore estimated growth and consumption for this size class should be considered a maximum estimate. More accurate growth and diet data are needed to increase the precision of consumption estimates.

Model Outputs using MW_i

Model simulations for 2007 indicated that juvenile bull trout in tributary habitats were feeding between 28% and 36% of C_{max}. The age 3 fish transitioning from tributary to main stem habitats exhibited a higher apparent feeding rate at 62% of C_{max}. Sub-adults and mature fish were feeding between 20% and 25% of their theoretical C_{max}. Growth efficiencies (GE) in tributary habitats ranged 7-10%. Age 3 fish exhibited 21% GE and sub-adult and first time spawners ranged 11-13%, and GE for larger mature fish ranged 3%-11% (Table A3).

In winter and spring 2008 juvenile bull trout in the tributaries and transitional age 3 were feeding at 28%-35% C_{max} while the sub-adult and adult fish fed at 19%-25% C_{max}. Growth efficiency in tributary habitats ranged from 13%-

18%, age 3 fish had a GE of 39% and sub-adults and adults showed growth efficiencies of 5%-13% for the two seasons (Table A3).

Simulations for 2007 predicted that a unit population of 1,000 bull trout >300mm consumed 1,896 kg of food annually of which 634 kg were fish (Figure A1). The top five contributors to annual bull trout diets were: 478 kg of Pacific salmon carcass flesh, 394 kg of fish eggs (primarily Pacific salmon), 296 kg of resident fishes (primarily sculpin spp. and dace spp.), 289 kg of aquatic invertebrates, and 128 kg of Pacific salmon fry/alevin. Predation on juvenile Pacific salmon was higher in winter and spring 2007 and 2008. Those values are as follows: in winter and spring 2007, the top five diet contributors were; aquatic invertebrates 197kg, Pacific salmon carcass 172kg, Pacific salmon fry/alevin 102kg, resident fishes (primarily sculpin spp. and dace spp.) 77kg, and steelhead/rainbow trout 58kg. Chinook salmon contributed 23 kg of the total consumption of which 22 kg were consumed in winter and spring. In winter/spring 2008 bull trout consumed 817kg of food, 348kg were fish, with aquatic invertebrates 244kg, Pacific salmon carcass 133kg, Pacific salmon fry/alevin 106kg, resident fishes 78kg (primarily dace spp. and mountain whitefish), and pink salmon 73kg, and comprising the top five contributors to total consumption (Figure A1**)**. In winter spring 2008 50.7 kg of Chinook salmon fry/parr and 29kg of steelhead/rainbow trout were consumed.

Model Outputs using W_i

Model simulations for 2007 indicated that juvenile bull trout in tributary habitats were feeding between 28% and 35% of C_{max}. The age 3 fish transitioning from tributary to main stem habitats exhibited a high feeding rate at 54% of C_{max}. Sub-adults and mature fish were feeding between 20% and 25% of their theoretical C_{max}. Growth efficiencies (GE) in tributary habitats ranged from 7% -10%. Age 3 fish exhibited 24% GE, sub-adult and first time spawners ranged from 13%-15%, and larger mature fish ranged from 3%-11% (Table A3).

In winter and spring 2008 juvenile bull trout in the tributaries and transitionary age 3 were feeding at 28%-35% C_{max} while the sub-adult and adult fish fed at 16%-22% C_{max}. Growth efficiency in tributary habitats ranged from 13%-17%, age 3 fish had a GE of 41% and sub-adults and adults showed growth efficiencies of 0%-12% for the two seasons (Table A3).

Simulations for 2007 predicted that a unit population of 1000 bull trout >300mm consumed 1739kg of food annually including 976 kg of fish (Figure A2). The top five contributors to annual bull trout diets were: 451kg of resident fishes (primarily sculpin spp. and dace spp.), 440 kg of fish eggs (primarily Pacific Salmon), 327 kg of steelhead/rainbow trout, 144 kg of Pacific salmon carcass, and 93 kg of aquatic insects (Figure A2). In winter and spring, 1000 bull trout consumed 735 kg of food 531 of which were fish. Major contributors to bull trout diets were; steelhead/rainbow trout 268 kg, Pacific salmon carcass 144kg, resident fishes 70kg, coho salmon 65kg, and Chinook salmon fry and parr 48kg. In winter and spring 2008 1000 bull trout consumed 640 kg of food 407 of which were fish. Top contributors to bull trout diets were: steelhead/rainbow trout 140kg, resident fishes 91 kg, pink salmon 77kg, aquatic insects 69kg, and other 63kg. In winter spring 2008 5kg of Chinook salmon fry and parr were consumed (Figure A2).

Estimated Energy Budgets

The contributions of various prey to the annual energy budget (total consumption x energy density of prey) of bull trout varied by size class. On an annual basis MW_i (Figure A3) predicted that ages 1-3 are supported in tributary habitats primarily by aquatic invertebrates (99% for age 1and 2, and 60% for age 3), age 4 and older are supported mostly by eggs (38-40%), resident fishes (age 4 and 5 11% and age 6-9 21%-22% primarily sculpin and dace spp), and carcass flesh (age 4 and 5 16% and age 6-9 8%-9%) with lower contributions from juvenile salmon and steelhead/rainbow trout and invertebrates. Winter and spring were predicted as the seasons where the majority of energy intake occurs in age 1-2 bull trout at 44%. In age 3 transitionary bull trout energy intake was highest, 75%, in summer and spring. In the larger size classes fall and summer were the seasons of highest energy intake and showed the following pattern: 301-450mm 66%, and >450 68%. This differed from total consumption (Figure A1) where summer followed by spring uniformly comprised the majority of consumption for all sized bull trout (30-300mm 72%-78% and >300mm 61%-62%). The proportion of annual consumption in fall always ranked 3rd after summer and spring while the majority of energy intake always occurred in fall (37%-38%) in fish >300mm. Winter consumption and energy intake ranked consistently last in all size classes.

