FEATURE: INTRODUCED SPECIES

Western Lake Trout Woes

STATE OF COLORADO.

Lake trout can provide a trophy component in coldwater fisheries. Governor Bill Ritter congratulates anglers who caught consecutive state record lake trout from Blue Mesa Reservoir, Colorado.

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ABSTRACT: In the western United States, the ability of non-native lake trout (*Salvelinus namaycush*) to attain large sizes, > 18 kg under favorable conditions, fueled the popularity of lake trout fisheries. In the past, restrictive regulations were adopted to increase lake trout abundance and produce trophy specimens. More recently, lake trout have become increasingly problematic because they prey upon and potentially compete with native and sport fishes. We review the experiences of agencies in seven western states which are considering or implementing strategies to address lake trout impacts despite management difficulties due to mixed public perception about lake trout's complex interactions with native or introduced fauna. Special regulations protecting lake trout have often been liberalized or rescinded to encourage their harvest and reduce their negative effects. More intensive methods to control or reduce lake trout abundance include promoting or requiring lake trout harvest, commercial-scale netting, disrupting spawning, and stocking sterile lake trout.

Penurias con la trucha de lago

RESUMEN: En el oeste de los Estados Unidos de Norteamérica la capacidad de la trucha de lago, especie foránea (*Salvelinus namaycush*), de alcanzar grandes tamaños, > 18 kg bajo condiciones favorables, impulsó su popularidad en las pesquerías. En el pasado se adoptaron medidas restrictivas para incrementar la abundancia de la especie y producir especímenes de trofeo. Más recientemente, la trucha de lago se ha convertido en un problema creciente ya que depredan y potencialmente compiten con especies nativas y de pesca recreativa. Se hace una revisión de las experiencias por parte de las agencias en siete estados del oeste que están considerando o implementando estrategias para lidiar con los impactos de la trucha de lago, a pesar de las dificultades de manejo debidas a la mezcla de percepciones por parte del público acerca de las complejas interacciones de esta especie con la fauna nativa o introducida. Las regulaciones que protegen a la trucha de lago se han decretado o revocado para fomentar su captura y reducir sus efectos negativos. Métodos más intensivos para controlar o reducir la abundancia de la trucha de lago incluyen la promoción o requerimiento de captura de la especie, el uso de redes a escala comercial, interrupción del desove y producción de individuos estériles.

INTRODUCTION

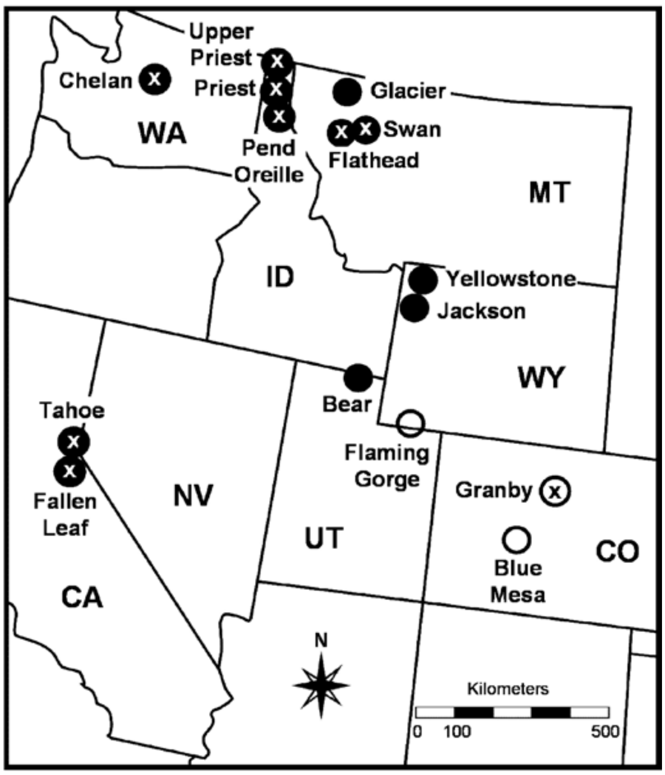
Lake trout (*Salvelinus namaycush*), or mackinaw, have been widely introduced outside of their native range into lakes and reservoirs in the western United States (Crossman 1995). In their native range in North America, including northern Canada, Alaska, the Great Lakes, and parts of New England, lake trout fill an important ecological niche as a keystone predator in food webs of lakes (Ryder et al. 1981) and support socially and economically valuable recreational, commercial, or subsistence fisheries (Healy 1978; Sellers et al. 1998; Mackenzie-Grieve and Post 2005). Angling for native lake trout is often strictly regulated to enhance reproduction and to perpetuate trophy-sized individuals (Payne et al. 1990; Dextrase and Ball 1991; Trippel 1993). In contrast, lake trout add a trophy component in many waters where they have been introduced, but they have often become problematic predators on and potential competitors with native fishes and other popular sport fishes.

Commercial fishery consultants from Hickey Brothers, LLC (Baileys Harbor, Wisconsin), and Idaho Department of Fish and Game personnel lift deepwater trap nets deployed to capture lake trout in Lake Pend Oreille, Idaho.

NED HORNER

Lake trout are adapted to deep, cold oligotrophic lakes where their life history is characterized by longevity, slow growth, late maturity, low reproductive potential, and slow replacement of adults (Shuter et al. 1998). Despite their restrictive habitat requirements and long generation time, lake trout often become the dominant top predator and reach large sizes in many unproductive northern waters due to the availability of sympatric prey such as opossum shrimp (*Mysis relicta*) and lake whitefish (*Coregonus clupeaformis*; Scott and Crossman 1973; Johnson 1976). Among North American salmonids, lake trout are second in size only to Chinook salmon (*Oncorhynchus tshawystcha*; Donald and Alger 1986). The largest recorded lake trout was just over 45 kg and 127 cm total length (TL; Scott and Crossman 1973). The species commonly exceeds 18 kg under favorable conditions (Donald and Alger 1986). Its large size often exceeds that of other sport fish, both native and non-native, earning it the devotion of some anglers who demand that it be maintained or maximized in western fisheries despite demonstrable depletions of its prey (Yule and Luecke 1993; Johnson and Martinez 2000; Beauchamp et al. 2007). Herein, we review lake trout management and impacts on local resources in 18 western lakes and reservoirs.

Figure 1. Lakes (solid dots) and reservoirs (open circles) in the western U.S. with management issues concerning introduced lake trout. Waters marked with an "x" indicate the presence of non-native *Mysis relicta*.



BIOLOGICAL AND MANAGEMENT ATTRIBUTES OF LAKE TROUT IN THE WEST

Fifteen lakes and three reservoirs are included in this review of lake trout in the western United States (Figure 1). These


BRIAN FREDENBERG

Lake trout are highly resistant to starvation. This emaciated 96.5 cm TL, 7.7 kg (W_r = 60) lake trout was caught nearly a decade after kokanee were eliminated as its primary food source.


SCOTT TOLENTINO

Triploid lake trout produced at the Grace State Fish Hatchery, Idaho, for stocking into Bear Lake, Utah-Idaho. Double fin clips, adipose and right pelvic, are applied prior to stocking to facilitate evaluating the performance of triploid lake trout in the fishery.

waters vary greatly in size, depth, and altitude (Table 1). Waters that span the boundary between two states include Lake Tahoe, Flaming Gorge Reservoir, and Bear Lake. Six lakes lie within national parks: Jackson, Yellowstone, Bowman, Kintla, Logging, and McDonald. Nine waters contain non-native *M. relicta:* Tahoe, Fallen Leaf, Granby, Pend Oreille, Priest, Upper Priest, Flathead, Swan, and Chelan (Figure 1). Many of these waters, including Blue Mesa Reservoir, are leading destinations for lake trout anglers in the western United States and have produced state record lake trout (Table 2).

In the 1980s and early 1990s, restrictive regulations were used to enhance angling opportunities for trophy-sized lake trout in several western states (Table 3; Johnson and Martinez 1995), but this focus on trophy fisheries in some waters initially failed to

Table 1. Physical attributes of lake trout waters in the western United States. State(s) in which the water is located is shown in parentheses.

Water	Surface area (ha)	Elevation (m)	Mean depth (m)	Maximum depth (m)
Tahoe (CA/NV)	49,491	1,900	305	501
Fallen Leaf (CA)	567	1,953	53	120
Blue Mesa (CO)	3,709	2,293	31	104
Granby (CO)	2,939	2,525	23	67
Pend Oreille (ID)	34,814	629	164	351
Priest (ID)	9,461	743	38	112
Upper Priest (ID)	541	743	13	32
Flathead (MT)	49,854	881	47	118
Bowman (MT)	691	1,229	Unknown	77
Kintla (MT)	688	1,222	Unknown	119
Logging (MT)	444	1,162	Unknown	60
McDonald (MT)	2,763	961	Unknown	142
Swan (MT)	1,312	935	16	43
Chelan (WA)	13,500	335	144	453
Bear (UT/ID)	28,350	1,806	28	63
Flaming Gorge (UT/WY)	17,018	1,843	64	133
Jackson (WY)	10,420	2,062	37	136
Yellowstone (WY)	35,427	2,359	48	133

Table 2. Lengths and weights of state record lake trout caught by angling in selected waters of the western United States.

State	Water	Year	Record lake trout size	
			Length (cm)	Weight (kg)
California	Tahoe	1974	NA	16.9
Colorado	Blue Mesa	2007	112	22.8
	Granby	1995	100	17.4
Idaho	Pend Oreille	1995	NA	19.7
	Priest	1971	125	26.1
Montana	Flathead	2004	108	19.2
Utah	Flaming Gorge	1988	115	23.4
Washington	Chelan	2001	NA	16.1
Wyoming	Flaming Gorge	1995	122	22.7
	Jackson	1983	117	22.7

consider the massive prey demand by lake trout. Likewise, other ecological and economic consequences of stockpiling even modest numbers of large, piscivorous lake trout were not adequately scrutinized (Johnson and Martinez 1995, 2000).

Lake trout grow more rapidly and achieve higher densities in more productive waters with extended growing seasons (Johnson and Martinez 2000). Protective length limits that increase the abundance and sizes of lake trout can hasten or exacerbate the demise of prey populations, including fish not necessarily intended to feed lake trout (Luecke et al.1994; Johnson and Martinez 1995). In the western United States, for example, prey populations exploited by lake trout invariably include sport fish stocked from hatcheries (Fredenberg et al. 1999; Johnson and Martinez 2000; Haddix and Budy 2005). Further, larger lake trout can consume fusiform prey up to 50% of their own body length (Keeley and Grant 2001; Ruzycki et al. 2003; Beauchamp et al. 2007) and thus are capable of consuming adults of other lacustrine salmonids. This may be especially problematic if the accumulation of larger, piscivorous lake trout results from rapid growth, low exploitation, or protective length limits. Predation by lake trout can be considerable even if their abundance is not enhanced by stocking, restrictive bag limits, or protective length limits. Lake trout that grow more slowly and exist at lower densities in less productive waters can still exert considerable predation. Lake trout exhibiting slow growth consume more prey to reach the same size as lake trout in more productive waters due to lower growth efficiencies (Johnson and Martinez 2000).

These characteristics of lake trout populations and the predation they exert can complicate management of other taxa at an ecosystem level as well. A variety of fish species and terrestrial vertebrates, including grizzly bear (*Ursus arctos*), bald eagle (*Haliaeetus leucocephalus*), and osprey (*Pandion haliaetus*), could be vulnerable to direct or indirect effects of excessive lake trout predation on other fishes in waters of the western United States (Spencer et al. 1991; Schullery and Varley 1995; Table 4). In some waters the preservation, recovery, or restoration of five subspecies of native cutthroat trout (*Oncorhynchus clarkii* subspp.) may be in jeopardy due in part to excessive lake trout predation (Quist and Hubert 2004; Ruzycki 2004). Bull trout (*Salvelinus confluentus*), which are listed as threatened under the Endangered Species Act, appear to be especially vulnerable. Lake trout not only prey on bull trout but also compete with them, and due to a shorter lifespan and more rigorous spawning and rearing requirements, bull trout are at a considerable disadvantage when the two species are in sympatry (Donald and Alger 1993; USFWS 1998; Fredenberg 2002).

CALIFORNIA

Tahoe and Fallen Leaf lakes contain a variety of introduced salmonids and *M. relicta*. The potential reestablishment of native Lahontan cutthroat trout (*O. clarkii henshawi*) is a recent management consideration for both waters and a potential challenge for managing multiple species.

