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Seasonal movements of non-native lake trout in a connected lake and river system

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Abstract Non-native lake trout, *Salvelinus namaycush* (Walbaum), threaten native salmonid populations in the western United States. Effective management of lake trout requires understanding movements within connected lake and river systems. This study determined the seasonal movements of subadult lake trout in the Flathead River upstream of Flathead Lake, Montana, USA using radio telemetry. The spatiotemporal distribution of lake trout in the river was related to water temperature. Lake trout were detected in the river primarily during autumn, winter and spring, when water temperatures were cool. By contrast, fewer were detected when temperatures were warmest during summer and during high spring flows. Downriver movements to Flathead Lake occurred throughout autumn and winter when water temperature decreased below 5 °C, and in late spring as water temperature rose towards 15 °C and river discharge declined following spring runoff. Upriver movements occurred primarily in October, which coincided with migrations of prey fishes. These results suggest that lake trout are capable of moving throughout connected river and lake systems (up to 230 km) and that warm water temperatures function as an impediment to occupancy of the river during summer. Controlling source populations and maintaining natural water temperatures may be effective management strategies for reducing the spread of non-native lake trout.

KEYWORDS: introduced species, Montana, salmonids, *Salvelinus namaycush*, telemetry, water temperature.

Introduction

Introductions of non-native fishes into aquatic ecosystems threaten native species and the biodiversity of aquatic ecosystems worldwide (Vitousek *et al.* 1997). Lake trout, *Salvelinus namaycush* (Walbaum), are large, long-lived, top-level predators native to deep, cold and oligotrophic lakes of Canada and northern parts of the USA, including the Great Lakes (Crossman 1995). However, lake trout were widely introduced into lakes and reservoirs outside their native range during the late 19th and early 20th centuries (Behnke 1992). More recently, non-native lake trout populations are expanding in the western USA through dispersal and unauthorised translocations (Martinez *et al.* 2009). Although lake trout occupy an important ecological niche as a top-level predator in lakes where they are native, they have become predators of and competitors with native fishes in waters where they have been introduced (Ruzycki *et al.* 2003; Koel *et al.* 2005; Martinez *et al.* 2009; Kalinowski *et al.* 2010), resulting in dramatic declines in native salmonid and desired sport fish populations (Martinez *et al.* 2009). Effective management requires an understanding of the movements of lake trout within freshwater systems to either suppress non-native populations or to prevent their spread.

In 1905, lake trout were introduced from the Great Lakes into Flathead Lake, Montana, USA, the largest natural freshwater lake (510 km^2 surface area) in the western United States. Lake trout abundance remained at a relatively low level until the opossum shrimp, *Mysis diluviana* Audzijonytë and Väinölä, invaded Flathead Lake during the 1980s after being introduced from 1968 to 1976 into five lakes upstream of Flathead Lake (Ellis *et al.* 2011). The subsequent boom in this

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shrimp population was followed by an increase in the abundance of lake trout and non-native lake whitefish, *Coregonus clupeaformis* (Mitchill), and extirpation of formerly abundant non-native kokanee salmon, *Oncorhynchus nerka* (Walbaum), by 1989 (Ellis *et al.* 2011). Native bull trout, *Salvelinus confluentus* (Suckley), a federally protected species, and westslope cutthroat trout, *Oncorhynchus clarkii lewisi* (Girard), populations also declined in the early 1990s in the upper Flathead River and Flathead Lake because of these major community changes in Flathead Lake. Concurrently, there were broad declines in bull trout numbers and corresponding increases in lake trout abundance in several natural lakes in Glacier National Park that are connected to Flathead Lake (Fredenberg 2002). The incidence of lake trout entering the Flathead River was rarely observed prior to 1989, yet angler creel data suggested that lake trout use of the Flathead River substantially increased in the 1990s (Christenson *et al.* 1996; Montana Fish, Wildlife & Parks, unpublished data).

