Population Dynamics and Trophic Ecology of Nonnative Lake Trout in Priest Lake, Idaho

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Authorization to Submit Thesis

This thesis of Elizabeth L. Ng, submitted for the degree of Master of Science with a Major in Natural Resources and titled “Population Dynamics and Trophic Ecology of Nonnative Lake Trout in Priest Lake, Idaho,” has been reviewed in final form. Permission, as indicated by the signatures and dates below, is now granted to submit final copies to the College of Graduate Studies for approval.

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Abstract

Nonnative Lake Trout have provided a recreational fishery in Priest Lake, Idaho, since their introduction in 1925. However, changes in the fish assemblage, declines in Lake Trout body condition, and negative interactions between Lake Trout and fishes of conservation and economic importance have prompted questions about future management goals for this Lake Trout population. Given the lack of fishery-independent information, I evaluated the demographics and trophic ecology of Lake Trout in Priest Lake. I used age-structured population models to synthesize biological information and evaluate the feasibility and trade-offs associated with eradication, trophy, and balance management scenarios. I also used stable isotope analysis to evaluate Lake Trout in a food-web context. These studies contribute directly to effective management of Lake Trout in Priest Lake, and more broadly, to our understanding of Lake Trout populations throughout North America.

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Dedication

This thesis is dedicated to my family.

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Chapter 1: General Introduction

Freshwater ecosystems have been modified extensively over the last two centuries (Warren Jr. and Burr 1994; Cowx and Gerdeaux 2004). Water resource development, nonnative species introduction, and overexploitation have contributed to changes in physical habitat, water quality, and species diversity (Moyle and Leidy 1992; Warren and Burr 1994; Wilcove et al. 1998; Sala et al. 2000; Chapin et al. 2000). Many nonnative species have been introduced accidentally or illegally (Sala et al. 2000; Sakai et al. 2001; Hickley and Chare 2004), although a substantial portion of nonnative fishes were introduced intentionally by natural resources managers, often to meet demands from the public for aquaculture or angling opportunities (Gozlan 2008; Vitule et al. 2009).

Initial attempts at stocking or transferring fishes by state and federal governments in the United States began in the early 1850s, but most were small in scale and achieved limited success (Nico and Fuller 1999). By the early 20th century, however, stocking of fishes for food and recreation became widespread. Of the seventeen most commonly introduced species in the United States, thirteen were introduced as sport fish (Rahel 2000). Like other introduced species, nonnative sport fishes may have negative interactions with native species. The practice of stocking piscivorous sport fishes can be particularly problematic because piscivores can alter prey species richness, demographics, and abundance (Findlay et al. 2000; Carpenter et al. 2001; Eby et al. 2006; Byström et al. 2007).

Despite well-documented cases of catastrophic fish introductions (Vitule et al. 2009), a minority of introduced fishes will actually become invasive (Britton et al. 2011; Hansen et al. 2013). Furthermore, self-sustaining populations of nonnative sport fishes can support socially and economically desirable recreational fisheries (e.g., Peck et al. 1999). These naturalized populations may integrate into new ecosystems with little threat to native species (Copp et al. 2005). Even if negative interactions between native and nonnative species are observed, the costs and risks of eradication may outweigh the benefits of removal (Copp et al. 2005; Zipkin et al. 2009). A pragmatic approach for some nonnative species may be to accept them as members of the fish assemblage and manage them accordingly (Copp et al. 2005). These types of management decisions depend on judgment about the costs and benefits of self-sustaining nonnative fish populations and require careful consideration of the social, economic, and biological feasibility of desired management objectives.

Like many waterbodies in the western United States, the fish assemblage in Priest Lake, Idaho, has been diversified through a series of species introductions. Historically, Priest Lake supported Westslope Cutthroat Trout *O. clarikii lewisi* and Bull Trout *Salvelinus namaycush* fisheries (Kemmerer et al. 1924; Bjornn 1957; Rieman et al. 1979). The first road to Priest Lake was constructed in 1900 and the first hotels and resorts soon followed. Although the remoteness of Priest Lake kept angler exploitation low, the lake supported an annual harvest of over 5,000 Cutthroat Trout and 2,500 Bull Trout (Bjornn 1961; Davis et al. 2000). Lake Trout *S. namaycush* were introduced to Priest Lake in 1925, but they initially remained at low abundance and contributed only a few hundred fish to the annual harvest (Crossman 1995; Martinez et al. 2009).

A late-spawning strain of kokanee *Oncorhychus nerka* was introduced to the system in 1942, 1943, and 1944, and quickly became established (Bjornn 1961; Rieman et al. 1979). The kokanee fishery was highly popular, and by the mid-1950s, kokanee contributed over 100,000 fish annually and composed nearly 95% of the harvest. Lake Trout continued to remain at low abundance, but the new prey base provided by kokanee allowed both Lake Trout and Bull Trout to reach trophy sizes (Rieman et al. 1979). In addition to trophy Lake Trout and Bull Trout, kokanee continued to provide a high-yield fishery, while Westslope Cutthroat Trout were targeted by smaller numbers of specialized anglers (Bjornn 1961; Liter et al. 2008). The balance of this artificially diverse fishery was disrupted in the late-1960s by the introduction of opossum shrimp, *Mysis diluviana*. During 1965-1967, approximately 995,000 *M. diluviana* from Kootenay Lake, British Columbia, were introduced to Priest Lake in an effort to enhance the prey base and increase kokanee production (Leusink 1968; Bowles et al. 1991). As early as 1969, *M. diluviana* had begun reproducing (Heimer 1970), and in 1972 were abundant in trawl surveys (Irizarry 1973; Bowles et al. 1991).

As with many introduced species, there was a lag in the effects of *M. diluviana* introduction. In 1974 and 1975, trophy kokanee rivaling the national record at 3.0 kg were taken from Priest Lake (Rieman et al. 1979). Lake Trout growth also increased, and in 1971, Priest Lake produced the largest Lake Trout caught by an angler outside the Great Lakes, a 1,250-mm fish weighing 26.1 kg (Martinez et al. 2009). Shifts in the maximum size attained by both kokanee and Lake Trout indicated that *M. diluviana* had altered the food web. However, neither kokanee nor Lake Trout harvest deviated substantially from pre-introduction rates for nearly 10 years post-mysid introduction (Davis et al. 2000). But in 1976, the kokanee fishery collapsed, and by 1978 only 4,593 kokanee were harvested in Priest Lake (Rieman et al. 1979; Fredericks et al. 2009). The 1978 creel survey was also the last time that kokanee, Cutthroat Trout, or Bull Trout had a significant presence in the creel. By the next creel survey in 1983, it was estimated that only 66 kokanee, 105 Cutthroat Trout, and 92 Bull Trout were caught (Rieman et al. 1979; Horner and Rieman 1984).

Despite efforts to protect Bull Trout from increasing exploitation, a 510-mm length limit failed to improve population trends, and the Bull Trout fishery was closed in 1984 (Rieman and Horner 1984; Mauser 1986a). Similarly, closures of Westslope Cutthroat Trout tributary fisheries and implementation of a 380-mm minimum length limit failed to increase abundance (Mauser 1986b). Harvest of Cutthroat Trout was eliminated on Priest Lake in 1988 (Liter and Horner 2008), and by the 1990s, Bull Trout numbers were severely depressed (Venard and Scarnecchia 2005). By 1987, the total abundance of adult kokanee in the lake was reduced to approximately 2,800 fish (Liter and Horner 2008). With few other opportunities available, anglers focused their attention on Lake Trout. From 1956 to 1978, angler harvest of Lake Trout varied from 3,528 to 5,724 fish, but by 1994 the harvest rate more than doubled to 13,987 (Davis and Horner 1995).

Given the timing of these declines, it appears that the introduction of *M. diluviana* facilitated the invasive effects of Lake Trout, which had previously existed in the system with little ill effect (Ricciardi 2001). *M. diluviana* provided a new, abundant source of deep-water prey for juvenile Lake Trout and thereby eliminated a recruitment bottleneck (Bowles et al. 1991; Stafford et al. 2002; Ellis et al. 2011). Although mysids were introduced widely in the western United States to benefit kokanee, most of the deep lakes where they were stocked provided refugia for bottom-dwelling mysids, which made them inaccessible to kokanee (Bowles et al. 1991). A 1978 Idaho Department of Fish and Game (IDFG) survey of Lake Trout diets in Priest Lake indicated that fish less than 510 mm consumed mostly *M. diluviana* (Rieman et al. 1979). Once Lake Trout grew to 510 mm, fish composed over 50% of the diet, and by the time they reached 760 mm, Lake Trout fed predominantly on kokanee. A small-scale mark recapture-abundance estimate at that time also indicated that

Priest Lake contained at least 30,000 Lake Trout over 0.9 kg, of which 10,000 were 4.5 kg or greater (Rieman et al. 1979). The predatory pressure of the growing Lake Trout population made enhancing kokanee and Westslope Cutthroat Trout populations challenging, if not impossible.

Numerous efforts were made by IDFG over the next decade to restore kokanee and Westslope Cutthroat Trout fisheries through stocking. Although initial attempts in the early 1980s appeared promising (Rieman 1983), the efforts were plagued by poor survival of hatchery-produced fish and low return to the creel (Mauser 1986a). Furthermore, it was estimated that 2 to 5 million kokanee and 50,000 Westslope Cutthroat Trout would need to be released annually to reestablish consumptive fisheries, demands that could not be satisfied by production rates at the time (Rieman et al. 1979; Horner and Rieman 1984; Mauser 1986b). Lake Trout predation in the main lake and Brook Trout *S. fontinalis* in tributaries were implicated in the poor success of stocking efforts (Horner and Rieman 1984). Despite releases of over 6.8 million kokanee fry between 1984 and 1986 (Mauser et al. 1988) and over 235,000 fingerling Westslope Cutthroat Trout from 1989 to 1991 (Davis and Horner 1995), stocking efforts were deemed unsuccessful and terminated.

Depressed kokanee and Westslope Cutthroat Trout populations have also had consequences for the Lake Trout population, which has experienced a number of changes since the trophy-period in the 1970s. The quality of the Lake Trout fishery remained high after the initial collapse of kokanee (Rieman et al. 1979), and Lake Trout continued to feed on kokanee despite low kokanee abundance (Horner and Rieman 1984). However, managers quickly recognized that predation by Lake Trout would be a major impediment to restoring the kokanee fishery and would reduce the quality of the Lake Trout fishery. A bag limit of six Lake Trout, with only two over 410 mm, was implemented to concentrate exploitation and reduce predatory pressure (Mauser 1986a). Lake Trout growth and body condition continued to decline in the mid-1980s, which prompted managers to retarget kokanee stocking goals towards stabilizing the Lake Trout population size-structure (Mauser 1986b; Mauser et al. 1988). Stocked kokanee may have temporarily bolstered the Lake Trout population, but average mass of Lake Trout in the harvest had declined from 5.5 kg in the 1970s to 1.6 kg at the end of the 1980s (Horner et al. 1988; Mauser et al. 1988). Concerns over the declining Lake Trout population size structure grew, but population models indicated that the necessary harvest restrictions would be too restrictive to garner much support from anglers (Horner et al. 1988; Mauser et al. 1988). Then, in 1991, regulations were modified to increase harvest of smaller Lake Trout while allowing for a trophy component; the limit was reduced from six to three, with none 660 to 813 mm, and only one Lake Trout over 813 mm (Davis and Horner 1995).

Following the change in regulations, the abundance of Lake Trout in Priest Lake appears to have continued to increase (Fredericks et al. 2002), although the mean length of fish harvested has decreased. The slot limit implemented in 1991 failed to improve the size-structure because Lake Trout grew too slowly to exit the slot (Davis et al. 2000). Exploitation was estimated to be low (7%), and the bag limit was subsequently liberalized to two Lake Trout per day with no size restrictions (Fredericks et al. 2003). In the early 2000s, management goals for Priest Lake began to focus once again on native species conservation. In an effort to reduce Lake Trout predation on native species and to bring Priest Lake regulations in line with other north Idaho fisheries, the bag limit was raised to a six fish limit of any length (Fredericks et al. 2003). Although the Priest Lake fishery continues to be dominated by Lake Trout, IDFG reopened the kokanee fishery in 2011 (Maiolie et al. 2013). Surprisingly, anglers were able to catch kokanee, and the combined fishery generated as much as US$5.9 million for the local economy (Maiolie et al. 2013). The resurgence of the kokanee fishery, in addition to the Lake Trout removal efforts on nearby Lake Pend Oreille (Hansen et al. 2008; Wahl et al. 2015) have prompted questions about the feasibility and desirability of Lake Trout removal in Priest Lake.

Further incentive to remove Lake Trout lies just north of Priest Lake, in Upper Priest Lake, which is connected to Priest Lake by a short channel called the Thorofare. In contrast to Priest Lake, no Lake Trout or *M. diluviana* were stocked in Upper Priest Lake, and for decades the upper lake remained a refuge for native species (Martinez et al. 2009; DuPont et al. 2011). However, Lake Trout are highly mobile (Martin and Olver 1980) and in the mid-1980s they were first detected in Upper Priest Lake (Martinez et al. 2009; DuPont et al. 2011). In 1997, an abundance estimate indicated that a small but growing population of Lake Trout had become established in Upper Priest Lake (Fredericks et al. 2000). Recognizing the need to protect the remaining Bull Trout and Cutthroat Trout populations in the Priest Lake watershed, IDFG began Lake Trout removal efforts in 1998 (Fredericks et al. 2000; Fredericks and Venard 2001). Idaho Department of Fish and Game staff continued removal efforts using gill nets, and in 2006, commercial gillnetters were contracted to increase the intensity of removal efforts (DuPont et al. 2009). Connectivity between the two lakes remains problematic. Several studies have found high Lake Trout movement rates between the lakes, and the population in Upper Priest Lake continues to persist, despite removal efforts (Liter and Maiolie 2003; Venard and Scarnecchia 2005; Maiolie et al. 2013). Maintaining separate management strategies for Upper Priest Lake and Priest Lake may be problematic. Given the high degree of connectivity between these two lakes, Upper Priest Lake removal efforts may be ineffective without action on the lower lake.

Despite depressions in Westslope Cutthroat Trout, Bull Trout, and kokanee populations in Priest Lake, the Lake Trout fishery remains popular with many anglers. The recent success of the kokanee fishery in Priest Lake may also reduce the need to alter management strategies. Furthermore, removal efforts are costly and the outcomes are uncertain. Therefore, the goal of this thesis was to provide managers with information about the demographic and trophic status of Lake Trout in Priest Lake, which would help to identify the biological constraints of different management strategies. There were two main objectives for this research: (1) to describe the biological and demographic characteristics of the Lake Trout population and synthesize the information in a population model, and (2) to describe the trophic ecology of Lake Trout and the Priest Lake food web using stable isotope analysis.

Thesis Organization

This thesis is composed of four chapters. The second chapter describes the population dynamics of Lake Trout in Priest Lake and evaluates alternative management scenarios using an age-structured population model. Chapter two will be submitted to the *North American Journal of Fisheries Management*. The third chapter investigates the trophic structure of Priest Lake. Chapter three will be submitted to *Ecology of Freshwater Fish*. The fourth chapter provides general conclusions, integrating the results of each chapter to address the consequences of this research for Lake Trout management in Priest Lake, Idaho.

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Chapter 2: Population Dynamics and Evaluation of Alternative Management Goals for Nonnative Lake Trout in a Large Western Lake

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Abstract

Lake Trout *Salvelinus namaycush* have been introduced widely throughout the western United States to enhance recreational fisheries, but high predatory demand and inertia can create challenges for management of yield and trophy fisheries alike. Lake Trout were introduced to Priest Lake, Idaho, during the 1920s, but little fishery-independent data are available to guide current or future management actions. We evaluated population dynamics and potential management scenarios using an age-structured population model. Lake Trout in Priest Lake were characterized by fast growth at young ages, which resulted in young age at maturity. However, growth rates were lower for adults and body condition declined with length. High rates of skipped spawning (>50%) were also observed. Model projections indicated that the population was growing ($\lambda = 1.03$). Eradication could be achieved by increasing annual mortality to 0.32, approximately twice the current rate. A protected slot length limit could increase population length-structure, but few fish grew fast enough to exit the slot. In contrast, a juvenile removal scenario targeting age-2 to age-5 Lake Trout maintained short-term harvest of trophy-length individuals while reducing overall population abundance.

Introduction

Inland freshwater fishery management in the western United States has been defined by the extensive introduction of nonnative fishes over the past two centuries (Nico and Fuller 1999). Although some species were unintentionally introduced, many were purposefully added to enhance recreational or subsistence fisheries (Stapp and Hayward 2002; Gozlan 2008; Mitchell and Knouft 2008). Additionally, many introduced sport fish are piscivorous, which has resulted in widespread conflicts with native species. Through a variety of mechanisms, piscivores instigate top-down effects that can result in altered prey species richness, composition, and abundance (Findlay et al. 2000; Carpenter et al. 2001; Eby et al. 2006; Byström et al. 2007). Piscivores can also influence community dynamics and biogeochemical processes through behavioral modification of prey species (Hölker et al. 2007). Therefore, management of nonnative populations depends on social and economic values, as well as the biological feasibility of management outcomes desired by the public.

Lake Trout *Salvelinus namaycush* are recognized throughout their native and introduced distributions for their ability to attain trophy sizes (>45 kg) and provide valuable recreational and commercial fisheries (Martin and Olver 1980; Shuter et al. 1998). In their native distribution, this desirability has often resulted in recruitment overfishing and population collapse (Healey 1978; Richards et al. 2004; Tsehaye et al. 2014). Beyond the native distribution, this desirability has led to widespread introduction of Lake Trout, where populations are sustained by natural reproduction or stocking (Crossman 1995; Martinez et al. 2009). However, like many other nonnative species, Lake Trout introduction is associated with a number of ecological consequences.

Lake Trout often exhibit fast growth, and as a top-level consumer, demand for prey is high. Supporting nonnative Lake Trout populations can therefore have high economic, ecological, and social consequences. In an evaluation of the costs associated with stocking prey fishes in Colorado reservoirs, Johnson and Martinez (2000) found that Lake Trout cost US$200 per fish. For species of conservation concern, such as Yellowstone Cutthroat Trout *Oncorhynchus clarkia bouvieri* in Yellowstone Lake, Wyoming, the cost of Lake Trout consumption is immeasurable in economic terms (Ruzycki et al. 2003). In addition to the high demand for prey fishes, Lake Trout also exhibit predatory inertia and resistance to starvation (Eby et al. 1995; Schoen et al. 2012). These long-lived predators can subsist on sub-optimal prey for prolonged periods and quickly respond to increased prey availability (Martinez et al. 2009). However, as prey resources decline, the quality of Lake Trout fisheries also declines.

Lake Trout can also destabilize ecological interactions, potentially creating trophic cascades, which further complicate the ability to achieve management goals (Eby et al. 2006). For example, in Flathead Lake, Montana, the interaction of introduced Lake Trout with introduced opossum shrimp *Mysis diluviana* created both top-down and bottom-up pressures that ultimately extirpated kokanee *O. nerka* (Ellis et al. 2011). The lack of coevolutionary history between nonnative Lake Trout and other members of the fish assemblage can produce unstable food-web interactions (Eby et al. 2006). The combination of long life, vulnerability to overharvest, piscivory, predatory inertia, and food-web instability makes managing Lake Trout fisheries challenging.