W_i estimated energy budget (Figure A4)for ages 1-2 in tributary habitats is primarily (95%-96%) aquatic invertebrates, age 3 energy budget was more varied with aquatic invertebrates (34%), terrestrial invertebrates (29%), and resident fishes (18% unidentified non-salmonid) as major contributions to annual energy budget. Age 4 and older fish are supported mostly by eggs (38%-43%), resident fishes (age 4and 5 20% and age 6-9 26%-27% primarily sculpin and dace spp., and mountain whitefish), and steelhead/rainbow trout (15-18%) with lower contributions from juvenile Pacific salmon and Pacific salmon carcass. W_i structured total seasonal energy budget was similar for juveniles and sub-adults and varied from that of fish >300mm. Fall and summer were predicted as the seasons where the majority of energy intake occurs. This differs from total consumption (Figure A2) where summer followed by spring uniformly comprised the majority of consumption for all size classes. The proportion of annual consumption in fall always ranked 3rd after summer and spring while the majority of energy intake always occurred in the fall in fish >300mm. Winter consumption and energy intake ranked consistently last in all size classes.

Predation Estimates

Total predation by an estimated 1,600 bull trout >300mm on key salmonids ranged seasonally in the Skagit River with the majority of predation occurring in the main stem in the winter during emergence and in the spring during out-migration.

Estimates using MW_i

Total stream-type (yearling) estimated Chinook salmon predation by bull trout was 589 in 2007 with none detected in 2008. Yearling steelhead/rainbow trout were consumed in greater numbers compared to yearling Chinook salmon in 2007, 9,986, and 5,484 in 2008. Estimated ocean-type Chinook fry and parr predation was 31,410 in 2007 and 207,915 in 2008. Steelhead/rainbow trout fry/parr saw a loss of 13,559 in 2007 and 2,458 in 2008. Coho predation was estimated in 2007 at 11,120 yearlings consumed and no sub-yearlings compared to 128,133 sub-yearlings and no yearlings consumed in 2008. Chum salmon were consumed in high numbers with 808,919 consumed in 2007 and none detected in 2008. Pink salmon experienced high predation rates in 2008 with a loss of 907,826 individuals. Unidentified Pacific salmon fry, parr, and alevin showed the highest number of individuals consumed, 969,851, in 2007 and 1,638,619 in 2008 **(**Table A4**)**.

Estimates using W_i

Total stream-type (yearling) estimated Chinook salmon predation by bull trout was 876 in 2007 with none detected in 2008. Yearling steelhead/rainbow trout were consumed in higher numbers than yearling Chinook salmon in 2007, 42,022, and 30,058 in 2008. Estimated ocean-type Chinook fry and parr predation was 68,325 in 2007 and 22,786 in 2008. Steelhead/rainbow trout fry/parr saw a loss of 14,426 in 2007 and 905 in 2007. Coho predation was estimated in 2007 at 20,515 yearlings consumed and no sub-yearlings compared to 295,206 sub-yearlings and no yearlings consumed in 2008. Chum salmon were consumed in high numbers with 249,772 consumed in 2007 and none detected in 2008. Pink salmon experienced high predation rates in 2008 with a loss of 937,549 individuals. Unidentified Pacific salmon fry, parr, and alevin showed the highest number of individuals consumed, 451,340, in 2007 and 735,747, in 2008 **(**Table A5**)**.

Consumption Scenarios

The above total predation rates were calculated for a population level of 1600 bull trout based on the base unit of n = 1000 bull trout >300mm. It is also informative to think of predation in a system-wide context. Since the total basin-wide population level is unknown it is useful to consider predation rates on key species by different population sizes of bull trout (Tables A6 and A**7**). This allows researchers and natural resource managers to gauge the impact of predation on the population as a whole.

Both diet indices predicted predation mortality for stream-type and ocean-type anadromous salmonids with W_i predicting higher predation than MW_i for stream-type fish. Both estimates should be considered when assessing the potential impact of bull trout predation with W_i estimates constituting an upper bound and MW_i representing a mid point for total predation. Both indices indicated a possible negative effect on steelhead/rainbow trout yearlings in 2007 and 2008 and a negligible effect on Chinook populations for both years.

