The influence of lake and stream conditions on survival of migratory rainbow trout in the Bois Brule (Wisconsin) and Knife (Minnesota) rivers.

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Dedication

This thesis is dedicated to my mother, Jean Ann Kaspar, who passed away August 2001. She was always proud and supportive of me and my accomplishments and I know she still is today.

Abstract

Rainbow trout (*Oncorhynchus mykiss)* were introduced to the Laurentian Great Lakes from the Pacific Coast and make up an important part of the sport fishery. The potamodromous life history variant (migratory rainbows or steelhead) is most prevalent among wild populations in the Great Lakes, where they hatch in-stream, migrate to the lake as juveniles, and return to the stream as adults to spawn. Large inter-annual variability in survival of steelhead populations from the Bois Brule River, WI, and Knife River, MN, in western Lake Superior has been observed, but the underlying mechanisms have not been well explained. The focus of my study was to identify the underlying mechanisms that influence variability in survival of wild maiden spawning adults. Multiple linear regression analyses were used to identify in-stream and in-lake (western Lake Superior) sources of variability, and to indicate the environment (stream or lake) that was most limiting. Data for wild maiden spawning rainbow trout, including abundance, stream age and lake age, were provided by the WI and MN Departments of Natural Resources. The in-stream analyses included stream temperature, flow, precipitation, and winter minimum air temperature. The lake analyses included surface temperature, lake trout (*Salvelinus namaycush*) (predator) abundance and forage abundance.

For in-stream influences, I found that total September precipitation was negatively correlated with survival during the first stream year for Brule River steelhead. Total winter precipitation was positively correlated with survival of Knife River juveniles in their first stream year. However, first year survival of juvenile steelhead in the Knife River was negatively correlated with high stream temperatures (degree days > 20°C).

The number of Brule River first returning steelhead (maiden returns) was positively correlated with surface temperature in western Lake Superior in their first lake year. Maiden returns of Knife River steelhead were negatively correlated with cisco density (kg/ha) in their second lake year. Overall, my results suggest that variability in maiden returning steelhead for both populations is better explained by conditions in their river of origin than conditions in western Lake Superior, which have a secondary influence and may better explain variability in repeat spawning and stocked steelhead.

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Introduction

Rainbow trout (*Oncorhynchus mykiss)* are an important and popular sport fish in the Laurentian Great Lakes (Dubois and Pratt 1994, Daugherty *et al*. 2003, Schreiner *et al*. 2006). It is a cosmopolitan salmonine species that exhibits two life histories including anadromy and freshwater residency, and is classified as partially anadromous in its native range (Hendry *et al*. 2004). Anadromous migration takes these fish from freshwater streams to the ocean as juveniles to grow and mature, then they return to streams to spawn (Hendry *et al*. 2004). In the Great Lakes rainbow trout exhibit similar behavior; however, they are considered potamodromous because they migrate among bodies of freshwater (Negus *et al*. 2011). Anadromous and potamodromous rainbow trout are commonly referred to as a steelhead, which describes their steel blue coloration when in the sea (or lake) (Behnke 2002). In contrast, stream resident rainbow trout spend their entire life cycle in the stream without substantial migration out of the lotic environment and retain a much more spotted appearance, with a pronounced red stripe along their side and head.

Steelhead in North America

In North America, rainbow trout are native to the Pacific northwest with a coastal distribution extending from the Bering Sea and Bristol Bay, Aleutian Islands, Alaska, south throughout British Columbia, Washington and Oregon to southern California (Crawford and Muir 2008). In their native range, steelhead are anadromous and migrate from freshwater streams as juveniles during the early-mid summer months to the ocean where they grow and mature into adults. They later return as adults to their natal stream (where they hatched) to spawn through homing (McDowall 2001). Studies have shown a wide variation in the number of years steelhead spend in the stream before smolting and the number of years spent in the ocean before migrating to the stream to spawn for the first time as a maiden spawner. Busby *et al*. (1996) suggest that the majority of steelhead on the U.S. Pacific Coast smolt at ages 2 and 3 and spend on average 2 years in the ocean before returning to spawn. However, the number of ocean years may depend on latitude such that steelhead usually spend 2-3 years in the ocean in the north but only 1-2 years in more southern portions of their native range (Busby *et al*. 1996).

As juvenile steelhead migrate to the ocean, they go through a process referred to as smolting. When juveniles smolt, they lose parr marks (vertical bars), their scales develop silver flecking, and their body undergoes physiological changes for osmoregulation. Changes in the gills, kidney, gut, and urinary bladder increase their tolerance for the increased salinity of the ocean and enable them to make the transition from freshwater (McCormick and Saunders 1987). Juveniles that smolt and out-migrate are found to have increased growth and fecundity as they mature compared to those that stay in the stream (Hendry *et al*. 2004). As adults, steelhead can reach sizes of 102 cm or more in the ocean because of the available space and abundant foraging opportunities. They feed on abundant squid, other fish, and crustaceans that are not available in freshwater streams (Behnke 2002).

The ability of adults to return thousands of miles to their natal stream sites has been shown to include olfactory cues that were imprinted during the juvenile phase. The chemical cues of a given stream enable adults to locate these spawning grounds after traveling long distances at sea (McDowall 2001). Steelhead are known to migrate up to

5370 km from their natal site on the Pacific Coast and were still able to return to natal streams (Quinn and Meyers 2004). Their homing ability is thought to increase spawning success because it reduces the effort to search for suitable spawning sites (McDowall 2001). When at sea, steelhead are considered pelagic and generally stay near the surface waters while making periodic dives to greater depths (Quinn and Meyers 2004).

Steelhead in the Great Lakes

In the Great Lakes, rainbow trout are non-native and were purposely introduced from the Pacific Coast by the U.S. Fish Commission to increase sport fishing opportunities in the late 1800’s and early 1900’s (Behnke 2002). The initial introduction to the Great Lakes occurred in 1876 when they were stocked into tributaries to Lakes Huron and Michigan (Crawford and Muir 2008). Introductions of rainbows also occurred in Lake Superior in the Bois Brule River (hereafter called the Brule River), WI, in 1892 (Scholl *et al*. 1984) and in Minnesota tributaries in 1895 (Hassinger *et al*. 1974). The strain introduced into many Lake Superior tributaries likely included a mix of anadromous and resident rainbow trout from the McCloud River in California (Behnke 2002). According to additional unpublished stocking records, some Brule River steelhead may have originated from the Klamath River basin in Northern California (Bill Blust, WDNR Advanced Fisheries Technician, Superior, personal communication 4/03/2012). Since their introduction, steelhead have become naturalized and have naturally reproducing populations in all five Great Lakes (Biette *et al*. 1981).

In the Great Lakes, as in their native range, smolting takes place, during which juveniles lose their parr marks, attain silver flecking on their scales, and emigrate from the stream in early to mid-summer to grow and mature in the lake (Biette *et al*. 1981).

This is likely due to better growth conditions in the lake that include increased space and forage. Unlike on the Pacific Coast, juveniles in the Great Lakes can migrate to the lake as parr, and these early migrants may significantly contribute to certain populations (Seelbach 1993). Homing behavior also persists in the Great Lakes where migrations have been found to be extensive (Niemuth 1970, Beitte *et al*. 1981, Scholl *et al*. 1984). Niemuth (1970) and Scholl *et al*. (1984) followed tag returns for steelhead from the Brule River and found that some individuals roamed in Lake Superior as far as the Ontario border (225+ km) up Minnesota's north shore and east along the south shore as far as Keweenah Bay, Michigan (274+ km). The majority of the tagged fish reported by anglers returned to the Brule River to spawn the following year. When in the lake, steelhead are pelagic, as they are in the Pacific, where they generally stay near the surface and periodically dive during bouts of foraging (Höök *et al*. 2004). An archival tag study performed by the Minnesota Department of Natural Resources indicated that steelhead (wild and stocked) from the French and Knife Rivers spend >50% of their time in the top 1 m, about 80% in the top 2 m, and about 96% of their time in the top 10 m when in western Lake Superior (Mary Negus, MNDNR Lake Superior Area Research Scientist, personal communication 3/12/2012).

In the Great Lakes, similar variation in the number of year spent in the natal rivers (stream years) relative to those spent in the lake (lake years) is observed as in native populations along the Pacific Coast that grow as adults in the ocean. Juveniles tend to spend 1-3 years in the stream before smolting, and adults spend 1-3 years in the lake before returning to spawn (Hassinger *et al*. 1974, Biette *et al*. 1981, Seelbach 1993, DuBois and Pratt 1994, Daugherty *et al*. 2003, Ward 2010). This life history strategy is not only maintained in Great Lakes steelhead, but is also maintained in other exotic steelhead populations. For example, steelhead introduced to the Santa Cruz River, Argentina, spend 2-3 years in the stream before smolting and 1-2 years in the ocean before spawning (Rossi *et al*. 2007). This variability in stream years and lake years has been thought to be advantageous and likely maintained because when only some individuals of a year class smolt in a particular year and only some return to spawn in a particular year, only part of the year class is lost if conditions are poor in either the ocean/lake or the stream (Hendry *et al*. 2004).

Populations of Interest

In western Lake Superior two of the best known populations of steelhead occur in the Brule River in Wisconsin and the Knife River in Minnesota. These rivers support sport fisheries that target steelhead (DuBois and Pratt 1994 and Schreiner *et al*. 2006). Because of their popularity, fisheries management has been essential in maintaining and protecting these populations.