Nonnative Lake Trout management has centered around three primary goals in the western United States: eradication, trophy, and balance (Martinez et al. 2009). Because of the social and economic costs of Lake Trout, managers of some waters have pursued eradication. For example, in Yellowstone Lake, Lake Trout threaten to extirpate Yellowstone Cutthroat Trout via predation (Ruzycki et al. 2003; Quist and Hubert 2004; Syslo et al. 2011). Given the risks that Lake Trout pose both to Yellowstone Cutthroat Trout and broader ecosystem linkages, large-scale Lake Trout suppression effort using gill nets and trap nets was initiated in 1995 (Syslo et al. 2011). Similarly, in Lake Pend Oreille, Idaho, Lake Trout predation reduced kokanee abundance, forcing managers to close the popular kokanee fishery and begin a suppression program using gill nets and large trap nets in 2006 (Hansen et al. 2008). Additionally, an angler incentive (i.e., bounty) program was established to increase mortality of Lake Trout. These and other suppression efforts seek to exploit vulnerabilities in Lake Trout life history (i.e., slow growth, late maturation) to cause recruitment overfishing and collapse populations (Martinez et al. 2009).

In contrast to the eradication management goal, many nonnative Lake Trout fisheries are managed to produce trophy-length individuals (Johnson and Martinez 2000, Martinez et al. 2009). As in their native distribution, Lake Trout may be protected by restrictive harvest limits to reduce mortality and facilitate the production of trophy individuals (Dextrase and Ball 1991). For example, in Payette Lake, Idaho, strict harvest regulations and a maximum length limit exist to “maximize the numbers of large, mature” Lake Trout (Janssen et al. 2012; Idaho Department of Fish and Game 2013). In some Colorado reservoirs, such as Lake Granby, bag limits of one or two fish and minimum length limits were implemented to increase the size structure of nonnative Lake Trout populations (Johnson and Martinez 2000). Therefore, by increasing Lake Trout survival, regulations can increase Lake Trout population size-structure and provide a trophy fishery.

The final approach to nonnative Lake Trout management is a compromise between the trophy and eradication management goals. The predatory inertia of Lake Trout requires a delicate balance between consumer demand and prey fish availability, which may not be fully understood when restrictive regulations are implemented (Johnson and Martinez 1995, 2000). By targeting specific Lake Trout size-classes for harvest or removal, the goal is to reduce the overall abundance and negative side-effects of Lake Trout predation while still retaining sufficient numbers of Lake Trout to provide a fishery (Pate et al. 2014). In Blue

Mesa Reservoir, Colorado, managers hope to provide both a trophy Lake Trout fishery and an abundant kokanee fishery (Pate et al. 2014). However, recent declines in abundance of kokanee and body condition of Lake Trout have necessitated intervention. Simulations indicated that the two fisheries could be maintained with adequate harvest of young (e.g., age-4 to age-9) Lake Trout, which are the greatest numerical consumers of kokanee. The targeted removal of small fish would reduce undesirable interactions with other fishes, while still allowing for a trophy Lake Trout fishery (Pate et al. 2014). Likewise, in Flaming Gorge Reservoir, Wyoming-Utah, managers evaluated trade-offs between increasing the abundance of trophy-length Lake Trout and decreasing prey fish abundance through predation (Luecke et al. 1994). After evaluating several slot limits, Luecke et al. (1994) found that a 711-914 mm slot length limit would provide a slight increase in trophy catch rates without increasing consumptive demand substantially. “Balanced” approaches to Lake Trout population management generally use mechanical (e.g., gill nets) removal of targeted size classes to reduce predatory pressure, while retaining a fishery.

Lake Trout were introduced to Priest Lake, Idaho, in 1925, but initially remained at low abundance (Crossman 1995; Martinez et al. 2009). Kokanee were introduced in the mid-1940s, and quickly became established (Bjornn 1961; Rieman et al. 1979). Although Lake Trout abundance remained low, the new prey base allowed Lake Trout to reach trophy sizes (Rieman et al. 1979). In the late-1960s, *M. diluviana* were introduced to increase kokanee production (Leusink 1968; Bowles et al. 1991). After mysid introduction, both kokanee and Lake Trout growth increased. In 1971, Priest Lake produced the largest Lake Trout caught by an angler outside the Great Lakes, a 125-cm long fish weighing 26.1 kg (Martinez et al. 2009). Although downward shifts in the maximum length attained by Lake

Trout indicated that *M. diluviana* had altered the food web, neither kokanee nor Lake Trout harvest deviated much from pre-introduction rates for nearly 10 years post-mysid introduction (Davis et al. 2000). In 1976, the kokanee fishery collapsed, and by 1978 only 4,500 kokanee were harvested in Priest Lake (Rieman et al. 1979; Fredericks et al. 2009). By 1987, the total abundance of adult kokanee in the lake was approximately 2,800 fish (Liter and Horner 2008). From 1956 to 1978, angler harvest of Lake Trout varied from 3,528 to 5,724 fish, but the harvest rate more than doubled to 13,987 by 1994 (Davis and Horner 1995).

Although Lake Trout continue to dominate the recreational fishery in Priest Lake, recent increases in kokanee harvest in nearby Lake Pend Oreille following Lake Trout suppression have raised questions about management goals for Priest Lake. Therefore, the objectives of this study were to assess current population dynamics of Lake Trout in Priest Lake and to evaluate potential management scenarios. Using an age-structured population model, we evaluated three different harvest scenarios that represent three general strategies for Lake Trout populations: an eradication-type effort with constant age-specific fishing mortality, a protected slot limit to promote trophy fish production, and a juvenile removal effort to “balance” predation with yield and size structure. We incorporated uncertainty in model projections with a parametric bootstrap procedure and used sensitivity analysis to identify vital rates that are likely to play key roles in regulating population size and growth.

Methods

Study area—Priest Lake is a 9,461-ha dimictic lake located in the Columbia River basin of northern Idaho (Figure 2.1). The roughly 1,554 km^2 watershed is granitic and dominated by coniferous forest cover (Bjornn 1957; Maiolie et al. 2013). Formed by glacial action, this oligotrophic lake has steep sides with little littoral habitat (Bjornn 1957). Priest Lake is at an elevation of 743 m and has a surface area of 9,461 ha (Martinez et al. 2009), a mean depth of 38 m, and a maximum depth of 112 m (Bowles et al. 1991). Approximately 19% of the lake is less than 12 m deep (Rieman et al. 1979). Portions of the lake may become ice covered from January to April (Bjornn 1957). Thermal stratification generally occurs mid-July through the end of October, with a thermocline at a depth of about 35 to 50 m and summer surface water temperatures reaching 26°C in shallow areas (Kemmerer et al. 1924; Bjornn 1957; Rieman et al. 1979).

The native fish assemblage includes Bull Trout *S. confluentus*, Westslope Cutthroat Trout, Mountain Whitefish *Prosopium williamsoni*, Pygmy Whitefish *P. coulterii*, Largescale Sucker *Catostomus macrocheilus*, Longnose Sucker *C. catostomus*, Northern Pikeminnow *Ptychocheilus oregonensis*, Redside Shiner *Richardsonius balteatus*, Peamouth *Mylocheilus caurinus*, and Slimy Sculpin *Cottus cognatus* (Bjornn 1957; Rieman et al. 1979; Maiolie et al. 2011). In addition to Lake Trout and kokanee, at least seven other fish species have been introduced: Brook Trout *S. fontinalis*, Tench *Tinca tinca,* Largemouth Bass *Micropterus salmoides*, Smallmouth Bass *M. dolomieui*, Northern Pike *Esox lucius*, Green Sunfish *Lepomis cyanellus*, and Yellow Perch *Perca flavescens* (Fredericks et al. 2009).

Field sampling and laboratory processing—A mark-recapture study was conducted from March-May, 2013 to estimate Lake Trout abundance. A stratified random sampling design was used (Thompson 2012). The lake was divided into north and south strata of equal area, which were sampled systematically on alternate days. The lake was then divided by a one-square kilometer grid. One to seven locations were selected randomly each day for sampling. Lake Trout were captured using sinking monofilament gill nets (1.8 m deep × 30.5 m long), which consisted of one of eight mesh sizes (50.8, 63.5, 76.2, 88.9, 101.6, 114.3, 127.0, 139.7-mm stretch mesh). Twelve nets were combined to form a 1,463 m-long gang where each mesh size was represented at least once and no more than twice. Gangs were set during daylight hours in a serpentine pattern along an isobath (mean maximum depth, 37 m), soaked for one hour, and lifted slowly with a hydraulic lifter.

Eight large, nylon multimesh traps nets were also used to capture Lake Trout: six larger trap nets and two smaller “juvenile” trap nets. The pots of the large trap nets were 6.10 m × 6.10 m × 12.19 m, with 9.14-m high leads that varied in length from 213.36 m to 274.32 m. The hearts and wings were 9.14-m tall, and the wings extended 30.48 m from the heart. Half of the large trap nets used larger mesh: 114-mm stretch mesh on the pot and 228-mm stretch mesh on the lead and wings. The other three large trap nets used 102-mm stretch mesh on the pots and 204-mm stretch mesh on the lead and wings. The pots of the smaller trap nets were 3.66 m × 3.50 m × 6.10 m and were constructed with 64-mm stretch mesh. The 152-mm stretch mesh leads extended to a maximum of 152.4 m from the pot. One trap net had a heart with 114-mm stretch mesh and the other had 152-mm stretch mesh. Locations in each stratum with suitable bathymetry and substrate type were identified, and trap-net locations were randomly selected. Four trap nets were placed in the north stratum and four were placed in the south stratum. In mid-April, four of the trap nets were moved to new locations. Trap nets were allowed to soak for two to three nights and then lifted.

Lake Trout captured in both gill nets and trap nets were measured (mm, total length) and tagged in the dorsal musculature with a uniquely numbered T-bar tag (Floy Tag, Seattle, Washington). Approximately every fifth Lake Trout was also tagged with a uniquely numbered spaghetti tag (Floy Tag) to evaluate tag loss (Pine et al. 2003). In addition to the identification number, tags included a toll-free telephone number, which anglers could use to report their catch to the Idaho Department of Fish and Game tag-reporting program (Meyer et al. 2012). Two-hundred spaghetti tags (38% of spaghetti tags) were marked as US$50 reward tags.

Because trauma from handling can result in post-release mortality, each Lake Trout was assessed for gill-net trauma and barotrauma using three-level condition ratings (mild, moderate, or severe; Ng et al. *in press*). For gill-net trauma, fish with no apparent injuries were assigned a mild rating; fish with minor bruising, scale loss, or damaged fins were assigned a moderate rating; and fish with extensive bruising, extensive scale loss, torn fins, torn maxillaries, or bleeding gills were assigned a severe rating. For barotrauma, fish that were upright, without any distension of the abdomen, and swimming normally were assigned a mild rating; fish that were visibly bloated or had difficulty swimming were assigned a moderate rating; and fish with rigid bodies, inability to swim, or bleeding in the eyes (hemorrhage) were assigned a severe rating.

Gill-net captured Lake Trout in mild condition (i.e., able to orient and swim) were released alongside the boat after they were processed. Trap-net captured fish were retained in a holding tank and released away from the leads and pot once the trap net was lowered. Fish experiencing barotrauma or exhaustion were allowed to recuperate and then released directly into the open lake or with a weighted deep-release cage (0.9 m × 0.6 m × 1.2 m). The cage was lowered to approximately 30 m and held at depth to allow fish to swim out of the open bottom. After 10 min, the cage was lifted. If fish remained inside the cage, it was lowered to 30 m for an additional 10 minutes.

Sagittal otoliths were collected from all handling mortalities during the mark-recapture study. Sex was also recorded. Additionally, five gangs (three north stratum, two south stratum) were randomly selected to collect age and growth information from all fish captured. Age structures were collected and length, weight (nearest g), and sex were recorded. Saggital otoliths from 10 Lake Trout per 10-mm length group were aged. Otoliths were mounted in epoxy, thin-sectioned with a low speed saw (Beuhler, Lake Bluff, IL), and viewed under a dissecting scope using transmitted light (Quist et al. 2012).

Body condition for Lake Trout captured in the spring was evaluated using relative weight (W_r ; Piccolo et al. 1993; Hubert et al. 1994; Neumann et al. 2012). Relative weight for an individual Lake Trout is the observed weight divided by the length-specific standard weight for Lake Trout (W_s) multiplied by 100. Mean relative weight was calculated for each of the standard length categories for Lake Trout: stock (≥280 mm), quality (≥500 mm), preferred (≥700 mm), memorable (≥850 mm), and trophy (≥1,000; Piccolo et al. 1993).

Because Lake Trout gonadal maturation does not occur until autumn (Goetz et al. 2011), a separate netting effort was conducted in October 2013 prior to peak spawning to evaluate maturity schedule and fecundity. Lake Trout were collected using gill nets in the same manner as spring 2013. Two sites in the north stratum and three sites in the south stratum were randomly selected for sampling. Length, weight, and sex were recorded for each fish, and otoliths were collected as in the spring. Maturity status of female Lake Trout was assessed macroscopically in the field during autumn sampling (Sitar et al. 2014). Small, translucent ovaries that had granular, undersized eggs (≤1 mm diameter) were categorized as immature. Ovaries that were large and contained well-developed or loose eggs (>3 mm diameter) were categorized as mature. Sexually-mature female Lake Trout may not spawn every year (Sitar et al. 2014); skipped spawners were identified by their thinner, less developed ovaries and smaller eggs (1-2 mm diameter). Presence of atretic follicles was also used to distinguish skip-spawners from immature fish. Maturity and reproduction ogives (i.e., age-specific probability of maturity or spawning) were modeled using logistic regression (Sitar et al. 2014).

Intact ovaries from mature females were preserved in a 15% formaldehyde solution. Fecundity (*f*) was estimated gravimetrically (Murua et al. 2003). Each ovary was weighed to the nearest 0.01 g, and three cross-sectional subsamples were taken from each ovary (anterior, medial, and posterior sections) and weighed to the nearest 0.01 g. Vitellogenic eggs (≥3 mm in diameter) were counted. Mean egg density was estimated for each ovary and multiplied by total ovary mass. Mean fecundity at age was estimated using linear regression.

Data summarization—Lake Trout abundance was estimated using a robust-design Huggins closed-population model with two periods and weekly sampling intervals using Program MARK (Huggins 1991; White and Burnham 1999). Detection probability and survival were specified as constant across sampling events. Estimated abundance was corrected for post-release mortality using post-release mortality rates from a separate survival study (see below).

The subsample of aged Lake Trout was used to create an age-length key. Because of missing age classes, multinomial logistic regression of age on length was used to estimate length-specific age frequency (Gerritsen et al. 2006). Population length-frequency was estimated from gill-net catch rates using relative retention probability estimated for 97 length classes using the SELECT method (Millar and Fryer 1999). All combinations of five parametric forms for selectivity, three specifications for fishing power, and a correction for entangling were evaluated. The model with the lowest mean model deviance was chosen as the top model (Jonsson et al. 2013). Population age-frequency distribution was then approximated by applying the age-length key to gill-net selectivity-corrected length-frequencies (Millar 1992). A von Bertalanffy growth model was fit to observed length-at-age data to obtain parameters used to estimate natural mortality (see below):

$$L_t = L_\infty\left[1 - e^{-k(t-t_0)}\right]$$

where L_t is the length at age t, L_∞ is the asymptotic length, k is a growth constant, and t_0 is the theoretical age when length is 0 mm (Gallucci and Quinn II 1979).

Annual survival (S) was estimated from gill-net selectivity-corrected catch-at-age for age-3 to age-35 fish. The Chapman-Robson estimator was used with peak-plus criterion and corrected for overdispersion (Chapman and Robson 1960; Smith et al. 2012). Because catch of age-1 and age-2 Lake Trout was low and because no data on survival of age-0 Lake Trout were available for Priest Lake, survival rates of age-0, age-1, and age-2 Lake Trout were obtained from the literature (Shuter et al. 1998; Sitar et al. 1999).

Exploitation (μ) for age-3 and older Lake Trout was estimated using tags reported through the Idaho Department of Fish and Game tagging hotline during the one-year period following tagging. The number of tags returned was corrected for non-reporting using average reporting rates developed by Meyer et al. (2012) for Idaho fisheries. Meyer et al. (2012) found that 54.2% of non-reward tags were reported and 91.7% of US$50 reward tags were reported. The number of fish available for harvest was corrected for post-release mortality (Ng et al. *in press*). After excluding fish that had been reported as harvested during the tagging period ($n = 3$), the total number of tagged fish available was estimated. The following logistic regression model was used to estimate post-release mortality (P_m) for Lake Trout in Priest Lake:

$$P_m = \frac{e^{\eta_i}}{1 + e^{\eta_i}},$$

$$\eta_i = \beta_0 + \beta_1 x_{iDeep} + \beta_2 x_{iTL} + \beta_3 x_{iB2} + \beta_4 x_{iB3} + \beta_5 x_{iGill2} + \beta_6 x_{iGill3} + \beta_7 x_{iTL} x_{iDeep},$$

where $\beta_0, \dots, \beta_7$ are estimated coefficients, x_{iDeep} is an indicator variable for treatment with a deep release cage, x_{iTL} is the total length (mm) scaled by 0.01, x_{iB2} is an indicator variable for moderate barotrauma, x_{iB3} is an indicator variable for mild barotrauma, x_{iGill2} is an indicator variable for moderate gill-net trauma, x_{iGill3} is an indicator variable for mild gill-net trauma, and $x_{iTL} x_{iDeep}$ is the interaction between length and deep-release treatment. The predicted probability of mortality was calculated for each released fish. The estimated expected number of total post-release mortalities was the sum of the predicted probabilities. The estimated number of mortalities was subtracted from the total number of available fish for harvest to obtain a corrected number of available fish. Exploitation was estimated by dividing the number of reported tags by the respective reporting rate (i.e., for US$0 and US$50 tags), then dividing by the corrected number of fish available for harvest. Exploitation was converted to instantaneous fishing mortality (F) using the relationship for a Type 2 fishery: $F = \mu Z / A$ (Ricker 1975).

Instantaneous natural mortality (M) was obtained by $M = Z - F$ (Ricker 1975). Additionally, to account for uncertainty in estimates of natural mortality, M was also estimated using equations from Hoenig (1983) and Shuter et al. (1998). Hoenig (1983) used a regression estimator based on data for fishes, mollusks, and cetaceans to develop the following relationship between M and maximum observed age (t_{max}):

$$\ln(M) = 1.44 - 0.982 \cdot \ln(t_{max}).$$

Using information on Lake Trout populations in Ontario, Shuter et al. (1998) developed an estimator for M based on Pauly (1980), which incorporates a population's von Bertalanffy growth parameters and mean environmental temperature. The simplified estimator is:

$$M = 2.064 \cdot \omega^{0.655} \cdot L_{\infty}^{-0.933},$$

where $\omega = K \cdot L_{\infty}$, and K and L_{∞} are parameters of the von Bertalanffy growth model. The average of these three estimates was used as the final estimate of M in population models.

Population modeling—An age-structured, female-based matrix (i.e., Leslie matrix) model was used to evaluate Lake Trout population growth trajectory and dynamics (Caswell 2001; Morris and Doak 2002). Analyses were conducted in R using functions from the popbio package (Stubben and Milligan 2007; R Core Team 2014). The matrix model included 35 age-classes (i.e., maximum age observed) and a pre-breeding census:

$$\boldsymbol{A} = \begin{bmatrix} R_1 & R_2 & \cdots & R_{34} & R_{35} \\ S_1 & 0 & \cdots & 0 & 0 \\ 0 & S_2 & & \vdots & \vdots \\ \vdots & & \ddots & 0 & 0 \\ 0 & \cdots & 0 & S_{34} & 0 \end{bmatrix},$$

where S_i is the survival of age-class i and R_i is the reproductive rate of age-class i, given by:

$$R_i = P_i \cdot f_i \cdot S_0 \cdot a,$$

where P_i is the probability of spawning for age-class i, f_i is the fecundity of age-class i, and a is the proportion of female offspring. The observed age of first maturity was 6 years old.