Figures and Tables

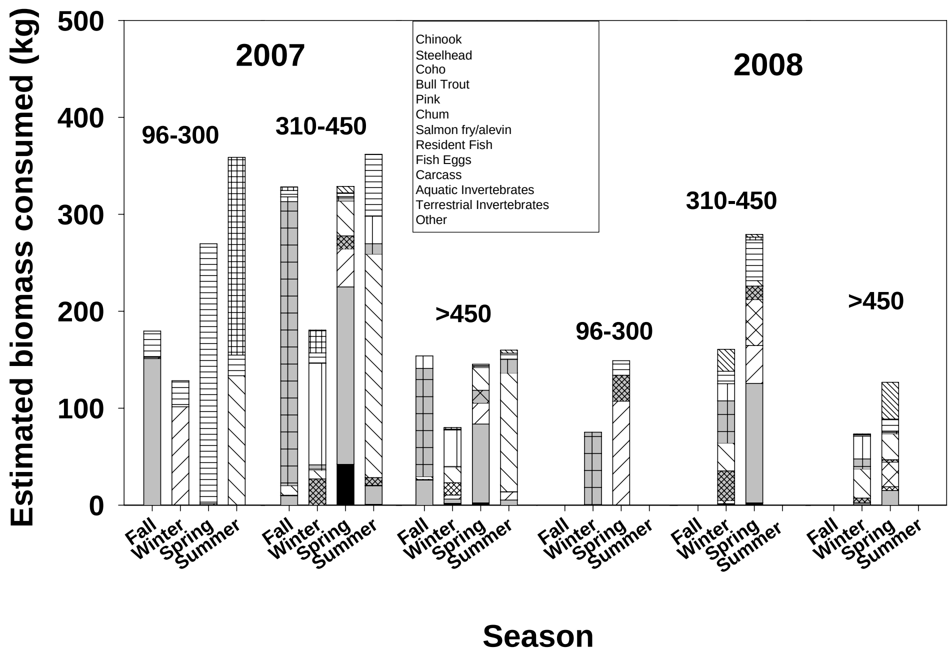

Figure A1. Population-level consumption estimates for a unit population of n = 1000 Skagit River bull trout >300mmcaught in 2007 and winter and spring 2008, based on diet composition computed with the MW_i method.

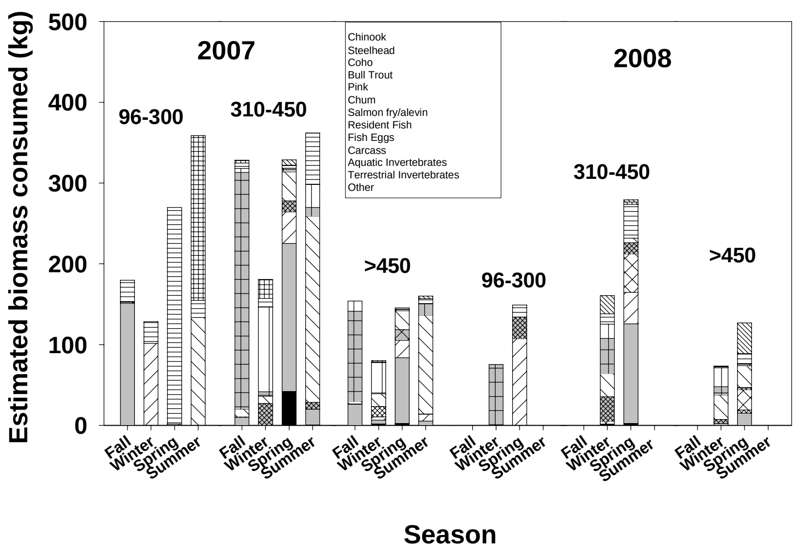

Figure A2. Population-level consumption estimates for a unit population of n = 1000 Skagit River bull trout >300mm caught in 2007 and winter and spring 2008, based on diet composition computed with the W_i method.

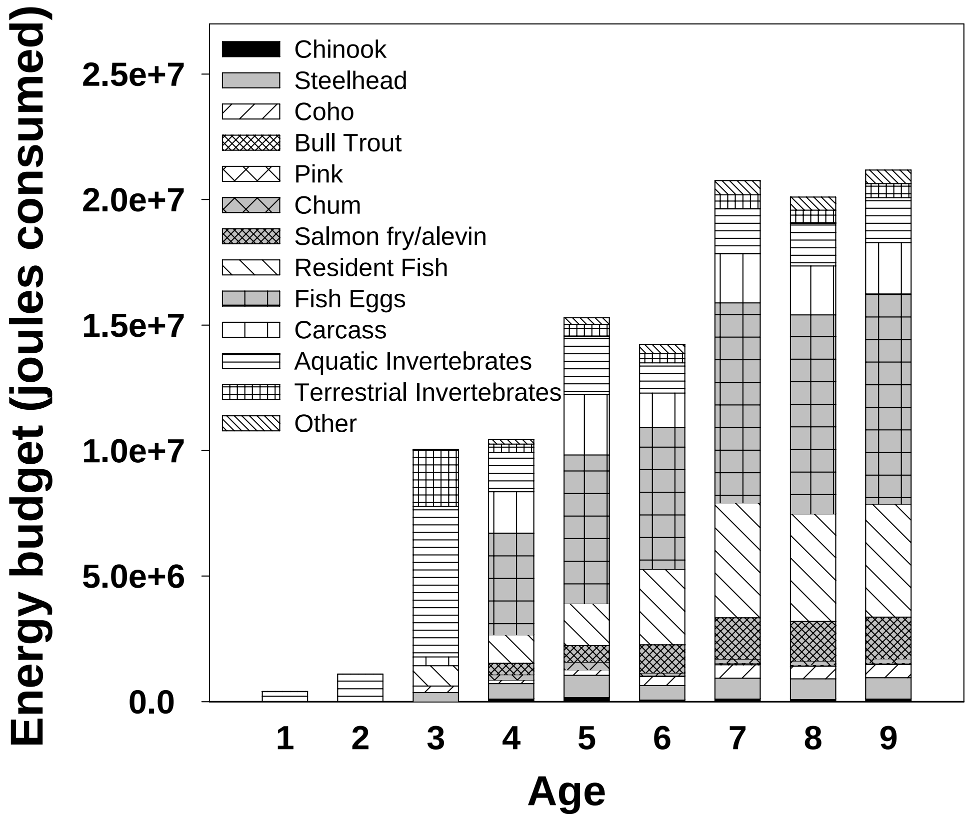

Figure A3. The estimated contribution of each prey category to the annual energy budget, by age, of bull trout, based on diets computed with the MW_i method.