Lake Tahoe

Lake trout were introduced into Lake Tahoe in the late 1880s (Frantz and Cordone 1970) and have been a component in the fishery for nearly 100 years (Beauchamp et al. 1992). Lake trout predation in Lake Tahoe may have been responsible for substantial reductions in native fishes and fluctuations

Table 3. Comparison of lake trout bag (K = must-kill) and length limits (M = minimum; X = maximum; slot limit range denoted by hyphen) in 18 waters in the western United States since 1980, showing prevailing regulations during 5-year intervals, including current lake trout regulations. Minimum length limits allow harvest of only one or two fish longer than the designated length; slot limits restrict harvest to only one fish longer than the upper length. TH = Lake Tahoe and FL = Fallen Leaf Lake (California-Nevada); BM = Blue Mesa Reservoir and GR = Granby Reservoir (Colorado); PO = Lake Pend Oreille, PR = Priest Lake, and UP = Upper Priest Lake (Idaho); FH = Flathead Lake, GP = Glacier National Park which includes Bowman, Kintla, Logging, and McDonald lakes, and SW = Swan Lake (Montana); BR = Bear Lake (Utah-Idaho); FG = Flaming Gorge Reservoir (Utah-Wyoming); CH = Lake Chelan (Washington); and JK = Jackson Lake and YS = Yellowstone Lake (Wyoming). Prior to their discovery in Yellowstone Lake in 1994, lake trout inadvertently fell under the lake's two trout < 33 cm maximum length limit.

Water	Bag limit (N = none)							Length limit in cm (N = none)						
	1980	1985	1990	1995	2000	2005	current	1980	1985	1990	1995	2000	2005	current
TH	2	2	2	2	2	2	2	N	N	N	N	N	N	N
FL	5	5	5	5	5	5	5	N	N	N	N	N	N	N
BM	2	1	1	8	8	8	8	N	51–M	56–86	N	N	N	N
GR	2	1	1	4	2	4	4	N	51–76	66–91	66–91	66–91	51–M	N
PO	6	6	2	4	N	N	N	41-M	41–M	N	N	N	N	N
PR	6	6	2	3	6	6	6	41-M	41–M	N	66–81	N	N	N
UP	0	0	0	0	6	6	6	N	N	N	N	N	N	N
FH	5	5	10	10	16	20	50	N	71–M	66–91	76–91	76–91	76–91	76–91
GL	2	2	2	2	15	15	N	N	N	N	N	N	N	N
SW	5	5	10	10	10	10	10	N	N	N	N	N	N	N
BR	2	2	2	2	2	2	2	N	N	N	N	N	N	N
FG	2	2	2	2	3	6	8	N	51–M	66–91	86-M	71–M	71–M	71–M
CH	2	2	2	2	2	2	N	38-M	38–M	38–M	38–M	38–M	38–M	N
JK	6	6	6	6	6	6	6	61-M	61–M	61–M	61–M	61–M	61–M	61–M
YS	2	2	2	K	K	K	K	33-X	33–X	33–X	N	N	N	N

Table 4. Fish and wildlife species impacted by lake trout that were purposefully introduced (standard font), entered from other waters (bold), or were illegally transplanted (bold italics) in 18 waters in the western United States. Waters:
TH = Tahoe; FL = Fallen Leaf; BM = Blue Mesa; GR = Granby; PO = Pend Oreille; PR = Priest; UP = Upper Priest; FH = Flathead; GL = Glacier National Park; SW = Swan; BR = Bear; FG = Flaming Gorge; CH = Chelan; JK = Jackson; and YS = Yellowstone. Glacier National Park includes four lakes: Bowman, Kintla, Logging, and McDonald. NA = not applicable.

	CA		CO		ID			MT			UT		WA	WY	
Species	TH	FL	BM	GR	PO	PR	**UP**	FH	**GL**	**SW**	BR	**FG**	CH	**JK**	***YS***
Native cutthroat trout (*Oncorhynchus clarkii* subspp.)															
Bonneville *O. c. utah*	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	X	NA	NA	NA	NA
Lahontan *O. c. henshawi*	X	X	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
Snake River *O. c. bouvieri* spp.	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	X	NA
Westslope *O. c. lewisi*	NA	NA	NA	NA	X	X	X	X	X	X	NA	NA	X	NA	NA
Yellowstone *O. c. bouveri*	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	X
Other native vertebrates															
Bull trout *Salvelinus confluentus*	NA	NA	NA	NA	X	X	X	X	X	X	NA	NA	X	NA	NA
Whitefishes (*Prosopium* spp.)	NA	X	NA	NA	X	X	X	X	X	X	X	NA	X	X	NA
Catostomids, cyprinids *or* cottids	X	NA	NA	NA	NA	NA	NA	NA	NA	NA	X	NA	NA	NA	NA
Grizzly bear *Ursus arctos*	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	X
Bald eagle *Haliaeetus leucocephalus*	NA	NA	NA	NA	NA	NA	NA	X	X	NA	NA	NA	NA	NA	X
Osprey *Pandion haliaetus*	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	X
Non-native sport fish (*Oncorhynchus* spp.)															
Kokanee *O. nerka*	X	NA	X	X	X	X	X	X	X	X	NA	X	X	NA	NA
Rainbow trout *O. mykiss*	NA	NA	X	X	X	NA	NA	NA	NA	NA	NA	X	X	NA	NA

in the abundance of introduced kokanee (*O. nerka*; Theide 1997). Native Lahontan cutthroat trout were extirpated from the lake in the late 1930s due to a combination of factors including introduced salmonids (Gerstung 1988), particularly lake trout (Vander Zanden et al. 2003). The combined effects of lake trout and *M. relicta*, first introduced in the early 1960s (Richards et al. 1975), restructured the pelagic food web (Richards et al. 1991). Further, the diel vertical behavior of *M. relicta* may have redistributed epilimnetic nutrients to the hypolimnion (Jassby et al. 1992; Jassby 1998). The establishment of *M. relicta* coincided with the disappearance of *Daphnia* and *Bosmina*, but as *M. relicta* densities declined, cladocerans reappeared (Richards et al. 1991). Self-sustaining lake trout, the primary sport fish in Lake Tahoe, prey most heavily on *M. relicta* (Theide 1997). Lake trout also eat kokanee and native fishes such as Paiute sculpin (*Cottus beldingi*), Lahontan redsides (*Richardsonius egregious*), Tui chub (*Gila bicolor*), and Tahoe sucker (*Catostomus tahoensis*; Frantz and Cordone 1970; Thiede 1997).

These changes in food web dynamics illustrate the complexity of this system and now complicate the multiple fishery management objectives for the lake. Richards et al. (1991) reported that some fishery managers believed that a decline in the number of larger lake trout warranted stricter lake trout regulations. More recently, however, the feasibility of reintroducing Lahontan cutthroat trout has been explored, but food web alterations (Vander Zanden et al. 2006) and social obstacles may limit the restoration potential of Lahontan cutthroat trout in Lake Tahoe. Lake trout currently occupy the historic niche of Lahontan cutthroat trout, and the lake trout reductions needed to restore Lahontan cutthroat trout would be poorly received by anglers and associated commercial interests (Vander Zanden et al. 2003). Further, *Daphnia*, a key prey of Lahontan cutthroat trout, continue to be suppressed by *M. relicta* and reducing the abundance of *M. relicta* is not currently feasible (Vander Zanden et al. 2003).

Fallen Leaf Lake

Fallen Leaf Lake also has been studied to assess the potential for reintroduction of Lahontan cutthroat trout (Allen et al. 2006). Despite the presence of several non-native aquatic species, its food web remains comparatively more intact (Vander Zanden et al. 2006). Lake trout were found to consume primarily Lahontan cutthroat trout, mountain whitefish (*Prosopium williamsoni*), and smaller lake trout. While larger lake trout displayed increased piscivory and consumption of Lahontan cutthroat trout, smaller lake trout (< 425 mm) represented the greatest predation threat to salmonids due to their high abundance (Al-Chokhachy et al., in press). Other nonnative species pose competitive (*M. relicta* and kokanee), predatory (brown trout *Salmo trutta*) or hybridization (rainbow trout *O. mykiss*) threats to reintroduced Lahontan cutthroat trout, but lake trout represent the critical limiting factor for juvenile Lahontan cutthroat trout. An epilimnetic thermal refuge protects Lahontan cutthroat trout from lake trout predation during periods of stratification; however, lake trout continue to impede the reestablishment of Lahontan cutthroat trout due to the spatial overlap of these species during the remainder of the year. Among the proposed strategies to reintroduce Lahontan cutthroat trout into Fallen Leaf Lake is the active removal of lake trout (Al-Chokhachy et al., in press).

COLORADO

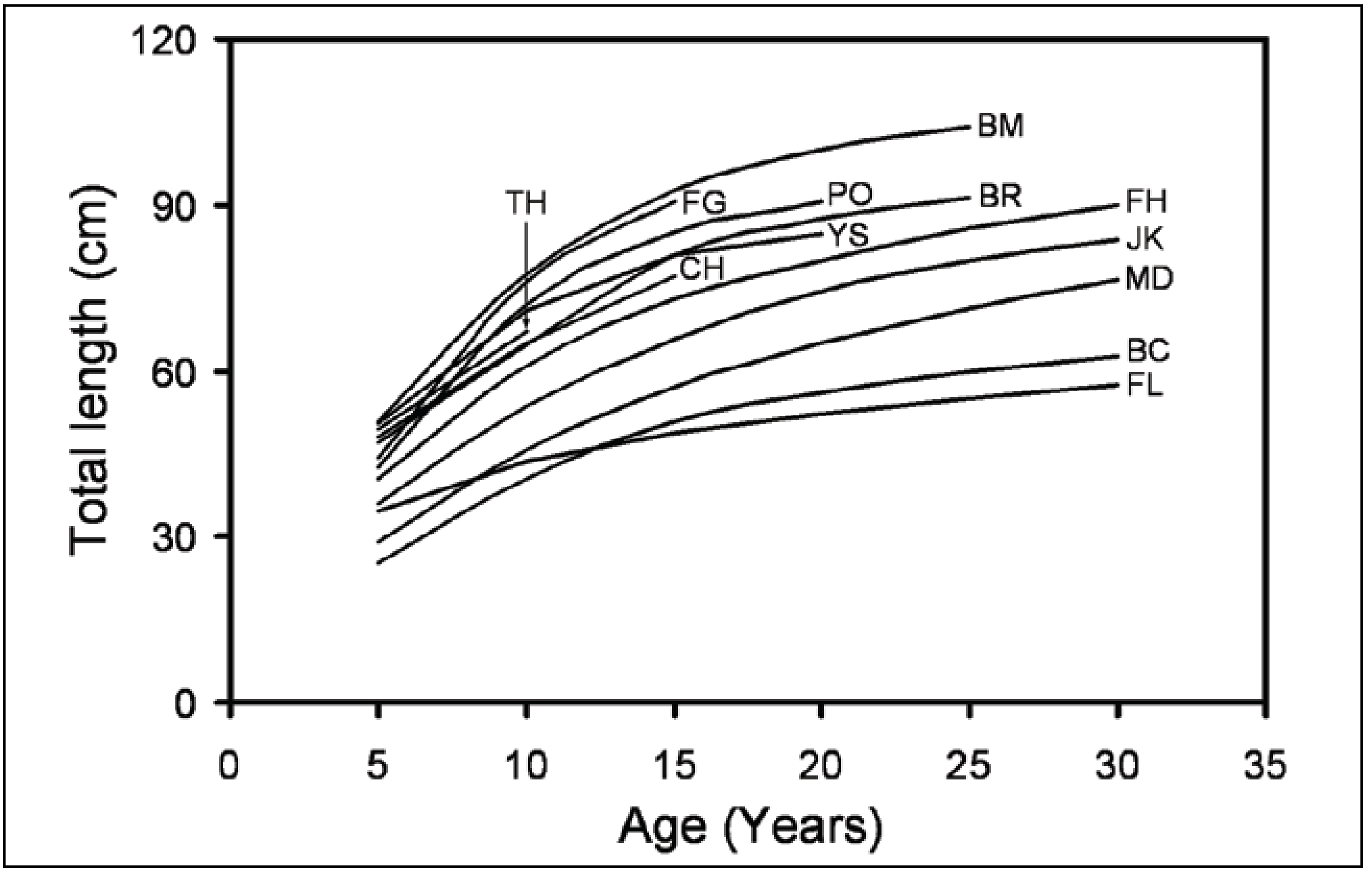
Lake trout concerns in Blue Mesa and Granby reservoirs do not involve native fishes. The issues in these reservoirs concern the impact of lake trout predation on the stability and quality of fisheries for multiple, introduced species. Both reservoirs also contain introduced kokanee, rainbow trout, and brown trout, and both have lost some fishing opportunities as lake trout predation increased (Johnson and Martinez 2000). These losses include reductions in the kokanee bag limit at Granby and fishing opportunities for mature kokanee in spawning runs. Of greatest importance, however, is the annual collection of kokanee eggs from these reservoirs for restocking kokanee populations (Martinez 2005). In any given year, either Blue Mesa or Granby are the leading suppliers of kokanee eggs in the state, making their annual production of eggs essential for producing kokanee fry (Martinez 2005).