The proportion of female offspring produced was specified as 0.5 since the observed sex ratio did not differ significantly from 0.5 (0.45 female; 95% CI: 0.39-0.51).

Asymptotic population growth rate was estimated by calculating the dominant eigenvector of $\boldsymbol{A}$. We also evaluated the transient dynamics of the Lake Trout population because transient dynamics provide more realistic estimates of population growth over the short-term (Morris and Doak 2002). Projected age-specific abundance ($\boldsymbol{n_{t+1}}$) was calculated by multiplying the estimated Leslie matrix by the vector of age-specific abundances at time ($\boldsymbol{n_t}$): $\boldsymbol{n_{t+1}} = \boldsymbol{A n_t}$. The population was projected over a period of 5, 10, or 20 years. Population growth over each time step was calculated by:

$$\lambda_{t+1} = \frac{N_{t+1}}{N_t},$$

where N_t is total abundance at time *t*. The average population growth rate (λ) over the given period (e.g., 5 years) was calculated as the geometric mean of the population growth rate at each time step (i.e., one year) over the projection period. We varied *F* from 0 to 1.5 in 0.01 increments to evaluate effects of different harvest levels.

In addition to λ, we estimated average population size, number of fish harvested, biomass, biomass harvested, and abundance and number of Lake Trout harvested by incremental standard length category over a 10-year period. Abundance and biomass are given for the female half of the population only (i.e., the direct results of population projections). Biomass was calculated by multiplying age-specific abundance by observed mean-weight at age. We used a multinomial regression of length on age to convert harvest by age class to harvest by incremental size class. The number of Lake Trout harvested per age class for a given value of *F* was calculated using:

$$C_i = \frac{F_i}{F_i + M_i} N_{i\bullet},$$

where C_i is the harvest for age class i, F_i is the fishing mortality for age class i, M_i is the natural mortality for age class i, and $N_{i\bullet}$ is 10-year average abundance for age class i (Quinn and Deriso 1999).

Parametric bootstrap was used to incorporate uncertainty in all of the vital rate estimates and to obtain 95% confidence intervals for estimates of abundance, biomass, and harvest (Morris and Doak 2002). Age-specific survival rates and probability of spawning were modeled as beta distributions with the mean set to the observed value and the variance set to the observed standard error. For literature values of survival where no standard errors were available, we specified the variance of the beta distribution equal to 20% of the mean (Syslo et al. 2011; Cox et al. 2013). Fecundity was modeled using a stretch-beta distribution, with the maximum number of eggs set to three-times the mean number of eggs, since variation in fecundity is not uncommon in fishes (Healey 1978). Confidence intervals were estimated as the 97.5th and 2.5th percentiles of 1,000 bootstrap samples.

We evaluated the outcome of each management goal (i.e., eradication, trophy, and balance) at varying fishing intensities. The eradication goal assumed constant F across age classes ≥age 3 (Dux et al. 2011). The trophy goal modeled the implementation of a protected slot length limit that was based on a historical regulation for Priest Lake (Davis et al. 2000) that protected fish 660-813 mm. Based on mean-length-age data, the regulation would protect age-23 to age-35 Lake Trout. The balance goal incorporated targeted mechanical removal and recreational angling. We modeled a mechanical removal effort that targeted juvenile Lake Trout and sought to compromise between maintaining a Lake Trout fishery and reducing the abundance of Lake Trout. Asymptotic sensitivity analysis (Caswell

1988) indicated that population growth rate was most sensitive to changes in survival of age 2-5 Lake Trout. Therefore, these age classes were targeted in simulations to maximize the effect of a removal effort, while minimizing the effects on recreationally desirable fish (i.e., less than quality length [500 mm]). In addition to the mechanical removal of juvenile fish, we assumed that angler exploitation would remain constant at the observed rate for age-3 and older Lake Trout.

For each scenario, outcomes were evaluated for values of *F* varying from 0 to 1.5 in 0.01 increments on the targeted age-classes for each scenario (i.e., ≥age 3 [eradication], age 3-age 22 [trophy], and age 2-age 5 [balance]). In the eradication scenario, we evaluated λ over 5, 10, and 20 years. In the scenarios that maintained a fishery (i.e., trophy and balance), we estimated λ and median population size, number of fish harvested, biomass, biomass harvested, and abundance and number of Lake Trout harvested by incremental standard length category over a 10-year period. For the balance scenario, harvest was calculated for the portion of fishing effort due to angling, excluding mechanical removal harvest. Bootstrap confidence intervals were calculated as above. For all bootstrap simulations, age-specific standard errors from the observed survival rates (i.e., Chapman-Robson estimator) were used.

We performed a sensitivity analysis for λ to provide insight into potential effects of density-dependent responses of Lake Trout to increased *F*. We evaluated the effect of a 20% increase in probability of spawning to reflect a potential increase in food resources for adult Lake Trout following increases in *F*. We also evaluated the effect of a 20% increase in mean fecundity at age, representing a potential increase in growth rate since fecundity is most closely correlated with body size. Reproductive rates were increased across all ages and average population growth was estimated over a 10-year period for both vital rates.

Results

In spring 2013, 4,392 individual Lake Trout were captured of which 2,959 were released alive. One-hundred and four individuals were recaptured during the spring netting, and one individual was recaptured three times. After correcting for post-release mortality (41%), the estimated population size was 43,210 (95% CI: 31,569-59,451) or 4.6 fish/ha (95% CI: 3.3-6.3 fish/ha). Mean catch rate for trap nets was 1.26 fish/net night (SD = 2.11 fish/net night). Mean catch rate for gill nets was 24.70 fish per/gang/hour (SD = 27.23 fish/gang/hour). Catch rates were not significantly different between strata for gill nets ($t = -0.58$, $df = 126$, $P = 0.57$) or trap nets ($t = 0.30$, $df = 121$, $P = 0.77$).

Lake Trout varied in length from 174 to 1,130 mm (mean ± SD; 549 ± 114 mm). The majority of Lake Trout captured were quality length (PSD = 71, PSD-P = 7, PSD-M = 2, PSD-T = 0). On average, Lake Trout in Priest Lake were in good condition (mean W_r = 90 ±13 SD). However, there was a slight but statistically significant negative relationship between W_r and length ($\beta_1 = -0.072$, $P < 0.0001$). Stock-length fish had an average W_r of 95 (± 10 SD). Quality-length fish had an average W_r of 83 (±12 SD). Both preferred- and memorable-length fish had mean W_r of 76 (±10 SD). Lake Trout (n = 628) varied in age from 2 to age 35 (Figure 2.2). The estimated von Bertalanffy growth model (Figure 2.3) was:

$$L_t = 789\left[1 - e^{-0.0646(t+5.4404)}\right].$$

After correcting for gill-net selectivity, peak abundance in the catch occurred at age 3 (Figure 2.2). Total instantaneous mortality for age-3 and older fish was 0.108 (95% CI: 0.084—0.133) and *S* was 89.7% (95% CI: 87.5—91.9%). Between May 10, 2013 and May 10, 2014, 23 reward-tagged and 164 non-reward-tagged Lake Trout were reported harvested (Table 2.1). After correcting for reporting rate, an estimated 25 reward-tagged Lake Trout and 303 non-reward-tagged Lake Trout were harvested during the period. Although 2,959 Lake Trout were released during the tagging period, we estimated that 554 died after release. Thus, after correcting for non-reporting and post-release mortality, μ was estimated to be 0.136 and *F* was 0.143 (Table 2.2). Based on observed *F* and *Z*, *M* was -0.037. The estimate of *M* was 0.054 using Shuter et al. (1998) and 0.129 using Hoenig (1983). The average of the three estimates of *M* was 0.048.

One-hundred-thirty-three female Lake Trout were captured during the 2013 autumn netting. Minimum observed age of maturity was 6 years old. Age at 50% maturity was 7.5 years (95% CI: 6.7-8.3 years; Figure 2.4). However, age at 50% reproductivity (i.e., excluding non-spawning fish) was 19.9 years (14.8-24.9 years; Figure 2.5). The reproductive schedule of female Lake Trout was described by the following logistic regression equation:

$$P_{reproductive} = \frac{e^{0.12Age-2.43}}{1 + e^{0.12Age-2.43}}.$$

Fecundity tended to increase with age (Figure 2.5). Mean fecundity was 2,443 eggs (*n* = 32; 2,150-2,735 eggs) and varied from 1,206 to 5,847 eggs per female. Mean relative fecundity was 1,392 (1,304-1,482) eggs/kg body mass.

Asymptotic population growth rate for the observed population matrix was 1.03, but mean population growth rate from transient dynamics analysis indicated more rapid average growth in the short term. At current levels of exploitation, the simulated 5-year λ was 1.26 (95% CI: 1.14-1.50), the 10-year λ was 1.12 (95% CI: 1.03-1.21), and the 20-year λ was 1.07 (95% CI: 1.00-1.15). Average annual abundance projected over 10 years was 83,099 Lake Trout (95% CI: 49,035-117,163), with an average annual harvest of 11,408 Lake Trout (95% CI: 8,260-14,557). Projected average biomass was 36,810 kg (95% CI: 26,124-47,496 kg), with a harvest of 13,693 (95% CI: 11,436-15,950). The number of S-Q length fish was projected to be 30,000 (95% CI: 13,893-46,108), with 5,957 (95% CI: 3,468-8,445) in the harvest. The number of Q-P length fish was projected to be 9,045 (95% CI: 7,698-10,393), with 4,790 (95% CI: 4,154-5,426) in the harvest. Simulated abundance of M-T (366, 95% CI: 355-377) and trophy-length Lake Trout (171, 95% CI: 165-178) was much lower than for the other length categories. Harvest of M-T (201, 95% CI: 195-207) and trophy-length Lake Trout (94, 95% CI: 90-98) was also low.

Population projections for the eradication scenario indicated that causing the population to decline would be possible (Figure 2.6). The level of F associated with replacement rate (i.e., $\lambda = 1$) decreased as the duration of fishing increased. To achieve $\lambda < 1$, on average, over a period of 5 years, F would need to be maintained at nearly five times the current level of fishing mortality ($F = 0.68$, $A = 0.51$). Over a 10-year period, F would need to be maintained at 0.34 ($A = 0.32$). Finally, over a 20-year period, F would need to be maintained at 0.26 ($A = 0.27$), less than twice the current exploitation rate.

Compared to the eradication scenario, the scenarios that maintained a Lake Trout fishery exhibited slower declines in λ with increasing F because fishing mortality was applied to fewer age classes in the latter two scenarios (Figure 2.7). For example, mean λ reached replacement rate for the 10-year eradication scenario at $F = 0.26$. Mean λ did not reach replacement until *F* = 0.38 for the trophy scenario and *F* = 0.72 for the balance scenario. Trends in abundance and biomass at varying levels of *F* for the trophy and balance scenarios corresponded to trends in λ. In the trophy scenario, peak number of fish harvested occurred at a higher level of *F* than peak biomass harvested. Peak number harvested occurred at *F* = 0.10 (23,460 fish/yr, 12,498-34,422) and peak biomass harvested occurred at of *F* = 0.09 (15,870 kg/yr, 11,201- 20,538). In the balance scenario, peak harvest by anglers occurred in the scenario without any removal effort (i.e., observed conditions).

Abundance and number of fish harvested for each length category were generally lower for the trophy scenario than the balance scenario (Figure 2.8). The exception was that the protected slot limit in the trophy scenario maintained higher abundances of trophy-length fish in the population for all values of *F*, though fewer trophy-length fish were harvested. In contrast, the balance scenario maintained nearly constant numbers of preferred-length fish in the population across a wide range of *F*, and allowed for harvest. Harvest rate of trophy-length fish in the balance scenario was unchanged from the current conditions in Priest Lake.

Transient sensitivity analysis of the Lake Trout population was consistent with the asymptotic sensitivity analysis, which indicated that λ was less sensitive to reproductive rates than to juvenile survival rates. Increasing fecundity or probability of spawning by 20% resulted, on average, in a 2.2% increase in λ over a 10-year period.

Discussion

In this study, we coupled a biological evaluation of the nonnative Lake Trout population in Priest Lake with a demographic model to evaluate trade-offs in implementation of three potential management scenarios. Length at age indicated that individual Lake Trout grew rapidly at young ages, but that growth rates declined with age. Slow adult growth rates coupled with declining body condition with length and high rates of skipped spawning may be caused by low prey availability for piscivorous age classes. These types of density-dependent restrictions in adult growth rate and reproductive rate have implications for the success of eradication, trophy, and balance management scenarios.

Population length structure is a useful indicator of growth rates and growth potential. Fish populations with ample prey resources, low densities, and hence low competition, generally grow faster and larger. Lake Trout can reach lengths up to 1,570 mm (Martin and Olver 1980). Although the largest fish captured during sampling was 1,130 mm, few fish captured were longer than memorable length. Furthermore, L_∞ was only 789 mm, which was lower than for many nonnative Lake Trout populations, including Yellowstone Lake (L_∞= 812 mm, Syslo et al. 2011), Lake McDonald, Montana (L_∞= 922 mm, Dux et al. 2011), Quartz Lake, Montana (L_∞= 1,033 mm, Fredenberg 2014), Swan Lake, Montana (L_∞= 1,112 mm, Cox et al. 2013), and Blue Mesa Reservoir (L_∞= 1,151 mm, Pate et al. 2014). Reductions in growth rates can occur in Lake Trout populations where prey resources are limited, either due to high Lake Trout density or low density of prey fishes (Pazzia et al. 2002). Further evidence for the low prey abundance in Priest Lake is the high variability in individual growth rates, which spanned as much as 546 mm within one age class (age 14, 297-843 mm). Variability in individual growth rates is another indication of prey limitations for Lake Trout (Eby et al. 1995).

In Priest Lake, *Mysis diluviana* likely provide an abundant food source for juvenile Lake Trout, while kokanee and other fishes are important for larger Lake Trout (Bowles et al. 1991). The body condition of adult Lake Trout showed several signs that current prey resources are inadequate. Furthermore, prey density alone may not be sufficient to maintain good condition of larger Lake Trout, since prey size is also an important consideration (Kerr 1971; Johnson and Martinez 2000; Pazzia et al. 2002). Based on these biological factors, we found evidence of a mismatch between carrying capacity for juvenile versus adult Lake Trout.

Patterns in body condition of Lake Trout in Priest Lake also provided evidence of a mismatch between adult and juvenile prey availability. The average body condition of Lake Trout in Priest Lake was in the 50th percentile for 58 North American stocks (Hubert et al. 1994) and W_r decreased with length. Furthermore, catch of preferred- and memorable-length fish was rare, and for those captured, relative weights were below the 5th percentile (Hubert et al. 1994). Food supply is a major factor influencing Lake Trout body condition (Martin and Olver 1980). For example, generally poor (1st-5th percentile) Lake Trout body condition in Lake McDonald, Glacier National Park, was attributed to limited food resources (Dux et al. 2011). In contrast, in Blue Mesa Reservoir, high kokanee availability has historically allowed Lake Trout to reach trophy sizes and excellent body condition (mean $W_r > 150$; Pate et al. 2014). However, recent declines of kokanee in Blue Mesa Reservoir by as much as 90% coincided with decreases in W_r to 108 for trophy-length fish. Lake Trout in Yellowstone Lake were also in better condition (median $W_r \geq 100$) than Lake Trout in Priest Lake. The good condition of Lake Trout in Yellowstone Lake is likely representative of superior prey resources due to higher productivity (Syslo 2010). Thus, reduced prey fish abundance can lead to declines in body condition such as those observed in Priest Lake.

Reproductive rates can also be used to evaluate population status (Trippel 1995). Age at first maturity in Lake Trout populations varies from 4-13 years for female Lake Trout (Martin and Olver 1980), and is closely tied to lake productivity and individual growth rates (Trippel 1993). Female Lake Trout in Priest Lake matured at relatively young ages; we first observed maturity at age 6, and by age 8, over 50% of the population was mature. Although age at maturation was indicative of high individual growth rates, the high rate of skipped spawning (0.54) suggests energetic limitations later in life. For example, skipped-spawning was linked to high Lake Trout density and reduced availability of the prey fish Cisco *Coregonus artedii* in Greenwich Lake, Ontario (Trippel 1993). Furthermore, previous studies of Canadian populations noted that skip-spawning is more frequent at northern latitudes, where rates may be as high as 87% (Healey 1978; Sitar et al. 2014). Skip spawning is also know to occur at lower latitudes, where high rates are related to restriction in food supply (Martin and Olver 1980; Sitar et al. 2014). Reproductive parameters in Priest Lake further suggest energetic mismatches between juvenile and adult Lake Trout.

Our population models indicate that the population in Priest Lake is growing slower than other introduced populations in the western United States. For example, in nearby Lake Pend Oreille, time series analysis of abundance data indicated λ was 1.63 in 2005 prior to the initiation of Lake Trout removal efforts (Hansen et al. 2008). Density of adult Lake Trout (>age 5) in Priest Lake (3.2 fish/ha) was nearly three times the density in Lake Pend Oreille (0.3 fish/ha). Total density of Lake Trout in Priest Lake (4.8 fish/ha) was over 10 times the density in Lake Pend Oreille (0.9 fish/ha) prior to eradication efforts. Despite the differences in population growth rates, the density of fish in Priest Lake is close to the average for North American populations (mean adult density = 4.4 fish/ha, range = 0.9-14.2

fish/ha; Hansen et al. 2008). Cox et al. (2013) evaluated asymptotic population growth rate for a population of nonnative Lake Trout in Swan Lake, a moderate-sized (1,335 ha), glacially-formed lake. Matrix models indicated that the Swan Lake population was growing at a rate of $\lambda = 1.35$, about 30% greater than that estimated for Priest Lake. Like Lake Pend Oreille and Priest Lake, Swan Lake contains *M. diluviana*. However, Lake Trout in Swan Lake were in better condition, likely reflecting higher productivity in Swan Lake (TDS = 112 mg/L) than Priest Lake (8.36 mg/L; Bowles et al. 1991). More similar to Priest Lake, Lake Trout in Quartz Lake, Montana, were below the 50th percentile in mean W_r and experienced similar levels of natural mortality ($M = 0.06$; Fredenberg 2014). Twenty-year average population growth rate for Lake Trout in Quartz Lake was 1.23, whereas λ was 1.07 for Priest Lake over 20 years. Although Quartz Lake lacks *M. diluviana*, the main difference between populations appears to the high rate of skipped-spawning among Lake Trout in Priest Lake. Thus, trends in population growth rates and characteristics throughout the region further support observations that the Priest Lake population is slow-growing and near carrying capacity.