Changes in the thermal characteristics of the Flathead River also may have affected lake trout distribution in the system (Fig. 1). Prior to the installation of a temperature-control device on Hungry Horse Dam, hypolimnetic releases of water at 4–6 °C artificially cooled the lower South Fork and mainstem Flathead rivers during 1952–1995. In August of 1996, a selective-withdrawal system was installed on the dam to control temperatures in the tailrace, which restored downstream river temperatures to near pre-dam conditions (Christenson *et al.* 1996; Marotz *et al.* 1996). Since then, dam discharge temperatures during late June through September have frequently exceeded 10.6 °C,

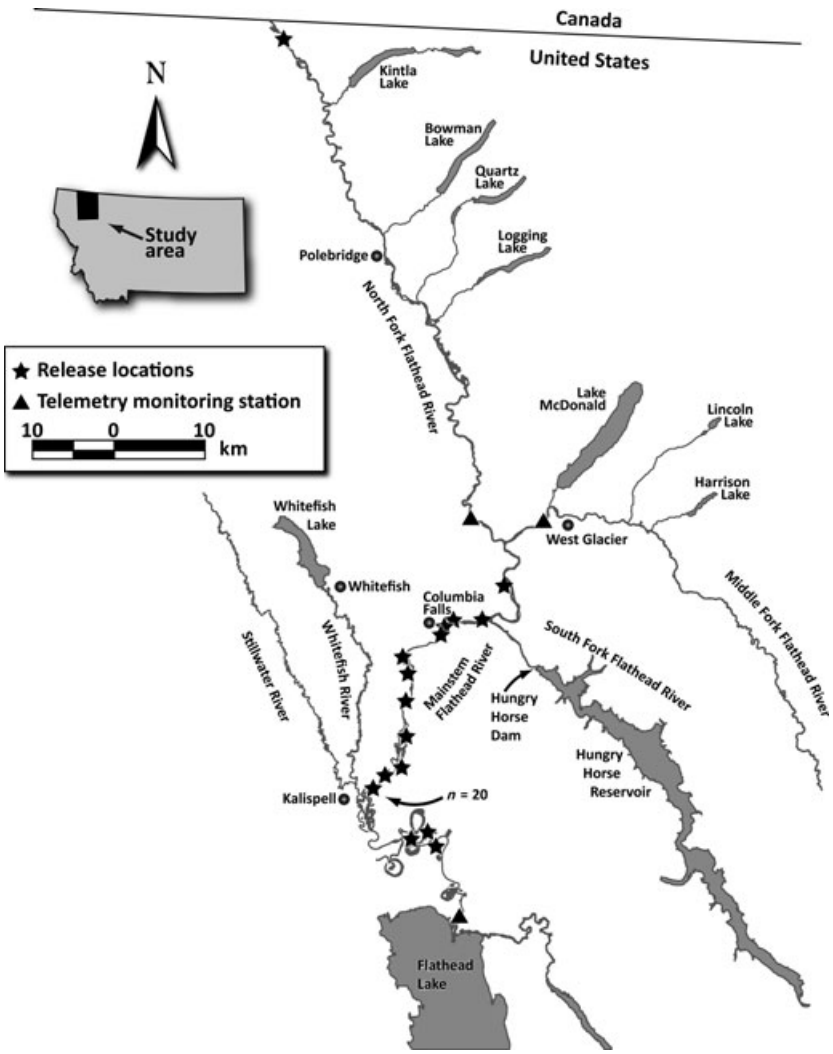

Figure 1. Study area in the upper Flathead River system, including the capture and release locations of the radio-tagged lake trout. Lakes supporting non-native lake trout populations are identified. The number of lake trout tagged at one location near Kalispell (n = 20) is noted.

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the peak feeding temperature for adult lake trout (Stewart *et al.* 1983), and often exceeded their typical daytime temperature range of 4–15 °C (Stewart *et al.* 1983; Sellers *et al.* 1998). Thus, operation of selective withdrawal and restoration of natural water temperatures may act as a thermal impediment to lake trout use of the river system during the warm summer months. However, no information exists regarding the relationship between water temperature and lake trout movements and use of the Flathead River.

The purported increase in lake trout abundance and distribution in the Flathead River and concomitant decrease in native salmonid populations prompted research to investigate the seasonal movements of non-native lake trout in the Flathead River upstream of Flathead Lake. Specifically, this study sought to determine whether water temperature may reduce the abundance of lake trout in the Flathead River system upstream of Flathead Lake. The objectives of this study were: (1) to describe the seasonal movements and distribution of lake trout in the Flathead River; and (2) to relate movements to water temperatures in the river.