Blue Mesa Reservoir

Blue Mesa Reservoir is highly productive and supports very high growth rates for kokanee and lake trout (Johnson and Martinez 2000; Hardiman et al. 2004). Lake trout in Blue Mesa Reservoir exhibit rapid growth, reaching 76 cm TL within 10 years (Figure 2), and in recent years, the reservoir has produced several consecutive state records for lake trout (Crockett et al. 2006; Table 2). However, creel survey data over the past decade indicate that the kokanee fishery attracts the most anglers and supplies the most fish (Dan Brauch, Colorado Division of Wildlife [CDOW], unpublished data).

Correlations in the declines of kokanee and rainbow trout with lake trout predation indicate that these main prey items of lake trout in Blue Mesa are in serious trouble (CDOW 2009). The kokanee population was in decline in the early-1990s before the slot-limit protecting large lake trout was rescinded (Table 3). In ensuing years, kokanee and rainbow trout were found in equal proportions in the lake trout diet, and predation also led to steep declines in the rainbow trout fishery (Johnson and Martinez 2000; Martinez 2005). Creel and sonar surveys demonstrated that the kokanee population in Blue Mesa has not rebounded to desired levels despite increasing the annual stocking rate from 1.2 million fry to 2.8 million fry (Martinez 2005). Average relative weights (W_r) of large lake trout (Hubert et al. 1994) in the reservoir, which had been high in the past (110-150), showed some decline for fish > 70 cm TL in 2006 (Dan Brauch, CDOW, unpublished data). These find-

Figure 2. Growth rates of introduced lake trout in lakes and reservoirs of the western United States compared to that of lake trout populations exhibiting slow growth in lakes in northern British Columbia (BC; deLeeuw 1991). Lake Tahoe (TH), California-Nevada (Thiede 1997); Fallen Leaf Lake (FL), California (Allen et al. 2006); Blue Mesa Reservoir (BM), Colorado (Martinez 2004); Flaming Gorge Reservoir (FG), Utah-Wyoming (Luecke et al. 1994); Lake Pend Oreille (PO), Idaho (Hansen 2007); Bear Lake (BR), Utah-Idaho (Ruzycki et al. 2001); Yellowstone Lake (YS), Wyoming (Ruzycki et al. 2003); Flathead Lake (FH), Montana, (Beauchamp 1996); Jackson Lake (JK), Wyoming (Rhea 2007); Lake McDonald (MD), Montana (Dux 2005); Lake Chelan (CH), Washington (Shoen 2007). Fork length (FL) was converted to total length (TL) by TL=1.023 + (1.045 FL) for fish < 68 cm, and TL = 1.488 + (1.032 FL) for fish > 68 cm (Conrad and Gutmann 1996).



ings heightened concern for the overall fishery, particularly for kokanee which may now also face predation and competition from illegally introduced yellow perch (*Perca flavescens*).

Granby Reservoir

Granby Reservoir formerly had a large kokanee population that supported a popular fishery and a spawning run that supplied several million eggs annually (Martinez and Bergersen 1991; Martinez and Wiltzius 1995). Martinez and Bergersen (1991) indicated that while *M. relicta* (established by the late-1970s) predation on *Daphnia* diminished conditions for kokanee, kokanee could persist in the reservoir. However, a shift in the mid-1980s to management that emphasized lake trout was associated with a severe decline in the kokanee fishery by the early 1990s and ultimately the loss of kokanee egg production in 1998.

The virtual elimination of kokanee in Granby Reservoir by the late 1990s was likely due to the combined effects of *M. relicta* and lake trout. Kokanee were strongly influenced by cyclic trends in reservoir storage which influenced the creation of a thermal refuge for *Daphnia* that excluded *M. relicta* from the warm surface waters (Martinez and Wiltzius 1995). *Daphnia* and kokanee benefited from warmer thermal conditions during years of reservoir drawdown, but *M. relicta* and lake trout were favored during years when higher reservoir levels associated with cooler thermal conditions allowed greater access to their prey. In the mid-1990s when the reservoir was near capacity, *M. relicta* density peaked at about 1,300/m^2 and *Daphnia* were severely reduced (Martinez 2005). During this period of depleted food resources for kokanee, lake trout stocking and the protection afforded by a slot length-limit contributed to an overabundance of lake trout (Martinez 2005). Further, consumption of *M. relicta* by lake trout, particularly juveniles (Johnson and Martinez 2000; Johnson et al. 2002), likely enhanced the recruitment of lake trout.

Excessive lake trout predation in Granby Reservoir, which suppressed the kokanee population and eventually caused lake trout relative weights to plummet by the mid-1990s, led to removal of the slot length-limit by 2001 (Table 3). Lake trout growth eventually stalled, toppling the reservoir's reputation as a producer of trophy lake trout. Some lake trout recaptured 10 years after tagging had grown less than 2.5 cm, with most fish over 50.8 cm TL showing minimal or no increase in length after several years (Martinez 2005, 2006). This poor growth and the emaciated condition of lake trout resulted in the removal of all length-limits for lake trout in Granby Reservoir in 2006 (Table 3). Recent data suggest that the removal of protective length limits for lake trout has helped reduce predation by lake trout, facilitating recovery of the kokanee population and its egg production, and restoring normal growth and condition of lake trout (Billy Atkinson, CDOW, pers. comm.).

IDAHO

Pend Oreille and Priest lakes have similar management issues of lake trout negatively impacting both sport and native fish, while impacts to native fishes are the primary concern in Upper Priest Lake. At all three lakes, regulations limiting the harvest of lake trout have been liberalized (Table 3), while native bull trout and westslope cutthroat trout (*O. clarkii lewisi*) are presently protected by harvest closures. These lakes also contain native mountain whitefish and pygmy whitefish (*P. coulteri*), but only Lake Pend Oreille contains introduced lake whitefish. Kokanee, present in all three lakes, declined dramatically in Pend Oreille and Priest lakes, despite efforts to restock them (IDFG 2007). *M. relicta* is established in the three lakes and is believed to enhance lake trout recruitment (Mauser et al. 1988; Bowles et al. 1991; IDFG 2007). Fish managers are seeking to minimize the lake trout populations in Pend Oreille and Upper Priest lakes, while accepting that a lake trout fishery may be the most practical management option for Priest Lake.

Lake Pend Oreille

Lake trout were introduced into Lake Pend Oreille in 1925, but contributed little to the sport fishery until the mid-1990s. The lake supports one of the most abundant adfluvial bull trout populations in the Pacific Northwest and a remnant population of westslope cutthroat trout. Kokanee were established in the lake by the mid-1930s and supported a sport and commercial fishery catch that averaged one million fish per year through the 1960s. Kokanee were also the primary prey of bull trout, lake trout, and rainbow trout in the lake (Vidergar 2000; Maiolie et al. 2002; Clarke et al. 2005). Gerrard (Kamloops) rainbow trout were introduced in 1941, producing a popular sport fishery. The kokanee population began to decline in the mid-1960s and reached extremely low levels by 2000 (Maiolie et al. 2002). Several factors have contributed to reduced kokanee abundance and slowed their recovery including alteration of the zooplankton community by introduced *M. relicta* (Clarke et al. 2005), changes in lake level management that altered shoreline spawning habitat (Maiolie et al. 2002), and more recently and most importantly, excessive predation by both rainbow trout and lake trout.

The abundance of immature and mature lake trout in Lake Pend Oreille in 1999, 2003, and 2005, described by an exponential growth model, was projected to double every 1.4 years, reaching nearly 400,000 by 2010 if the population did not reach carrying capacity sooner (Hansen et al. 2008). Aggressive action began in 2006 to curb the expanding lake trout population to prevent a complete collapse of the kokanee population and negative impacts to bull trout. Fishery managers experimented with a variety of harvest options to reduce the number of lake trout in the lake. Approved in 2003, 10 licenses for a commercial rod-and-reel fishery for lake trout were issued in the first year. Strict Food and Drug Administration requirements for fish handling and processing and a limited market for lake trout subsequently limited participation to 3–4 licenses per year and a total commercial harvest since its inception of less than 2,000 lake trout. In 2006, sport anglers paid to harvest rainbow trout and lake trout removed nearly 6,000 rainbow trout and over 11,000 lake trout (Hansen et al. 2006) at a cost of about $241,000. A $10 bounty per fish proved more effective than rewards based on tagged fish ($100-$2,000), lottery tickets, or monthly cash drawings. The bounty was increased to $15 per fish in 2007 with $500,000 budgeted annually for the program (Ned Horner, personal observation). Through 2008, anglers participating in these harvest incentive programs removed 18,784 rainbow trout and 41,726 lake trout (Jim Fredericks, Idaho Department of Fish and Game [IDFG], pers. comm).

Commercial trap netting gear for suppressing lake trout in Lake Pend Oreille was evaluated and utilized by IDFG personnel and commercial fishery consultants (Peterson and Maiolie 2005). In 2005, deep-water trap netting and intensive, targeted gill netting harvested another 5,015 lake trout, contributing to an exploitation rate of 44% and a total annual mortality of 58% (Hansen et al. 2008). By August 2007, an exploitation rate of 57% and an estimated total annual mortality of 81% were achieved (Ned Horner, unpublished data). Through 2008, netting had removed a total of 21,871 lake trout for a combined total of 63,597 lake trout being removed by netting and angling. Modeling predicted that this use of multiple gear types (angling, trap nets, and gill nets) would be more effective in collapsing the lake trout population in Lake Pend Oreille than any one gear type alone (Hansen et al. 2008). Lake trout populations elsewhere were reportedly unable to withstand total annual mortality higher than 50% (Healy et al. 1978; Hansen 2007). Total annual mortality of lake trout in Lake Superior ranged from 50% just before and up to 90% during their collapse (Hansen et al. 1995). If this high mortality could be sustained, the lake trout population in Lake Pend Oreille should collapse. Kokanee in Lake Pend Oreille appeared to be responding to the reduction of lake trout. Survival of age 1 to age 2 kokanee increased from 10% in 2007 to 30% in 2008. Similarly, survival of age 2 and age 3 kokanee increased from 4% in 2007 to 51% in 2008 (Jim Fredericks, IDFG, pers. comm.).

Priest Lake

Lake trout were also introduced into Priest Lake in 1925 and have created similar management challenges for sport and native fish. The lake trout fishery was dominated by relatively few large fish until *M. relicta* was established by the early 1970s. *M. relicta* increased lake trout recruitment, resulting in an increase in lake trout abundance and predation that ultimately led to the collapse of kokanee by 1976 (Bowles et al. 1991). Priest Lake produced the U.S. angling record for lake trout outside of the Great Lakes (Table 2), but the loss of kokanee ended the lake's reputation as a premier producer of trophy lake trout. The fishery is now dominated by lake trout averaging 50 cm and 0.5 kg (Mark Liter, IDFG, unpublished data). Bull trout formerly supported a productive fishery in Priest Lake, but they were nearly extirpated from the lake by the late 1990s due to competition with lake trout (Venard and Scarnecchia 2005). Lake trout regulations were liberalized in 2002 to reduce impacts on native fishes (IDFG 2007). However, given the combined effects of *M. relicta* and lake trout, and other habitat and biological factors limiting recovery of bull trout and westslope cutthroat trout, Priest Lake will continue to be managed primarily as a sport fishery for lake trout (IDFG 2007).

Upper Priest Lake

In contrast to Priest Lake, the management of Upper Priest Lake will emphasize the protection and restoration of native fishes, including the suppression of lake trout. Lake trout were first detected in Upper Priest Lake in the mid-1980s, invading upstream from Priest Lake via a 3.2 km long channel (IDFG 2007). Intensive annual gillnetting by agency personnel since 1998 and by commercial fishery consultants since 2007 (Table 5) has been attempted to prevent lake trout from proliferating in Upper Priest Lake (Dupont et al. 2004; Dupont et al. in press), but re-invasion of lake trout from the large population in Priest Lake remains problematic. Movement of lake trout through the channel connecting the two lakes occurs primarily at night, and is restricted by warm water temperatures (over 15° C) in July and August (Venard and Scarnecchia 2005). Installation of a behavioral barrier (strobe light; Liter and Maiolie 2003) or trap netting in the channel between Priest and Upper Priest lakes are being considered to control lake trout movement during part of the year (IDFG 2007).