Due to their slow growth and late maturity, Lake Trout populations are thought to be susceptible to overexploitation (Healey 1978; Martin and Olver 1980). Because of the reduced reproductive rate of female Lake Trout in Priest Lake, less effort would be required to collapse the population than in other western lakes. We found that total annual mortality rates as low as 27% could cause the population to decline, lower than the frequently cited assertion that Lake Trout populations cannot sustain total annual mortality rates greater than 50% (Healey 1978). For example, the young and rapidly growing Lake Trout population in Yellowstone Lake required an estimated total annual mortality greater than 39% over a 20-

year period to reduce the population (Syslo et al. 2011). Similarly, in Lake McDonald, simulations indicated that the Lake Trout population would decline if total annual mortality was between 44% and 49% (Dux 2005). In Lake Pend Oreille, Hansen (2007) evaluated the level of mortality required to reduce Lake Trout abundance and prevent collapse of kokanee or other sport fish populations. A threshold of 1,792 fish was identified as the target for suppression, based on previous estimates of abundance (Hansen et al. 2006; Hansen 2007). Hansen (2007) found that the Lake Trout population would be suppressed after 10-15 years of gill netting for A from 0.45 to 0.50. Using the same threshold for suppression, the Lake Trout population in Priest Lake would be suppressed after 10 years of netting for $A = 0.51$. Lower rates of mortality would require longer periods to reach suppression; for $A = 0.32$ suppression would be projected to occur within 25 years, and for $A = 0.27$, mortality would need to be maintained for 43 years to achieve suppression. Therefore, it appears that removal of Lake Trout in Priest Lake is possible and would require less effort than in other lakes.

Protected slot length limits are designed to promote the growth and survival of trophy individuals, and our simulation indicated that such a limit would successfully maintain the number of trophy individuals across a wide range of fishing intensities. However, increasing abundance of trophy-length individuals could further exacerbate prey-limitations in Priest Lake. In Flaming Gorge Reservoir, population models indicated that regulations maximizing catch of trophy Lake Trout also maximized prey consumption (Luecke et al. 1994). Furthermore, although we designated trophy status by length, somatic weight is often the determining factor for recreational angler satisfaction (Johnson and Martinez 2000). Fish in low-productivity systems may require more prey resources to attain the same growth rates as fish in more productive waters because prey density affects foraging efficiency (Mason et al. 1998). Large Lake Trout in Priest Lake are already in poor condition, and increasing their abundance through protective limits would likely exacerbate the problem and eventually result in angler dissatisfaction.

Removing juvenile Lake Trout (i.e., ages 2-5) has the potential to decrease population density and increase individual growth rates, but would not guarantee reduction in consumption rates. If juvenile removal reduces Lake Trout abundance such that the overall predatory pressure of Lake Trout in Priest Lake is reduced, sport fishes (e.g., kokanee) may increase in abundance. However, management with this goal in mind should be pursued cautiously because of the foraging efficiency and predatory inertia of Lake Trout (Eby et al. 1995; Schoen et al. 2012). Even if Lake Trout density is decreased, remaining individuals may increase consumption of prey fish. If maintaining a Lake Trout fishery with more ideal length-composition is desirable, the juvenile removal scenario may provide the best option to increase effort without risk of collapsing the population. Another benefit of the juvenile removal scenario is that it does not assume any changes in angler effort or exploitation. In this scenario, a limited mechanical removal of juvenile fish could be conducted, but there is no dependence on angler effort, which can be difficult to manipulate (Radomski et al. 2001).

We used a deterministic exponential growth model, which does not incorporate density-dependent dynamics. Although these types of matrix models have previously been used to evaluate population growth of Lake Trout populations (Syslo et al. 2011; Cox et al. 2013; Fredenberg 2014), slow growth and poor condition of Lake Trout in Priest Lake are indicators that density-dependent forces are already governing this population. Indeed, density-dependent responses are not only possible, but are also potentially desirable consequences of increasing exploitation in Priest Lake. Lake Trout populations have demonstrated density-dependent responses to harvest and prey abundance, including compensatory responses in growth and age-at-maturity (Sitar et al. 1999, Syslo et al. 2013). For example, individual Lake Trout growth rates increased in response to increasing exploitation in Ontario (Healey 1978). This response indicated that increased body growth may be an important compensating mechanism in exploited Lake Trout populations (Healey 1978). Since Lake Trout generally appear to mature at a fixed size, rather than age, increased individual growth rates under high exploitation can lead to earlier age of maturation (Healey 1978; Ferreri and Taylor 1996). Maternal effects, such as egg size and quality may also be density-dependent (Trippel 1993), as is skipped spawning (Sitar et al. 1999). We evaluated the potential short-term consequences of such density-dependent responses in length-at-age and probability of spawning using sensitivity analysis. Interestingly, the effect was smaller than expected; a 20% change in either vital rate resulted in less than 20% change in population growth rate.

Another potential density-dependent response is increased survival. Consistent with other studies of Lake Trout population dynamics, we found that population growth rate was most sensitive to age-0 (and juvenile) survival rates (Cox et al. 2013). Because juvenile survival rates were unavailable for Priest Lake, we used literature values corresponding to the Lake Superior (age-0 survival; Sitar et al. 2014) and Ontario lakes (age-1 and age-2 survival; Shuter et al. 1998), where different factors, such as Sea Lamprey *Petromyzon marinus* predation and low population density influences survival rates. However, as discussed above, density-dependent responses in adult Lake Trout growth rates are common.

In a simulation study using an age-structured population model, Rose (2005) demonstrated that when adult and juvenile density-dependence occurred simultaneously, they dampened each other. Therefore, although density-dependent effects across multiple age-classes may be present, such forces may ultimately cancel each other. In the absence of data for Priest Lake, we chose to omit density-dependent effects on recruitment and adult growth from the model.

Fisheries management is an iterative process because fish populations are highly dynamic (Parrish et al. 1995). This study provides insight on the short-term (10-year) population dynamics under three management scenarios representing alternative management scenarios for Lake Trout populations. As with any study using population models, projections are uncertain because variation in vital rates depends on intrinsic, biotic, and abiotic factors (Shuter et al. 1998), as well as stochastic environmental processes (Morris and Doak 2002). Despite these limitations, population models are useful for synthesizing information and comparing management actions. Our research provides a foundation for assessing biological feasibility of potential management actions, and serves as a baseline for future monitoring and assessment. More broadly, these types of models help advance understanding of the intrinsic factors that regulate fish populations and provide a basis for formulating hypotheses about the drivers of population growth and decline. Moving forward, management “experiments” and monitoring will allow us to test hypotheses about fish population dynamics.

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Table 2.1. Number of tagged and released Lake Trout ($\boldsymbol{N_{tag}}$), and the number reported harvested ($\boldsymbol{N_{rep}}$) during May 10, 2013-May 10, 2014 from Priest Lake, Idaho. Number of tagged fish available for capture was corrected for post-release mortality ($\boldsymbol{\widehat{N}_{tag}}$) and number of harvested fish was corrected for non-reporting ($\boldsymbol{\widehat{N}_{rep}}$) before calculating exploitation (μ).

Reward	N_{tag}	$\widehat{N}_{tag}$	N_{rep}	$\widehat{N}_{rep}$	μ
$50	188	177	23	25	14.2
$0	2,771	2,238	164	303	13.5
Mean	2,959	2,415	187	327	13.6

Table 2.2. Mean and standard deviation (in parentheses) of age-specific characteristics and vital rates used in population simulations for Lake Trout in Priest Lake, Idaho; female abundance (*N*), survival (*S*), probability of spawning (*P*), and fecundity (*f*, number of eggs).

Age (i)	TL (mm)	Mass (g)	N_i	S_i	P_i	f_i
0	–	–	–	0.0043 (0.001)[a]	0.00 (0.00)	0 (0)
1	–	–	2241	0.450 (0.090)[b]	0.00 (0.00)	0 (0)
2	301	258	1996	0.780 (0.156)[b]	0.00 (0.00)	0 (0)
3	332	338	1556	0.825 (0.012)	0.00 (0.00)	0 (0)
4	360	425	1125	0.825 (0.012)	0.00 (0.00)	0 (0)
5	387	519	649	0.825 (0.012)	0.00 (0.00)	0 (0)
6	412	618	666	0.825 (0.012)	0.15 (0.04)	2097 (235)
7	436	721	1045	0.825 (0.012)	0.17 (0.04)	2137 (218)
8	458	827	1342	0.825 (0.012)	0.19 (0.04)	2177 (202)
9	479	935	1160	0.825 (0.012)	0.21 (0.04)	2217 (188)
10	498	1044	1280	0.825 (0.012)	0.23 (0.04)	2257 (175)
11	516	1153	1152	0.825 (0.012)	0.25 (0.04)	2297 (164)
12	533	1262	1173	0.825 (0.012)	0.28 (0.04)	2337 (154)
13	549	1369	1314	0.825 (0.012)	0.30 (0.05)	2377 (148)
14	564	1476	813	0.825 (0.012)	0.33 (0.05)	2417 (144)
15	579	1580	854	0.825 (0.012)	0.36 (0.05)	2457 (144)
16	592	1682	447	0.825 (0.012)	0.38 (0.06)	2497 (146)
17	604	1781	716	0.825 (0.012)	0.41 (0.06)	2537 (152)
18	616	1877	605	0.825 (0.012)	0.44 (0.07)	2577 (160)
19	627	1971	265	0.825 (0.012)	0.47 (0.07)	2617 (171)
20	637	2061	112	0.825 (0.012)	0.50 (0.08)	2657 (184)
21	646	2148	356	0.825 (0.012)	0.53 (0.08)	2697 (198)
22	655	2231	252	0.825 (0.012)	0.56 (0.09)	2737 (213)
23	664	2311	184	0.825 (0.012)	0.59 (0.09)	2777 (229)
24	671	2388	196	0.825 (0.012)	0.62 (0.10)	2817 (247)
25	679	2461	205	0.825 (0.012)	0.65 (0.10)	2857 (264)
26	686	2531	105	0.825 (0.012)	0.68 (0.10)	2897 (283)
27	692	2598	154	0.825 (0.012)	0.70 (0.10)	2937 (301)
28	698	2662	171	0.825 (0.012)	0.73 (0.10)	2976 (320)
29	704	2723	270	0.825 (0.012)	0.75 (0.10)	3016 (340)
30	709	2780	69	0.825 (0.012)	0.78 (0.10)	3056 (359)
31	714	2835	167	0.825 (0.012)	0.80 (0.10)	3096 (379)
32	719	2887	58	0.825 (0.012)	0.81 (0.10)	3136 (399)
33	723	2936	22	0.825 (0.012)	0.83 (0.09)	3176 (419)

Table 2.2 continued

34	728	2983	3	0.825 (0.012)	0.85 (0.09)	3216 (439)
35	731	3027	25	–	0.86 (0.08)	3256 (459)

[a] Vital rate estimate from Shuter et al. (1998) with standard deviation equal to 20% of the mean.

[b] Vital rate estimate from Sitar et al. (1999) with standard deviation equal to 20% of the mean.

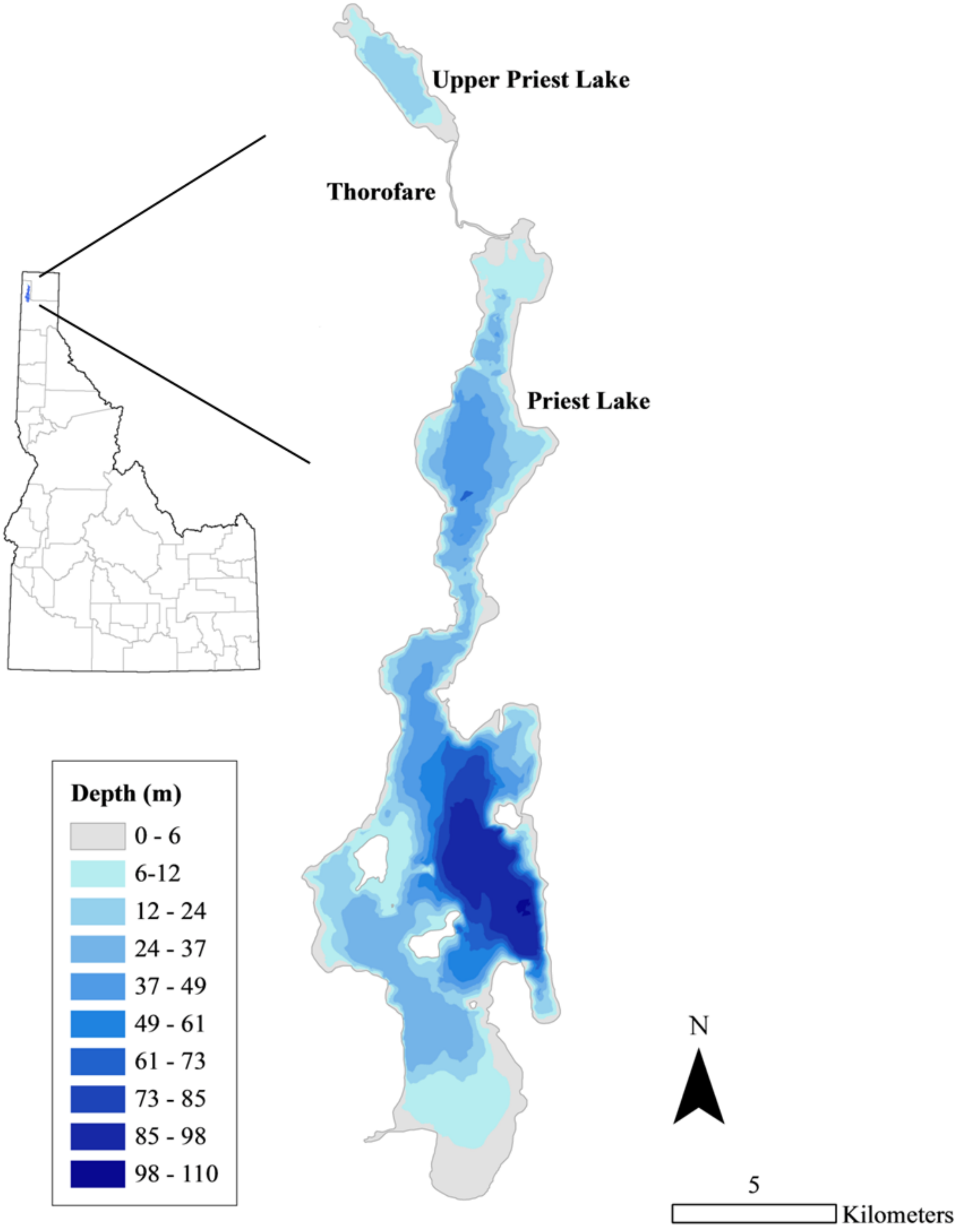

Figure 2.1. Location of Priest Lake in the northern Idaho panhandle.

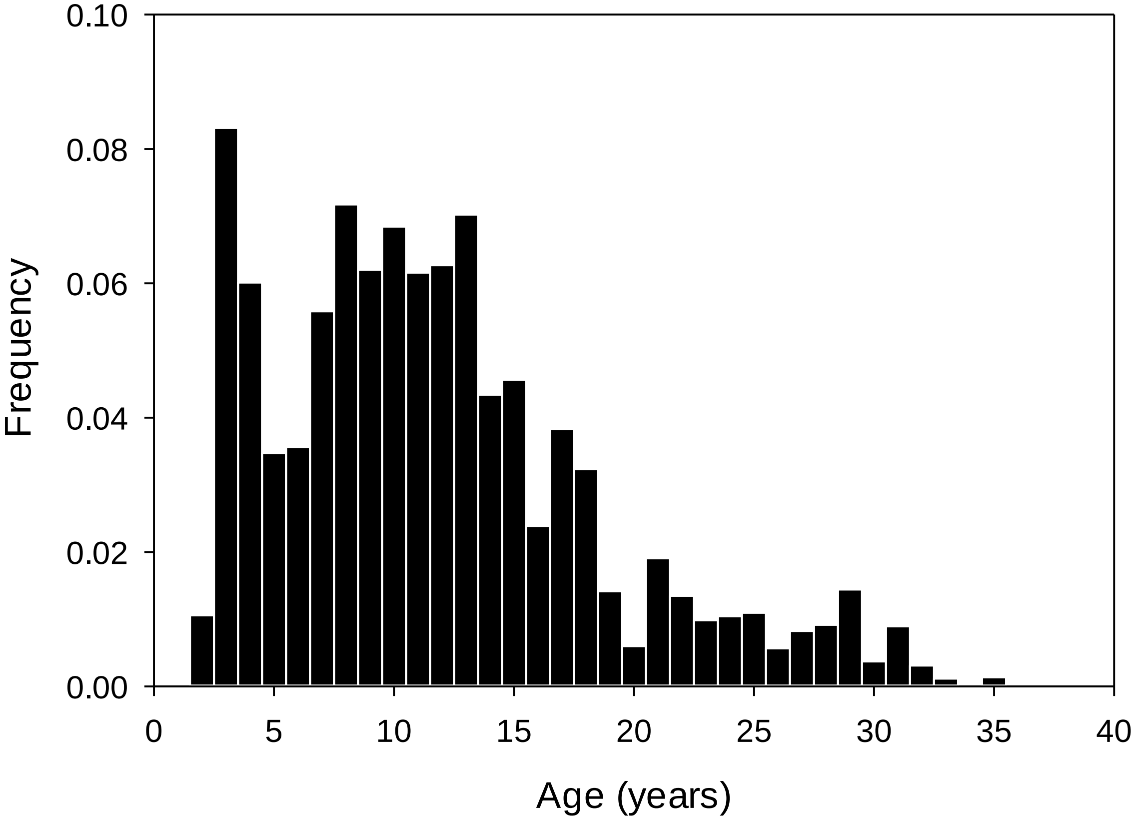

Figure 2.2. Age-frequency distribution of Lake Trout sampled in spring 2013 from Priest Lake, Idaho. Data are for gill-net captured fish corrected for selectivity.

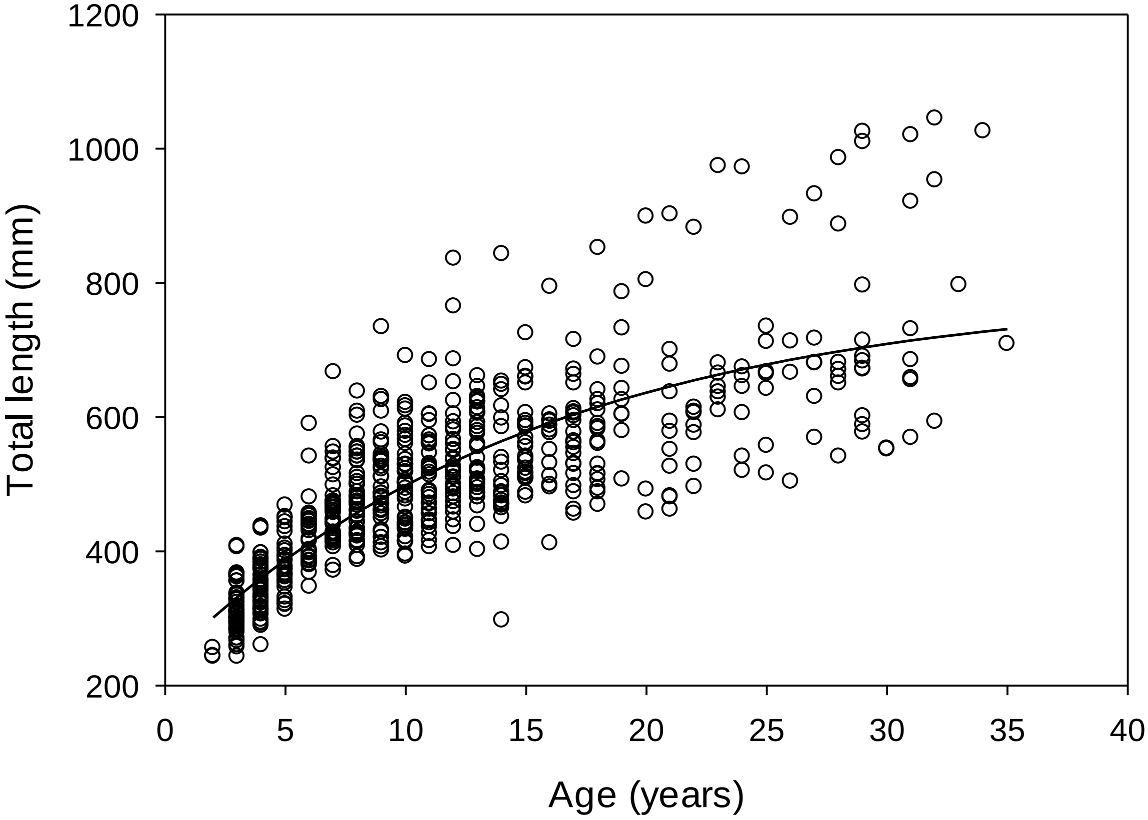

Figure 2.3. Von Bertalanffy growth model fit to length-at-age data for Lake Trout sampled in 2013 from Priest Lake, Idaho.