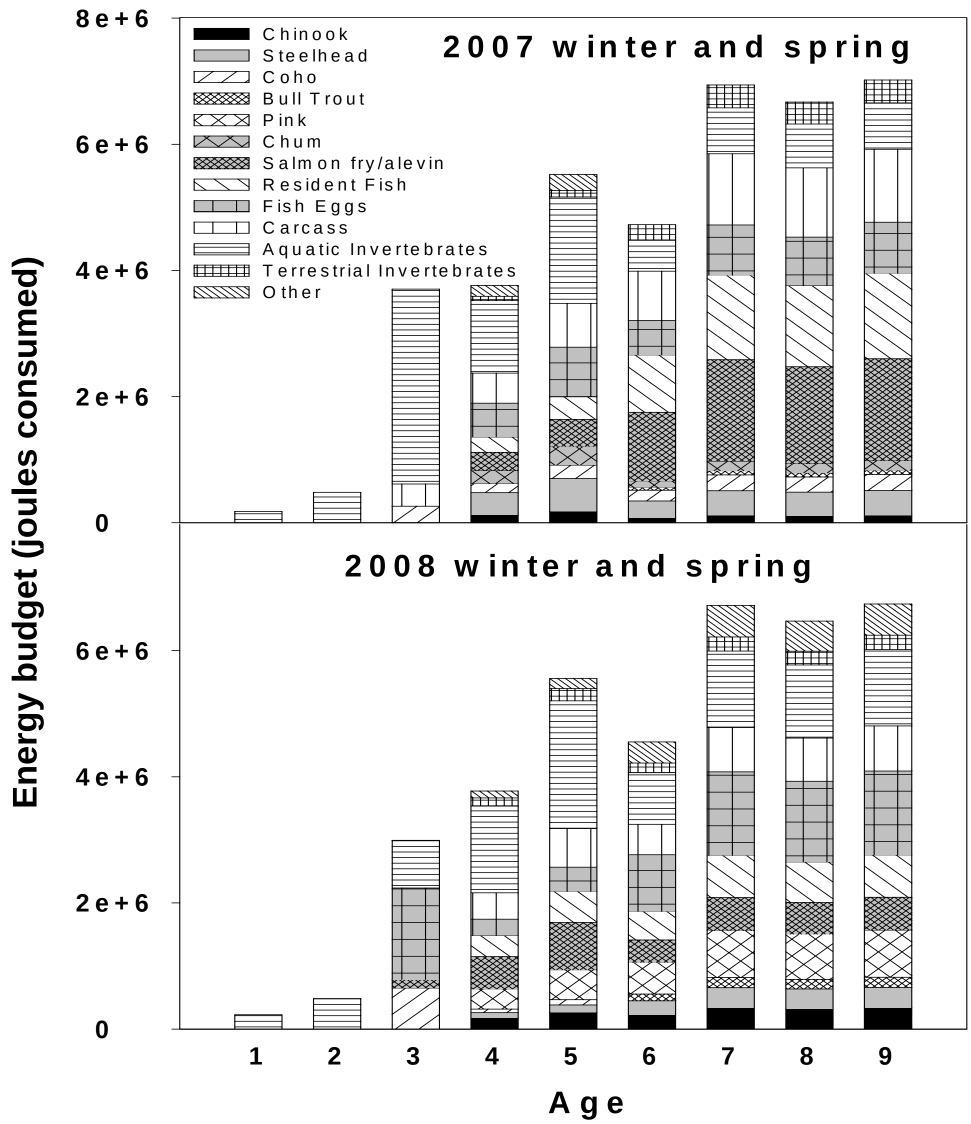

Figure A3 continued. The estimated contribution of each prey category to the energy budget in winter spring of 2007 and 2008, by age, of bull trout, based on diets computed with the MW_i method.

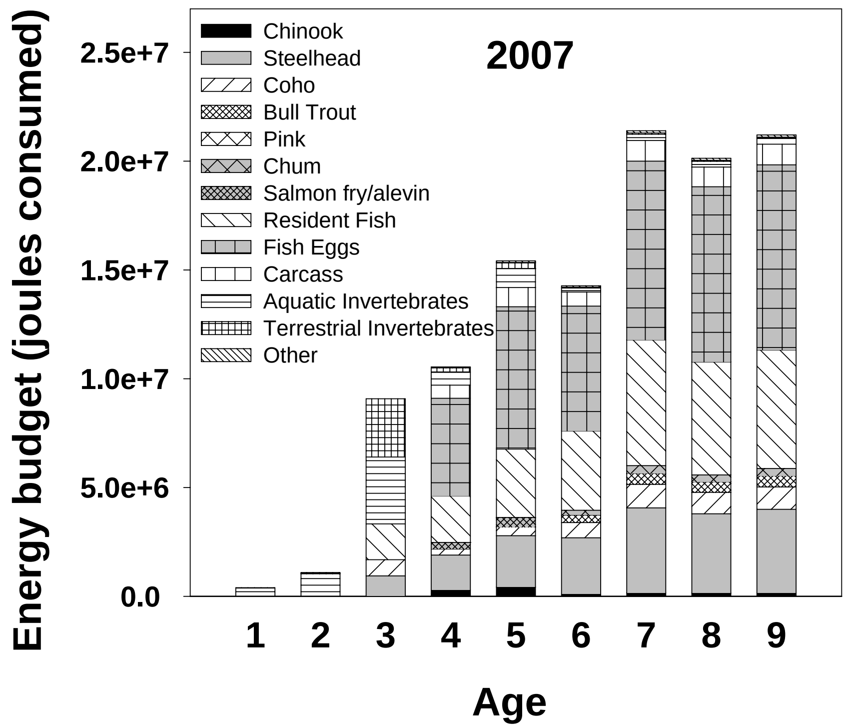

Figure A4. The estimated contribution of each prey category to the annual energy budget by age of bull trout, based on the diets computed with the W_i method.