Brule River Steelhead

In the Brule River, like all other tributaries to the Great Lakes, steelhead spawn in the spring. The Brule River population is unique in that a substantial portion of returning adults ascend the river in autumn (September to December). In fact, the majority- (~80%) of the steelhead migrate upstream and reside in the deeper pools over winter. The remainder of the spawning adults ascend the river in a spring run (March to May) (DuBois and Pratt 1994). These two distinct spawning runs are similar to the summer and winter runs typically found on the Pacific Coast (Behnke 2002).

Brule River adult steelhead range in age from 3-10 years and show a wide variation between the number of years spent in the stream versus in the lake (Niemuth 1970, Scholl *et al*. 1984). Scholl *et al*. (1984) found that juveniles smolt and migrate during the summer months at ages of 1 (59%), 2 (38%), and 3 (3%). Number of stream years of returning adults, which was determined by fish scale analysis, indicated the majority of the surviving adults spent 2 years in the stream. This suggests a discrepancy in survival between age 1, 2, and 3 down-migrating juveniles. DuBois (2001) conducted a comprehensive study (1987-91) on the Brule River to estimate population density, growth, smolting, and sport fishery data for steelhead as well as other salmonid species. For steelhead, he found that nearly half of the down-migrating juveniles were smolts that emigrated at age 2.

Survival and growth rate upon entering the lake are dependent on age of smolting. Despite the enhanced survival and contribution to returns of age 2 smolts, growth rates of smolts with one stream year are higher (Scholl *et al*. 1984). Length at age analyses indicated faster initial growth rates for steelhead that entered the lake at age 1, but steelhead that entered at age 2 were found to reduce the size gap after 2-3 years in the lake. Age 2 smolts were larger in size than age 1 when entering the lake. Steelhead that had entered the lake at age 3 were initially larger than age 2 fish, but were found to have decreased growth in the lake. Length at age was found to vary as much as 33 cm within age groups, while similar-sized steelhead could vary as much as 6 years in age. This is thought to be due to a combination of the variation in the number of stream years and the number of years spent in the lake before returning to spawn, which is typically 2-3 years.

Knife River Steelhead

The Knife River population has a combination of wild steelhead and hatchery reared steelhead. Steelhead in the Knife River spawn in the spring with the peak period for spawning occurring in early May (Hassinger *et al*. 1974). The Knife River contains approximately 290 km of steelhead spawning habitat, as well as nursery and juvenile rearing habitat (Negus *et al*. 2011). It also contains approximately 43% of the spawning and nursery habitat for potamodromous fish on the north shore (Hassinger *et al*. 1974, Ward 2010).

As in the Brule River, juveniles in the Knife River smolt and migrate to the lake during the summer months. The number of years the wild juvenile steelhead spend in the stream before migrating was found to be 0, 1, 2, or 3, where the majority of them migrate to the lake after age 1 (mostly parr), and the majority of returning adults (survivors) had migrated at age 2 (mostly smolts) (Ward 2010). The Knife River has a fish trap that captures both migrating adults and emigrating smolts. Of the migrating juveniles that passed through the juvenile trap on the Knife River between 1997-2009, 5% were age 0, 76% were age 1, 19% were age 2, and 0.005% were age 3 (Ward 2010). Adults returning to spawn for the first time typically spent 2-3 years in the lake (Ward 2010).

Potential Limiting Factors for Lake Superior Populations

Although populations in the Brule and Knife Rivers reproduce naturally, there is significant variability in the number of wild steelhead that return from the lake to spawn each year. Schreiner *et al*. (2010) suggest that there is similar variability among steelhead populations from the Brule, Knife, and French rivers (1980-2005) that may be related to conditions in western Lake Superior. The mechanisms underlying observed variations in survival have not been well studied. Given that steelhead spend part of their life in the stream and part of their life in the lake, managers have not been able to identify which environment most limits the survival of steelhead year classes.

In-Stream Variables

The stream environment can be highly variable depending on its geographic location and watershed. In close proximity to the Knife River, Close and Anderson (1997) examined four representative North Shore streams for factors that limit survival of young of the year (YOY), age 1, and smolts (age 1+) steelhead. Their results suggested June floods (shortly after stocking fish) and small substrate/particle size (no cobble or boulders for current breaks) were most limiting for YOY, while an early winter (metabolic stress, anchor ice), low summer discharge (low DO and higher temperatures), and lack of woody debris (cover, pool habitat) were most limiting to age 1 and smolting juveniles. Other limiting factors mentioned included beaver dams (migration barriers) and clear cutting of the forest in the watershed (causing an increase in stream temperature and flood potential).

DuBois and Pratt (1994) suggested similar limiting factors for the Brule River, including spring floods (dislodges eggs before they hatch), June floods (while fry are small), stream location (lower river is less stable in temperature and flow than the upper river), and spring river temperature (warm spring increases growth and survival of juveniles). Compared to the Knife River, the Brule River has seasonally stable flow conditions and moderate temperatures that are not as limiting to steelhead survival and contribute to it being ice-free early in the spring (February or March typically) without anchor ice (DuBois and Pratt 1994).

In-Lake Variables

The environment in Lake Superior is large and diverse. Lake Superior is a deep (average depth 147 m, max depth 482 m), clear lake and is classified as oligotrophic due to low nutrient loads from bedrock runoff and a cold average lake temperature (4 °C) (Schreiner *et al*. 2006). Four fish habitat zones are defined in Schreiner *et al*. (2006) in the Lake Superior basin including nearshore (<80 m), offshore (>80 m), embayments (harbors, estuaries, and bays subject to seiches), and tributary reaches not subject to seiches. Many possible factors and interactions could influence steelhead survival as they enter the lake as juveniles. Since the populations of steelhead in the Brule and Knife Rivers are located in the western arm, it represents a common nursery for juveniles and adults alike.

Adult steelhead typically stay within the western arm of Lake Superior, but have been found to disperse from their natal sites great distances (Niemuth 1970 and Scholl *et al*. 1984). Survival of juvenile steelhead to adulthood and adult survival have been thought to be effected by predation, forage, lake surface temperature, and angler harvest, as well as other environmental factors (Höök *et al*. 2004, Anonymous 2010). The most abundant and most likely predators for steelhead during their first year in Lake Superior are lake trout (*Salvelinus namaycush*), which have been found to eat juvenile salmonids (Negus *et al*. 2007).

Steelhead diets in Lake Superior are likely composed primarily of insects and invertebrates (Keough *et al*. 1996, Negus *et al*. 2007). Keough *et al*.*'s* (1996) stable isotope analysis of ^{15}N (an indicator of trophic status) indicated a diet largely composed of invertebrates. Diet data for steelhead in the western arm of Lake Superior showed their diet was composed of mostly invertebrates (crustaceans) and insects for their first year in the lake, with an addition of rainbow smelt (*Osmerus mordax*) and other small fish for older fish (Negus *et al*. 2007). Recent findings showed that age 2 (1 year in the lake) steelhead diets contained mostly *Mysis diluviana* (crustacean, formerly *Mysis relicta*), followed by insects for all ecoregions (western tip, Apostle Islands, and the north shore), while the diet of age 3+ (more than 1 year in lake) steelhead had more insects, fewer *Mysis diluviana*, and also contained fish (Negus *et al*. 2008).

Lake surface temperatures may influence steelhead growth and survival, especially in their first lake years, because steelhead spend most of their time near the surface (Höök *et al*. 2004, Anonymous 2010). A recent study by Negus *et al*. (2011) found a positive correlation between survival of steelhead stocked in the Knife River (stocked yearlings) and the nearby French River (stocked fry and yearlings) and mean summer lake temperature taken from the French River hatchery water intake (depth 18.3 m). In the coolest years of the study (1992 and 1993), they found low survival for all stocked fish, and in the warmest year (1998) they found the highest survival from the fish stocked as yearlings. However, this relationship with mean summer lake temperature was not found for the Kamloops strain, which were stocked as yearlings.

Although there is information available regarding variables that can influence survival of these steelhead populations in the stream and lake environment, few studies have been performed to quantify these relationships. Also, it is not known whether the stream environment in the river of origin or the environment in western Lake Superior has the strongest influence on their survival, which may have implications for their management. The primary objectives of this study were to determine whether the stream (early life stage) or lake (adult stage) environment has the most influence on the survival and abundance of maiden returning steelhead (first time spawners), and whether controlling factors vary by river of origin. I sought to identify the relative influence of in-stream factors including temperature (°C), discharge (cms), total precipitation (cm), and winter minimum air temperatures (°C) from the Brule and Knife River on the juvenile life stages of steelhead in each river system. In addition, factors in western Lake Superior (surface temperature (°C), lake trout (predator) abundance (#/1,000 m night), and forage abundance (kg/ha)) that influence the abundance and success of maiden returning adults were to be identified. Multiple regression analyses were used to determine the factors that have the strongest influence in each environment (stream and lake) and whether multiple factors provided the best explanation. If similar lake factors have the strongest relationship with both populations and variability in maiden returns are similar, then conditions in western Lake Superior would likely have the strongest influence. If in-stream conditions have the strongest relationships, explain more variability in maiden returns, and patterns are dissimilar between populations, then conditions in the river of origin will likely have the strongest influence.