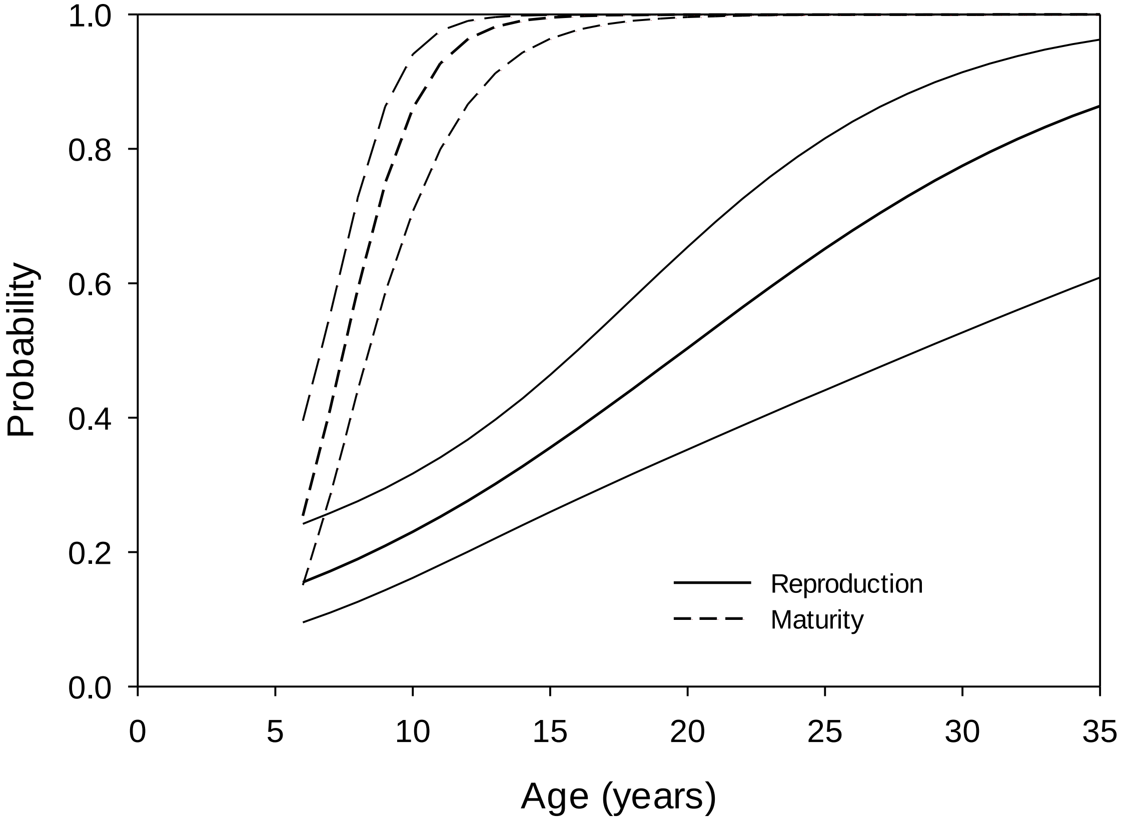

Figure 2.4. Maturity and reproductive ogives for Lake Trout sampled in autumn 2013 from Priest Lake, Idaho. Maturity ogive indicates the probability of maturity for Lake Trout at age. Reproductive ogive represents the probability of spawning at a given age. Lines are predicted probability and 95% confidence intervals.

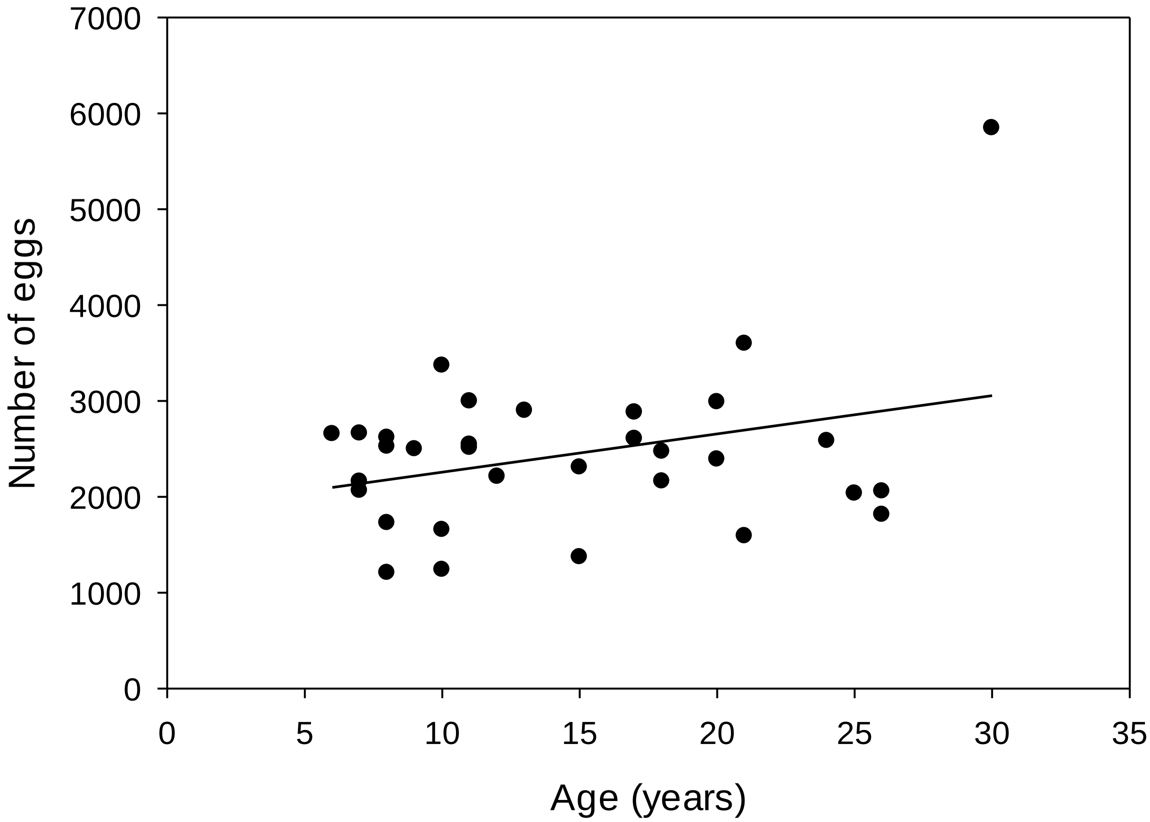

Figure 2.5. Observed fecundity at age for female Lake Trout sampled in autumn 2013 from Priest Lake, Idaho.

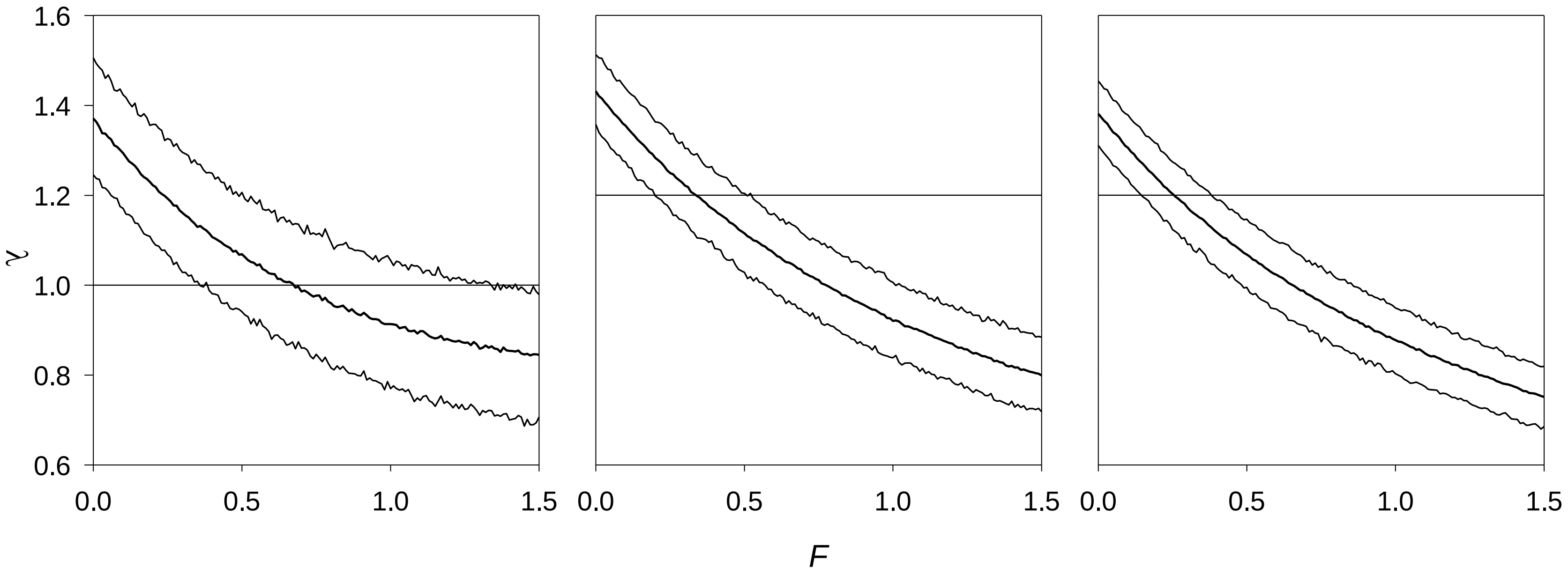

Figure 2.6. Median population growth rate (λ) with 95% confidence intervals for the eradication scenario at varying levels of fishing mortality (*F*) over 5- (left), 10- (center), or 20-year (right) periods for Lake Trout in Priest Lake, Idaho. The horizontal reference line indicates λ = 1 (replacement).

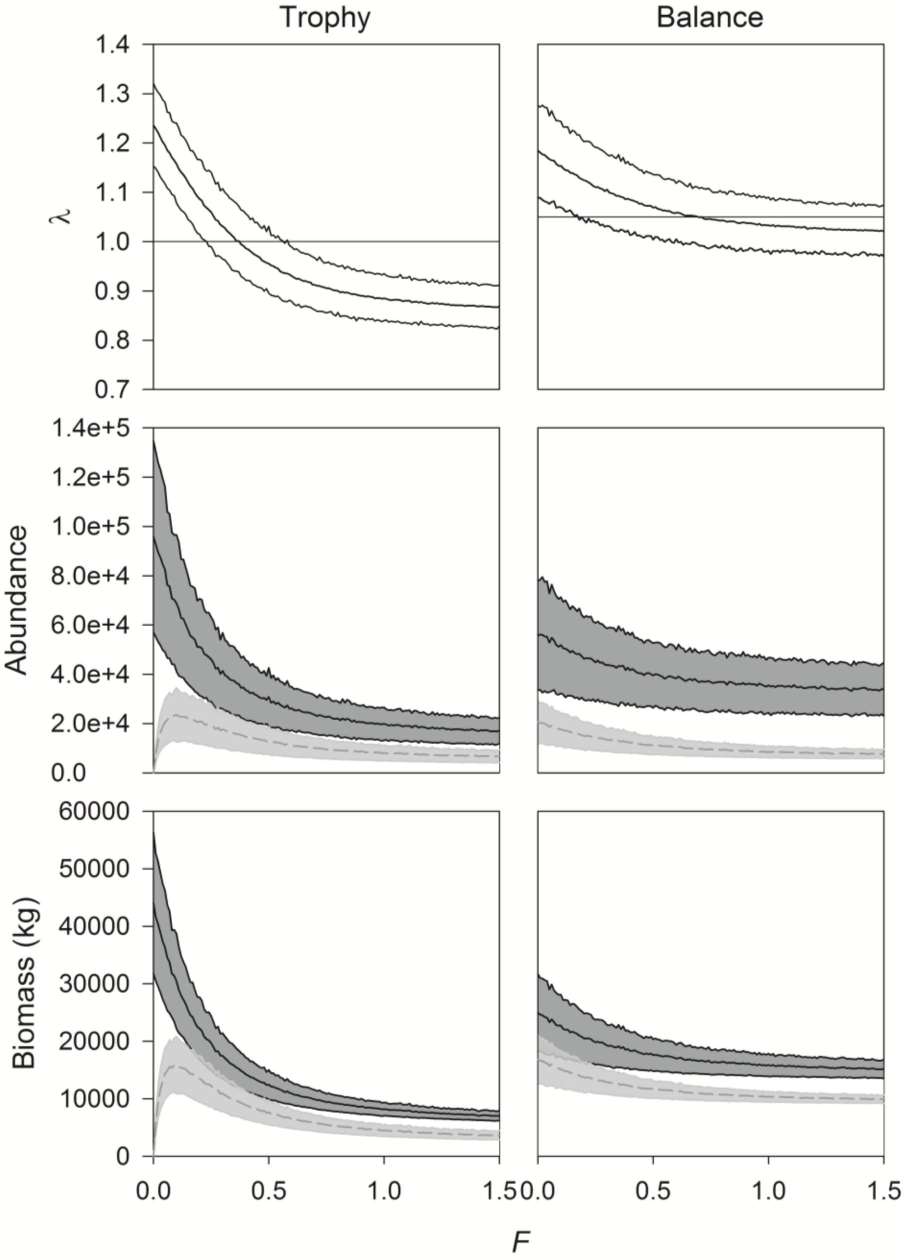

Figure 2.7. Population growth rate (λ), abundance, and biomass under two management scenarios at varying levels of fishing mortality (*F*) over a period of 10 years for Lake Trout in Priest Lake, Idaho. Mean population growth is shown with a reference line indicating λ = 1 (replacement). Median population abundance (solid line) and median number fish harvested (dashed line) are in the second row. Median population biomass (kg; solid lines) and median biomass harvested (dashed line) are in the bottom row. Ninety-five percent confidence intervals are shown. Management scenarios are trophy (left), a protected slot limit for fish age 23 and above; and balance (right), a mechanical juvenile removal scenario for age-2 to age-5 Lake Trout.

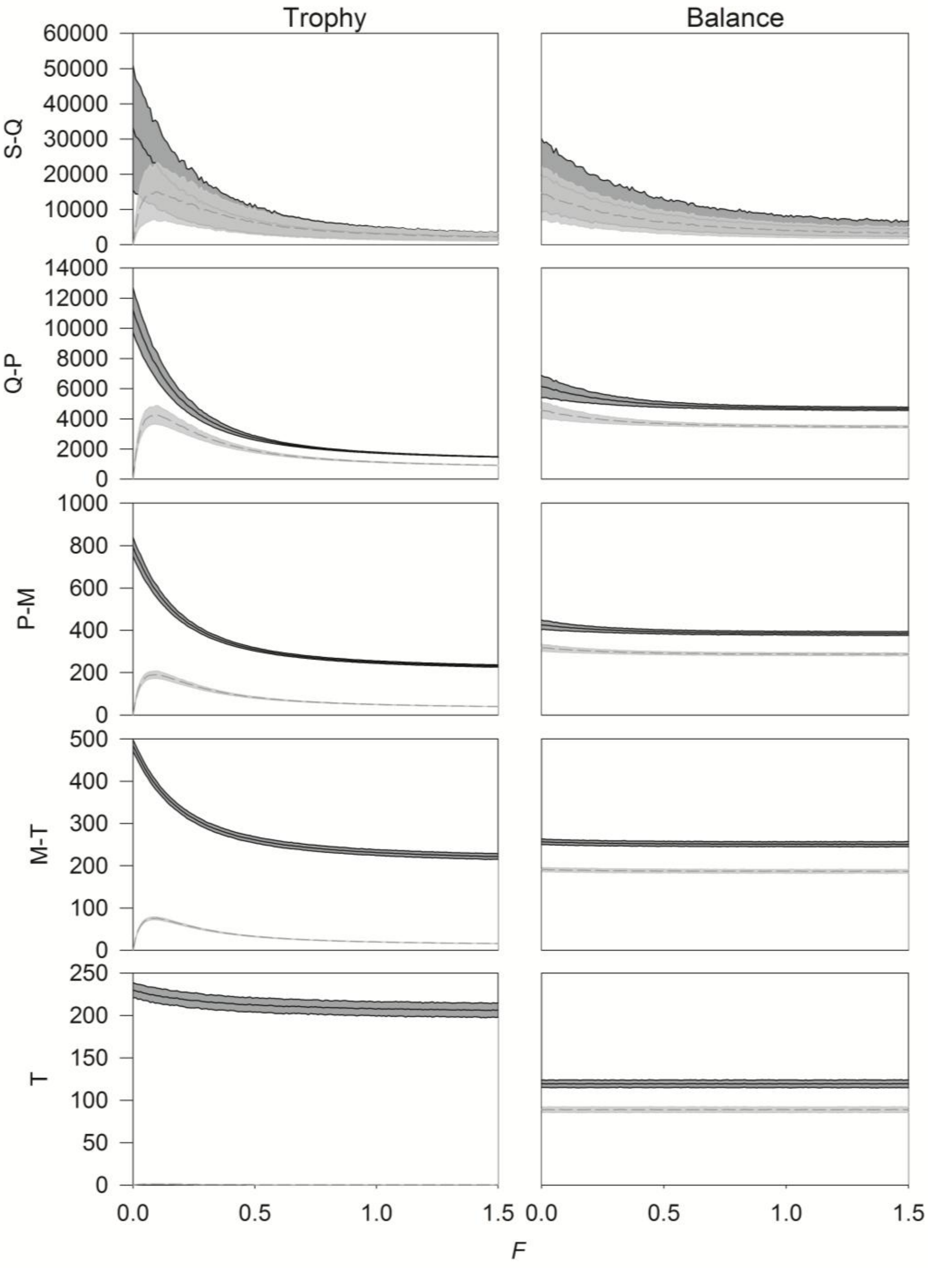

Figure 2.8. Abundance of Lake Trout by incremental-standard-length categories under two management scenarios at varying levels of fishing mortality (*F*) in Priest Lake, Idaho. The length categories, from top to bottom row, are stock–quality (280–500 mm), quality-preferred (501–700), preferred-memorable (701–850 mm), memorable-trophy (851–1,000 mm), and trophy (>1,000 mm). Median abundance (solid lines) and median number harvested (dashed lines) are shown with 95% confidence intervals. Management scenarios are trophy (left), a protected slot limit (660–813 mm, age 23 and above); and balance (right) where age-2 to age-5 Lake Trout were removed.