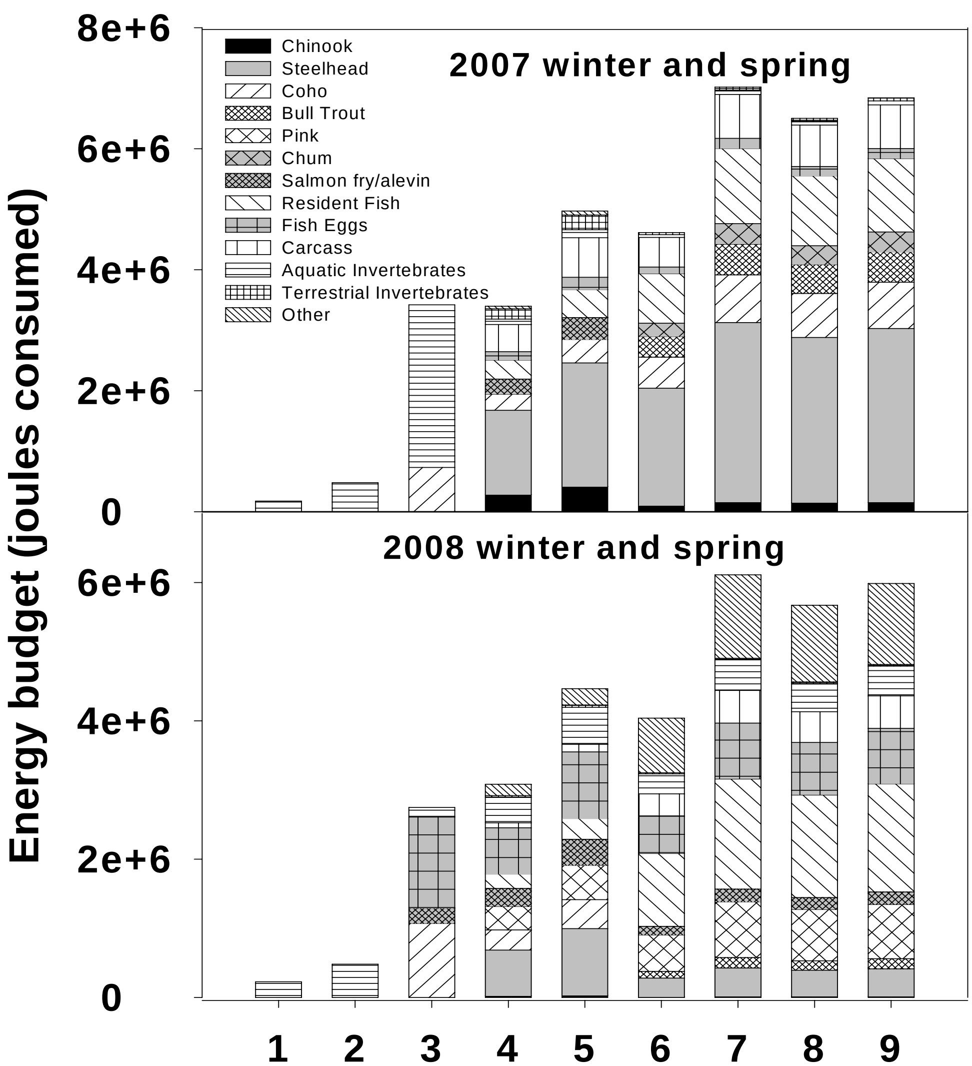

Figure A4continued. The estimated contribution of each prey category to the energy budget in winter spring of 2007 and 2008, by age, of bull trout, based on diets computed with the W_i method.

Table A1. Seasonal and size structured diet proportions of bull trout captured in 2007 and winter and spring 2008 calculated using the MW_i diet index (“M” and “T” indicate main stem and tributary habitats. Where n = 0 diet composition was not estimated.