Study Area

Brule River

The Brule River is located in the township of Brule, WI, in Douglas County in the northwestern part of the state (DuBois and Pratt 1994) (Figure 1). It is approximately 76 km in length and flows northward to the south shore of Lake Superior with a drainage area of 306 km^2 (USGS online: http://waterdata.usgs.gov/nwis). The upper and middle sections flow through glacial drift (silt, sand and gravel) underlain by igneous rock, while the lower section flows through glacial lake deposits of red clay underlain by sandstone

(Scholl *et al*. 1984). The Brule River receives significant groundwater from springs in the upper river section, creating a moderate thermal regime and stable flows compared to many other WI streams (Sather and Johannes 1973, as cited by Scholl *et al*. 1984). In the middle section, the average discharge (1943-2011) is 4.8 cms (169.6 cfs), with daily average flows ranging from 1.9 to 43.0 cms (67 to 1520 cfs) (USGS online: http://waterdata.usgs.gov/nwis).

Knife River

The Knife River is located in St. Louis County in northeastern Minnesota on the north shore of Lake Superior (Ward 2010) (Figure 1). The Knife River is approximately 41 km in length and flows south to Lake Superior with a drainage area of 217 km^2 (USGS online: http://waterdata.usgs.gov/nwis). This tributary, like other north shore tributaries in MN, flows through bedrock, boulders, gravel, and rubble; most of the flow is maintained by runoff in the summer months due to minimal groundwater inputs that occur primarily in headwater areas (Hassinger *et al*. 1974, Waters 1977 and Ostazeski and Schreiner 2004). Lack of groundwater input causes extreme fluctuations in flow that can lead to high summer water temperatures and anchor ice in the winter (Hassinger *et al*. 1974 and Anonymous 2010). The average discharge (1973-2011) is 2.5 cms (89.8 cfs) with daily average flows ranging from 0 to 137 cms (0 to 4,841 cfs) (USGS online: http://waterdata.usgs.gov/nwis).

Methods

Steelhead Estimates

Brule River

WDNR estimated annual migratory steelhead runs (fall: July to late-November and spring: March to June) from counts of fish that passed a viewing window at the Lamprey Barrier fishway located approximately 9.7 km upstream from the river mouth (Figure 1). Fish were recorded on time-lapsed VHS equipment and annual length-frequencies were estimated by using a stencil scaled to the viewing window to measure passing fish to the nearest inch on a viewing monitor. Age analysis, estimated numbers of years spent in the river and in the lake, and spawning status (maiden/repeat) were determined from scales taken in the fall from approximately 250 fish sampled annually using electrofishing (1986-2010). Length, gender, and presence/absence of an adipose clip (wild/stocked) were also recorded. Length-at-age data from the scales were applied to length-frequency data from the fishway to estimate the proportion of steelhead that were maiden or repeat spawners, and how long they spent in each environment. Data estimating year-class strength from 1987-1991 were provided from DuBois (2001) to test for a relationship with the number of maiden steelhead returning from each year-class. Estimates of all steelhead (wild and stocked, maiden and repeat spawning) returning annually to the Brule River were also provided to compare variability in survival to the Knife River population.

The number of years spent in the stream or wild maiden returning steelhead were estimated from scale analysis. These data were used to determine the year each fish had hatched to create year-classes, which I categorized as the first year they experienced effects from in-stream conditions during their stream (juvenile) life history (first stream year). I then determined the year that each fish would have spent their second year in the stream (second year they experienced effects from in-stream conditions as juveniles) to create a year-class category that included all fish spending their second year in the stream in a given year (second stream year), which excludes any fish that had only spent one year in the stream before migrating out to western Lake Superior. A summary of the total estimated wild maiden steelhead population migrating up the Brule River each year and the first and second stream year-class categories estimated from those totals are displayed in Table 1. Full cohorts (years that included estimates of the first and second stream year-class categories from all wild maiden steelhead life histories (stream and lake ages)) included: first stream year (1985-2004) and second stream year (1985-2005). Data for 1985 and 1986 were not included in the analysis due to limited years of data collected for independent variables.

The lake ages estimated for wild maiden steelhead using fish scales were then used to determine the year each fish had smolted and migrated out to western Lake Superior to create a lake year-class, which I categorized as the first year maiden steelhead experienced effects from in-lake conditions (during their lake life-history) before returning to spawn (first lake year). I then determined the year that each fish would have spent their second year in the lake (second year they experienced effects from in-lake conditions during their lake life-history) to create a year-class category that included all fish spending their second year in western Lake Superior in a given year (second lake year), which excludes any fish that had only spent one year in the lake before returning to the Brule River to spawn. A summary of the estimated first and second lake year-class categories is displayed in Table 1. Full cohorts (years that included estimates for the first and second lake year-class categories from all wild maiden steelhead lake life-histories (lake ages)) included 1986-2007 for both the first and second lake year-classes. Data for 1986 were not included in the analysis due to limited data collected for independent variables.

Knife River

Stream and lake life histories for the Knife River were determined using juvenile and adult steelhead trap data provided by MNDNR. Both traps are at the same location approximately 0.8 km upstream from the river mouth (Figure 1).

Stream effects on the riverine life-stage of wild maiden steelhead from the Knife River were assessed using counts of down-migrating juveniles and fish scale data from the juvenile trap (1997-2010) to determine the number of years juveniles spend in the stream (stream age) before entering western Lake Superior. Estimates for the total number of juveniles down-migrating to the lake each year were determined from the total trap catch (March-July) and the trap efficiency for that year (Ward and Blankenheim 2006). The fish scale data were used to determine stream-age and were taken from a subset of juveniles in the trap. These ages were then applied to the estimated juvenile catch based on length-at-age data. Annual estimates of the total number of out-migrating juveniles from the Knife River juvenile trap were also used to test for a relationship with the number of maiden steelhead that had smolted and migrated out to western Lake Superior in those years (first lake year) (1997-2005).

The stream ages estimated from the fish scales were used to determine the year each juvenile had hatched. Using this information, year-classes were identified, which I categorized as the first year they experienced effects from in-stream conditions (first stream year). I then determined the year that each juvenile would have spent their second year in the stream (second year they experienced effects from in-stream conditions) to create a year-class category that included all juveniles spending their second year in the stream in a given year (second stream year), which excludes any juvenile that had only spent one year in the stream before being caught in the trap. Age 0 juveniles that had down-migrated to the trap (and ultimately to western Lake Superior) were not included in our analyses because they do not survive to return as adults. A summary of the estimated total annual juvenile trap catch and the first and second stream year-class categories estimated from those totals are displayed in Table 2. Full cohorts (years that included estimates of the first and second stream year-class categories from all juveniles of stream ages 1, 2, and 3) included first stream year (1996-2007) and second stream year (1996-2008). Data for 1996 were not included in the analysis due to limited data collected for independent variables.

The number of years steelhead had spent in western Lake Superior (lake age) before returning as maiden spawning fish was estimated from counts of upstream migrating steelhead and fish scale data collected from the adult fish trap on the Knife River (1996-2010). Estimates of the total number of up-migrating steelhead were from the total trap catch (fall: September-November and spring: March-June) and the trap efficiency for that year (Ward and Blankenheim 2006). Scales were taken from all adults caught in the trap and used to estimate stream age, lake age and spawning status (maiden or repeat spawning). These estimates were then applied to the estimated adult trap catch based on the proportions of life histories (stream and lake years) and spawning status. Estimates of all steelhead (wild and stocked, maiden and repeat spawning) returning to the Knife River were also provided to compare variability in survival to the Brule River population.

The age of fish upon migration to the lake (lake ages), estimated using fish scales for the Knife River population of wild maiden steelhead, were used to determine the same first and second lake year-class categories as the Brule River (see above description for the Brule River). A summary of the estimated first and second lake year-class categories is displayed in Table 2. Full cohorts (years that included estimates for the first and second lake year-class categories from all wild maiden steelhead lake life-histories (lake ages)) include first lake year (1995-2005) and second lake year (1995-2006).

In-Stream Variables

Discharge

All discharge (cubic feet per second (cfs)) data for the Brule and Knife Rivers were obtained from the USGS National Water Information System website (http://waterdata.usgs.gov/nwis). The Brule River gage (Hydrologic Unit 04025500) is located 2.25 km downstream from Nebagamon Creek, and 2.74 km upstream from Little Bois Brule River in Brule, WI (N46°32'16", W91°35'43") (Figure 1). Daily discharge has been recorded from October 1942 to September 1981 and January 1984 to present. The Knife River gage (Hydrologic Unit 04015330) is located in Knife River Park (downstream of Highway 61) near Two Harbors, MN (N46°56'49", W91°47'32") (Figure 1). Daily discharge has been recorded from July 1974 to present. These data from the USGS National Water System website were summarized and provided by the MNDNR.

Average discharge was calculated for spring (April 1-May 31), June, summer (June-Sept.), September, and fall (Sept.-Nov.). To quantify years with above average discharge during each of those periods, daily averages for each year (Brule: 1986-2010, Knife: 1996-2010) were compared to the long-term daily average (Brule: 1943-2011, Knife: 1974-2011) along with two measures of high flow: the long-term average for a given date plus one standard error (SE) and plus two SEs. The amount of discharge over one SE for each day was summed for each period (discharge less than one was given a zero value) for each year. This was also done for two SEs above the long-term mean. Peak flows were also used for each period per year where the highest daily average discharge represented a given year. To quantify years with below average summer and fall discharge, the same procedure was used except the amount of discharge under the long-term average minus one and two SEs were summed for the summer and the fall period (average daily discharge greater than one or two SEs were given a zero value). The lowest daily average discharge was also used for both periods.