Chapter 3: Stable Isotope Evaluation of Population- and Individual-level Diet Variability in a Large, Oligotrophic Lake with Nonnative Lake Trout

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Abstract

Nonnative piscivores can alter food web dynamics; therefore, evaluating interspecific relationships is vital for conservation and management of ecosystems with introduced fishes. Priest Lake, Idaho, supports a number of introduced species, including Lake Trout *Salvelinus namaycush*, Brook Trout *S. fontinalis*, and opossum shrimp *Mysis diluviana*. In this study, we used stable isotopes (δ^{13}C and δ^{15}N) to evaluate the food web structure of Priest Lake and to test hypotheses about apparent patterns in individual heterogeneity in Lake Trout growth. We found that isotopic niches of species using pelagic-origin carbon did not overlap with those using more littoral-origin carbon. Species using more littoral-origin carbon, such as Brook Trout and Westslope Cutthroat Trout *Oncorhynchus clarki lewisi*, exhibited a high degree of isotopic niche overlap and high intra-population variability in resource use. Although we hypothesized that Lake Trout would experience an ontogenetic diet shift, resulting in decreasing dependency on pelagic *M. diluviana* and increasing trophic position with increasing length, no such patterns were apparent in isotopic signatures. Low variability in Lake Trout isotope signatures may result from dependence on *M. diluviana* across lengths, and opportunistic foraging on prey fishes. Lake Trout growth rates were not associated with patterns in δ^{15}N, indicating that causes of diversification in adult body composition may occur early in life. Understanding trophic relationships at both the individual and population levels provides a more complete understanding of the food web. Here, we identified potential competitive interactions among and within species in Priest Lake.

Introduction

Trophic interactions are one of the fundamental mechanisms by which ecological structuring and niche partitioning occur in aquatic environments. Predators can have strong effects on ecosystem structuring through both direct (e.g., Goldschmidt et al. 1993) and indirect (e.g., Hölker et al. 2007) pathways, especially in lentic ecosystems (Northcote 1988; Jackson et al. 2001). Because of the sensitivity of lacustrine ecosystems to predators, introduced fishes, which are commonly piscivores (Eby et al. 2006), have an outsized effect on lentic systems (Sala et al. 2000; Mitchell and Knouft 2008). In particular, introduced predators can have cascading effects on ecosystems (Carpenter et al. 2001; Cucherousset and Olden 2011). Evaluating interspecific relationships is therefore vital for conservation and management of ecosystems where introduced species have altered dynamics between coevolved species.

Population-level effects of introduced species are well-studied (Sakai et al. 2001; Cucherousset and Olden 2011), but focus has increasingly shifted to understanding the underlying contribution of intraspecific trait variation to population-level patterns (Bolnick et al. 2011; Ruffino et al. 2011; Svanbäck et al. 2015). Intraspecific patterns in trait diversity can have effects at the population level, including stability, competition, and fitness (Bolnick et al. 2003). Size, growth, and foraging patterns can drive individual heterogeneity in diets (e.g., Huss et al. 2008), so evaluating intraspecific variability can elucidate the origins of patterns that emerge at the population level. For example, Araújo et al. (2008) found that diet breadth of Threespine Stickleback *Casterosteus aceleatus* increased in response to increasing intraspecific competition (i.e., increasing Threespine Stickleback density). However, individual fish did not have equivalent diet breadths. Rather, a subset of individuals switched from preferred prey to new prey resources, reflecting phenotypic-dependent changes in foraging behavior (Svanbäck and Bolnick 2007). Therefore, within nonnative fish populations, generalist and specialist (e.g., piscivorous) individuals may contribute disproportionally to negative interactions with native species. Furthermore, we can understand the mechanisms driving patterns in diet by linking observed patterns in individual diet variability to individual phenotypic traits, such as growth rate or length (Svanbäck et al. 2015). Understanding trophic relationships at both the individual and population levels provides a more complete understanding of the effects of nonnative species.

Lake Trout *Salvelinus namaycush* have been introduced widely, often to provide a trophy component to recreational fisheries (Crossman 1995; Martinez et al. 2009). Within their native distribution, Lake Trout are apex predators (Ryder et al. 1981). As such, introductions of nonnative Lake Trout have caused conflicts with sport fish and fishes of conservation concern (Martinez et al. 2009). Nonnative Lake Trout are particularly challenging to manage because of their predatory intertia, which results from high rates of predation coupled with long life spans and resistance to starvation (Eby et al. 1995; Schoen et al. 2012). Predation by nonnative Lake Trout is problematic in many systems. For instance, in Yellowstone Lake, Wyoming, Lake Trout have contributed to the decline of Yellowstone Cutthroat Trout *Onchorynchus clarkia bouvieri* via direct predation (Ruzycki et al. 2003; Quist and Hubert 2004; Syslo et al. 2011). Furthermore, Lake Trout may also alter niche partitioning through competition with native predators, such as Bull Trout *S. confluentus* (Donald and Alger 1993; Meeuwig et al. 2011). Over longer periods of time, the introduction of Lake Trout, especially in systems with introduced opossum shrimp *Mysis* *diluviana*, can mediate trophic cascades and cause dramatic shifts in ecosystem structure (Bowles et al. 1991; Tronstad et al. 2010; Ellis et al. 2011).

The introduction of Lake Trout to Priest Lake, Idaho, in 1925 followed patterns similar to other western U.S. lakes, such as Flathead Lake and Lake Pend Oreille (Bowles et al. 1991; Martinez et al. 2009; Ellis et al. 2011). Lake Trout remained at low abundance and provided a trophy fishery following the successful introduction of kokanee *Onchorynchus nerka* in 1956. However, after the establishment of *M. diluviana* in the early 1970s, kokanee abundance declined and the Lake Trout fishery transitioned from a low-catch trophy fishery to a high-yield fishery with reduced size structure. Additionally, the previously abundant Bull Trout population declined sharply after the abundance of Lake Trout increased in the late 1970s (Venard and Scarnecchia 2005). By the late 1990s, Bull Trout were thought to be nearly extirpated from Priest Lake. Once-abundant Westslope Cutthroat Trout *O. clarki lewisi* in Priest Lake began to decline in the mid-1950s, and currently remain at low abundance (Mallet 2013). Although major changes in the fish assemblage have occurred, the relationship between nonnative species and a decline Westslope Cutthroat Trout abundance remain unclear. Furthermore, declines in the body condition of Lake Trout following reduction in kokanee abundance have spurred questions about prey availability and foraging capacity of Lake Trout in the system.

Individual Lake Trout growth rates and body condition depended on prey availability. In a study of six Lake Trout populations in Canada, Martin (1966) found that populations with access to suitable prey fishes grew faster than those that were restricted to invertebrates. When non-piscivorous Lake Trout were transplanted to lakes with abundant prey fishes, individual growth rates increased markedly (Martin 1966). In Lake Opeongo, Ontario, body condition of Lake Trout increased after the introduction of Cisco *Coregonus artedi*, a pelagic prey species (Martin 1970). Patterns in growth between Lake Trout populations with varying prey availabilities are common (Pazzia et al. 2002), but Lake Trout can also exhibit a high degree of intrapopulation plasticity (Zimmerman et al. 2006; McDermid et al. 2010; Muir et al. 2015). For example, Stafford et al. (2013) found evidence of a fast-growing shallow-water Lake Trout morphotype and a slow-growing deep-water morphotype in Flathead Lake. Dietary differences were also found between the two morphotypes, with shallow Lake Trout feeding opportunistically on fishes and deep Lake Trout feeding predominantly on *M. diluviana* (Stafford et al. 2013). Based on observations of Lake Trout in Priest Lake with low and high body condition, it has been hypothesized that two different stocks or morphotypes may be present in Priest Lake. Furthermore, these two groups of Lake Trout may respond differently to prey fish abundance.

Stable isotopes have been used extensively to study trophic interactions in aquatic ecosystems, including the effects of nonnative fishes. Isotopes are incorporated at the time of tissue synthesis, and for adult fish muscle tissue isotopic ratios represent about a year's worth of diet information (Vander Zanden et al. 1997). Isotopes can be used to identify the carbon source and trophic position of prey items because of differential assimilation of heavy versus light isotopes into consumer tissues (i.e., fractionation). Pelagic planktonic algae is generally depleted in the heavy carbon isotope (^{13}C) relative to littoral, benthic, or epilithic algae because turbulence in the pelagic zone reduces boundary-layer diffusion inhibition (France 1995). Furthermore, carbon isotopes do not fractionate strongly with increasing trophic position, so consumers retain the signature of the carbon source. The light nitrogen isotope (^{14}N) is preferentially excreted in nitrogenous waste. Therefore, consumer tissue is consistently enriched relative to prey tissue, and ^{15}N enrichment can be used as an indicator of trophic position (Minagawa and Wada 1984; Vander Zanden et al. 1997).

In this study, we used stable isotopes to evaluate the food web structure and to test hypotheses about apparent patterns in individual heterogeneity of Lake Trout in Priest Lake. Specifically, we hypothesized that Lake Trout would experience ontogenetic shifts from a diet dominated by pelagic *M. diluviana* to one that included more littoral prey fishes. We also hypothesized that the shift in diet would result in increasing trophic position of Lake Trout with increasing length.

Methods

Priest Lake is a 9,461-ha dimictic lake located in the Columbia River basin of northern Idaho (Figure 3.1). The roughly 1,554 km^2 watershed is granitic and dominated by coniferous forest cover (Bjornn 1957; Maiolie et al. 2013). Formed by glacial action, this oligotrophic lake has steep sides with little littoral habitat (Bjornn 1957). Priest Lake is at an elevation of 743 m and has a surface area of 9,461 ha (Martinez et al. 2009), a mean depth of 38 m, and a maximum depth of 112 m (Bowles et al. 1991). Approximately 19% of the lake is less than 12 m deep (Rieman et al. 1979). Portions of the lake may become ice-covered from January to April (Bjornn 1957). Thermal stratification generally occurs mid-July through the end of October, with a thermocline at a depth of about 35 to 50 m and summer surface water temperatures reaching 26°C in shallow areas (Kemmerer et al. 1924; Bjornn 1957; Rieman et al. 1979). Upper Priest Lake is located at the same elevation as the lower lake and the two lakes are connected by a short (3.2 km), shallow (2-3 m deep) channel called the Thorofare (Rieman et al. 1979). Upper Priest Lake is smaller and shallower than the main lake, with a surface area of 541 ha, a mean depth of 13 m, and a maximum depth of 32 m (Martinez et al. 2009). Upper Priest Lake has a higher percentage of littoral habitat than the lower lake (Bjornn 1957). Roughly a third of the upper lake is less than 6 m deep (Rieman et al. 1979).

The native fish assemblage includes Bull Trout, Westslope Cutthroat Trout, Mountain Whitefish *Prosopium williamsoni*, Pygmy Whitefish *P. coulterii*, Largescale Sucker *Catostomus macrocheilus*, Longnose Sucker *C. catostomus*, Northern Pikeminnow *Ptychocheilus oregonensis*, Redside Shiner *Richardsonius balteatus*, Peamouth *Mylocheilus caurinus*, and Slimy Sculpin *Cottus cognatus* (Bjornn 1957; Rieman et al. 1979; Maiolie et al. 2011). In addition to Lake Trout and kokanee, at least seven other fish species have been introduced: Brook Trout *S. fontinalis*, Tench *Tinca tinca*, Largemouth Bass *Micropterus salmoides*, Smallmouth Bass *M. dolomieui*, Northern Pike *Esox lucius*, Green Sunfish *Lepomis cyanellus*, and Yellow Perch *Perca flavescens* (Fredericks et al. 2009).

Fishes were collected from Priest Lake in spring and summer 2013 and 2014, Upper Priest Lake in early summer 2013 and 2014, and the Thorofare in autumn 2013. Fishes were sampled from Priest Lake and Upper Priest Lake using sinking monofilament gill nets (1.8 m deep × 30.5 m long), which consisted of one of eight mesh sizes (50.8, 63.5, 76.2, 88.9, 101.6, 114.3, 127.0, 139.7-mm stretch mesh). Twelve nets were combined to form a 1,463 m-long gang where each mesh size was represented at least once and no more than twice. Gangs were set during daylight hours in a serpentine pattern along an isobath. Priest Lake was divided into two strata of equal area (north and south) and then divided by a 1-km^2 grid. In April 2013, three sites in the northern stratum and two sites in the southern stratum were randomly selected for sampling; all fishes captured were sacrificed. In May 2014, one site was randomly selected for collection. Upper Priest Lake was small enough that gill nets covered most fishable areas in June 2013. In June 2014, nearshore areas were randomly selected from Priest Lake for sampling with floating monofilament experimental gill nets (1.8 m deep × 45 m long). Floating gill nets were composed of six panels of six mesh sizes (38, 50, 64, 76, 102, and 128-mm stretch mesh). Nets were set perpendicular to the shoreline and fished overnight with set times varying from 12 to 19 hours. Night electrofishing was also conducted in Priest Lake in June 2014. A boat-mounted Smith-Root 5.0 GPP electrofisher (Smith-Root Inc., Vancouver, WA) was used with pulsed DC (60 pulses per second). Electrofishing samples consisted of 10 min units of effort beginning at randomly chosen sites throughout Priest Lake. In summer 2014, muscle tissue was also collected from kokanee acquired from anglers during a creel survey. Finally, a large trap net was placed in the Thorofare from October to November 2013 to collect Lake Trout moving into Upper Priest Lake. The trap pot was placed in the middle of the channel with the leads (200-mm stretch mesh) extended to both shorelines.

Zooplankton was sampled from Priest Lake in summer 2013 and 2014. In August 2013, *M. diluviana* were collected during a sampling effort targeting kokanee with a midwater trawl (see Rieman and Myers 1992). In June 2014, a 500-µm mesh (0.5-m diameter) plankton net and a 300-µm mesh (0.2-m diameter) plankton net were used to sample *M. diluviana* and zooplankton in Priest Lake. Vertical tows were conducted at night through the layer of *M. diluviana* that was identified with sonar.

Captured fish were measured (nearest mm) and a small plug of white muscle tissue (about 5 g) was removed from the anterior dorsal musculature. Samples were placed on ice during field processing and immediately frozen (-24°C) in the laboratory until further processing. *M. diluviana* were isolated from other zooplankton in the lab. *M. diluviana* were separated into small (<1 cm) and large individuals, since diets can vary by size (Chipps and Bennett 2000). Individual *M. diluviana* were combined to reach a mass of approximately 5 g wet weight per sample. Bulk zooplankton samples (with *M. diluviana* removed) were separated into samples of roughly 5 g. Observation of bulk samples indicated that they were composed primarily of cladocerans and copepods.

All samples were processed for stable isotope analysis by the Washington State University Stable Isotope Core laboratory. Samples were dried at 60°C to constant mass and ground to a fine powder. One to two mg of each sample were placed into a tin cup and processed for δ^{13}C and δ^{15}N values using an elemental analyzer (ECS 4010, Costech Analytical, Valencia, CA) and a continuous flow isotope ratio mass spectrometer (Delta PlusXP, Thermofinnigan, Bremen; Brenna et al. 1998, Qi et al. 2003). Results were expressed as the relative difference between isotope ratios of the sample and a standard:

$$\delta = \frac{(R_{sample} - R_{standard})}{R_{standard}} \times 1{,}000,$$

where δ (‰) is the difference, R_{sample} is the isotopic ratio of the sample, and $R_{standard}$ is the isotopic ratio of the standard (Vienna Pee Dee Belemnite for ^{13}C/^{12}C and atmospheric N_2 for ^{15}N/^{14}N). Samples were normalized using three running standards: acetanilide, corn *Zea mays*, and keratin. Because lipids are generally depleted in ^{13}C relative to proteins and carbohydrates, variation in fat content can bias estimates. We therefore used a mathematical normalization for lipid content using the C:N ratio (Post et al. 2007).

Priest Lake trophic structure was evaluated qualitatively using δ^{13}C and δ^{15}N bi-plots. Sample sizes for individual taxa precluded statistical tests of differences between locations, seasons, and years, but visual observation indicated no major differences among sampling events. All analyses were conducted with samples pooled across time and location. Trophic position of individual taxa and overall food chain length were estimated by converting δ^{15}N values to trophic position. We assumed that zooplankton fed at trophic position 2 and determined successively higher trophic positions using the following equation:

$$TP_i = \frac{\delta^{15}\mathrm{N}_i - \delta^{15}\mathrm{N}_{pc}}{3.4} + 2,$$

where TP_i is the trophic position of the ith taxon, $\delta^{15}\mathrm{N}_i$ is the nitrogen signature of the ith taxon, and $\delta^{15}\mathrm{N}_{pc}$ is the nitrogen signature of primary consumers (zooplankton; Post 2002). Stable Isotope Bayesian Ellipses in R (SIBER; Jackson et al. 2011) was used to estimate standard ellipse area (i.e., isotopic niche space) for members of the Priest Lake food web. Standard ellipses are the bivariate extension of univariate standard deviations. Furthermore, the Bayesian implementation has been shown to be robust to differences in sample sizes (Jackson et al. 2011), in contrast to traditional convex-hull based metrics (e.g., Layman et al. 2012). In addition to niche size, we also evaluated area of niche overlap between taxa in Priest Lake. Linear regression was used to test hypotheses regarding patterns in the Lake Trout population. Specifically, we tested for significant increases in δ^{13}C and δ^{15}N with length to evaluate dietary partitioning by Lake Trout that may undergo ontogenetic shifts from *M. diluviana* to fish prey. All analyses were conducted in R (R Core Team 2014, version 3.1.2).

Finally, we evaluated the relationship between Lake Trout growth and trophic position. Saggital otoliths and fin rays were collected from Lake Trout sampled in 2013. Otoliths were mounted in epoxy, thin-sectioned with a low speed saw (Beuhler, Lake Bluff, IL), and viewed under a dissecting scope using transmitted light (Quist et al. 2012). A von Bertalanffy growth model was fit to observed length-at-age data:

$$L_t = L_\infty\left[1 - e^{-k(t-t_0)}\right]$$

where L_t is the length at age t, L_∞ is the asymptotic length, k is a growth constant, and t_0 is the theoretical age when length is 0 mm (Gallucci and Quinn II 1979). Standardized residuals were used as an indicator of individual growth rate. We compared the mean δ^{15}N values of Lake Trout in the upper and lower 25th percentiles of growth by age. We hypothesized that fast-growing Lake Trout (i.e., the upper 25th percentile of growth) would have elevated δ^{15}N values relative to slow-growing fish.

Results

Over the course of the study, 15 taxa were sampled (Table 3.1). Organisms collected in offshore areas, including zooplankton, *M. diluviana*, kokanee, and Lake Trout, tended to have depleted δ^{13}C values (Figure 3.2). Offshore species' standard ellipses did not overlap, except for the standard ellipse of Lake Trout, which overlapped 10% with the standard ellipse of Bull Trout (Table 3.2). A cluster of species with more enriched δ^{13}C values was centered around -25.0‰, and included Brook Trout, Mountain Whitefish, Westslope Cutthroat Trout, Longnose Suckers, Largescale Suckers, Peamouth, and Tench. These species exhibited a high degree of niche overlap (Table 3.2), but also had the most variable δ^{13}C values. For example, Mountain Whitefish had the second largest niche size, but it was entirely encompassed by the standard ellipse of Brook Trout. Westslope Cutthroat Trout had an intermediate-sized niche area, but overlapped 80% with Brook Trout, 80% with Mountain Whitefish, 70% with Largescale Sucker, 60% with Longnose Sucker, 30% with Northern Pikeminnow, and 50% with Peamouth (Table 3.2). The species with the most prominent littoral signatures were Yellow Perch and Smallmouth Bass (Figure 3.2); however, low sample sizes for these species precluded further analysis.