Table 5. Methods used to reduce or control lake trout abundance in 17 waters in the western United States. Numbers denote the year that a lake trout control strategy was first implemented. Question marks indicate control strategies that have been proposed or are being considered. FL = Fallen Leaf; BM = Blue Mesa; GR = Granby; PO = Pend Oreille; PR = Priest; UP = Upper Priest; FH = Flathead; GL = Glacier National Park; SW = Swan; BR = Bear; FG = Flaming Gorge; CH = Chelan; JK = Jackson; and YS = Yellowstone. Glacier National Park includes Bowman, Kintla, Logging, and McDonald lakes. NA = not applicable.

	CA	CO		ID			MT			UT		WA	WY	
Control Strategy	FL	BM	GR	PO	PR	UP	FH	GL	SW	BR	FG	CH	JK	YS
Cease lake trout stocking	NA	92	98	NA	NA	NA	NA	NA	NA	NA	NA	02	07	NA
Liberalize lake trout regulations	NA	96	06	00	02	02	90	00	NA	NA	94	04	NA	95
Promote harvest of lake trout	NA	00	06	00	NA	NA	01	00	NA	NA	94	01	NA	95
Monetary incentive to harvest lake trout	NA	NA	NA	06	NA	NA	02	NA	NA	NA	NA	NA	NA	NA
Intensive netting of lake trout	?	?	NA	06	NA	98	?	?	08	NA	NA	NA	NA	96
Commercial fishing for lake trout	NA	NA	NA	03	NA	NA	?	NA	NA	NA	NA	NA	NA	NA
Control lake trout movement	NA	NA	NA	NA	NA	?	NA	05	NA	NA	NA	NA	NA	NA
Stock sterile lake trout	NA	NA	NA	NA	NA	NA	NA	NA	NA	02	NA	NA	NA	NA
Control lake trout at spawning sites	NA	?	NA	07	NA	NA	?	?	?	NA	NA	NA	NA	04

MONTANA

The Columbia River headwaters in northwestern Montana currently support about 20 populations of nonnative lake trout, some of which were intentionally introduced, including the Flathead Lake population in 1905 (Spencer et al. 1991). Most of the non-introduced populations, however, have resulted from the natural dispersal of lake trout through interconnected waterways from the original population established in Flathead Lake. Complete colonization by lake trout of most or all lakes in the Flathead River basin that are not isolated by fish passage barriers is now considered likely (Fredenberg et al. 2007; Meeuwig 2008). Waters of the Flathead River basin, including Swan Lake and lakes within Glacier National Park, historically provided a stronghold for adfluvial bull trout and westslope cutthroat trout.

Flathead Lake

Flathead Lake is the largest freshwater lake in the western United States (Table 1). It formerly contained a small population of lake trout dominated by large fish that were typically caught by anglers in a specialized troll fishery that constituted less than 2% of the total angler catch of all species (Graham and Fredenberg 1983). The abundance of lake trout increased rapidly after *M. relicta* migrated downstream into Flathead Lake from upstream lakes, including Swan Lake, where they had been intentionally planted in 1968 to enhance growth of kokanee (Beattie and Clancy 1991). In Flathead Lake, *M. relicta* reached peak densities around 1986 (130 / m^2), only five years after they were first detected, and rapidly triggered trophic changes that cascaded through the entire food web (Spencer et al. 1991). Among these was the decline of cladocerans that contributed to the abrupt collapse of the popular kokanee fishery that had dominated the lake's sport fishery for 60 years (Beattie and Clancy 1991; Deleray et al. 1999; Spencer et al. 1999). From 1993 to1997, Montana Fish Wildlife and Parks and the Confederated Salish and Kootenai Tribes attempted to reestablish the kokanee fishery by stocking about 5.8 million kokanee (mostly yearling fish 13-15 cm TL) in Flathead Lake (Deleray et al. 1995; Fredenberg et al. 1999). Beauchamp et al. (2006) estimated that 87% of the stocked kokanee were consumed by lake trout within one year of their release. This provided evidence that the expanded lake trout population, rather than competition with *M. relicta*, was primarily responsible for the demise of kokanee (Carty et al. 1997; Deleray et al. 1999).

M. relicta shifted the energy flow in the Flathead Lake food web from pelagic pathways relied upon by planktivores, such as kokanee, to benthic pathways benefiting lake trout and lake whitefish (Tohtz 1993; Chess and Stanford 1998; Deleray et al. 1999). In Flathead Lake, *M. relicta* constituted up to 75% of the caloric intake of juvenile lake trout and up to 20% of the intake of lake whitefish (Beauchamp et al. 2006). *M. relicta* accelerated the expansion of lake trout and lake whitefish numbers to levels that ultimately suppressed *M. relicta* to about one-third of their peak levels (Wicklum 1999; Beauchamp et al. 2006).

While the lake trout expansion caused the rapid elimination of kokanee through predation, the effect on the remaining fish species in Flathead Lake has been more attenuated. Coincident with the increase in lake trout was a decline in adfluvial westslope cutthroat trout and a reduction in the bull trout spawning run in the Flathead River system, to roughly half their abundance in the 1980s (MFWP and CSKT 2001). The decline of these species was attributed to lake trout predation as bioenergetics simulations estimated that lake trout consumed high numbers of westslope cutthroat trout and bull trout in Flathead Lake (Beauchamp et al. 2006). This decline in the bull trout population contributed to the 1992 petition and eventual decision to protect bull trout, range-wide, as "threatened" under the Endangered Species Act in 1998.

The expansion of the lake trout population also transformed the recreational fishery of Flathead Lake. Kokanee provided annual harvests exceeding 200,000 fish from the 1950s into the 1980s (Graham and Fredenberg 1983), a period when lake trout were present, but largely preceding the arrival of *M. relicta*. During the 1980s, annual angler use at Flathead Lake averaged about 89,500 angler-days (MFWP 2008). Since the collapse of kokanee, recreational fishing has averaged about 54,000 angler-days annually (MFWP 2008). Further, the ongoing increase in lake trout resulted in density-dependent reductions in lake trout growth rate and condition, and increased age at maturity (CSKT and MFWP 2006).

Managers responded to the changes in the Flathead Lake fish community with an updated fisheries management plan (MFWP and CSKT 2001). The plan sought to conserve the remaining bull trout and westslope cutthroat trout by reducing lake trout abundance, while maintaining a viable recreational fishery. Because lake trout represented up to 90% of the recreational sport fish catch in Flathead Lake during the 1990s (Evarts et al. 1994), the decision to reduce lake trout numbers proved controversial. As a compromise with the angling public, a protective slot-limit was kept in place to maintain trophy lake trout (Table 3).

Beginning in 2001, the first strategy in a planned progression of measures to reduce lake trout was to encourage increased angler harvest of lake trout < 76 cm TL (Table 5). Advantages of this approach were its cost-effectiveness and the social acceptability of anglers harvesting surplus fish. While the harvest of lake trout increased from about 2,000/y before *M. relicta* to roughly 50,000/y recently, it remained uncertain whether recreational angling alone could offset the productive capacity of a lake trout population in a lake as large and well suited for lake trout as Flathead Lake. Attempts to achieve an even higher recreational harvest of lake trout have been limited by the propensity of anglers to release much of their catch, despite a very high bag limit (Table 3) and no seasonal fishing closures. Angling pressure for lake trout at Flathead Lake remained relatively low (about 3 h/ha/y; Evarts et al. 1994). To bolster angler interest in catching and harvesting lake trout, management agencies have sponsored annual spring and fall fishing contests since the fall of 2002, providing substantial monetary rewards to individual anglers based on the number of lake trout they harvest. The contests have grown rapidly, accounting for over 20,000 of the estimated 50,000 total lake trout harvested in 2007 and in 2008. However, none of the monitoring indicated that this level of harvest reduced the lake trout population. Managers continue to evaluate the amount of harvest necessary to reduce the lake trout population, while considering socially and economically compatible means to achieve it (CSKT and MFWP 2006).

Glacier National Park

Bull trout have declined over the last 25-30 years in the four largest lakes on the west side of Glacier National Park (Kintla, Bowman, Logging, and McDonald) in association with the establishment of lake trout (Fredenberg 2002; Meeuwig 2008). These lake trout populations, which invaded from downstream or adjacent populations, are a direct result of the initial introduction that occurred in Flathead Lake over 100 years ago. This colonization and proliferation by lake trout is ongoing in other former bull trout strongholds within Glacier National Park. Lake trout were recently documented in Harrison, Rogers, Lower Quartz, and Quartz lakes (Fredenberg et al. 2007; Meeuwig 2008). Lake trout dispersal apparently continues via migration throughout the interconnected headwater lakes in Glacier National Park.

Biologists are actively seeking means to control or eliminate lake trout in former bull trout strongholds in Glacier National Park (Fredenberg et al. 2007). Lake trout growth in Lake McDonald and other similarly oligotrophic headwater lakes is extremely slow (Figure 2). Consequently, the control of lake trout abundance is considered feasible (Dux 2005). In 2008, all lake trout bag and length limits were eliminated for lakes west of the Continental Divide in Glacier National Park (Table 3). However, limited access to most park waters and low levels of angler interest in lake trout hamper the potential for sport fishing to reduce lake trout numbers. Other successful means of suppressing lake trout will be necessary to combat the growing threat to native fish and ecosystems in Glacier National Park.

Glacier National Park also suffered repercussions from the lake trout-induced kokanee collapse in Flathead Lake. The demise of non-native kokanee in Flathead Lake ultimately had a cascading effect on birds and mammals feeding on spawning kokanee, their eggs, and carcasses in McDonald Creek (Spencer et al. 1991). This impact was best documented on the winter congregation of hundreds of bald eagles (Table 4). Because alternate food sources for eagles were unavailable in the area, the eagles moved to winter elsewhere in the western United States.

Swan Lake

Swan Lake was believed to be isolated from Flathead Lake by a century-old barrier preventing the upstream movement of fish. Despite this, lake trout were first detected in Swan Lake in 1998, raising concern that predation would threaten the lake's robust bull trout and kokanee populations and the popular fishery they support. In 2008, gill netting performed by commercial fishery consultants removed nearly 4,000 lake trout and estimated a population of 8,000 lake trout > 175 mm in the lake (Montana State University, unpublished data). In addition, following sonic-tagged lake trout led biologists to two major spawning locations. Based on the success of these initial investigations, management agencies are pursuing a 3-year experimental pilot project to drastically reduce the lake trout population in Swan Lake by aggressive gill netting. In 2009, lake trout that presumably migrated from Swan Lake were detected 90 km upstream in Lindbergh Lake (MFWP 2009).

UTAH

Bear Lake (Utah-Idaho) and Flaming Gorge Reservoir (Utah-Wyoming) represent contrasting management scenarios. In Bear Lake, the fishery includes a unique combination of endemic fishes that are preyed upon by lake trout. In Flaming Gorge Reservoir, the fishery is supported entirely by non-native fishes with lake trout as a top piscivore. Because fishery management of each of these waters is shared between two states, differences and compromises regarding lake trout management have occurred.

Bear Lake

The Bonneville cutthroat trout (*O. clarkii utah*) in Bear Lake evolved with a unique endemic fish assemblage including Bear Lake whitefish (*Prosopium abyssicola*), Bonneville cisco (*P. gemmifer*), Bonneville whitefish (*P. spilonotus*), and Bear Lake sculpin (*Cottus extensus*; Nielson and Lentsch 1988; Tolentino 2007b). Bonneville cutthroat trout in Bear Lake become piscivorous as they mature and they feed on the lake's endemic fishes (Nielson and Lentsch 1988). The three species of *Prosopium* are also popular sport fish with regulated harvest. Lake trout were first stocked into the lake in 1911 (Crossman 1995) and have been stocked annually in recent years (Ruzycki et al. 2001). Lake trout provide very popular yield and trophy components in the Bear Lake fishery in the Utah portion of the lake, and the notion of eliminating lake trout stocking is extremely unpopular with anglers. In a recent creel survey by Utah, anglers targeted lake trout more than native Bonneville cutthroat trout (Tolentino 2007a).

Concern about lake trout proliferation, competition with adult cutthroat trout, and predation on stocked juvenile cutthroat trout and endemic fishes has raised the issue of whether lake trout should continue to be stocked in Bear Lake (Ruzycki et al. 2001; Kennedy et al. 2006). Stocking lake trout decouples them from regulatory mechanisms such as prey abundance and their predatory inertia due to their long life and capacity to reach large size spans decades (Johnson and Martinez 1995; Ruzycki et al. 2001). However, lake trout continue to be stocked because reproductive success is apparently low due to egg predation, limited spawning habitat, and a unique water chemistry that precipitates calcium carbonate, suffocating lake trout eggs deposited in rocky substrate. Although natural recruitment of lake trout is limited, concern remains that unforeseen factors could facilitate lake trout recruitment which would increase predation on native species (Ruzycki et al. 2001). If increased predation by lake trout coincided with lowered lake levels known to reduce natural reproduction of Bonneville cutthroat trout and spawning substrate for the endemic prey fishes (Ruzycki et al. 1998), lake trout may suppress these species (Ruzycki et al. 2001). However, lowered lake levels would also reduce the amount of rocky habitat used by lake trout for spawning, potentially reducing lake trout recruitment as well.