	Season	Size class	n	Chinook Salmon	Steelhead / rainbow trout	Coho Salmon	Bull Trout	Pink Salmon	Chum Salmon	Pacific salmon fry/alevin	Resident Fishes	Fish Eggs	Pacific Salmon Carcass	Aquatic Invertebrates	Terrestrial Invertebrates	Other
2007	Autumn	30-95 T	19	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.98	0.02	0.00
	Winter	30-95 T	0	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Spring	30-95 T	8	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00
	Summer	30-95 T	26	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.99	0.01	0.00
	Autumn	96-300 T	16	0.00	0.28	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.69	0.00	0.03
	Winter	96-300 T	0	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Spring	96-300 T	2	0.00	0.00	0.40	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.60	0.00	0.00
	Summer	96-300 T	16	0.00	0.00	0.31	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.67	0.02	0.00
	Autumn	96-300 M	1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00
	Winter	96-300 M	1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00
	Spring	96-300 M	2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00
	Summer	96-300 M	5	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.16	0.00	0.00	0.42	0.42	0.00
	Autumn	301-450	46	0.00	0.04	0.00	0.00	0.00	0.00	0.02	0.14	0.55	0.23	0.02	0.00	0.00
	Winter	301-450	18	0.00	0.00	0.00	0.00	0.00	0.00	0.09	0.01	0.04	0.46	0.35	0.05	0.00
	Spring	301-450	16	0.05	0.13	0.06	0.00	0.00	0.10	0.08	0.09	0.07	0.06	0.29	0.00	0.07
	Summer	301-450	18	0.00	0.04	0.00	0.00	0.00	0.00	0.04	0.19	0.10	0.43	0.12	0.08	0.00
	Autumn	>450	38	0.00	0.05	0.00	0.00	0.00	0.00	0.00	0.01	0.59	0.30	0.05	0.00	0.00
	Winter	>450	27	0.03	0.01	0.01	0.02	0.00	0.00	0.03	0.13	0.08	0.62	0.05	0.02	0.00
	Spring	>450	40	0.01	0.07	0.05	0.00	0.00	0.04	0.35	0.21	0.03	0.05	0.13	0.06	0.00
	Summer	>450	12	0.00	0.03	0.05	0.00	0.00	0.00	0.00	0.54	0.10	0.00	0.15	0.03	0.10
2008	Winter	30-95	0	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Spring	30-95	6	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00
	Winter	96-300 T	1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00
	Spring	96-300 T	2	0.00	0.00	0.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.50	0.00	0.00
	Winter	96-300 M	2	0.00	0.00	0.00	0.00	0.50	0.00	0.00	0.00	0.00	0.00	0.43	0.07	0.00
	Spring	96-300 M	2	0.00	0.00	0.40	0.00	0.00	0.00	0.10	0.00	0.00	0.00	0.50	0.00	0.00
	Winter	301-450	32	0.13	0.00	0.00	0.00	0.01	0.00	0.15	0.11	0.06	0.26	0.24	0.01	0.04
	Spring	301-450	34	0.02	0.04	0.02	0.00	0.12	0.00	0.14	0.08	0.01	0.11	0.40	0.04	0.02
	Winter	>450	56	0.19	0.05	0.00	0.00	0.05	0.00	0.05	0.07	0.11	0.32	0.06	0.09	0.01
	Spring	>450	73	0.00	0.07	0.00	0.03	0.15	0.00	0.11	0.13	0.07	0.08	0.24	0.00	0.11

Table A2. Seasonal and size structured diet proportions of bull trout captured in 2007 and winter and spring 2008 calculated using the W_i diet index ("M" and "T" indicate main stem and tributary habitats. Where n = 0 diet composition was not estimates.

	Wi		n	Chinook salmon	Steelhead / rainbow trout	Coho Salmon	Bull Trout	Pink Salmon	Chum Salmon	Pacific Salmon fry/alevin	Resident Fish	Fish Eggs	Pacific Salmon Carcass	Aquatic Invertebrates	Terrestrial Invertebrates	Other
2007	Autumn	30-95 T	19	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.78	0.22	0.00
	Winter	30-95 T	0	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Spring	30-95 T	7	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00
	Summer	30-95 T	25	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.98	0.02	0.00
	Autumn	96-300 T	16	0.00	0.85	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.15	0.00	0.00
	Winter	96-300 T	0	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Spring	96-300 T	2	0.00	0.00	0.79	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.21	0.00	0.00
	Summer	96-300 T	16	0.00	0.00	0.83	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.17	0.00	0.00
	Autumn	96-300 M	1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00
	Winter	96-300 M	1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00
	Spring	96-300 M	2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00
	Summer	96-300 M	5	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.38	0.00	0.00	0.04	0.58	0.00
	Autumn	301-450	46	0.00	0.03	0.00	0.00	0.00	0.00	0.00	0.03	0.90	0.01	0.02	0.01	0.00
	Winter	301-450	18	0.00	0.00	0.00	0.00	0.00	0.00	0.15	0.05	0.03	0.58	0.06	0.13	0.00
	Spring	301-450	16	0.13	0.56	0.12	0.00	0.00	0.00	0.04	0.11	0.01	0.00	0.01	0.00	0.02
	Summer	301-450	18	0.00	0.04	0.00	0.00	0.00	0.00	0.02	0.65	0.03	0.08	0.18	0.00	0.00
	Autumn	>450	41	0.00	0.17	0.00	0.00	0.00	0.00	0.00	0.02	0.73	0.08	0.00	0.00	0.00
	Winter	>450	27	0.03	0.05	0.05	0.16	0.00	0.00	0.00	0.20	0.01	0.47	0.01	0.02	0.00
	Spring	>450	40	0.02	0.56	0.15	0.00	0.00	0.09	0.00	0.16	0.01	0.00	0.01	0.00	0.00
	Summer	>450	12	0.00	0.02	0.05	0.00	0.00	0.00	0.00	0.78	0.09	0.00	0.04	0.00	0.02
2008	Winter	30-95	0	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Spring	30-95	10	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00
	Winter	96-300 T	1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00
	Spring	96-300 T	2	0.00	0.00	0.99	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00
	Winter	96-300 M	2	0.00	0.00	0.00	0.00	0.63	0.00	0.00	0.00	0.00	0.00	0.32	0.05	0.00
	Spring	96-300 M	2	0.00	0.00	0.72	0.00	0.00	0.00	0.18	0.00	0.00	0.00	0.10	0.00	0.00
	Winter	301-450	32	0.01	0.00	0.00	0.00	0.02	0.00	0.18	0.18	0.28	0.11	0.08	0.00	0.14
	Spring	301-450	34	0.01	0.44	0.14	0.00	0.17	0.00	0.05	0.02	0.00	0.00	0.15	0.01	0.01
	Winter	>450	56	0.01	0.02	0.00	0.00	0.01	0.00	0.06	0.41	0.14	0.32	0.02	0.01	0.00
	Spring	>450	74	0.00	0.12	0.00	0.03	0.20	0.00	0.02	0.21	0.01	0.01	0.10	0.00	0.30

Table A3. Individual age structured consumption estimates of bull trout in the Skagit River using the MW_i, W_i indices fitted to initial and final mass, and spawning losses.