The Priest Lake food chain was relatively short, with a difference of only 2.2 trophic positions between zooplankton and the highest member, Lake Trout (4.2). Trophic position of Bull Trout (4.1) was nearly as high as for Lake Trout. Northern Pikeminnow, Yellow Perch, and Brook Trout had the next highest trophic position (3.8) followed by Mountain Whitefish (3.7) and Smallmouth Bass (3.6). Longnose Sucker, Largescale Sucker, and Westslope Cutthroat Trout appeared to feed at the same trophic position (3.5), followed closely by kokanee and Peamouth (3.4). The fish with the lowest trophic position was Tench (3.1). *M. diluviana* had an average trophic position of 2.7, but trophic position of smaller individuals (2.3) was lower than for large individuals (2.7).

Brook Trout had the largest niche space (Figure 3.3) followed by Mountain Whitefish, Northern Pikeminnow, and Largescale Sucker. Lake Trout had the smallest niche size, though zooplankton, *M. diluviana*, and kokanee also had small niche space. With small sample sizes (ca. $n < 30$), estimated niche space may be biased slightly low (Jackson et al. 2011).

Total length of Lake Trout was positively related to δ^{13}C value, but the relationship accounted for less than 10% of the variability in overall δ^{13}C values for Lake Trout (Figure

3.4). Neither Lake Trout length (Figure 3.4) nor growth rate (Figure 3.5) indicated strong relationships with δ^{15}N.

Discussion

Based on stable isotope analysis, several members of the Priest Lake fish assemblage appeared to use similar carbon sources (e.g., more littoral) and feed at a similar trophic level. Species included native species like Mountain Whitefish, Northern Pikeminnow, Westslope Cutthroat Trout, Longnose Sucker, Largescale Sucker, and Peamouth, as well as nonnative Brook Trout and Tench. These results were similar to stable isotope studies in nearby Lake Pend Oreille, which has a similar species composition to Priest Lake (Clarke et al. 2005). There, Clarke et al. (2005) found no difference in δ^{15}N values for Northern Pikeminnow, Westslope Cutthroat Trout, Peamouth, and Rainbow Trout, species that also had similar δ^{13}C values. Although the group of fishes using littoral-origin carbon sources in Priest Lake exhibited high levels of niche overlap, the niches also tended to be large, indicating high intraspecific variability in resource use. Diet breadth tends to increase with increasing competition for resources (Werner and Hall 1974). Diet breadth may also be highest at intermediate trophic levels (Svanbäck et al. 2015), reflecting trade-offs in individual foraging. However, population-level variability can arise from individual specialization on different resources, or by taking a snap-shot of individual generalists in time (Bearhop et al. 2004). High intrapopulation variability in isotopic niche may also occur because of spatial and temporal variability in food isotopic signatures, rather than from diet composition (Matthews and Mazumder 2004). Although we qualitatively determined that there were no temporal or spatial patterns in isotopic signatures, this would be a worthwhile area for future study. Given the high levels of overlap for mid-trophic level fishes in Priest Lake, including Brook Trout and Westslope Cutthroat Trout, further investigation of niche partitioning may shed light onto the decline of Westslope Cutthroat Trout in Priest Lake, and the effects of nonnative species like Brook Trout, Tench, Smallmouth Bass, and Yellow Perch on structuring the littoral fish assemblage.

Consistent with the view of Lake Trout as the archetypical apex predator, Lake Trout fed at the highest trophic position (4.2). Although we had low sample sizes for Bull Trout (*n* = 3), it appeared that Bull Trout and Lake Trout were both apical predators feeding on similar carbon sources. The positions of Lake Trout and Bull Trout were also found to be similar in Lake Pend Oreille (Clarke et al. 2005), though absolute trophic position was nearly half a trophic position lower for both Lake Trout and Bull Trout. In a study of native Lake Trout populations in Canada, Vander Zanden et al. (2000) found that in waters with *M. diluviana* and pelagic prey fishes (i.e., class 3 lakes), mean Lake Trout trophic position inferred from $\delta^{15}N$ was 4.3. Lake Trout in Priest Lake more closely resembled Lake Trout in waters that lacked pelagic prey fishes (i.e., class 2 lakes; TP = 4.2). Interestingly, Lake Trout trophic position was high (3.9) after initial introduction (1959-1966) in Lake Tahoe, but declined (3.5) in 1998-2000 after the establishment of *M. diluviana* (Vander Zanden et al. 2003). In a study of Ontario and Quebec lakes, Vander Zanden et al. (1999b) found that food chain length was positively related to fish species richness. Furthermore, food chain length may be reduced by increasing rates of diet generalization across trophic positions (Post et al. 2000). These factors, in conjunction with the overall shorter length of the food chain in Priest Lake, may be a result of lower abundances of prey fishes in Priest Lake and reliance of Lake Trout on *M. diluviana*.

Previous work has found that ontogenetic niche shifts and intraspecific niche partitioning can be detected in $\delta^{13}C$ and $\delta^{15}N$ signatures, but we did not find patterns in ^{13}C enrichment for Lake Trout in Priest Lake. In a study of Arctic Charr *S. alpinus* in Loch Tay, Scotland, smaller individuals had more enriched $\delta^{13}C$ than larger individuals (Power et al. 2012). These carbon signatures paralleled divergences in adult body size, indicating that both diet and growth separated two sub-populations of Arctic Charr in Loch Tay. Similarly, in Lake Pend Oreille, Clarke et al. (2005) found that $\delta^{13}C$ became less enriched in Rainbow Trout, Westslope Cutthroat Trout, and Northern Pikeminnow as length increased, indicating ontogenetic shifts from juvenile littoral invertivore feeding to pelagic piscivoroy as adults. In contrast, although $\delta^{13}C$ decreased significantly with length in Priest Lake, the effect size and amount of variability explained were very small. In a study of Lake Trout morphotypes (i.e., lean and siscowet-like) in Great Slave Lake, Northwest Territory, Zimmerman et al. (2009) found that large (>430 mm standard length) Lake Trout of both morphotypes were depleted in $\delta^{13}C$ relative to small Lake Trout. There, the shift from benthic- to pelagic-origin carbon with length was corroborated by increasing prevalence of pelagic fishes in the diet, and was consistent with previous studies of Lake Trout diets in Lake Superior and Lake Michigan. Keyse et al. (2007) also detected niche partitioning between large (>350 mm fork length) and small Lake Trout in a small arctic lake in Alaska, where large Lake Trout were enriched in $\delta^{13}C$ relative to small Lake Trout. In Priest Lake, the poor relationship between length and $\delta^{13}C$ indicates that Lake Trout of all sizes feed consistently on prey of predominantly pelagic-origin carbon signatures. The narrow niche space of Lake Trout further supports the observation that individuals feed similarly.

Patterns in $\delta^{15}N$ enrichment have been linked to fish growth, length, and the onset of piscivory. For instance, in a study of Arctic Charr on Baffin Island, Canada, Gallagher and Dick (2010) identified two trophic levels in the population. Although they found that $\delta^{13}C$ values did not differ significantly by group, older, larger individuals comprised the higher trophic level as indicated by higher $\delta^{15}N$ values. Similarly, Eloranta et al. (2010) evaluated stable isotope signatures of Arctic Charr in a subarctic lake in Lapland, Finland. Larger Arctic Charr (>500 mm) had grown faster and were in better condition than smaller individuals, indicating a shift to piscivory, which was corroborated by the positive relationship between length and $\delta^{15}N$. Grey (2001) was able to trace ontogenetic shifts from eggs to parr to adults in Brown Trout *Salmo trutta* in Loch Ness, Scotland. Small Brown Trout were gape-limited and restricted to macroinvertebrates, which was reflected in low enrichment of $\delta^{15}N$. Large Brown Trout, however, could consume fishes and $\delta^{15}N$ enrichment increased with length.

Lake Trout in Priest Lake and other systems do not generally appear to exhibit patterns in $\delta^{15}N$ enrichment with length, or they exhibit counterintuitive declines in $\delta^{15}N$ with length. In Lake Pend Oreille, Clarke et al. (2005) found no relationship between $\delta^{15}N$ and length of Lake Trout. Similarly, in a study of nonnative Lake Trout in two Colorado reservoirs, Johnson et al. (2002) found no evidence of a relationship between Lake Trout length and $\delta^{15}N$ enrichment. Even in native Lake Trout populations, relationships between $\delta^{15}N$ enrichment and Lake Trout length appear to be absent (Vander Zanden et al. 2000). Vander Zanden et al. (2000) attributed the lack of enrichment to the absence of a relationship between length of prey fishes and $\delta^{15}N$ enrichment. Zimmerman et al. (2009)

found that large (>430 mm standard length) lean-morphotype Lake Trout in Great Slave Lake were depleted in ^{15}N compared to small lean Lake Trout, and that δ^{15}N did not differ for small and large siscowet-like Lake Trout. A switch from ^{15}N-enriched sculpins *Cottus* spp. to ^{15}N-depleted coregonines was hypothesized to have caused the counterintuitive decrease in δ^{15}N (Zimmerman et al. 2009). Finally, Lake Trout in a small Arctic lake in Alaska also exhibited a negative relationship between ^{15}N enrichment and length (Keyse et al. 2007). Given the substantial differences in ^{15}N enrichment between *M. diluviana* and other fish species in Priest Lake, we would expect to see some intraspecific differences in δ^{15}N from Lake Trout that varied in length from 257 to 932 mm.

Despite well-known ontogenetic shifts in Lake Trout diets, the absence of relationships between δ^{15}N and length likely reflect dietary homogeneity. Although age-0 Lake Trout (<60 mm) consume exclusively invertebrates and juvenile Lake Trout feed extensively on *M. diluviana* (Martin and Olver 1980), Lake Trout may become piscivorous as early as age 2 (150-400 mm; Mittelbach and Persson 1998). Furthermore, instead of consuming higher trophic-position prey fishes as Lake Trout grow, Lake Trout may simply consume larger individuals of the same prey species (Martin and Olver 1980, Matuszek et al. 1990, Vander Zanden et al. 2000). Particularly in Priest Lake, where prey resources are thought to be limited (Bowles et al. 1991), intraspecific competition may prohibit individuals from increasing the proportion of fish in their diet. From field observations of Lake Trout stomach contents, many individuals, regardless of size, consumed *M. diluviana*. Finally, if the onset of piscivory is also accompanied by rapid growth, δ^{15}N in individuals may quickly become more enriched, since isotopic composition is determined by the rate of tissue growth (Hesslein et al. 1993). Future studies could corroborate these hypotheses by evaluating isotopic signatures closer to the period of transition to piscivory, which potentially occurs at shorter lengths than we evaluated in this study.

Given the lack of a relationship between $\delta^{15}N$ and Lake Trout length, it was not surprising that there was no apparent relationship between $\delta^{15}N$ and individual growth rates. Individual Lake Trout of high and low condition (i.e., members of the two “stocks”) may not be adequately identified by growth in length, or may be sufficiently rare in the population that we could not detect patterns. Even if two “stocks” of fish were identifiable, adult isotopic signatures may not be indicative of the underlying drivers of diversification. Juvenile environmental conditions, including nutritional status, can shape subsequent adult life history, including growth and body size (Metcalfe and Monaghan 2001; Taborsky 2006). If early life history status drives differential adult condition, adult muscle isotopic signatures may not contain information relevant to the critical period. Further work is needed to differentiate Lake Trout in Priest Lake into “stocks”, if such a division of the population truly exists; muscle carbon and nitrogen stable isotope signatures do not appear to be useful for “stock” identification.

Stable isotopes provide time-integrated perspectives on diet and niche partitioning questions that are challenging and labor-intensive to answer with traditional stomach content analyses (Zanden and Rasmussen 1999). As such, these methods provide considerable insight into the community- and individual-level effects of introduced species (Vander Zanden et al. 1999a; Svanbäck et al. 2015). In this study, we identified patterns in the clustering of fish species by carbon source and trophic position, consistent with previous studies. Substantial overlap in the niche space of Westslope Cutthroat Trout, a popular sport fish and species of conservation concern, with nonnative Brook Trout warrants future investigation. Furthermore, we did not identify trophic partitioning in this nonnative Lake Trout population, consistent with previous studies of native and nonnative Lake Trout. Given the importance of piscivores in structuring lacustrine ecosystems, this information enhances understanding of the food web structure in systems with nonnative piscivores.

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Table 3.1. Month, year, and location that samples were collected for stable isotope analysis from taxa in Priest Lake, Idaho. Locations were Priest Lake (PL), Thorofare (TF), and Upper Priest Lake (UPL). Taxa were collected by gill nets, electrofishing, angling, trawling, and zooplankton tows.

			n			
Taxa	Year	Month	PL	TF	UPL	Total
Brook Trout	2014	June	6	–	–	6
Bull Trout	2013	May	1		1	2
		October	–	1	–	1
Westslope Cutthroat Trout	2013	November	–	1	–	1
	2014	June	15	–	–	15
Kokanee	2013	May	–	–	2	2
		October	–	3	–	3
		November	–	8	–	8
	2014	May	4	–	–	4
		June	3	–	–	3
Lake Trout	2013	April	97	–	–	97
		May	273	–	–	273
	2014	May	46	–	–	46
Largescale Sucker	2013	April	4	–	–	4
		May	–	–	1	1
		November	–	2	–	2
	2014	June	1	–	–	1
Longnose Sucker	2013	May	–	–	2	2
		November	–	1	–	1
Mountain Whitefish	2013	October	–	6	–	6
		November	–	10	–	10
	2014	June	1	–	–	1
M. diluviana	2013	August	8	–	–	8
	2014	June	15	–	–	15
Northern Pikeminnow	2013	May	–	–	5	5
		November	–	1	–	1
	2014	June	12	–	–	12
Peamouth	2014	June	10	–	–	10
Smallmouth Bass	2014	June	1	–	–	1
Tench	2013	November	–	1	–	1
	2014	June	4	–	–	4
Yellow Perch	2013	November	–	1	–	1
Zooplankton	2014	June	11	–	–	11
Total			512	35	11	558

Table 3.2. Percent area of standard ellipse overlap for members of the Priest Lake food web. Standard ellipse areas were calculated from $\delta^{13}C$ and $\delta^{15}N$ signatures and represent isotopic niche space. Percent area of overlap is given for each taxa by column; darker shading represents a higher percent overlap. Taxa are organized by $\delta^{13}C$ (decreasing in enrinchment from left to right and top to bottom); codes are zooplankton (Zoop) , *M. diluviana* (MD), Lake Trout (LKT), kokanee (KOK) , Bull Trout (BLT), Brook Trout (BKT), Mountain Whitefish (MWF), Largescale Sucker (LSS), Westslope Cutthroat Trout (WCT), Peamouth (PEA), Longnose Sucker (LNS), Tench (TEN), and Northern Pikeminnow (NPM).

	Zoop	MD	LKT	KOK	BLT	BKT	MWF	LSS	WCT	PEA	LNS	TEN	NPM
Zoop	■	0	0	0	0	0	0	0	0	0	0	0	0
MD	0	■	0	0	0	0	0	0	0	0	0	0	0
LKT	0	0	■	0	0.1	0	0	0	0	0	0	0	0
KOK	0	0	0	■	0	0	0	0	0	0	0	0	0
BLT	0	0	0.11	0	■	0.16	0	0	0	0	0	0	0
BKT	0	0	0	0	0	■	0.52	0.22	0.12	0.13	0.15	0	0.3
MWF	0	0	0	0	0	■	■	0.37	0.22	0.17	0.3	0	0.25
LSS	0	0	0	0	0	0.6	0.54	■	0.28	0.39	0.18	0.11	0
WCT	0	0	0	0	0	0.79	0.79	0.69	■	0.52	0.59	0	0
PEA	0	0	0	0	0	0.51	0.34	0.54	0.29	■	0.33	0	0
LNS	0	0	0	0	0	0.69	0.68	0.29	0.39	0.39	■	0	0.05
TEN	0	0	0	0	0	0	0	0.29	0	0	0	■	0
NPM	0	0	0	0	0	0.79	0.35	0	0	0	0.03	0	■

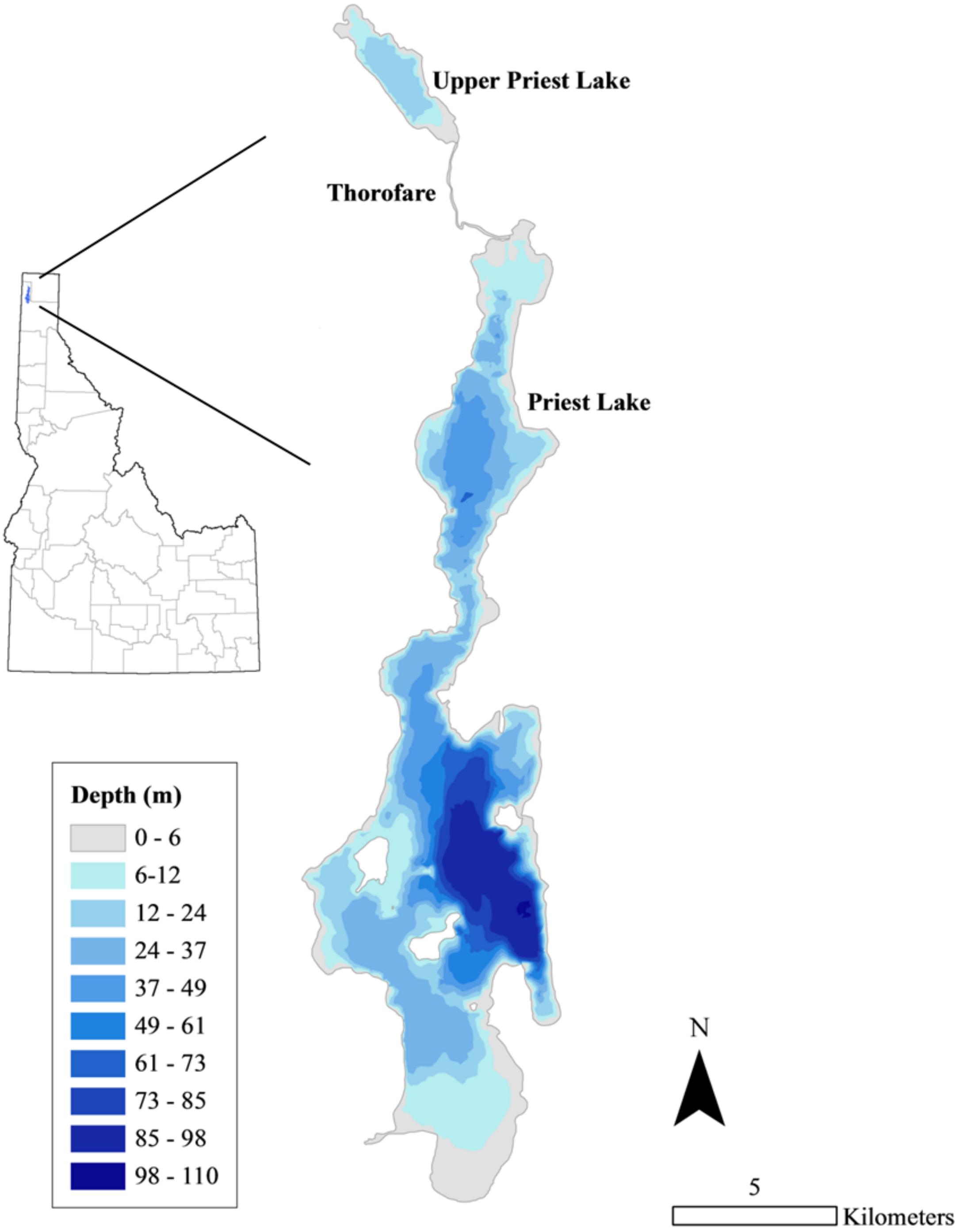

Figure 3.1. Location of Priest Lake in the northern Panhandle of Idaho.