Materials and methods

Study site

The upper Flathead River drainage originates in the Rocky Mountains of north-western Montana, USA and south-eastern British Columbia, Canada and includes the North Fork, Middle Fork, South Fork and mainstem Flathead rivers and Flathead Lake (Fig. 1). The drainage area is approximately 18 400 km^2 and is in the headwaters of the upper Columbia River Basin. Hungry Horse Dam, located on the South Fork Flathead River 8.5 km upstream of the confluence with the mainstem Flathead River, was completed in 1952. The dam regulates river discharge, impedes upstream fish migration and isolates fish populations upstream (Fig. 1). The current flow management strategy mimics the natural spring runoff event, within flood constraints, gradually reducing dam discharge towards stable flows during summer, autumn and winter, which maximises the availability of critical bull trout and westslope cutthroat trout habitats in the dam-influenced reaches of the mainstem Flathead River (Muhlfeld *et al.* 2011).

Lake trout were collected for transmitter implantation in the mainstem Flathead River downstream of the mouth of the South Fork Flathead River between October 1996 and July 1998 (Fig. 1). The mainstem Flathead River contains two distinct sections: a free-flowing (lotic) section and a lake-influenced (lentic) section. The free-flowing section (herein referred to as the mainstem) contains a single-thread channel that begins at the South Fork confluence and extends 17.6 km downstream and an anastomosing channel (multiple stable channels that have a large area covered by mature vegetation) that extends an additional 19.2 km downriver to the confluence with the Stillwater River. The lower section of the Flathead River is a lake-influenced section of the river (herein referred to as the 'lower river') that extends from the mouth of the Stillwater River to the north end of Flathead Lake. This 32-km section of the river is a deep (maximum depth = 27.5 m), low-gradient (<0.4 m km^{-1}) sinuous channel that contains connected slough habitats in lateral areas of the floodplain. This river portion is influenced by backwater effects caused by the impoundment of Flathead Lake by Kerr Dam, which is located near the outlet of Flathead Lake; variable lake levels transform the lower river from a lotic to a lentic environment.

Radio tracking

Thirty-eight lake trout (mean total length = 478 mm, range = 411–538 mm; mean weight = 752 g, range = 408–990 g) were captured by angling (n = 37) and passive (Merwin) trapping (n = 1), implanted with radio transmitters and released near their capture locations (Fig. 1). Captured fish were anaesthetised with tricaine methane sulphonate (MS-222), and transmitters were surgically implanted into the body

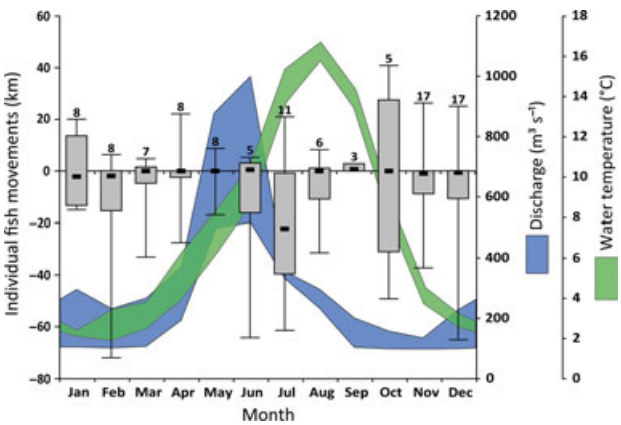

Figure 2. Movements by radio-tagged lake trout in relation to mean daily water temperature and mean daily discharge in the mainstem Flathead River, October 1996 to May 1999. Negative values represent downriver movements. Small black boxes represent median values, large grey boxes the 25th and 75th quartiles and whiskers the minimum and maximum values. The number of fish detected per month is noted above each box plot. The inter-annual ranges of mean daily water temperatures and discharges are shown.

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cavity. Total length (*TL*) of all lake trout was measured to the nearest mm, and mass was measured to the nearest g; these data were unavailable for two fish. Each anaesthetised fish was placed in a padded, V-shaped trough, and gills were irrigated with a 60 mg L^{-1} solution of MS-222 during surgery. A 10-mm incision was made immediately anterior of the pelvic girdle, and a sterilised transmitter was admitted into the body cavity with the antenna extended through the body wall immediately posterior of the pelvic girdle. Each incision was closed with three to four synthetic absorbable sutures. Each surgery lasted approximately 8–10 min, and no mortalities occurred during surgery or during the 0.5-h recovery period. Transmitters (MCFT2-3EM; Lotek Wireless Inc., Newmarket, ON, Canada) weighed 10.0 g in air and had a predicted life expectancy of 395 days. Each tag emitted a uniquely coded signal (12 pulses min^{-1}) in the frequency range of 148.750 MHz.