Although lake trout had been stocked in Bear Lake at a higher rate for over 90 years without developing a naturally recruiting population, the frequency of lake trout stocking and the number stocked have been reduced, The stocking rate was reduced to an average of 0.25/ha/y from 1990 to 2006 (Nielson and Tolentino 2002; Tolentino 2007a) despite bioenergetic simulations of predation by lake trout under different stocking rates that projected that Bear Lake could support an annual rate up to 0.6/ha (Albrecht et al. 2004). This lower stocking rate has reduced the number of lake trout in the lake based on lower catch rates of lake trout in standardized gill net sampling. Further, as a compromise to eliminating lake trout stocking in Bear Lake, Utah and Idaho agreed to stock only triploid lake trout. Effort began in 2000 to produce sterile lake trout (Bill Horton, IDFG, pers. comm.) using pressure treatment of fertilized eggs to produce triploid lake trout (Kozfkay et al. 2005). Future work will evaluate the fishery performance of triploid lake trout compared to previous years when diploid lake trout were stocked.

Flaming Gorge Reservoir

Since completion in 1962, Flaming Gorge Reservoir has been recognized for its salmonid fisheries (Teuscher and Luecke 1996), first for rainbow trout in the 1960s, trophy brown trout in the 1970s, and kokanee and trophy lake trout since the 1980s (Luecke et al. 1994). Initially, in the 1970s, brown trout feeding on abundant, introduced Utah chub (*Gila atraria*) produced trophy-sized fish exceeding 13.6 kg. By the early 1980s, abundances of brown trout and trophy-sized rainbow trout began to dwindle as prey densities declined. Kokanee were introduced in 1963 and have been stocked periodically thereafter (Gipson and Hubert 1993), but their abundance has been sustained primarily by natural reproduction (Yule and Luecke 1993). Lake trout entered the reservoir by downstream dispersal from Fremont Lake, Wyoming, and reached trophy sizes by the mid-1980s, producing the Utah state record in 1988 (Table 2). The decline in Utah chub and its replacement by kokanee as the most abundant pelagic fish in the reservoir by 1990 was attributed to the Utah chub's higher vulnerability to lake trout predation (Yule and Luecke 1993). From 1980 to 1988, the harvested biomass of lake trout decreased by 15%, likely due to overfishing or a decline in prey availability (Luecke et al. 1994). Luecke et al. (1994) confirmed that lake trout growth potential had declined during 1990-1993 due to decreased prey densities.

Agency concern over prey availability for lake trout and the possibility of excessive predation by lake trout stimulated discussions between Utah and Wyoming about maintaining the slot-limit regulation protecting large lake trout. Initially, anglers in the two states viewed the popularity of the trophy lake trout fishery in Flaming Gorge Reservoir differently. During the early 1990s, this discrepancy led to several years when the lake trout regulations differed between Utah and Wyoming. Wyoming retained the slot-length limit, which promoted the trophy lake trout fishery. Utah adopted a minimum-length limit for lake trout that de-emphasized lake trout, while striving to satisfy demand for a more family-oriented fishery consisting of rainbow trout and kokanee. Both states later agreed to the same minimum-length regulation (Table 1) and have since increased the bag limit incrementally due to concern about increasing lake trout predation on other salmonids. Haddix and Budy (2005) suggested that rainbow trout survival was reduced by lake trout predation and that rainbow trout growth was suppressed by predator avoidance behavior, and recommended a trophic economics approach (e.g., Johnson and Martinez 2000) to re-evaluate lake trout and rainbow trout management in the reservoir. Adding to the overall concern about demand for prey in the reservoir is the recent discovery of the piscivorous burbot (*Lota lota*).

WASHINGTON

Lake Chelan

Lake trout were introduced into Lake Chelan in the early 1980s to add a trophy component to the fishery. More recently, however, managers have become concerned about their predatory and competitive impacts to introduced kokanee and Chinook salmon, along with native westslope cutthroat trout and pygmy whitefish (Viola and Foster 2002). Stunting of kokanee and angler dissatisfaction with these small fish led to the introduction of *M. relicta* in 1968 to provide prey for kokanee (Brown 1984). Following the establishment of *M. relicta*, however, the kokanee population crashed and lake trout recruitment was enhanced (Brown 1984). Despite the increase in lake trout abundance, kokanee gradually rebounded to become the most abundant pelagic fish in the lake (Schoen 2007) and they currently support the most popular fishery (DES 2000). Comparisons of shallow and deep portions of Lake Chelan support the hypothesis that lake basins of decreasing depth sustain increased zooplankton production that remains available to kokanee despite the presence of *M. relicta* (Martinez and Wiltzius 1995; Schoen 2007). However, while lake trout exploitation of both profundal *M. relicta* and pelagic kokanee may be less efficient in deeper basins, the availability of *M. relicta* would still likely facilitate an increase in the number of lake trout that prey on kokanee and other pelagic fishes (Schoen 2007).

Naturally reproducing Chinook salmon crashed in 1999, due in part to competition with lake trout (Viola and Foster 2002). Further, the Washington Department of Fish and Wildlife recognized the threat that lake trout posed to kokanee and cutthroat trout in Lake Chelan. An increase in lake trout abundance would likely preclude increasing the abundance of westslope cutthroat trout and increase predation on pygmy whitefish. Bull trout were extirpated from the lake by the 1940s and it is believed that attempts to reintroduce them would be unsuccessful due to present lake trout abundance (Viola and Foster 2002). To slow or prevent a substantial increase in lake trout abundance, lake trout stocking was discontinued in 2002 (Table 5), and the length and bag limits for lake trout were removed in 2004 (Table 1).

WYOMING

Jackson and Yellowstone lakes lie within national parks where fishery management includes a growing emphasis on native fish species, including Yellowstone cutthroat trout (*O. clarkii bouveri*). Lake trout colonized Jackson Lake through downstream dispersal from Lewis and Shoshone lakes in

Yellowstone National Park, where they had been introduced in 1890 (Stephens and Gipson 2004). Lake trout were illegally moved into Yellowstone Lake from Lewis Lake, probably in the 1980s (Munro et al. 2005).

Jackson Lake

Jackson Lake lies within Grand Teton National Park and is home to native Snake River cutthroat trout, a morphotype of the Yellowstone cutthroat trout (*O. c. bouveri* spp.; Behnke 1992). The lake has been managed for trophy lake trout since 1937 and is closed to fishing in October to protect spawning lake trout (O'Ney and Gipson 2006). However, lake trout have been associated with a substantial decline in the lake's Snake River cutthroat trout (Behnke 1992). Jackson Lake is locally regarded as a top producer of trophy lake trout (Rhea 2007) and it produced a state record lake trout (Table 2). Given the popularity of this fishery, angler resistance toward efforts to restore Snake River cutthroat trout in lieu of lake trout would be anticipated (Quist and Hubert 2004).

Lake trout are the most abundant trout species in the lake and population simulations showed that angling was not limiting the production of trophy lake trout under either the Jackson Lake length limit of one trout over 61 cm TL or the statewide size limit of one trout over 50.8 cm TL (Rhea 2007). Lake trout have been stocked since 1937, including about 36,000 (20-25 cm TL) which have been stocked annually since 1988 (Stephens and Gipson 2004). However, lake trout stocking in Jackson Lake ended in 2006 because stocked lake trout were rarely caught by anglers and biologists were concerned that lake trout competed for zooplankton, contributing to reduced condition of other salmonids. It is believed that the elimination of lake trout stocking might benefit native fishes, including mountain whitefish and Snake River cutthroat trout (Stephens and Gipson 2004; O'Ney and Gipson 2006).

Yellowstone Lake

Yellowstone Lake, in Yellowstone National Park, has highlighted concerns about predatory impacts of non-native lake trout on salmonid fisheries. The high fishery quality and economic value of the Yellowstone cutthroat trout in Yellowstone Lake (Varley and Gresswell 1988) are threatened by lake trout, which were discovered in the lake in 1994 (Kaeding et al. 1996). National and international publicity of this fishery resource problem exceeds that of any similar situation involving lake trout and has probably helped to raise awareness about the threat of excessive predation by non-native lake trout in other western lakes and reservoirs.

After discovering lake trout in Yellowstone Lake, park officials convened a panel of experts to formulate strategies to control lake trout numbers and mitigate their predatory impact to Yellowstone cutthroat trout and other species (McIntyre 1995). A bioenergetic study of lake trout predation on Yellowstone cutthroat trout in the lake estimated that an average lake trout consumed 41 Yellowstone cutthroat trout per year. This posed a serious long-term threat to the sustainability of the cutthroat trout population if expansion of the lake trout population continued (Ruzycki et al. 2003). Similar to the demise of kokanee in Flathead Lake and the cascading impacts to bald eagles in Glacier National Park, the severe reduction of Yellowstone cutthroat trout in Yellowstone Lake has reduced a traditional food resource for local grizzly bears (Haroldson et al. 2005) and ospreys (Table 4). Due to their deepwater distribution most of the year and in-lake spawning, lake trout are largely unavailable to terrestrial vertebrates that once exploited seasonally abundant Yellowstone cutthroat trout in the lake's shallows and tributary streams (Schullery and Varley 1995; Stapp and Hayward 2002).

Given these massive ecosystem impacts, the park responded with an intensive program to reduce lake trout in Yellowstone Lake. Regulations implemented in 1995 require anglers to kill all lake trout caught in Yellowstone Lake or its tributaries (Table 1; Koel et al. 2005) and instruct anglers who do not want to keep the lake trout they catch to puncture the air bladder to sink the carcass (YNP 2009). Additionally, gill netting that began in 1996 was intensified in 2001, with the goal of maximizing removal rates for lake trout while minimizing by-catch of Yellowstone cutthroat trout (Bigelow et al. 2003). Further, electrofishing over aggregations of mature lake trout on known spawning reefs in the lake at night during the fall has been conducted in an effort to maximize the annual catch of lake trout. While these intensive efforts to remove lake trout appear to have slowed the expansion of lake trout numbers, lake trout predation has contributed to the continued decline in numbers of Yellowstone cutthroat trout (Koel et al. 2005). A 2008 review of the park's lake trout removal program recommended intensifying the removal of lake trout by employing commercial fishery consultants to hasten the reduction of lake trout (Gresswell 2009).

OVERVIEW OF LAKE TROUT CONTROL STRATEGIES

Various strategies have been applied or are being tested to reduce or control lake trout abundance (Table 5). Ceasing lake trout stocking is often the first and most logical starting point. However, only a few waters in Table 5 were being routinely or sporadically stocked with lake trout. An alternative is stocking sterile lake trout, which is being tested only at Bear Lake in Utah/Idaho (Table 5; Kozfkay et al. 2005). Heat- or pressure-shocking of eggs induces triploidy, but this may not be 100% effective in ensuring sterility (Kozfkay et al. 2006). The risk that some stocked lake trout remain fertile must be weighed against the need to protect valued or declining fish stocks that are vulnerable to lake trout predation or competition.

Protective bag and size limits that were employed to promote popular and valuable trophy lake trout fisheries tended to increase predation demand. Consequently, many of these regulations were liberalized or rescinded to facilitate increased harvest of lake trout (Table 5). Lake trout bag limits have been low historically due to the species' vulnerability to over-harvest across its native range. Bag limits have been increasingly relaxed since 1995 in response to fishery collapses or growing concerns about lake trout predation (Table 3). Increased bag limits have generally been accompanied by the rescission of protective lake trout length limits (Table 3). Slot-length limits that protected highly piscivorous lake trout caused greater predation than minimum length limits (Luecke et al. 1994). Further, modeling has shown that per capita consumption by lake trout increased as the slot-length limit protecting the population from harvest was adjusted upward (Johnson and Martinez 1995). Despite this liberalization of bag and length limits, trophy lake trout continue to be produced without stringently protective regulations. Problematic predation is not restricted solely to waters containing or managed for trophy lake trout; therefore, even populations not specifically managed for or having few trophy-size lake trout can create predation concerns as well.

Another strategy being employed to reduce lake trout abundance and predation urges anglers to maximize harvest of lake trout (Table 5). Often, the focus is on harvest of smaller lake trout to slow recruitment of older, larger, more piscivorous individuals. The potential success of angling in reducing or controlling lake trout abundance depends on several site specific factors, including remoteness, accessibility by boats, and willingness of anglers participating in the fishery to harvest lake trout. At Flathead Lake, agencies encouraged and rewarded the removal of lake trout, yet anglers released as much as half of their catch outside of contest periods (Les Evarts, Confederated Salish-Kootenai Tribes, pers. comm.). Paying anglers $15/fish to harvest lake trout in Lake Pend Oreille helped increase exploitation to a critical level, but there would be little interest in this fishery without monetary incentives. In Yellowstone Lake and Glacier National Park, low fishing pressure limits the capacity of anglers to harvest significant numbers of lake trout.