Stream Temperature

The Brule River water temperatures were taken at the Lamprey Barrier fishway by WDNR. Hourly data recorded from various thermographs were used to calculate daily averages and were provided for years 1987-1995 and1999-2010, with 1999 only having data from August 12 to September 30. Missing data were estimated from temperatures measured by a hand thermometer at the same location during the same time period by averaging the values from the day before and after the missing day. Degree days above 20°C were calculated for the summer period (June 1-September 30) using daily averages, with temperatures below 20°C given a zero value.

Knife River water temperatures (hourly data recorded by thermographs) were used from two sites: the adult/juvenile trap (1996-2010) and Nursery Road (1997-2010), located 0.8 km and 24.3 km upstream from the river mouth (Figure 1). I chose these locations because they were the furthest apart representing downstream and upstream temperatures that had data for the period of interest. I used the same method as the Brule River to calculate degree days for the same period (June 1-September 30) for each site.

Winter Minimum Air Temperatures and Precipitation Totals

For the Brule River, winter (December 1-March 31) air temperature data (daily minimum values) and total precipitation (cm) were obtained from the WDNR field station located in Brule, WI, on the Brule River for years 1986-2010. These same data were obtained for the Knife River (1996-2010) from the Duluth International Airport in Duluth, MN, which is approximately 33 km from the river mouth. On leap years, February 29 was used and March 31 was excluded for both air temperature and precipitation. For air temperature, degree days were calculated for each station with threshold temperatures ranging from 0°C to -15°C. Degree-day values above the threshold temperatures were given a zero value. Total precipitation was calculated for each station for spring (April-May), June, summer (June-Sept.), September, fall (Sept.-Nov.), and winter (Dec.-March).

Variables in Western Lake Superior

Surface Temperature

Surface temperatures in western Lake Superior were estimated from data collected at NOAA Buoy #45006 (N47°20'5" W89°47'34") located in the western arm of Lake Superior north of Ironwood, MI (Figure 1). I selected this buoy because it had the only long-term data set for surface temperatures in western Lake Superior and would best represent the lake temperatures for the Brule and Knife River steelhead. Temperatures were recorded hourly at 0.6 m below the surface. Degree days from June 1 to October 15 were calculated for each year (1980-1983, 1987-2010), with temperatures above 4°C summed for the period and divided by 24, and temperatures at or below 4°C given a zero value. I chose 4°C because it is the annual average surface temperature in Lake Superior. I chose June 1 to October 15 because surface temperatures rarely reached 4°C prior to June 1, and some years the buoy was taken out by October 15. Missing data were estimated for years 1980, 1981, 1984, 1985, 1986, 1987, 1996, 1998, 2006, and 2007 using Buoy #45001 (N48°3'49" W87°46'37") located in central Lake Superior NNE of Hancock, MI (Austin and Colman 2007). The positive correlation between the buoys was 0.91 with a restriction of 130 days.

Predators

Lake trout are the most abundant and most likely predators of young steelhead in their early lake stages. I used estimates of their abundance to assess predation effects on young steelhead survival. MN and WI DNRs conduct annual spring (May-June) lake trout assessments (wild and stocked) using gillnets. Halpern and Schreiner (2003) outline MNDNR methods, and Seider (2011) outlines WDNR methods. Management zones sampled include MN1, MN2, MN3, WI1, and WI2 (Figure 2). MNDNR uses 11.4-14 cm stretch mesh with nets set for one to two nights depending on the site. MNDNR sets all nets in MN1, and has assistance from permit fishers in MN2 and MN3. WDNR also uses 11.4 cm stretch mesh and typically sets nets for one night.

Data for both MN and WI DNR lake trout assessments were provided in standard units (the number of lake trout caught per 1,000 m-night). All stations sampled for each zone were combined annually for wild and hatchery fish, and geometric means $e^{\frac{lnxi}{n}}$ were calculated. To create an index of lake trout abundance (wild and stocked combined) for all of western Lake Superior, data from all zones (MN and WI) were combined and total geometric means were calculated for each year 1986-2007. This was done to limit the variability in catch per year and because it better represents the range that steelhead from both rivers would cover and the lake trout population they would encounter. In both WI zones, no lake trout assessments were performed for the years 1996 and 2001. These years were estimated for the combined western arm data from the combined MN zones ($r^2 = 0.97$).

Prey Fish Abundance

Estimates of forage fish abundance were available from annual bottom trawl surveys performed by USGS (Great Lakes Science Center, Lake Superior Biological Station, Ashland, WI). The surveys are performed during spring (April-June) using a bottom trawl (Yankee bottom trawl, 12-m head rope) in the nearshore waters of Lake Superior at various locations using standard methodology (Hoff and Bronte 1999). Trawls were completed during daylight hours when fish would likely be congregated on the bottom. Trawls crossed contours starting at depths < 15 m nearshore and ending in approximately 100 m depths offshore. Each species was identified, counted, measured, and weighed in aggregate to estimate relative density (fish/ha) and biomass (kg/ha).

To estimate forage abundance, I only used data for stations that were located in western Lake Superior and sampled every year (1986-2007) (Table 3). These stations were combined for each year for each species of interest and geometric means were calculated. I combined stations to best represent the relative biomass of prey fish steelhead would encounter since they are known to roam for long distances. The forage species captured included rainbow smelt (*Osmerus mordax*), cisco (*Coregonus artedi*), bloater (*C. hoyi*), kiyi (*C. kiyi*), nine-spine stickleback (*Pungitius pungitius*), slimy sculpin (*Cottus cognatus*), and trout perch (*Percopsis omiscomaycus*). These species were included as potential forage items because they are typically small enough in most life stages to be potential prey for steelhead. In addition to the total kg/ha data for rainbow smelt, cisco, and bloater (three of the principle prey species in Lake Superior), age 1 data (kg/ha) were used to determine whether only the early life stage would be a good prey source. I used the same method for combining stations for each year and calculated geometric means.

Statistical Analyses

All statistical analyses were performed using SAS 9.2 software (SAS Institute Inc. Cary, NC). Multiple linear regression analysis using least square estimates of parameter values was performed to identify variables associated with both in-stream and in-lake steelhead survival. There were two models of stream effects and two models of lake effects included for the Brule and Knife Rivers for a total of four models for each population. For these models and from here on, first year and second year spent in the natal stream are referred to first and second stream year. Similarly, first year and second years spent in the lake are referred to as first and second lake years.

The two stream models used for each of the wild maiden steelhead populations included first stream year and second stream year. For the Brule River, the first stream year model compared all maiden returning steelhead to stream variables measured and experienced during their first year in the stream. The model of the second stream year (which included only maiden steelhead that had spent at least two years in the stream before smolting and migrating out to western Lake Superior) compared the number of maiden steelhead to stream variables measured during their first stream year, then to the same variables measured during their second stream year to determine which of the years was more critical for maidens that had spent 2+ years in the stream as juveniles. For the Knife River stream models (first stream year and second stream year), these same analyses were performed on the juveniles estimated from the Knife River juvenile trap.

The two lake models used for each of the wild maiden steelhead populations included first lake year and second lake year. For both rivers, the first lake year model compared all maiden returning steelhead from each river to lake variables measured during their first lake year. The second lake year models (which included only maiden steelhead that had spent at least two years in the lake) compared the number of maiden steelhead to lake variables measured during their first lake year, then to the same variables measured during their second lake year to determine which of the years was more critical for survival of maidens that had spent 2+ years in western Lake Superior before returning to spawn.

The number of potential predictor variables differed between models of lake and stream effects. The models of stream effects included 31 potential independent variables. The models of lake effects included 12 potential predictors. The winter minimum air temperature threshold used for all stream models was -15°C because it was better correlated in each model than any other minimum temperature threshold. The station used for the Knife River stream temperature was Nursery Road because the temperatures were better correlated in each of the stream models than temperatures from the Knife River trap and better indicated actual habitat conditions experienced by juvenile steelhead.

Before including independent variables in each model, I used residual plots (e_i versus x_{ii} and e_i versus $\hat{y}_i$) to test for unequal variance and normal plots (normal score versus e_i) to test for normality of untransformed data, and compared them to $\log_e$-transformed data. The only stream variable that required a transformation was winter air temperature (degree days) for both rivers, which was $\log_e$-transformed. All lake variables were improved by $\log_e$-transformations, which were used in the multiple regression analyses. To account for zero values, $\log_e(x_i + 1)$ was used for all transformations. To select the best transformation of the dependent variables, Box Cox Power transformations ($y^\lambda = (y^\lambda - 1)/\lambda$, where $\lambda \neq 0$; $y^\lambda = \log_e(y_i)$, where $\lambda = 0$) were performed to provide the transformation with the best normality (Table 4). The recommended (λ) value was indicated by (<) where values that fell within the 95% confidence interval were indicated by (*). All transformations within the 95% confidence interval were tested to find the best fit based on residual and normal plots. To detect outliers, studentized residuals $\frac{ei}{\delta\ \overline{1-hii}}$ and R-student $\frac{ei}{Si\ \overline{1-hii}}$ were used. All outliers detected were left in the models because they were all biologically feasible.