Fish movements were monitored using a jet boat, fixed-wing aircraft and remote ground receiver stations. A Lotek radio receiver (Model SRX 400-W5; Lotek Wireless Inc., Newmarket, ON, Canada) and a three-element directional Yagi antenna were used to locate fish during ground and aerial surveys. Tracking surveys were conducted twice a month during the daytime. Aerial surveys were conducted at approximately 100 m above ground at an average speed of 27–31 m s^{-1}. Three permanent telemetry ground stations were installed near the terminus of the North Fork, Middle Fork and mainstem Flathead rivers (Fig. 1). Fish were detected by each ground station when they moved within 250 m of the receiver, and the stations continuously monitored fish movements. Each ground station consisted of a Lotek data-logging receiver equipped with a three-element directional Yagi antenna powered by a 12-volt deep-cycle marine battery.

For each location, the distance moved was calculated from the previous location and direction (upstream or downstream) was recorded. Monthly movements were averaged for each fish, and each location and movement was assigned to the date each fish was detected. Each location was recorded on a USGS topographical map (1:24 000). Location points were later transferred into ArcView (Version 3.1; ESRI, Redlands, CA, USA). Movements were calculated using ArcView by measuring the distance along the thalweg for each consecutive location. It was assumed that fish remained in Flathead Lake if a signal was not obtained after a fish passed through the ground station near the mouth at Flathead Lake. Movements and locations of fish that were harvested by anglers were also recorded. Daily mean water temperature and discharge data were obtained from the USGS flow monitoring station located in the mainstem Flathead River (Columbia Falls). Seasons were delineated based on temperature and flow data in the Flathead River during the study period and were classified as winter (1 December to 31 March), spring (1 April to 15 July), summer (16 July to 15 September) and autumn (16 September to 30 November).

Results

From 1996 to 1999, 37 lake trout were tracked an average of 105 days (range, 2–410), and each fish was relocated an average of five times (SD, 5). One implanted fish was never detected and was not included in any analyses. Four fish were consistently relocated in the same location for several months after making long-distance movements; these fish were presumed to either have died or expelled their tags, so their final locations were noted, and subsequent relocations were removed from analyses. The movements of four fish harvested by anglers were included in the analyses.

Most fish moved downriver into Flathead Lake or the lower (lake-influenced) Flathead River after capture and tagging. Downriver movements to Flathead Lake and the lower river occurred throughout the autumn and winter as water temperatures declined from 5 to 2 °C and in June and July as water temperatures rose towards 15 °C and as river discharge declined following peak spring runoff (Fig. 2). By contrast, some lake trout made upriver movements; several moved upriver within the mainstem; two moved to the South Fork Flathead River (one directly downstream of Hungry Horse Dam), and one fish moved 89 km upriver to Whitefish Lake (Figs 1 and 2).

Seasonal detections in the Flathead River, from the mouth of the South Fork downriver to Flathead Lake, revealed that radio-tagged lake trout used the river system primarily in the autumn and winter (62% of the observations) and spring (26%) when water temperatures were cool (Figs 2 and 3). By contrast, fewer lake trout (12%) were detected in the river when water temperatures were warmest during summer. Furthermore, of the fish that were detected in the river, most (87%) were located in the lake-influenced portion of the river, whereas 13% of the observations were in the mainstem.

1996 Tagging data

Sixteen lake trout were radio-tagged in the mainstem near Kalispell (n = 14) and the lower river (n = 2)

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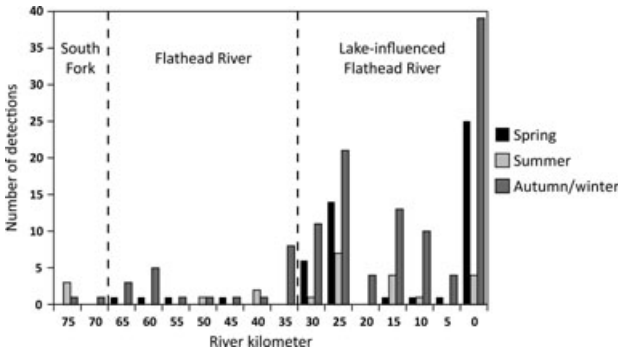