The potential for both recreational and commercial fishing to remove lake trout may also be compromised by health advisories which caution humans to limit their consumption of lake trout due to high levels of contaminants such as mercury, PCBs, and DDT. Waters in this review which have lake trout consumption advisories include Granby (CDPHE 2009), Pend Oreille and Priest (IDHW 2008), Flathead and Swan (MDPHHS 2007), and Chelan (WDOH 2006). Lake trout have a propensity to accumulate contaminants in their tissues because they are a top predator. This can be confounded by the presence of *M. relicta* (Cabana et al. 1994; Stafford et al. 2004). Large lake trout commonly display higher burdens of contaminants than other piscivores due to their older age at comparable sizes and their non-migratory behavior.

Where reduction of lake trout numbers by angling alone proves too slow or infeasible, mechanical removal may help (Koel et al. 2005 Hansen et al. 2008). Intensive removal of lake trout by agency personnel or commercial fishery consultants using commercial netting techniques is being applied in Pend Oreille, Upper Priest, Swan, and Yellowstone lakes (Table 5). Netting to control lake trout abundance can be costly in large lakes. At Yellowstone Lake, the annual budget for gill netting has been about $300,000. At Lake Pend Oreille, the annual cost to deploy deep-water trap nets and gill nets has been about $400,000. Public support for the removal of non-native salmonids to preserve native species may be more forthcoming in some national parks (Quist and Hubert 2004). However, even here, the cost of control programs competes with other management needs (Settle and Shogren 2002). In addition, incidental catch or mortality of non-target fishes, especially rare native fishes, must be avoided.

Development of technologies to control movement of lake trout would help in situations where lake trout pose an invasive threat to native fishes. The use of behavioral or physical barriers for limiting movement of lake trout, however, must be weighed against the collateral impacts on migratory native species such as bull trout (Muhlfeld and Marotz 2005).

Incorporating methods to remove or inflict mortality to lake trout at spawning sites originated at Yellowstone Lake (Table 5). Identification of lake trout spawning habitat using technologies such as GIS and LIDAR may optimize the application of treatments to hasten lake trout eradication (Shaw et al. 2008; Bigelow 2009). Electrofishing at night over shallow rocky reefs known to concentrate spawning lake trout in the fall adds substantially to the annual removal of lake trout by gill netting (Patricia Bigelow, unpublished data). By increasing the power output of the boat-mounted electroshocker, collateral mortality may increase on fish out of reach in deeper water and possibly extend to previously deposited lake trout eggs. Additional ideas that have been proposed for study to help reduce lake trout spawning success in Yellowstone Lake include biodegradable polymers that would serve as a deterrent to egg deposition or suffocate deposited eggs, ultrasound, microwaves, or piscicides (WTU 2008). At Lake Pend Oreille, "Judas" fish (sonic-tagged lake trout) led biologists to previously unknown lake trout spawning sites that were targeted with intensive gill netting to increase mortality.

CONCLUSIONS

Lake trout are widespread in the western United States, occurring in over 200 waters where they have been intentionally, illegally, or invasively established, including about 79 locations in Wyoming, 60 in Colorado, 27 in Montana, 13 in California, 7 in Washington, 7 in Idaho, and 4 in Utah, some of which we described here. Most of what we know about lake trout biology and ecology is from studies throughout the species' native range in the Great Lakes and central Canada. The prevailing assumption that lake trout populations are highly vulnerable to overexploitation (Healy 1978; Shuter 1998) is being confronted by a new paradigm emerging from the collective management challenges lake trout impose due to their overabundance in lakes and reservoirs across the western United States. An underlying ecological problem in all affected waters in the western United States is the evolutionary mismatch of lake trout with native fishes in these lakes, and most of the other sport fish established or stocked to sustain diverse and productive fisheries (Johnson and Martinez 1995). In these ecosystems where managers try to control artificial assemblages of native and/or non-native fish that did not coevolve, lake trout prey heavily on fish or compete for resources where niches overlap. This situation is exacerbated in waters containing *M. relicta* because they may shift food resources toward deepwater or benthic fishes, benefiting the recruitment, growth, and survival of juvenile lake trout (Bowles et al. 1991; Beauchamp et al. 2006; Hansen et al. 2008). Alternatively, *M. relicta* predation on zooplankton may reduce the food resources and abundance of planktivorous fishes that serve as prey for large lake trout, thereby reducing the growth of adult lake trout (Bowles et al. 1991; Stafford et al. 2002).

Because lake trout must consume large fish prey, even if they are rare, to reach larger body sizes (Hubert et al. 1994; Pazzia et al. 2002), introduced lake trout often prey on the adults of valued sport and rare native fishes in waters of the western United States. Excessive predation by lake trout could result in cascading impacts that extend beyond the confines of the affected water body, posing a threat to terrestrial portions of the ecosystem (Quist and Hubert 2004). The predatory inertia of lake trout (the ability to resist starvation, tolerate a depressed prey base for years, and then quickly respond to increased prey availability) can also create ecological or economic obstacles to reestablishing or rebuilding populations of fishes extinguished or depressed by lake trout predation. Furthermore, the collapse of highly preferred prey species, such as kokanee, can have a cascading impact on other salmonids that are next in order of prey preference (e.g., cutthroat trout or bull trout).

Kokanee in waters of the western United States are often considered to be innocuous (they do not hybridize with or prey upon other fishes) and ecologically valuable (Dunham et al. 2008), but they are exceedingly vulnerable to predation by lake trout. In Priest Lake, kokanee continued to be primary, preferred prey of lake trout after kokanee declined to well below historic levels (Mauser et al. 1988; Rieman et al. 1979; Bowles et al. 1991). Even after kokanee were no longer detectable in the sport fishery or in trawls, they continued to constitute 5–13% of the lake trout diet. In Flathead Lake, kokanee remained a dominant item in the diet of lake trout in the years immediately following their collapse (Stafford et al. 2002), despite there being no reported catches of kokanee by anglers (Spencer et al. 1991). The reduction or loss of kokanee as prey for lake trout can reduce growth rates or diminish trophy potential for lake trout. This has been documented at Flathead Lake (Stafford et al. 2002), Granby Reservoir (Martinez 2005), and Priest Lake (Bowles et al. 1991). Even at seemingly low densities, lake trout can be problematic. In Lake Pend Oreille, lake trout posed a predatory threat to kokanee at an estimated adult lake trout density of 0.28/ha and a total lake trout density of about 0.94/ha (Hansen et al. 2008). In Blue Mesa Reservoir, estimated densities for lake trout > 42.5 cm TL of 1.38/ha and for lake trout > 56.4 cm TL of 0.69/ha were associated with a decline in kokanee (Crockett et al. 2006). In Flathead Lake, where kokanee were eliminated, the abundance of lake trout >40 cm TL was estimated to be 5.12/ha (Deleray et al. 1999; Beauchamp et al. 2006). Further, lake trout are able to sustain high predation rates even at low prey densities, perhaps due to their large search volume (Eby et al. 1995) and tendency to be cruising predators (Vogel and Beauchamp 1999). Given these factors, if prey fishes were highly aggregated, as would be the case in strongly schooling species like kokanee, a decrease in prey abundance would not result in a lower rate of predation by lake trout until prey numbers were severely reduced (Eby et al. 1995).

In some popular media, the collective effort to control lake trout in various waters of the western United States has been described in terms such as the “War on Western Mackinaw.” As we have shown, lake trout management issues across this region—such as public demand for lake trout fisheries and the conflicts that arise when lake trout become an ecological or economic liability for the management of other valued sport or native fish—have much in common. Providing better information to the public about the ecological challenges of managing lake trout might help diffuse criticism focused on agencies or employees embroiled in local management controversies. Information for public distribution should outline concerns about the potential pitfalls of lake trout stocking and protective regulations, encourage anglers to harvest more lake trout, and provide recipes to help anglers prepare their catch for consumption. The emerging understanding of this issue should clarify this message to help address misinformation among anglers, reduce contentiousness, and facilitate management and protection of sport and native fish populations.

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REFERENCES

Albrecht, B., J. Robinson, C. Luecke, and **B. Kennedy.** 2004. Bioenergetics simulations assessing the consumption demand of different stocking regimes of sterile lake trout in Bear Lake Utah-Idaho. Final report to Idaho Department of Fish and Game. Department of Aquatic, Watershed, and Earth Resources, Utah State University, Logan.

Al-Chokhachy, R., M. Peacock, L. Heki, and **G. Thiede.** In press. Evaluating the reintroduction potential of Lahontan cutthroat trout (*Oncorhynchus clarkii henshawi*) in Fallen Leaf Lake, California. North American Journal of Fisheries Management.

Allen, B. C., S. Chandra, L. Atwell, J. Vander Zanden, and **J. E. Reuter.** 2006. Evaluation of the reintroduction of native Lahontan cutthroat trout, *Oncorhynchus clarkii henshawi*, in Fallen Leaf Lake, California, and development of management strategies for recovery. Final Report submitted to the U. S. Fish and Wildlife Service, Reno, Nevada.

Beattie, W. D., and **P. T. Clancey.** 1991. Effects of *Mysis relicta* on the zooplankton community and kokanee population in Flathead Lake, Montana. American Fisheries Society Symposium 9:39-48.

Beauchamp, D. A. 1996. Estimating predation losses under different lake trout population sizes and kokanee stocking scenarios in Flathead Lake. Final Report of Utah Cooperative Fisheries and Wildlife Research Unit to Montana Department of Fish Wildlife and Parks, Kalispell.

Beauchamp, D. A., B. C. Allen, R. C. Richards, W. A. Wurtsbaugh, and **C. R. Goldman.** 1992. Lake trout spawning in Lake Tahoe: egg incubation in deepwater macrophyte beds. North American Journal of Fisheries Management 12:442-449.

Beauchamp, D. A., M. W. Kershner, Overman, N. C., J. Rhydderch, J. Lin, and **L. Hauser.** 2006. Trophic interactions of nonnative lake trout and lake whitefish in the Flathead Lake food web. Report to the Confederated Salish-Kootenai Tribes. Washington Cooperative Fisheries and Wildlife Research Unit, University of Washington, Seattle.

Beauchamp, D. A., D. Wahl, and **B. M. Johnson.** 2007. Predator-prey interactions. Pages 765-842 *in* C. S. Guy and M. J. Brown, eds. Analysis and interpretation of inland fisheries data. American Fisheries Society, Bethesda, Maryland.

Behnke, R. J. 1992. Native trout of western North America. American Fisheries Society Monograph 6. Bethesda, Maryland.

Bigelow, P. E. 2009. Predicting areas of lake trout spawning habitat within Yellowstone Lake, Wyoming. Doctoral dissertation. University of Wyoming, Laramie.

Bigelow, P. E., T. M. Koel, D. Mahony, B. Ertel, B. Rowdon, and **S. T. Olliff.** 2003. Protection of native Yellowstone cutthroat trout in Yellowstone Lake—Yellowstone National Park, Wyoming. Technical Report NPS/NFWRD/NRTR-2003/314. National Park Service, Water Resources Division, Fort Collins, Colorado.

Bowles, E. C., B. E. Rieman, G. R. Mauser, and **D. H. Bennett.** 1991. Effects of introductions of *Mysis relicta* on fisheries in northern Idaho. American Fisheries Society Symposium 9:65-74.

Brown, L. G. 1984. Lake Chelan fishery investigations. Washington Department of Fish and Game, Olympia.

Cabana, G. A., Tremblay, J. Kalff, and **J. B. Rasmussen.** 1994. Pelagic food chain structure in Ontario lakes: a determinant of mercury levels in lake trout. Canadian Journal of Fisheries and Aquatic Sciences 51:381-389.

Carty, D., W. Fredenberg, L. Knotek, M. Deleray, and **B. Hansen.** 1997. Hungry Horse Dam fisheries mitigation: kokanee stocking and monitoring in Flathead Lake. Bonneville Power Administration, DOE/BP-60559-3, Portland, Oregon.

CDOW (Colorado Division of Wildlife). 2009. DOW working to balance fishery at Blue Mesa Reservoir. CDOW, Denver. Available at: http://wildlife.state.co.us/NewsMedia/PressReleases/. (July 2009).

CDPHE (Colorado Department of Public Health and Environment). 2009. Granby Reservoir fish consumption advisory. CDPHE, Denver. Available at: www.cdphe.state.co.us/wq/fishcon/09GranbyADVISO.pdf. (June 2009)

Chess, D. W., and **J. A. Stanford.** 1998. Comparative energetics and life cycle of the opossum shrimp (*Mysis relicta*) in native and non-native environments. Freshwater Biology 40:783-794.