To select variables for entry into the models, I used forward, backward and stepwise selection ($\alpha = 0.05$). If there was multicollinearity between independent variables, only the variable with the strongest relationship to the dependent variable was used. To account for an increased risk of making a Type I error (rejecting the null hypothesis when it is true) when making multiple comparisons, I used the Bonferroni method ($\alpha = \frac{\alpha}{m}$, where (m) is the number of predictors left in the model). Thus, in each model, the p-value for each β_i estimate was compared to $\frac{0.05}{m}$ to determine the significance of each variable.

Results

Steelhead Success and In-Stream Factors

Several variables associated with conditions within each river explained variability in steelhead survival. Variability in maiden steelhead survival from their juvenile stage for the Brule River was mostly explained by September precipitation measured during their first stream year. This was the only variable selected into any of the Brule River stream models with forward and backward stepwise selection.

During the first stream year of all maiden steelhead returning to the Brule River, high September precipitation had a negative influence on survival (Figure 3a, N = 18, F = 15.16, p = 0.001, r^2 = 0.49) (Table 5). Average September discharge measured during the first stream year also had a negative influence on survival of maiden steelhead (r^2 = 0.40), but was not used in the model because it was significantly correlated with September precipitation (r = 0.77) and had a weaker relationship. For maiden steelhead that had spent at least 2+ years in the stream as juveniles before out-migrating to western Lake Superior, high September precipitation experienced in their first stream year also negatively influenced survival (Figure 3b, N = 18, F = 16.92, p = 0.0008, r^2 = 0.51) (Table 5). No variables were associated with survival of maiden steelhead during their second stream year (N = 19) (Table 5).

The survival of juvenile steelhead in the Knife River was most influenced by conditions during their first stream year. Survival of juveniles in their first year was positively associated with high winter precipitation (Figure 4a). Conversely, survival of juveniles in the first stream year was negatively correlated with high summer stream temperatures (Figure 4b). Although both variables had a strong relationship ($r^2 = 0.56$, $r^2 = 0.36$), neither was significant when entered into a multiple regression model due to the multicollinearity between them ($r = -0.63$). When entered separately into the regression, winter precipitation had the strongest influence on survival ($N = 11$, $F = 11.58$, $p = 0.008$, $r^2 = 0.56$) (Table 5).

For juvenile steelhead that had spent at least 2+ years in the stream before out-migrating, high winter precipitation experienced during their first stream year had a positive influence on survival (Figure 4c, $N = 12$, $F = 10.87$, $p = 0.008$, $r^2 = 0.52$) (Table 5). No variables were associated with survival of maiden steelhead during their second stream year ($N = 12$) (Table 5).

Steelhead Success and Lake Factors

The success of steelhead within western Lake Superior was most associated with yearly variability in surface temperature. Variability in survival of maiden steelhead from the Brule River was only associated with lake surface temperatures experienced during their first lake year. There was significant positive influence of surface temperatures on all maiden steelhead during their first year in the lake (Figure 5a, $N = 21$, $F = 6.28$, $p = 0.0215$, $r^2 = 0.25$) (Table 6). For maiden steelhead that had spent 2+ years in the lake before returning to the Brule River, warm lake surface temperatures during their first lake year had a positive influence on survival (Figure 5b, $N = 20$, $F = 6.96$, $p = 0.0167$, $r^2 =$

0.28) (Table 6). No variables were associated with survival of maiden steelhead during their second lake year (N = 21) (Table 6).

For maiden steelhead returning to the Knife River, no variables were associated with survival during the first lake year of all maidens (N = 11). No variables were entered into the multiple regression model with forward or backward stepwise selection (Table 6). Survival of steelhead that had spent 2+ years in the lake before returning to the Knife River was not associated with any variables measured during their first lake year. During their second lake year, higher total cisco densities (kg/ha) in western Lake Superior had a negative influence on survival (Figure 6, N = 12, F = 19.48, p = 0.0013, r^2 = 0.66) (Table 6). Age one cisco density also had a negative influence on survival of Knife River steelhead during their second lake year (r^2 = 0.58), but was not used in the model because it was significantly correlated with total cisco density (r = 0.65) and had a weaker relationship.

Variability Among Steelhead Populations and the Relationship with Juvenile Production

There was substantial variability in steelhead survival within both the Brule and Knife River wild steelhead populations (Figure 7). When comparing the variability of wild maiden steelhead returning to the Brule River to the variability in the Knife River population, they do not follow a similar pattern (Figure 8a) and there is little correlation (r = -0.08). This suggests that the two populations do not co-vary significantly. However, when comparing the variability of all steelhead (wild and hatchery, maiden and repeat spawning) returning to each river, the pattern does indicate some coherence (Figure 8b) and shows they are positively correlated (r = 0.64).

The maiden returns of wild steelhead populations for both rivers were positively correlated to juvenile abundance in the river of origin. For the Brule River, estimated year class strength (abundance of age 0 parr) had a positive association with the number of steelhead returning from that year class (Figure 9a, $N = 5$, $F = 11.47$, $p = 0.04$, $r^2 = 0.79$). Although the regression model indicates a significant relationship, the trend is strongly influenced by data from 1987. The number of maiden steelhead returning to the Knife River had a positive association with the total number of juveniles (ages 1, 2, and 3) that had out-migrated to western Lake Superior during their first lake year (Figure 9b, $N = 9$, $F = 20.2$, $p = 0.003$, $r^2 = 0.74$). This indicates that when more juveniles out-migrate to western Lake Superior in a given summer, more returning adults are the result.

Discussion

Steelhead Success and In-Stream Factors

Variables associated with precipitation are important for in-stream survival of juvenile steelhead. September precipitation was related to the number of maiden returns to the Brule River. This information is consistent with previous findings that show a secondary peak of down migrating juveniles occurring in autumn (late August to November) that consists of mainly age 0 parr with some age 1 parr (DuBois 2001). In autumn, the peak emigration of age 0 parr usually occurred in September (1987-91).

The downstream movement of parr in fall may be associated with out migration or to seek large pools that serve as overwintering habitat. According to Seelbach (1987), juvenile steelhead are relatively inactive as winter approaches (water temperature < 5°C) and they take up residence under log and rock cover and at the bottom of deep pools. If there were high rain fall events leading to high discharge during migration, this may have a negative effect on survival. The Brule River is large and can have unstable hydrologic conditions during periods of heavy rain (DuBois 2001). The upper river has relatively stable flow (high ground water inputs), while the lower river flows through a red clay region characterized by high runoff, which is associated with high turbidity and siltation (DuBois and Pratt 1994). During periods of high rain (which is strongly correlated with high discharge) during their downstream movement, age 0 parr may be more vulnerable to increased turbidity and siltation in the lower river where larger substrate is not available for refuge.

When examining variables measured during the second stream year of Brule River maiden steelhead, no associations were found. This indicates that for juveniles spending more than one year in the stream before out-migrating to western Lake Superior, conditions in their first stream year are the most important for survival. This is consistent with previous studies that posit there is increased survival of juveniles after their first stream year due to increased size (Hassinger *et al*. 1974, DuBois 2001). However, other studies have suggested there is decreased survival for age 1+ parr compared to age 0 parr during the winter months in certain populations (Bustard and Narver 1975 and Seelbach 1987).

Bustard and Narver (1975) suggest that age 0 parr can burrow into bottom substrates (gravel, cobble) that age 1 parr cannot, leaving age 1 parr more vulnerable to high water when at higher densities. This may be more prevalent in streams with limited pool and large cover (log and rock) habitats, which are used by larger fish during the winter. The Brule River has abundant pool habitats suitable for larger fish over winter, which may increase their survival (Scholl *et al*. 1984). Results from Seelbach's (1987) study of the Little Manistee River, MI, steelhead population indicated that rivers with stable discharge and abundant spawning populations may primarily be limited by the carrying capacity of age 1+ parr and winter conditions prior to smolting because there is high production and good survival of age 0 parr. The Brule River does have stable flow (from abundant groundwater inputs) compared to most WI streams and an abundant spawning population similar to the Little Manistee River. However, the Brule River (especially the lower section) can be hydrologically unstable, which may cause increased mortality of age 0 parr.

Analyses of the Knife River juveniles indicated total winter precipitation (cm) during the first stream year was most influential on fish that had spent either one or more than one year(s) in the stream before out-migrating to western Lake Superior. My analyses indicated a strong positive relationship. This is consistent with the findings of Close and Anderson (1997), who studied juvenile steelhead survival for other north shore streams in MN. They found a positive correlation ($r = 0.57$) between the survival of age 1 steelhead parr and the amount of snowfall by January 15th. They suggested that the snow may insulate the stream from extreme air temperatures and limit the incidence of anchor ice, which occurs on the Knife River as well as other north shore streams and has been thought to contribute to winter mortality (Hassinger *et al*. 1974).

High stream temperatures during their first year were associated with reduced survival of Knife River juveniles. We found summer stream temperatures > 20°C to negatively influence survival during the first stream year when including all juveniles. This is consistent with what has been hypothesized by MNDNR (Anonymous 2010).