Figure 3. Seasonal lake trout detections in the mainstem Flathead River, October 1996 to May 1999.

from 29 October through 12 December 1996 (Table 1; Fig. 1). One of these tagged fish was harvested by an angler 12 days after its release. The majority of the remaining fish moved to Flathead Lake (n = 13), whilst two fish moved downriver into the lower river. Downriver movements to Flathead Lake and the lower river occurred from 2 November 1996 to 3 May 1997 when mean daily water temperatures ranged from 2 to 5.5 °C and river discharge generally remained at base flows. One lake trout moved 38 km upstream to the South Fork Flathead River in late January and then moved 72 km downstream and entered Flathead Lake on 25 February 1997. Two lake trout that migrated to Flathead Lake moved back upriver in the Flathead River during the autumn of 1997 when water temperatures declined below 8 °C. One of these lake trout migrated 46 km upriver in October and then progressively moved 20 km downriver from November through December. The other lake trout was located in the lower river near the ground station at the mouth of Flathead Lake during November.

1997 Tagging data

Four fish were tagged in the mainstem from 11 July through 23 July (Table 1; Fig. 1). One fish moved 67 km downriver and entered Flathead Lake 4 days after its release as river water temperatures approached 15 °C. The three remaining fish made extensive movements in the river system in July but were consistently detected at their same respective locations in August, suggesting they had died or expelled their tag. One of these fish moved 21 km upriver to a canyon upriver of the South Fork Flathead River and then moved 25 km downriver to the mainstem Flathead River as temperatures approached 15 °C. The two remaining fish moved 40 and 54 km downriver in the mainstem.

Six lake trout were radio-tagged in the mainstem near Kalispell from 22 October through 12 December 1997. Five of these fish moved 35 km downriver and entered Flathead Lake 12–93 days following release whilst water temperatures declined from 5 to 2 °C during the autumn and winter. One of these fish moved 37 km upriver to the South Fork in early November and then moved 65 km downriver and entered Flathead Lake on 26 December 1997. The remaining fish moved downstream to the lower river in November and was not subsequently relocated. One of the migrants to Flathead Lake returned to the lower Flathead River on 23 May 1998 and then moved 89 km upriver into the Whitefish River where it was subsequently caught by an angler in Whitefish Lake on 2 June 1998.

1998 Tagging data

Eleven lake trout were tagged from 22 June through 8 July 1998 throughout the Flathead River (Table 1; Fig. 1). Five lake trout moved 37–65 km downriver to Flathead Lake from 5 July to 9 July, as temperatures increased to 15 °C. Four fish were detected downstream in the lake-influenced portion of the river in July and remained there through the autumn and winter. One lake trout tagged near the mouth of the South Fork moved 8 km upstream to the base of Hungry Horse Dam where it remained in August and September during maximum summer water temperatures (Fig. 2) and then moved 23 km downstream to the mainstem in October.

Table 1. Collection dates, sample sizes, mean total lengths (TL), mean weights (g) and tracking information for radio-tagged lake trout in the Flathead River, Montana. Standard deviations are in parentheses

Tagging year	Dates released	N	Mean TL (mm)	Mean weight (g)	Mean number of relocations	Mean days tracked
1996	29 October to 12 December	16	452 (24)	762 (131)	7 (6)	158 (151)
1997	11 July to 23 July	4	486 (2)	714 (53)	3 (1)	21 (14)
1997	22 October to 10 November	6	492 (2)	794 (96)	4 (2)	66 (71)
1998	22 June to 21 July	10	507 (14)	725 (193)	4 (4)	75 (93)

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One lake trout that was captured and released during summer in the North Fork Flathead River (upstream of Polebridge; Fig. 1) moved a total distance of 231 km during its 136-day monitoring period. On 31 August 1998, this fish was detected in British Columbia, Canada, 39 km upriver of its capture and release location; no temperature data were available. During September, it incrementally moved a total distance of 133 km downstream to the confluence of the North Fork and Middle Fork, after temperatures declined to below 15 °C, and then moved 6 km upriver through the Middle Fork ground station where it remained in the river or possibly Lake McDonald, through mid-October. In November, this fish moved 53 km downriver to the mainstem and was subsequently harvested by an angler in December.