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

Conrad, R. H., and **J. L. Gutmann.** 1996. Conversion equations between fork length and total length for Chinook salmon (*Oncorhynchus tshawytscha*). Northwest Fishery Resource Bulletin, Project Report Series 5. Northwest Indian Fisheries Commission, Olympia, Washington.

Crockett, H. J., B. M. Johnson, P. J. Martinez, and **D. Brauch.** 2006. Modeling target strength distributions to improve hydroacoustic estimation of lake trout population size. Transactions of the American Fisheries Society 135:1095-1108.

Crossman, E. J. 1995. Introduction of the lake trout (*Salvelinus namaycush*) in areas outside of its native distribution: a review. Journal of Great Lakes Research 21 (Supplement 1): 17-29.

CSKT and MFWP (Confederated Salish and Kootenai Tribes, and Montana Fish, Wildlife and Parks). 2006. Phase II of the five year review of the Flathead Lake and River Fisheries Co-Management Plan, technical synopsis and management recommendations section. CSKT and MFWP, Pablo/Kalispell, Montana.

deLeeuw, A. D., D. J. Cadden, D. H. G. Ableson, and **S. Hatlevik.** 1991. Lake trout management strategy for northern British Columbia. British Columbia Ministry of Environment, Fisheries Branch, Prince George.

Deleray, M., W. Fredenberg, and **B. Hansen.** 1995. Kokanee stocking and monitoring, Flathead Lake – 1993-1994. Report DOE/BP-65903-6. Bonneville Power Administration, Portland, Oregon.

Deleray, M., L. Knotek, S. Rumsey, and **T. Weaver.** 1999. Flathead Lake and River system fisheries status report. DJ report F-78-R-1 through 5, Element 1, Project 1 and 2, SBAS Project 3131. Montana Fish, Wildlife and Parks, Kalispell.

Dextrase, A. J., and **H. E. Ball.** 1991. Hooking mortality of lake trout angled through the ice. North American Journal of Fisheries Management 11:477-479.

Donald, D. B., and **D. J. Alger.** 1986. Stunted lake trout (*Salvelinus namaycush*) from the Rocky Mountains. Canadian Journal of Fisheries and Aquatic Sciences 43:608-612.

_____. 1993. Geographic distribution, species displacement, and niche overlap for lake trout and bull trout in mountain lakes. Canadian Journal of Zoology 71:238-247.

DES (Duke Engineering and Services). 2000. Lake Chelan fisheries investigation. Lake Chelan Hydroelectric Project 637. Prepared for Public Utility District 1, Chelan County, Bellingham, Washington.

Dunham, J., C. Baxter, K. Fausch, W. Fredenberg, S. Kitano, I. Koizumi, K. Morita, T. Nakamura, B. Rieman, K. Savvaitova, J. Stanford, E. Taylor, and **S. Yamamoto.** 2008. Evolution, ecology, and conservation of Dolly Varden, white-spotted char, and bull trout. Fisheries 33(11):537-530.

DuPont, J., M. Liter, and **N. Horner.** 2004. Panhandle Region mountain lakes investigations. 2001 annual performance report. Idaho Fish and Game, Coeur d'Alene.

_____. In press. Regional fisheries management investigations. Idaho Department of Fish and Game, Federal Aid in Fish Restoration, F-71-R-30 Subproject 1, Job a, Performance Report, Boise.

Dux, A. M. 2005. Distribution and population characteristics of lake trout in Lake McDonald, Glacier National Park: implications for suppression. Master's thesis. Montana State University, Bozeman.

Eby, L. A., A. G. Rudstram, and **J. F. Kitchell.** 1995. Predator responses to prey population dynamics: an empirical analysis based on lake trout growth rates. Canadian Journal of Fisheries and Aquatic Sciences 52:1564-1571.

Evarts, L., B. Hansen, and **J. DosSantos.** 1994. Flathead Lake angler survey, 1992-1993. Report DOE/BP-60479-1. Bonneville Power Administration, Portland, Oregon.

Frantz, T. C., and **A. J. Cordone.** 1970. Food of lake trout in Lake Tahoe. California Fish and Game 56:21-35.

Fredenberg, W. 2002. Further evidence that lake trout displace bull trout in mountain lakes. Intermountain Journal of Sciences 8:143-152.

Fredenberg, W., D. Carty., M. Deleray, L, Knotek, and B. Hansen. 1999. Hungry Horse Dam fisheries mitigation: kokanee stocking and monitoring in Flathead Lake. Final Report to the U.S. Department of Energy. Bonneville Power Administration, Portland Oregon.

Fredenberg, W., M. Meeuwig, and C. Guy. 2007. Action plan to conserve bull trout in Glacier National Park. U.S. Fish and Wildlife Service, Kalispell, Montana.

Gerstung, E. R. 1988. Status, life history, and management of the Lahontan cutthroat trout. American Fisheries Society Symposium 4:93-106.

Gipson, R. D., and **W. A. Hubert.** 1993. Spawning-site selection by kokanee along the shoreline of Flaming Gorge Reservoir, Wyoming-Utah. North American Journal of Fisheries Management 13:475-482.

Graham, P., and **W. Fredenberg.** 1983. Flathead Lake fisherman census. Flathead River Basin environmental impact study. Montana Department of Fish, Wildlife and Parks, Kalispell.

Gresswell, R. E. 2009. Scientific review panel evaluation of the National Park Service lake trout suppression program in Yellowstone Lake. Northern Rocky Mountain Science Center Final Report U.S. Geological Survey. Bozeman, Montana.

Haddix, T., and **P. Budy.** 2005. Factors that limit growth and abundance of rainbow trout across ecologically distinct areas of Flaming Gorge Reservoir, Utah-Wyoming. North American Journal of Fisheries Management 25:1082-1094.

Hansen, M. 2007. Predator-prey dynamics in Lake Pend Oreille. Idaho Department of Fish and Game Fishery Research Report 07–53, Boise.

Hansen, M. J., N. J. Horner, M. Liter, M. P. Petersen, and **M. A. Maiolie.** 2008. Dynamics of an increasing lake trout population in Lake Pend Oreille, Idaho, USA. North American Journal of Fisheries Management 28:1160-1171.

Hansen, M. J., M. Liter, S. Cameron, and **N. Horner.** 2006. Mark-recapture study of lake trout using large trap nets in Lake Pend Oreille. Idaho Department of Fish and Game, Fishery Research Report 07–19, Boise.

Hansen, M. J., J. W. Peck, R. G. Schorfharr, J. H. Selgeby, D. R. Schreiner, S. T. Schramm, B. L. Swanson, W. R. MacCallum, M. R. Burnham-Curtis, G. L. Curtis, J. W. Heinrich, and **R. J. Young.** 1995. Lake trout (*Salvelinus namaycush*) populations in Lake Superior and their restoration in 1959-1993. Journal of Great Lakes Research 21 (Supplement 1): 152-175.

Hardiman, J. M., B. M. Johnson, and **P. J. Martinez.** 2004. Do predators influence the distribution of age-0 kokanee in a Colorado reservoir? Transactions of the American Fisheries Society 133:1366-1378.

Haroldson, M. A., K. A. Gunther, D. P. Reinart, S. R. Podrunzy, C. Cegelski, L. Waits, T. Wyman, and **J. Smith.** 2005. Changing numbers of spawning cutthroat trout in tributary streams of Yellowstone Lake and estimates of grizzly bears visiting streams from DNA. Ursus 16:167-180.

Healy, M. C. 1978. The dynamics of exploited lake trout populations and implications for management. Journal of Wildlife Management 42:307-328.

Hubert, W. A., R. D. Gipson, and **R. A. Whaley.** 1994. Interpreting relative weights of lake trout stocks. North American Journal of Fisheries Management 14:212-215.

IDFG (Idaho Department of Fish and Game). 2007. Fisheries management plan: 2007-2012. IDFG, Boise. Available at: http://fishandgame.idaho.gov/fish/programs/fish_plan.pdf. (January 2008).

IDHW (Idaho Department of Health and Welfare). 2008. Eat fish, be smart, choose wisely: safe fish eating guideline for fish caught in Idaho waters. Bureau of Community and Environmental Health, IDHW, Boise. Available at: www.healthandwelfare.idaho.gov/DesktopModules/Documents/DocumentsView.aspx?tabID=0&ItemID=11810&MId=12869&wversion=Staging. (January 2009).

Jassby, A. D. 1998. Interannual variability at three inland water sites: implications for sentinel ecosystems. Ecological Applications 8:277-287.

Jassby, A. D., C. R. Goldman, and **T. M. Powell.** 1992. Trend, seasonality, cycle, and irregular-fluctuations in primary productivity at Lake Tahoe, California-Nevada, USA. Hydrobiologia 246:195-203.

Johnson, L. 1976. Ecology of arctic populations of lake trout, *Salvelinus namaycush*, lake whitefish, *Coregonus clupeaformis*, Arctic char, S. alpinus, and associated species in unexploited lakes of the Canadian Northwest Territories. Journal of the Fisheries Research Board of Canada 33:2459-2488.

Johnson, B. M., and **P. J. Martinez.** 1995. Selecting harvest regulations for recreational fisheries: opportunities for research/management cooperation. Fisheries 20(10):22-29.

______. 2000. Trophic economics of lake trout management in reservoirs of differing productivity. North American Journal of Fisheries Management 20:127-143.

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

Kaeding, L. R., G. D.Boltz, and **D. G. Carty.** 1996. Lake trout discovered in Yellowstone Lake threaten native cutthroat trout. Fisheries 21(3):16-20.

Keely, E. R., and **J. W. A. Grant.** 2001. Prey size of salmonids in streams, lakes, and oceans. Canadian Journal of Fisheries and Aquatic Sciences 58:1122-1132.

Kennedy, B. M., B. W. Thompson, and **C. Luecke.** 2006. Ecological differences between two closely related morphologically similar benthic whitefish (*Prosopium spilonotus* and *Prosopium abyssicola*) in an endemic whitefish complex. Canadian Journal of Fisheries and Aquatic Sciences 63:1700-1709.

Koel, T. M., P. E. Bigelow, P. D. Doepke, B. D. Ertel, and **D. L Mahoney.** 2005. Nonnative lake trout result in Yellowstone cutthroat trout decline and impacts to bears and anglers. Fisheries 30(11):10-19.

Kozfkay, J. R., J. C. Dillon, and **D. J. Schill.** 2006. Routine use of sterile fish in salmonid sport fisheries: are we there yet? Fisheries 31(8):392-401.

Kozfkay, J. R., E. J. Wagner, and **D. Aplanalp.** 2005. Production of triploid lake trout by means of pressure treatment. North American Journal of Aquaculture 67:93-97.

Liter, M., and **M. A. Maiolie.** 2003. Upper Priest Lake lake trout removal and Priest Lake Thorofare strobe light evaluations. Idaho Department of Fish and Game, Fishery Research Report 03-36, Boise.

Luecke, C., T. C. Edwards, Jr., M. W. Wengert, Jr., S. Brayton, and **R. Schneidervin.** 1994. Simulated changes in lake trout yield, trophies, and forage consumption under various slot limits. North American Journal of Fisheries Management 14:14-21.

Mackenzie-Grieve, J. L., and **J. R. Post.** 2005. Projected impacts of climate warming on production of lake trout (*Salvelinus namaycush*) in southern Yukon lakes. Canadian Journal of Fisheries and Aquatic Sciences 63:788-797.

Maiolie, M. A., K. Harding, W. Ament, and **W. Harryman.** 2002. Lake Pend Oreille fishery recovery project. Idaho Department of Fish and Game, Completion Report to Bonneville Power Administration, Contract 194-047-00, Portland, Oregon.

Martinez, P. J. 2004. Coldwater reservoir ecology. Colorado Division of Wildlife, Federal Aid in Fish and Wildlife Restoration Project F-242-R11, Progress Report, Fort Collins.

______. 2005. Coldwater reservoir ecology. Colorado Division of Wildlife, Federal Aid in Fish and Wildlife Restoration Project F-242-R12, Progress Report, Fort Collins.

______. 2006. Coldwater reservoir ecology. Colorado Division of Wildlife, Federal Aid in Fish and Wildlife Restoration Project F-242-R13, Progress Report, Fort Collins.

Martinez, P. J., and **E. P. Bergersen.** 1991. Interactions of zooplankton, *Mysis relicta*, and kokanees in Lake Granby, Colorado. American Fisheries Society Symposium 9:49-64.

Martinez, P. J., and **W. J. Wiltzius.** 1995. Some factors affecting a hatchery-sustained kokanee population in a fluctuating Colorado reservoir. North American Journal of Fisheries Management 15:220-228.