Interestingly, this variable was negatively correlated (r = -0.63) with the total winter precipitation prior to summer. This indicates that in years with higher winter precipitation, summer stream temperatures may be cooler than in years with lower winter precipitation. This may be due to an increase in runoff during the spring in years with higher winter precipitation, which could increase stream flow for a longer period of time into summer compared to years with lower winter precipitation, and potentially moderate summer stream temperatures during that period. While the two variables are confounded, and winter precipitation appears to be more strongly correlated with juvenile steelhead survival, this trend may indicate a climatic pattern that drives success in the Knife River population.

High summer stream temperatures have been found to limit parr production, especially during periods of low flow (Close and Anderson 1997, Mathews and Berg 1997, Godby *et al*. 2007). Close and Anderson's (1997) results suggest that higher flows during periods with high water temperature (> 23°C) may decrease mortality in north shore streams. This was not examined in my analysis, and may account for the relationship not being strongly significant. Mathews and Berg (1997) suggest that steelhead tend to avoid (when possible) pool areas when temperatures are ≥ 21.5°C while temperatures > 25°C are considered lethal for trout. In the Knife River, pools can reach these temperatures in the summer, especially during low flow, due to limited ground water sources. Godby *et al*. (2007) found a correlation between high mortalities of parr and water temperatures > 21°C in the Muskegon River, Michigan, which is also consistent with our findings.

No variables appeared to influence survival of Knife River juveniles in their second year. This suggests that even for juveniles spending more than one year in the stream before out-migrating to western Lake Superior, conditions in their first stream year are the most important for survival. This is consistent with my findings for the Brule River as well as those identified by Hassinger *et al*. (1974) and Dubois (2001), who suggest there is increased survival of juveniles after their first stream year due to increased size.

Steelhead Success and Lake Factors

Brule River maiden steelhead returns showed increased survival when surface temperatures in western Lake Superior were warmer during their first year in the lake. This was also true for fish that had spent more than one year in western Lake Superior before returning as maiden spawners. This result is consistent with studies that have shown that steelhead spend the majority of their time at the surface (Höök *et al*. 2004, Anonymous 2010, Mary Negus, MNDNR Lake Superior Area Research Scientist, personal communication 3/12/2012). Höök *et al*. (2004) further suggest that steelhead in Lake Michigan prefer warmer surface temperatures, which is consistent with a study by Walker *et al*. (2000) in which a steelhead tagged with a data storage unit spent most of the study in temperatures 9-12°C in the Gulf of Alaska. Since Lake Superior is cooler than the other Laurentian Great Lakes, years with longer periods of above average surface temperatures may enhance growth and survival. Negus *et al*. (2011) found low returns in the coolest years of their study (1992 and 1993), and in the warmest year (1998), they had the highest return rate from the stocked steelhead. My results were similar in that the lowest returns of maidens had spent their first lake year in 1992 and

1993, but returns from 1998 were not the highest in my study period.

Survival of the Knife River maiden steelhead was not associated with any variables measured during their first lake year. This is in contrast to my findings for the Brule River and unpublished results from Negus *et al*. (2011). However, data for maiden returning steelhead were not available for 1992 and 1993, which could influence any observed relationships. In these years, lake temperatures were considerably cooler than other years in the study period, and results from my Brule River analyses and from Negus *et al*. (2011) indicated fewer fish surviving from those years. However, in contrast to Negus *et al*. (2011), 1998, the warmest year of the study period, showed relatively low returns of Knife River maiden steelhead that had first entered the lake that year. This may suggest there is more influence of Knife River conditions on the wild population before they migrate than from conditions in western Lake Superior after migration.

The analyses of in-lake variables measured during the second lake year of Knife River maiden steelhead indicated a strong negative relationship with cisco density (kg/ha). A similar negative relationship was found when only age-1 cisco were included in the analyses. Cisco are a forage fish (especially at age 1), but a negative correlation is not consistent with the positive influence associated with higher food resource availability for young trout. Previous studies show that steelhead diets are a mix of invertebrates and forage fish (Keough *et al*. 1996, Höök *et al*. 2004, and Negus *et al*. 2007). Results from Negus *et al*. (2007) suggest that in Lake Superior, steelhead diets are mostly composed of invertebrates (*Mysis diluviana* and aquatic and terrestrial insects) in their first lake year, and forage fish become part of their diet after two or more lake years. Although there is some overlap between cisco and steelhead diets, competition is not likely to be limiting at any life stage, especially during the second lake year when steelhead incorporate more fish species into their diet. No studies have suggested there is competition between cisco and steelhead. The relationship observed in this study is likely indirect and further research is needed to understand this relationship.

In-Stream Conditions versus Conditions in Western Lake Superior

If conditions in western Lake Superior have the strongest influence on the Brule and Knife River maiden steelhead populations, I would expect to see strong influences from similar lake variables and similar variation in survival each year. In my analyses, in-stream variables had the strongest influence and no in-lake variables were found in common between the Brule and Knife Rivers that explained variability in survival. When comparing the variability in wild maiden steelhead survival between the two rivers, I did not observe a similar trend. This suggests that conditions in-stream for at least one of the populations are more influential than conditions in western Lake Superior. This may also indicate differing causes of survival variability in each river, which is quite possible due to differences in their river morphology and geographic location.

Schreiner *et al*. (2010) provided a similar comparison between the Brule and Knife River populations that included all steelhead (wild and stocked, maiden and repeat spawning) and found similar variation in survival between the populations from 1996-2005. This pattern suggests that in-lake conditions may be the primary source of variability for both populations, and is in contrast with my results for wild maiden returns. When I did the same comparison and included all steelhead for each river from 1996-2010, my results were consistent with Schreiner *et al*. (2010), with the trend observed in each population being similar. One possible explanation may be that stocked and repeat spawning steelhead are more influenced by in-lake conditions than wild maiden spawning steelhead.

Steelhead that have been raised in a hatchery do not reflect in-stream influences that would affect wild fish. Many juveniles from the Brule and Knife Rivers were stocked as yearlings, spending their first year in the hatchery environment. These fish would have a limited stream life history and would not have been influenced by in-stream conditions at what may be their most vulnerable stage (age 0 parr). Stocked fish may also be more vulnerable to lake trout predation when entering western Lake Superior shortly after being stocked into the stream. Although I did not find any correlation between lake trout abundance and survival of maiden steelhead, a study did show that lake trout eat juvenile salmonids (Negus *et al*. 2007). Since lake trout are a long lived species compared to steelhead, variation in their abundance (as indicated by gill net catch) may be small compared to what is observed in steelhead and may mask their influence.

The observed variability of repeat spawning steelhead returning to each river would likely be influenced by in-lake conditions because they have already spawned one or more times and have experienced multiple years in the lake. This indicates that the variation I observed may be related to conditions that influence the number of times these fish are able to spawn, which is likely most influenced by conditions in western Lake Superior.

I found a positive relationship between number of juveniles produced and first returning or maiden adults for both the Brule and Knife River. In the Brule River, total age 0 parr production had a positive relationship with the number of maiden returns from those year classes. Although this relationship appeared to be strong, it was strongly influenced by data from 1987 and thus must be interpreted with caution. In the Knife River, the estimated number of juveniles that out-migrated to western Lake Superior had a positive influence on the number of maidens that survived from those lake years. These results suggest that year-class strength and the number of smolts that out-migrate may best predict the adult populations of both rivers, and further indicates that in-stream conditions experienced as juveniles have more of an influence on survival than in-lake conditions experienced as adults. This is consistent with findings from Scarnecchia (1981) for coho salmon (*Oncorhynchus kisutch*) on the Pacific coast, where in-stream conditions experienced during the juvenile stage best predicted adult abundance.

Summary and Conclusions

This study examined the influences of in-stream and in-lake habitat variability on the wild-maiden spawning steelhead populations of the Brule River, WI, and Knife River, MN. In each case, in-stream variables seemed to be the most important for steelhead survival. My analyses indicated that precipitation variables were associated with steelhead survival in their natal streams. My results for Brule River steelhead suggest that total September precipitation experienced during their first stream year (as age 0 parr) has a significant negative influence on maiden returns, and surface temperature in western Lake Superior experienced during their first year in the lake has a significant positive influence. For the Knife River, high winter precipitation had the most significant (positive) influence on juvenile survival in their first stream year. A negative association between total winter precipitation and high summer stream temperature may further indicate the importance of weather phenomena in influencing steelhead success in Lake Superior drainages along the north shore. For Knife River steelhead, a negative correlation was found with cisco density (kg/ha) encountered during their second lake year. This is almost certainly an indirect effect that needs further investigation to elucidate.

These results indicate that, overall, in-stream conditions have the strongest influence on wild maiden returning steelhead for both rivers, while conditions in western Lake Superior may act as a secondary influence and may be more influential on repeat spawning and stocked steelhead. This last finding indicates the importance of excluding repeat spawning and stocked steelhead from analyses and focusing on naturally-reproducing populations because they may mask the effects of in-stream conditions on age 0 parr. In particular, stocked steelhead experience a limited time in the stream, and are typically stocked as older fish (age 1+) that do not experience in-stream conditions as age 0 parr. My analyses also demonstrated how climatic factors can differentially influence the Brule and Knife River steelhead populations due to the morphological and geographical differences between the rivers.

Table 1. Estimates of total maiden returning steelhead for the Brule River (1987-2010) and their first and second stream and lake year-classes. Estimates of age and spawning status were based on fish scale analyses, for which results from sub-samples captured by electrofishing were applied to the estimated annual spawning run. Data were provided by WDNR, Superior, WI.