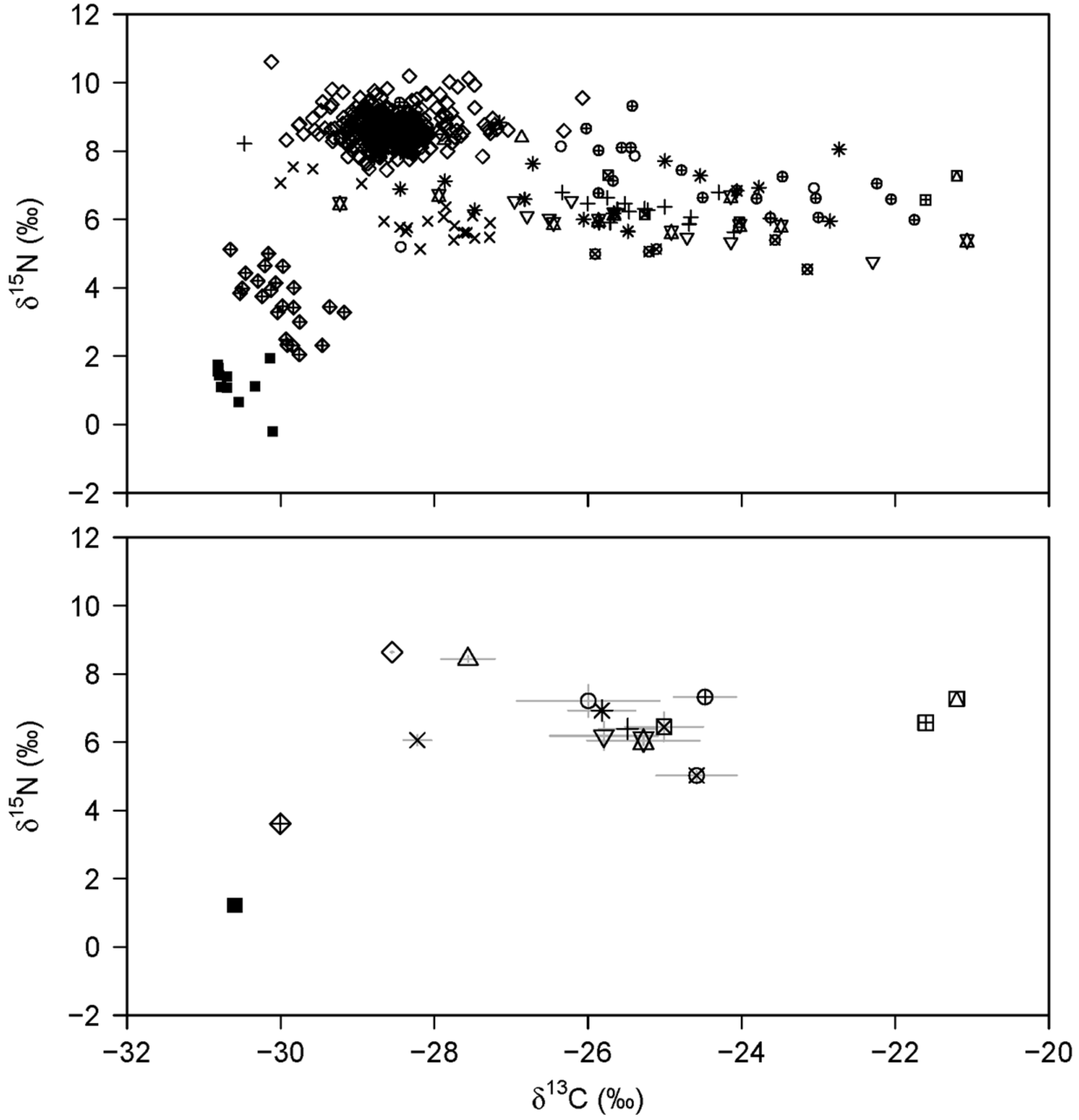

Figure 3.2. Bi-plot of stable isotope values for members of the fish assemblage in Priest Lake, Idaho, sampled in 2013 and 2014. Taxa included Brook Trout (○), Bull Trout (△), Westslope Cutthroat Trout (+), kokanee (✕), Lake Trout (◇), Largescale Sucker (▽), Longnose Sucker (⊠), Mountain Whitefish (✳), *M. diluviana* (⟐), Northern Pikeminnow (⊕), Peamouth (✡), Smallmouth Bass (⊞), Tench (⊗), Yellow Perch (⧄), and zooplankton (■). Individual samples (top panel) and taxa means (bottom panel) are shown as points. Error bars represent one standard deviation of the mean.

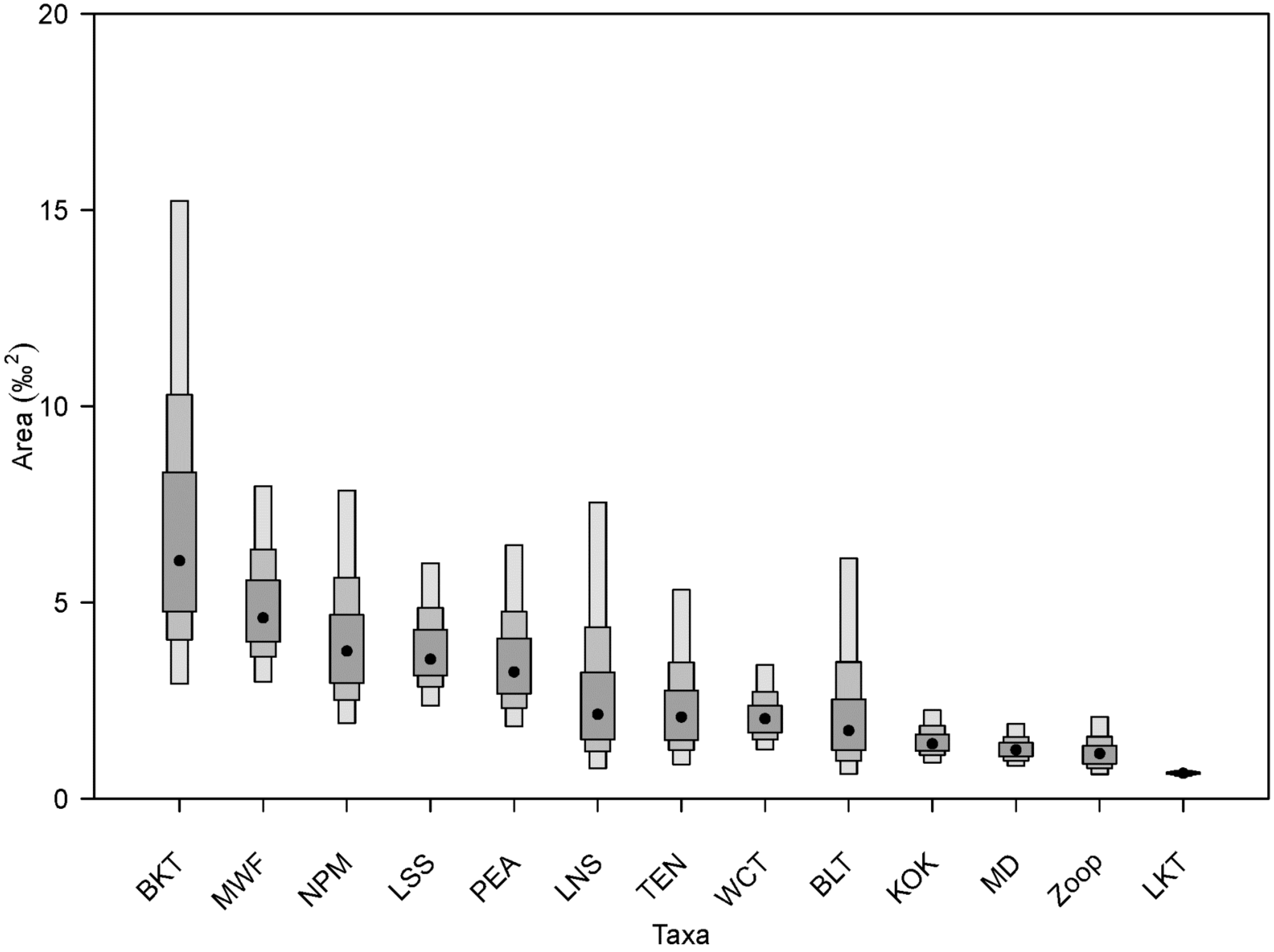

Figure 3.3. Plot of 95% credible intervals for estimated ellipse area of taxa sampled in 2013 and 2014 from the Priest Lake food web. Shaded boxes (from dark to light) represent 50%, 75% and 95% credible intervals. Taxa codes are Brook Trout (BKT), Mountain Whitefish (MWF), Northern Pikeminnow (NPW), Largescale Sucker (LSS), Peamouth (PEA), Longnose Sucker (LNS), Tench (TEN), Westslope Cutthroat Trout (WCT), Bull Trout (BLT), Kokanee (KOK), *M. diluviana*(MD), zooplankton (zoop), and Lake Trout (LKT).

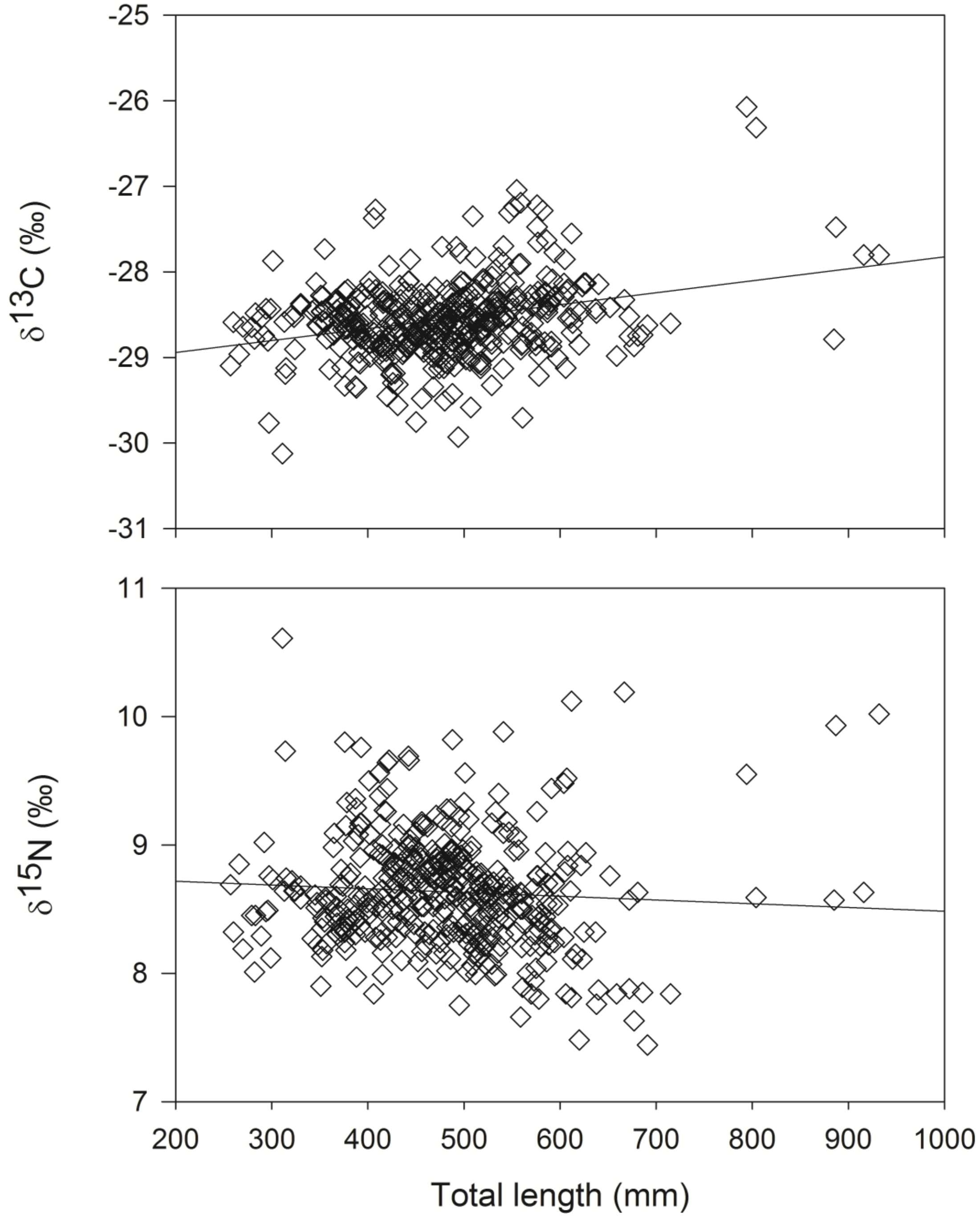

Figure 3.4. Relationship between Lake Trout total length and δ^{13}C values (top) and δ^{15}N (bottom) sampled from Priest Lake, Idaho, in 2013 and 2014. Lines represent simple linear regression models.

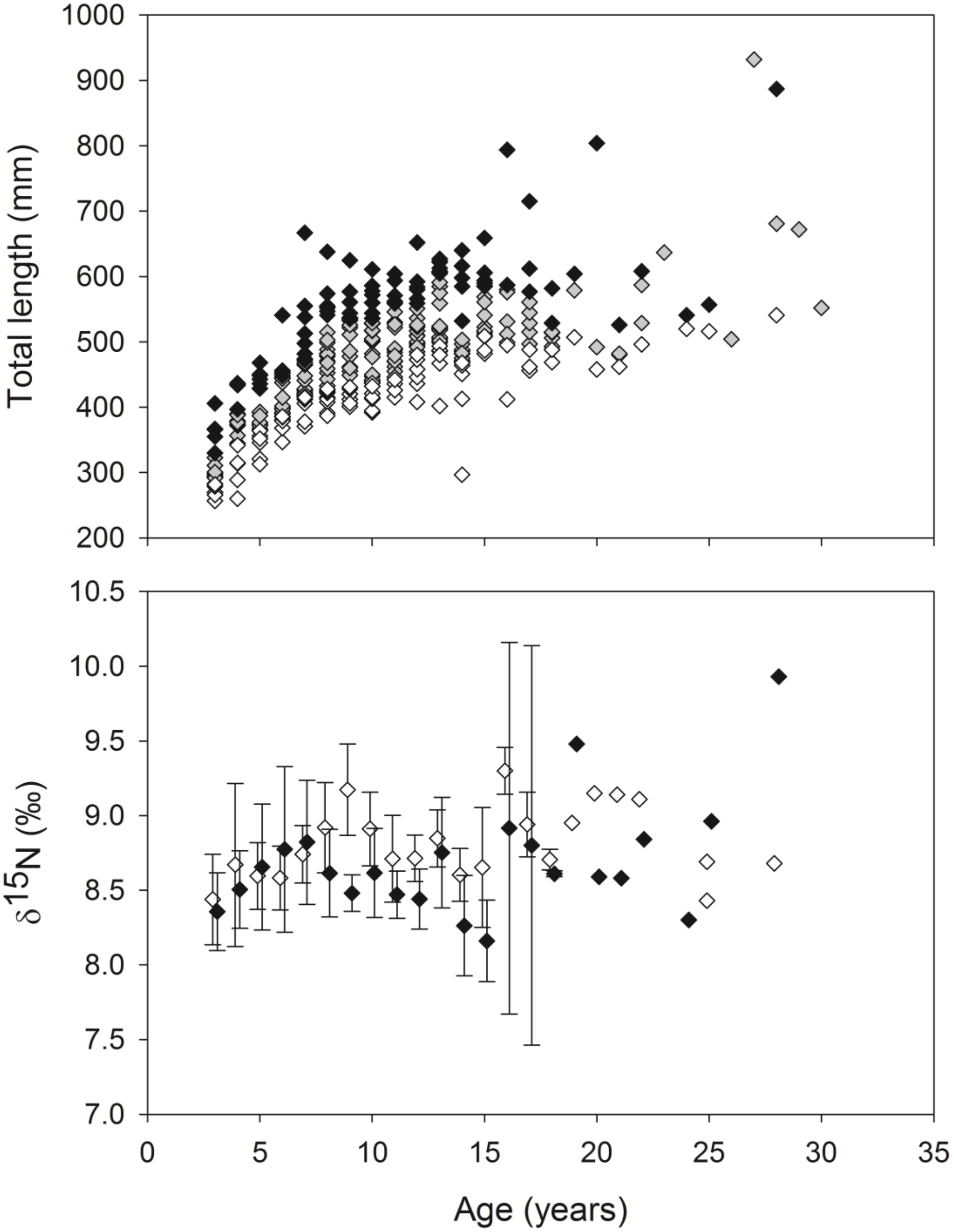

Figure 3.5. Length-at-age at capture (top panel) and relationship between growth and $\delta^{15}N$ (bottom panel) for Lake Trout sampled from Priest Lake during spring 2013. A von Bertalanffy model was fit and individuals with growth in the upper 25th percentile (black diamonds) and lower 25th percentile (white diamonds) by age were isolated. Mean $\delta^{15}N$ with 95% confidence intervals was plotted for each group. Sample sizes after age 18 were insufficient to calculate confidence intervals (*n* < 2).

Chapter 4: General Conclusions

Lake Trout *Salvelinus namaycush* are highly plastic and exhibit high variability in response to environmental conditions and trophic relationships, both in their native and nonnative distributions. Studying Lake Trout populations across large spatial scales contributes to our understanding of the mechanisms regulating population and individual growth, which ultimately improves the capacity for insightful fishery management. This thesis contributed to the broader understanding of Lake Trout demographics and ecology by characterizing a long-naturalized population in Priest Lake, Idaho. Additionally, this thesis directly addressed questions related to the management of Lake Trout in Priest Lake. Population modeling and demographic study evaluated alternative management goals for the fishery and the biological feasibility of implementation. Stable isotope analysis was also used to address the nature of the relationships between members of the aquatic community in Priest Lake.

The population assessment and modeling in chapter two indicated that the Lake Trout population is growing, but may be experiencing limited prey resources. Individuals were generally characterized by fast initial growth, followed by declining growth rates with age. Body condition also declined with increasing length. Interestingly, more than half of mature females were found to skip spawning, despite young age at maturity in the population. These finding are consistent with a population that readily feeds on opossum shrimp *Mysis diluviana* at young ages, but experiences difficulty transitioning to a piscivorous diet later in life. These findings were further corroborated by stable isotope analysis in chapter three, which showed little variation within the Lake Trout population isotopic niche. Lake Trout trophic position did not appear to increase with length, as would be expected for a successful shift to piscivory. As a result of these energetic restrictions, the population growth rate was lower than for other nonnative Lake Trout populations in the western United States.

Population modeling showed that eradication, trophy, and balance management goals could be achieved with the appropriate harvest strategy. However, management actions should be pursued cautiously and monitored closely. This fishery-independent study also supports many of the hypotheses about the Lake Trout population that had been gleaned from creel surveys and small-scale research projects, such as the effects of reduced prey availability following the collapse of the kokanee *Oncorhynchus nerka* population. Effective fishery management requires careful consideration of the biological, social, and economic constraints of management goals. Demographic study and stable isotope analysis have provided a foundation for future research and management in Priest Lake.