Discussion

The seasonal movements and habitat requirements of lake-dwelling lake trout have been well described in North America, with a substantial emphasis on populations inhabiting the Great Lakes region (Martin 1952; Stewart *et al.* 1983; Schmalz *et al.* 2002; Kapuscinski *et al.* 2005). These studies demonstrate that temperature, oxygen and prey availability are important factors influencing movements by lake trout in lentic environments. Prior to this study, however, only one published study had investigated the seasonal movements and factors influencing movements of lake trout in a lotic system outside their native range (Venard & Scarnecchia 2005). The spatiotemporal distribution and movement of lake trout within the connected Flathead Lake and River system was primarily a function of water temperature. Lake trout used the Flathead River primarily in the autumn, winter and spring when water temperatures were cool and apparently avoided the river during the warm summer months. Furthermore, few lake trout were detected in the river during peak spring runoff, suggesting that high spring flows may also limit lake trout use of the riverine environment. The results demonstrate the dispersal capabilities of non-native lake trout within connected lake and river systems and how summer water temperatures and high spring flows may function as impediments to lake trout occupancy of rivers.

Sustained water temperatures in excess of 15 °C are likely not conducive to lake trout occupancy of river systems. Lake trout moved downriver to Flathead Lake as river temperatures approached 15 °C, and fewer lake trout were detected in the river during the warm summer months. The few fish that occupied the river during summer were located in areas coinciding with potential cool water refugia (e.g. Canadian headwaters, Whitefish Lake, Lake McDonald and tailwaters of Hungry Horse Dam). Studies have suggested that 15 °C is the upper temperature threshold limiting vertical movement of lake trout in lakes (Kennedy 1941; Martin 1952; Snucins & Gunn 1995; Dux *et al.* 2011). Martin (1952) reported that lake trout moved to deeper water when surface waters warmed to 14 °C or 15 °C in mid-June in Red Rock Lake, Ontario. Dux *et al.* (2011) found lake trout avoided warm surface waters (> 12 °C) in Lake McDonald, Montana, and the maximum observed temperature used by the sonic-tagged fish was 15.7 °C. Venard and Scarnecchia (2005) found non-native lake trout moved frequently between Upper Priest and Priest lakes in northern Idaho in the spring and autumn when water temperatures were cool but did not move when water temperature exceeded 15 °C. In general, adult lake trout prefer temperatures of about 10 °C, whereas juvenile lake trout select deeper water and cooler temperatures of approximately 6 °C (Crossman 1995). Although mean daily temperature provides a good indicator of overall thermal suitability for lake trout, other metrics associated with seasonal and daily extremes (e.g. maximum, maximum weekly maximum temperature) may also affect movement in river and lake systems.

Restoration of natural, warmer summer water temperatures in the Flathead River may function as an impediment to lake trout occupancy of the river during summer months. Prior to the installation of the selective water-withdrawal system at Hungry Horse Dam in 1995, water temperatures in the South Fork Flathead River remained 4–7 °C all year (Marotz *et al.* 1996), and water temperatures in the mainstem Flathead River only sporadically exceeded 10 °C from June through early August depending on the timing and magnitude of cold water discharges from the dam (Christenson *et al.* 1996). In 1996, selective withdrawal restored nearly natural summer water temperatures in the South Fork and downstream in the mainstem Flathead River by replacing hypolimnetic discharges with stratified releases from the reservoir; water temperatures since 1996 consistently have exceeded 10 °C from late June through September (Christenson *et al.* 1996; Marotz *et al.* 1996). Eliminating cold, hypolimnetic discharges during summer appears to have influenced lake trout distribution and movements by removing a cold water refuge in the South Fork Flathead River downstream of the dam.