	Stream years		**Lake years**		
Year	**1st**	**2nd**	**1st**	**2nd**	**Total maidens**
*1985	4,321	2,976	-	-	-
*1986	3,691	3,980	3,320	3,487	-
1987	5,627	3,345	4,230	2,244	4,555
1988	921	5,168	3,851	2,858	3,792
1989	2,143	881	5,173	2,246	4,284
1990	1,052	1,787	1,322	2,761	5,165
1991	694	885	1,946	589	3,362
1992	2,716	668	934	1,040	2,104
1993	2,429	2,580	768	588	1,121
1994	2,084	2,386	2,662	634	820
1995	2,243	1,879	2,535	1,685	1,633
1996	2,538	2,132	2,004	1,678	1,750
1997	3,045	2,054	2,419	1,775	1,473
1998	2,654	2,475	2,847	2,005	2,193
1999	2,171	2,275	2,856	2,163	3,124
2000	4,224	1,988	2,422	2,409	3,010
2001	3,567	4,084	1,941	2,181	2,277
2002	1,928	3,202	4,649	1,581	2,459
2003	3,980	1,883	3,204	3,339	3,171
2004	6,687	3,822	2,073	2,158	3,767
2005	-	5,207	5,278	1,704	2,989
2006	-	-	5,853	3,010	3,938
2007	-	-	2,513	4,200	4,176
2008	-	-	-	-	3,606
2009	-	-	-	-	3,833
2010	-	-	-	-	2,527

*Indicates years not included in the analysis.

Table 2. Estimates of total juveniles (not including age-0 parr) (1997-2010) and total wild maiden returning steelhead (1996-2010) for the Knife River. Estimates of first and second stream year-classes of juveniles were based on fish scale analyses of annual juvenile trap catch and were applied to the estimated total trap catch. Estimates of first and second lake year-classes and spawning status were from fish scale analyses of annual adult trap catch and were applied to the estimated annual spawning run. Data were provided by MNDNR, Duluth, MN.

	Stream year			**Lake year**		
Year	**1st**	**2nd**	**Total juveniles**	**1st**	**2nd**	**Total maidens**
1995	-	-	-	269	189	-
1996	4,892	363	-	141	259	51
1997	3,015	1,221	4,031	89	100	278
1998	11,011	836	3,401	67	84	209
1999	20,183	3,442	8,377	61	47	190
2000	10,824	964	22,706	276	56	77
2001	3,312	1,779	10,017	194	260	62
2002	1,225	845	4,214	110	165	152
2003	14,047	657	1,377	68	91	198
2004	33,789	6,912	7,701	85	63	202
2005	17,057	7,028	33,817	207	85	98
2006	11,801	3,243	20,712	-	192	48
2007	9,969	3,564	11,537	-	-	139
2008	-	2,255	11,243	-	-	212
2009	-	-	21,106	-	-	175
2010	-	-	20,072	-	-	172

Table 3. Sampling locations for forage fish in western Lake Superior during the annual United States Geological Survey (USGS) nearshore spring bottom trawl surveys (1986-2007). All locations were sampled in every year of the study period. Data provided by USGS, Ashland, WI. See Figure 2 for zone locations.

Port	Location	Management Unit
36	Two Harbors	MN1
186	Lester River	MN1
172	Baptism River	MN2
65	Grand Marais	MN3
191	Wauswaugoning Bay	MN3
151	NE Herbster (Bark Point)	WI1
205	Port Wing	WI1
210	Superior Entry	WI1
2	Stockton Island	WI2
24	Michigan Island	WI2
45	Cat Island	WI2
71	Raspberry Island (PT.DET)	WI2
75	Bear Island	WI2
86	Basswood Island	WI2
87	NW Stockton Island	WI2
139	W Sand Island	WI2

Table 4. Results from Box Cox transformation analyses ($y^{\lambda} = (y^{\lambda} - 1)/\lambda$, where $\lambda \neq 0$; $y^{\lambda} = \log_e(y_i)$, where $\lambda = 0$) of all dependent (y) variables. Analyses were performed using SAS 9.2 software (SAS Institute Inc., Cary, NC).

(y)	**λ (<)**	**λ (*)**	**95% CI**
Brule Stream1	0.25	0.25	(-0.25,1)
Brule Stream2	0.5	0 ($\log_e$)	(0,1)
Knife Stream1	0.25	0 ($\log_e$)	(-0.25,0.75)
Knife Stream2	-0.25	0 ($\log_e$)	(-0.75,0.25)
Brule Lake 1	-0.25	0.25	(-0.25,0.75)
Brule Lake 2	0.75	0.75	(0.25,1.25)
Knife Lake 1	-0.5	-0.5	(-1,0)
Knife Lake 2	-0.75	-0.5	(-1.25,-0.25)

(<) indicates the (λ) value selected by the Box Cox method to transform (y).
(*) indicates the (λ) value used to transform (y).
($\log_e$) is the transformation used when $\lambda = 0$.

Table 5. Significant stream model results for the Brule and Knife Rivers selected from multiple regression analyses. All analyses were performed with SAS 9.2 software (SAS Institute Inc. Cary, NC). Sept. (cm) and Winter (cm) indicate September and winter precipitation. Degree days indicates stream water temperature.

Brule	**# Obs**	**Predictor(s)**	**r**	**Stream models**	**r^2**	**F-value**	**p-value**	**β_0 p-value**	**β_1 p-value**
1^{st}	18	x_1= Sept. (cm)	-0.70	$Y^{0.25} = 8.48 - 0.153x_1$	0.49	15.16	0.001	< 0.0001	0.001
2_{nd} (1^{st})	18	x_1 = Sept. (cm)	-0.72	$\log_e(Y) = 8.50 - 0.089x_1$	0.51	16.92	0.0008	< 0.0001	0.0008
2_{nd}	19	-	-	-	-	-	-	-	-
Knife									
1^{st}	11	x_1 = Winter (cm)	0.75	$\log_e(Y) = 6.29 + 0.24x_1$	0.56	11.58	0.008	< 0.0001	0.008
	11	x_1 = Degree days	-0.6	$\log_e(Y) = 9.99 - 0.04x_1$	0.36	5.15	0.05	< 0.0001	0.05
2_{nd} (1^{st})	12	x_1 = Winter (cm)	0.72	$\log_e(Y) = 5.32 + 0.198x_1$	0.52	10.87	0.008	< 0.0001	0.008
2_{nd}	12	-	-	-	-	-	-	-	-

(-) Indicates there was not a significant model

Table 6. Significant lake model results for the Brule and Knife Rivers selected from multiple regression analyses. All analyses were performed with SAS 9.2 software (SAS Institute Inc. Cary, NC). Degree days indicates lake surface temperature and Cisco indicates cisco density (kg/ha).

Brule	**# Obs**	**Predictor(s)**	**r**	**Lake models**	**r^2**	**F-value**	**p-value**	**β_0 p-value**	**β_1 p-value**
1^{st}	21	x_1 = Degree days	(+)0.5	$Y^{-0.25} = 0.65\ (+)\ 0.07\log_e(x_1)$	0.25	6.28	0.0215	0.005	0.0215
2_{nd} (1^{st})	20	x_1 = Degree days	0.53	$Y^{0.75} = -2532.15 + 395.23\ \log_e(x_1)$	0.28	6.96	0.0167	0.03	0.0167
2_{nd}	21	-	-	-	-	-	-	-	-
Knife									
1^{st}	11	-	-	-	-	-	-	-	-
2_{nd} (1^{st})	12	-	-	-	-	-	-	-	-
2_{nd}	12	x_1 = Cisco	(-)0.81	$Y^{-0.5} = 0.0354\ (-)\ 0.0786\log_e(x_1)$	0.66	19.48	0.0013	0.0406	0.0013

- Indicates there was not a significant model.

(-) (+) Indicate the relationship before a negative power transformation was applied.

Figure 1.