2007						MW_i Approach			W_i Approach	
Age	Size Classes	Initial/Final Mass (g)	Spawning Loss (% body weight)	Total Growth (g)	p-Value	Total Consumption (g)	Growth Efficiency	p-Value	Total Consumption (g)	Growth Efficiency
1	30-95	0.3-11	0	10	0.36	107	10%	0.35	107	10%
2	30-95	11-26	0	15	0.28	220	7%	0.28	219	7%
3	96-300	26-442	0	417	0.62	1998	21%	0.54	1744	24%
4	301-450	442-676	0	233	0.23	1778	13%	0.20	1607	15%
5	301-450	676-972	9.8%	296	0.25	2605	11%	0.22	2350	13%
6	>450	972-1044	11.6%	72	0.20	2313	3%	0.23	2171	3%
7	>450	1044-1408	13.7%	364	0.25	3396	11%	0.25	3297	11%
8	>450	1408-1543	13.7%	135	0.22	3270	4%	0.20	3067	4%
9	>450	1543-1668	13.7%	125	0.22	3444	4%	0.20	3229	4%
2008										
1	30-95	2.3-8.4	0	8	0.35	47	18%	0.35	47	17%
2	30-95	19-23	0	13	0.28	100	13%	0.28	100	13%
3	96-300	90-316	0	170	0.30	438	39%	0.28	399	41%
4	301-450	695-707	0	85	0.25	821	10%	0.17	607	5%
5	301-450	1024-1041	9.8%	150	0.27	1209	12%	0.19	880	7%
6	>450	1274-1138	11.6%	45	0.19	916	5%	0.16	831	0%
7	>450	1500-1495	13.7%	182	0.24	1352	13%	0.22	1259	12%
8	>450	1830-1683	13.7%	100	0.20	1302	8%	0.18	1167	3%
9	>450	1990-1823	13.7%	95	0.20	1356	7%	0.18	1232	3%

Table A4**.** Estimated individual prey fish consumed by a unit population of n=1000 bull trout >300mm in the Skagit River in 2007 and winter/spring 2008, using the MW_i index. Numbers for bull trout <300 mm represent tributary feeding.

	Winter		Spring		Summer		Fall		
	# Consumed	FL (mm)	# Consumed	FL (mm)	# Consumed	FL (mm)	# Consumed	FL (mm)	Total 2007
Chinook Salmon	222	80	4,196	65	146	65	-	-	19,999
	2,346	35	13,089	35	-	-	-	-	-
Steelhead/rainbow trout	141	78	2,751	106	8,475	60	851	126	14,716
	-	-	2,499	78	-	-	-	-	-
<300mm	-	-	-	-	-	-	41,418	49	41,418
Coho Salmon	160	73	4,774	76	2,016	70	-	-	6,950
	-	-	-	-	-	-	-	-	-
<300mm	6,971	73	86	76	-	70	119	70	7,175
Chum Salmon	-	-	492,831	27	12,743	27	-	-	505,574
Pink Salmon	-	-	-	-	-	-	-	-	-
Pacific Salmon Fry/Alevin	149,522	27	386,295	27	9,511	55	60,830	20	606,157
	-	-	-	-	-	-	-	-	-
<300mm	-	-	-	-	-	-	-	-	-
Resident Fishes	1,460	90	2,607	90	16,565	82	11,781	66	49,243
	-	-	5,998	90	10,831	82	-	-	
<300mm	-	90	-	90	4,618	55	-	66	4,618

Table A4. Continued Estimated individual prey fish consumed by a unit population of n=1000 bull trout >300mm in the Skagit River in 2007 and winter/spring 2008, using the MW_i index. Numbers for bull trout <300 mm represent tributary feeding.

	Winter		Spring		
	# Consumed	FL (mm)	# Consumed	FL (mm)	Total 2008
Chinook Salmon	103,040	36	26,907	34	129,947
	-	-	-	-	-
Steelhead/rainbow trout	1,536	59	3,428	83	4,964
	-	-	-	-	-
<300mm	-	-	-	-	-
Coho Salmon	-	-	8,421	40	8,421
	-	-	-	-	-
<300mm	-	-	71,662	40	71,662
Chum Salmon	-	-	-	-	-
Pink Salmon	69,932	24	497,459	27	567,391
Pacific Salmon Fry/Alevin	284,994	27	276,548	25	1,024,137
	-	-	462,595	45	-
<300mm	-	27	172,549	25	172,549
Resident Fishes	813	115	15,148	65	15,962
	-	-	-	-	-
<300mm	-	-	-	-	-

Table A5**.** Estimated individual prey fish consumed by a unit population of n=1000 bull trout >300mm in the Skagit River in 2007 and winter/spring 2008, using the W_i index. Numbers for bull trout <300 mm represent tributary feeding.