Some lake trout displayed long-distance movements throughout the upper Flathead River drainage. For

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example, one fish captured and released in the upper North Fork moved a total distance of 231 km throughout the upper North Fork (Canada and USA), Middle Fork and mainstem Flathead River during its monitoring period. Another lake trout moved 89 km upriver into Whitefish Lake, and several others moved throughout the Flathead River and South Fork Flathead River downstream of Hungry Horse Dam. The origin of lake trout 'pioneering' the Flathead River system remains uncertain. The increased observations of lake trout in the river beginning in the late 1980s may reflect a density-dependent response because of the dramatic expansion of lake trout in Flathead Lake following the establishment of *Mysis* shrimp (Ellis *et al*. 2011); however, little anecdotal or empirical evidence exists of these behaviours prior to *Mysis*. Another possibility is that these fish originated from lakes in Glacier National Park (e.g. Kintla, Bowman, Quartz, Logging, McDonald, Lincoln and Harrison lakes; Fig. 1) and subsequently migrated downstream into the Flathead River system. Although the origins of the study fish are unknown, several fish returned to the river from Flathead Lake, suggesting that Flathead Lake was likely a source of the study fish; however, additional research is needed to determine the origin of lake trout using the river system. Nevertheless, full-time residency by lake trout in the river system is unlikely because of presently unsuitable environmental conditions (i.e. warm summer temperatures, high spring flows) and the species' evolutionary adaptations to lentic environments (Crossman 1995).

One lake trout moved upriver to Hungry Horse Dam and remained there during the summer months. These data support the fact that Hungry Horse Dam has restricted the movement of non-native lake trout from downriver sources into waters upstream of the dam, (Hungry Horse Reservoir and the upper South Fork Flathead River) that currently support a native fish assemblage, including some of the last remaining strongholds for native bull trout and westslope cutthroat trout.

An additional influence for lake trout use of the river system may be that they were following prey fishes during their spawning or migration periods. Lake trout movements and occupancy of the river overlapped with upriver autumn spawning migrations of native pygmy whitefish, *Prosopium coulterii* (Eigenmann & Eigenmann), and non-native lake whitefish, *Coregonus clupeaformis* (Mitchill), from Flathead Lake and downriver migrations of native bull trout and westslope cutthroat trout to Flathead Lake and the lower Flathead River (Shepard *et al*. 1984; Muhlfeld & Marotz 2005). Lake trout diet studies conducted in the Flathead River near Kalispell revealed that pygmy whitefish (< 200 mm) formed the majority (> 95%) of the biomass of prey items consumed by 450–550 mm lake trout during the autumn and winter (Montana Fish, Wildlife & Parks, unpublished data), and Beauchamp *et al*. (2006) found that pygmy whitefish appeared in the diets of 200–500 mm lake trout in Flathead Lake during summer and autumn. Moreover, subadult (< 300 mm) bull trout and westslope cutthroat trout emigrate from their natal tributaries primarily in the spring (Fraley & Shepard 1989; Liknes and Graham 1988) and then migrate downriver into lower portions of the Flathead River and Flathead Lake in the spring and autumn (Shepard *et al*. 1984; Fraley & Shepard 1989; Muhlfeld & Marotz 2005; Muhlfeld *et al*. 2011). Lake trout are highly piscivorous (Crossman 1995) and consume prey fishes at lengths up to 50% of their body length in the Flathead system (Beauchamp *et al*. 2006). A bioenergetics model estimated that approximately 13 t of westslope cutthroat trout and 2 t of bull trout are consumed annually by lake trout in Flathead Lake (Beauchamp *et al*. 2006).

Three of the four lake trout that were radio-tagged during June and July in 1997 made extensive movements immediately following tagging and then apparently died or expelled their tags. By contrast, all 11 of the fish tagged in June and July 1998 apparently survived. Performing surgical implantations when water temperatures ranged from 11 to 14 °C may have contributed to the mortality of the three study fish. Alternatively, these fish may have been naturally stressed by high metabolic demands associated with river temperatures near their maximal thermal tolerance during July and August. The reasons for the differential survival of fish captured and implanted in the summer between years remain unknown.

Lake trout have been intentionally or unintentionally established in more than 200 waters in the western United States (Martinez *et al*. 2009) and, in many cases, prey on or compete for resources with native fishes, resulting in cascading food web impacts (Ellis *et al*. 2011). The results of this study provide a better understanding of the movements of lake trout within freshwater systems and may be used to inform management and recovery programmes aimed to restore native and desired fish populations threatened by non-native lake trout invasion in the western USA. Results suggest that warm water temperatures appear to function as an impediment to lake trout occupancy of the river during summer months and that lake trout are capable of moving long distances

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throughout connected river and lake systems. Controlling non-native source populations and maintaining natural water temperatures, therefore, may be effective management strategies for reducing the spread of non-native lake trout to conserve native fish populations in the Flathead River system and elsewhere.

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