Mauser, G. R., R. W. Vogelsang, and **C. L. Smith.** 1988. Enhancement of trout in large north Idaho lakes. Federal Aid in Fish Restoration Project F-73-R-10, Completion Report. Idaho Department of Fish and Game, Boise.

McIntyre, J. D. 1995. Review and assessment of possibilities for protecting the cutthroat trout of Yellowstone Lake from introduced lake trout. Pages 28-33 *in* J. D. Varley and P. Schullery, eds. The Yellowstone Lake crisis: confronting a lake trout invasion. National Park Service, Yellowstone Center for Resources, Yellowstone National Park, Wyoming.

MDPHHS (Montana Department of Public Health and Human Services). 2007. Montana sport fish consumption guidelines: what you need to know about mercury and PCBs in Montana's sport fish. MDPHHS, Helena. Available at: http://fwp.mt.gov/content/getItem.aspx?id=28187. (November 2008).

Meeuwig, M. H. 2008. Ecology of lacustrine-adfluvial bull trout populations in an interconnected system of natural lakes. Doctoral dissertation. Montana State University, Bozeman.

MFWP (Montana Fish, Wildlife and Parks). 2008. Montana statewide angling pressure. Mail survey 2007. MFWP, Bozeman.

_____. 2009. Lake trout confirmed in Lindbergh Lake. MFWP, Kalispell. http://fwp.mt.gov/news/article_8146.aspx. (June 2009).

MFWP and CSKT (Montana Fish, Wildlife and Parks and Confederated Salish and Kootenai Tribes). 2001. Executive summary: Flathead Lake and River fisheries co-management plan, 2001-2010. MFWP and CSKT, Kalispell/Pablo, Montana.

Muhlfeld, C. C., and **B. Marotz.** 2005. Seasonal movement and habitat use by subadult bull trout in the upper Flathead River system, Montana. North American Journal of Fisheries Management 25:797-810.

Munro, A. R., T. E. McMahon, and **J. R. Ruzycki.** 2005. Natural chemical markers identify source and date of introduction of an exotic species: lake trout (*Salvelinus namaycush*) in Yellowstone Lake. Canadian Journal of Fisheries and Aquatic Sciences 62: 79-87.

Nielson, B. R., and **L. Lentsch.** 1988. Bonneville cutthroat trout in Bear Lake: status and management. American Fisheries Society Symposium 4:128-133.

Nielson, B. R. and **S. A. Tolentino.** 2002. Fisheries investigations-Bear Lake cutthroat trout enhancemnt program-January 1995-December 1999. Publication 02-09. Utah Division of Wildlife Resources, Salt Lake City.

O'Ney, S. and **R. Gipson.** 2006. A century of fisheries management in Grand Teton National Park. Pages 131-134 *in* A. Wondrak Biel, ed. Greater Yellowstone public lands: a century of discovery, hard lessons, and bright prospects. Proceedings of the 8th Biennual Scientific Conference on the Greater Yellowstone Ecosystem. Yellowstone Center for Resources, Yellowstone National Park, Wyoming.

Payne, N. R., R. M. Korver, D. S. MacLennan, S. J. Nepszy, B. J. Shuter, T. J. Stewart, and **E. R. Thomas.** 1990. The harvest potential and dynamics of lake trout populations in Ontario. Ontario Ministry of Natural Resources, Toronto.

Pazzia, I., M. Trudel, M. Ridgeway, and **J. B. Rasmussen.** 2002. Influence of food web structure on the growth and bioenergetics of lake trout (*Salvelinus namaycush*). Canadian Journal of Fisheries and Aquatic Sciences 59:1593-1605.

Peterson, M. P., and **M. A. Maiolie.** 2005. Evaluation of large trap nets for lake trout removal in Lake Pend Oreille, Idaho. Idaho Department of Fish and Game, Fishery Research Report 04-35, Boise.

Quist, M. C., and **W. A.** Hubert. 2004. Bioinvasive species and the preservation of cutthroat trout in the western United States: ecological, social, and economic issues. Environmental Science and Policy 7:303-313.

Rhea, D. 2007. Growth and mortality of lake trout in Jackson Lake, with simulated effects in changes in exploitation. Fish Division Administrative Report. Wyoming Game and Fish Department, Cheyenne.

Rieman, B. E., B. Bowler, J. B. Lukens, and **P. F. Hassemer,** 1979. Priest Lake fisheries investigations. Federal Aid in Fish Restoration, Project F-73-R-1, Job Completion Report, Idaho Department of Fish and Game, Boise.

Richards, R., C. R. Goldman, E. Byron, and **C. Levitan.** 1991. The mysids and lake trout of Lake Tahoe: a 25-year history of changes in the fertility, plankton, and fishery of an alpine lake. American Fisheries Society Symposium 9:30-38.

Richards, R. C., C. R. Goldman, T. C. Frantz and **R. Wickwire.** 1975. Where have all the *Daphnia* gone? The decline of a major cladoceran in Lake Tahoe, California-Nevada. Internationale Vereinigung fur theoretishe und angewandte Limnologie Verhandlungen 19:835-842.

Ruzycki, J. R. 2004. Impact of lake trout introductions on cutthroat trout in selected western lakes of the continental United States. Doctoral dissertation. Utah State University, Logan.

Ruzycki, J. R., D. A. Beauchamp, and **D. L. Yule.** 2003. Effects of introduced lake trout on native cutthroat trout in Yellowstone Lake. Ecological Applications 13:23-37.

Ruzycki, J. R., W. A. Wurtsbaugh, and **C. Lay.** 1998. Reproductive ecology and early life history of a lacustrine sculpin. Environmental Biology of Fishes 53:117-127.

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

Ryder, R. A., S. R. Kerr, W. W. Taylor, and **P. A. Larkin.** 1981. Community consequences of fish stock diversity. Canadian Journal of Fisheries and Aquatic Sciences 38:1856-1866.

Schoen, E. R. 2007. Pelagic trophic interactions in contrasting basins of Lake Chelan. Master's thesis. University of Washington, Seattle.

Schullery, P., and **J. D Varley.** 1995. Cutthroat trout and the Yellowstone ecosystem. Pages 12-21 *in* J. D Varley and P. Schullery, eds. The Yellowstone Lake crisis: confronting a lake trout invasion. National Park Service, Yellowstone Center for Resources, Yellowstone National Park, Wyoming.

Scott, W. B., and **E. J. Crossman.** 1973. Freshwater fishes of Canada. Fisheries Research Board Bulletin 184.

Sellers, T. J., B. R. Parker, D. W. Schindler, and **W. M.** Tonn. 1998. Pelagic distribution of lake trout (*Salvelinus namaycush*) in small Canadian Shield lakes with respect to temperature, dissolved oxygen, and light. Canadian Journal of Fisheries and Aquatic Sciences 55:170-179.

Settle, C., and **J. F. Shogren.** 2002. The economics of invasive species management: modeling native-exotic species within Yellowstone Lake. American Journal of Agricultural Economics 84:1323-1328.

Shaw, J. A., J. H. Churnside, J. J. Wilson, N. E. Lerner, R. R. Tiensvold, P. E. Bigelow, and **T. M. Koel.** 2008. Airborne lidar mapping of invasive lake trout in Yellowstone Lake. Proceedings of the 24th International Laser Radar Conference Volume II:905-908.

Shuter, B. J., M. L. Jones, R. M. Korver, and **N. P. Lester.** 1998. A general, life history based model for regional management of fish stocks: the inland lake trout (*Salvelinus namaycush*) fisheries of Ontario. Canadian Journal of Fisheries and Aquatic Sciences 55:2161-2177.

Spencer, C., R. McClelland, and **J. Stanford.** 1991. Shrimp introduction, salmon collapse and bald eagle displacement: cascading interactions in the food web of a large aquatic ecosystem. Bioscience 41:1-14-21.

Spencer, C. R., D. S. Potter, and R. T. Bukantis, and **J. A. Stanford.** 1999. Impact of predation by *Mysis relicta* on zooplankton in Flathead Lake, Montana, USA. Journal of Plankton Research 21:51-64.

Stafford, C. P., B. Hansen, and J. A. Stanford. 2004. Mercury in fishes and their diet items from Flathead Lake, Montana. Transactions of the American Fisheries Society 133:349-357.

Stafford, C. P., J. A. Stanford, F. R. Hauer, and **E. B. Brothers.** 2002. Changes in lake trout growth associated with *Mysis relicta* establishment: a retrospective analysis using otoliths. Transactions of the American Fisheries Society 131:994-1003.

Stapp, P., and **G. D. Hayward.** 2002. Effects of an introduced piscivore on native trout: insights from a demographic model. Biological Invasions 4:299-316.

Stephens, T. J., and **R. D. Gipson.** 2004. Summary of Jackson Lake fishery investigations 1971-2003 with management recommendations. Fish Division Administrative Report. Wyoming Game and Fish Department, Cheyenne.

Teuscher, D., and **C. Leucke.** 1996. Competition between kokanees and Utah chub in Flaming Gorge Reservoir, Utah-Wyoming. Transactions of the American Fisheries Society 125:505-511.

Thiede, G. P. 1997. Impact of lake trout predation on prey populations in Lake Tahoe: a bioenergetics assessment. Master's thesis. Utah State University, Logan.

Tohtz, J. 1993. Lake whitefish diet and growth after the introduction of *Mysis relicta* to Flathead Lake, Montana. Transactions of the American Fisheries Society 122:629-635.

Tolentino, S. A. 2007a. Bear Lake biological report for calendar year 2006. Publication 07-20. Utah Division of Wildlife Resources, Salt Lake City.

_____. 2007b. Population status and trends of four Bear Lake endemic fishes. Transactions of the American Fisheries Society Symposium 53:77-84.

Trippel, E. A. 1993. Relations of fecundity, maturation, and body size of lake trout, and implications for management in northwestern Ontario Lakes. North American Journal of Fisheries Management 13:64-72.

USFWS (U. S. Fish and Wildlife Service). 1998. Bull trout *Salvelinus confluentus* facts. Public Affairs Office, USFWS, Portland, Oregon. Available at: library.fws.gov/Pubs1/bulltrout.pdf. (October 2005).

Vander Zanden, J. M., S. Chandra, B. C. Allen, J. E. Reuter, and **C. R. Goldman.** 2003. Historical food web structure of native aquatic communities in the Lake Tahoe (California-Nevada) basin. Ecosystems 6:274-288.

Vander Zanden, M. J., J. D. Olden, and **C. Gratton.** 2006. Food-web approaches in restoration ecology. Pages 165-189 *in* D. A. Falk, M. A. Palmer, and J. B. Zedler, eds. Foundations of restoration ecology. Island Press, Washington, DC.

Varley, J. D., and **R. E. Gresswell.** 1988. Ecology, status, and management of the Yellowstone cutthroat trout. American Fisheries Society Symposium 4:13-24.

Venard, J. A., and **D. L. Scarnecchia.** 2005. Seasonally dependent movement of lake trout between two northern Idaho lakes. North American Journal of Fisheries Management 25:635-639.

Vidergar, D. T. 2000. Population estimates, food habits, and estimates of consumption of selected predatory fishes in Lake Pend Oreille, Idaho. Master's thesis. University of Idaho, Moscow.

Viola, A. E., and **J. H. Foster.** 2002. Lake Chelan comprehensive fishery management plan. Washington Department of Fish and Wildlife, Olympia.

Vogel, J. L., and **D. A. Beauchamp.** 1999. Effects of light, prey size, and turbidity on reaction distances of lake trout (*Salvelinus namaycush*) to salmonid prey. Canadian Journal of Fisheries and Aquatic Sciences 56:1293-1297.

WDOH (Washington Department of Health). 2006. Lake Chelan fish consumption advisory. WDOH, Olympia. Available at: www.doh.wa.gov/ehp/oehas/fact%20sheets%20pdf/fs-lkchelan2006.pdf. (February 2006).

Wicklum, D. 1999. The ecology of *Mysis relicta* in Flathead Lake, Montana. Report to the Confederated Salish and Kootenai Tribes. Pablo, Montana.

WTU (Wyoming Trout Unlimited). 2008. Save the Yellowstone cutthroat: TU, the NPS and the USGS team in lake trout effort. WTU, Lander. Available at: www.wyomingtu.org/site/c.deIILOOpGnF/b.3942035/. (May 2008).

YNP (Yellowstone National Park). 2009. Fishing regulations. YNP, Wyoming. www.nps.gov/yell/planyourvisit/upload/fishreg09.pdf. (June 2009).

Yule, D. L., and **C. Luecke.** 1993. Lake trout consumption and recent changes in the fish assemblage of Flaming Gorge Reservoir. Transactions of the American Fisheries Society 122:1058-1069.