	Winter		Spring		Summer		Fall		
	# Consumed	FL (mm)	# Consumed	FL (mm)	# Consumed	FL (mm)	# Consumed	FL (mm)	Total 2007
Chinook Salmon	213	80	9,710	65	334	65	-	-	43,250
	2,252	35	30,741	35	-	-	-	-	-
Steelhead/rainbow trout	676	78	12,588	106	9,016	60	1,359	126	35,280
	-	-	11,640	78	-	-	-	-	-
<300mm	-	-	-	-	-	-	108,628	49	108,628
Coho Salmon	771	73	9,964	76	2,087	70	-	-	12,822
	-	-	-	-	-	-	-	-	-
<300mm	19,520	73	247	76	-	-	322	70	20,089
Chum Salmon	-	-	152,251	27	3,857	27	-	-	156,108
Pink Salmon	-	-	-	-	-	-	-	-	-
Pacific Salmon									
Fry/Alevin	203,896	27	63,205	27	3,876	55	11,111	20	282,087
	-	-	-	-	-	-	-	-	-
<300mm	-	-	-	-	-	-	-	-	-
Resident Fishes	2,867	90	2,404	90	34,649	82	3,000	66	71,141
	-	-	5,530	90	22,691	82	-	-	
<300mm	-	-	-	-	9,503	55	-	-	9,503

Table A5. (continued) Estimated individual prey fish consumed by a unit population of n=1000 bull trout >300mm in the Skagit River in 2007 and winter/spring 2008, using the W_i index. Numbers for bull trout <300 mm represent tributary feeding.

	Winter		Spring		
	# Consumed	FL (mm)	# Consumed	FL (mm)	Total 2008
Chinook Salmon	5,601	36	8,640	34	14,241
	-	-	-	-	-
Steelhead/rainbow trout	565	59	18,786	83	19,352
	-	-	-	-	-
<300mm	-	-	-	-	-
Coho Salmon	-	-	3,315	40	3,315
	-	-	-	-	-
<300mm	-	-	181,189	40	181,189
Chum Salmon	-	-	-	-	-
Pink Salmon	44,986	24	540,983	27	585,968
Pacific Salmon Fry/Alevin	275,143	27	65,167	25	459,842
	-	-	119,531	45	-
<300mm	-	27	283,320	25	283,320
Resident Fishes	1,645	115	10,352	65	198,678
	186,682	-	-	-	-
<300mm	-	-	-	-	-

Table A6. Consumption scenarios using the MW_i diet index based on bioenergetics model simulations for various population sizes of bull trout in the Skagit River, WA.

MWi		Bull trout Population size						
2007	Age Class (length range (mm))	n = 1,000	n = 1,600	n = 2,000	n = 4,000	n = 10,000	n = 15,000	n = 30,000
Chinook	0+ (30-90)	19,632	31,410	39,263	78,526	196,315	294,473	588,945
	1+ (>90)	368	589	736	1,472	3,680	5,519	11,039
Steelhead	0+ (25-65)	8,475	13,559	16,949	33,899	84,747	127,120	254,240
	1+ (65-150)	6,242	9,986	12,483	24,966	62,415	93,623	187,245
	0+ (Tributary)	41,418	66,268	82,835	165,670	414,175	621,263	1,242,526
Coho	0+ (30-60)	-	-	-	-	-	-	-
	1+ (60-90)	6,950	11,120	13,900	27,800	69,500	104,250	208,499
	1+ (Tributary)	7,175	11,481	14,351	28,701	71,753	107,630	215,260
2008								
Chinook	0+ (30-40)	129,947	207,915	259,893	519,786	1,299,466	1,949,199	3,898,397
	1+ (40-90)	-	-	-	-	-	-	-
Steelhead	0+ (25-65)	1,536	2,458	3,073	6,146	15,365	23,047	46,094
	1+ (65-150)	3,428	5,484	6,855	13,711	34,277	51,416	102,832
Coho	0+ (30-60)	80,083	128,133	160,166	320,332	800,830	1,201,244	2,402,489
	1+ (60-90)	-	-	-	-	-	-	-
	0+ (Tributary)	71,662	114,660	143,325	286,649	716,623	1,074,935	2,149,869

Table A7. Consumption scenarios using the W_i diet index based on bioenergetics model simulations for various population sizes of bull trout in the Skagit River, WA.

		Bull trout Population size						
2007	Age Class (length range (mm))	n = 1,000	n = 1,600	n = 2,000	n = 4,000	n = 10,000	n = 15,000	n = 30,000
Chinook	0+ (30-90)	42,703	68,325	85,406	170,813	427,032	640,548	1,281,096
	1+ (>90)	547	876	1,094	2,189	5,472	8,208	16,416
Steelhead	0+ (25-65)	9,016	14,426	18,032	36,065	90,162	135,243	270,486
	1+ (65-150)	26,264	42,022	52,528	105,056	262,640	393,960	787,920
	0+ (Tributary)	108,628	173,805	217,257	434,513	1,086,284	1,629,426	3,258,851
Coho	0+ (30-60)	-	-	-	-	-	-	-
	1+ (60-90)	12,822	20,515	25,644	51,289	128,222	192,332	384,665
	1+ (Tributary)	20,089	32,142	40,178	80,356	200,889	301,334	602,668
2008								
Chinook	0+ (30-40)	14,241	22,786	28,482	56,964	142,409	213,614	427,228
	1+ (40-90)	-	-	-	-	-	-	-
Steelhead	0+ (25-65)	565	905	1,131	2,261	5,653	8,480	16,960
	1+ (65-150)	18,786	30,058	37,573	75,146	187,865	281,797	563,594
Coho	0+ (30-60)	184,504	295,206	369,008	738,015	1,845,038	2,767,558	5,535,115
	1+ (60-90)	-	-	-	-	-	-	-