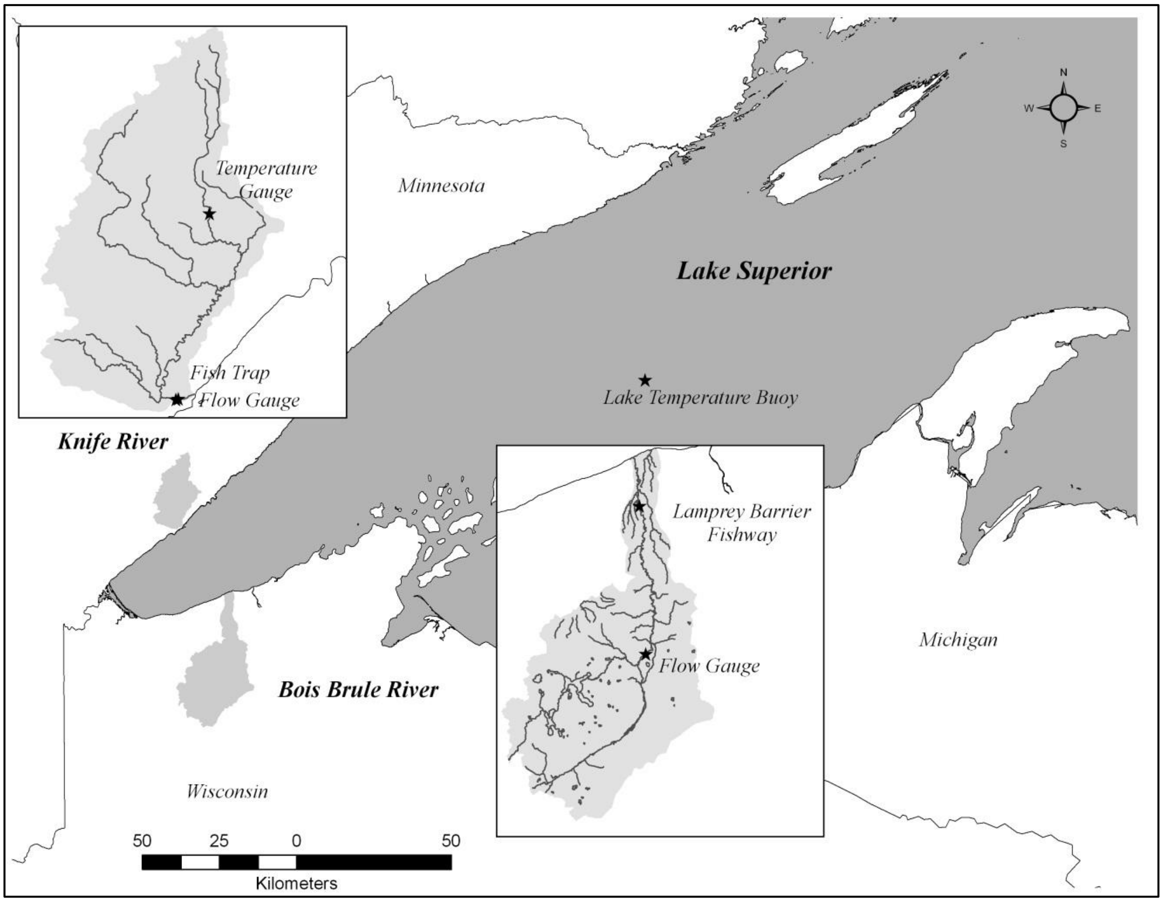

Temperature Gauge
Fish Trap
Flow Gauge
Knife River
Minnesota
Lake Superior
Lake Temperature Buoy
Lamprey Barrier Fishway
Flow Gauge
Michigan
Bois Brule River
Wisconsin
N
W
E
S
50
25
0
50
Kilometers

Figure 2.

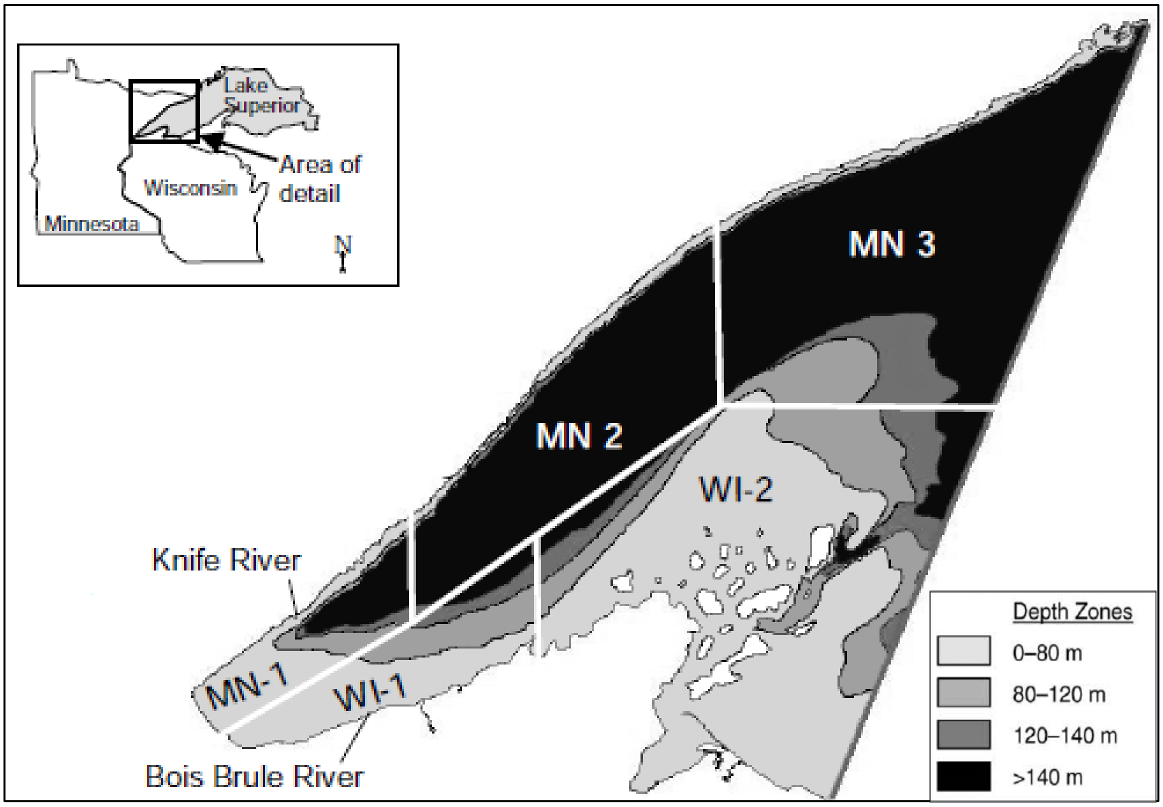

Lake Superior
Area of detail
Wisconsin
Minnesota
N
MN 3
MN 2
WI-2
Knife River
MN-1
WI-1
Bois Brule River
Depth Zones
0–80 m
80–120 m
120–140 m
>140 m

Figure 3.

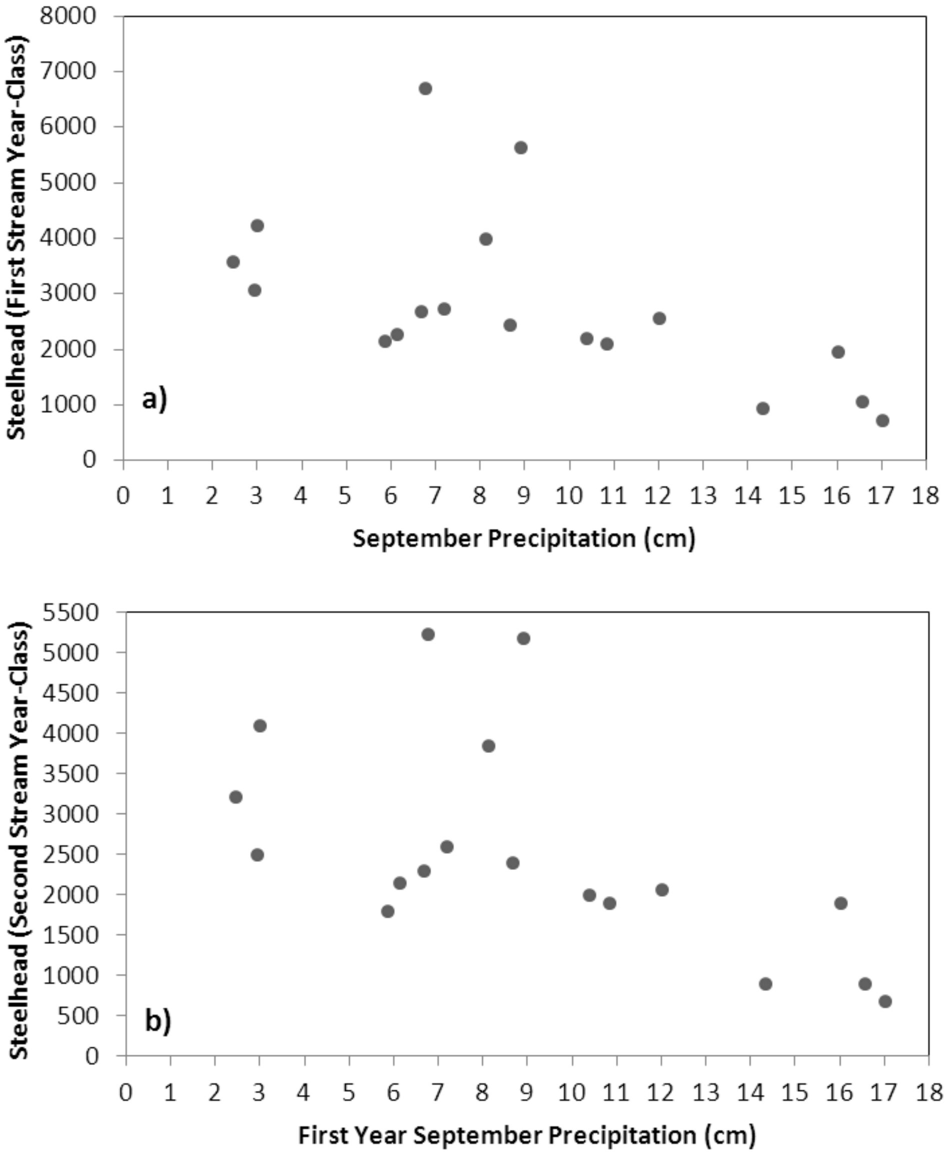

Steelhead (First Stream Year-Class)
8000
7000
6000
5000
4000
3000
2000
1000
0
a)
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18
September Precipitation (cm)
Steelhead (Second Stream Year-Class)
5500
5000
4500
4000
3500
3000
2500
2000
1500
1000
500
0
b)
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17 18
First Year September Precipitation (cm)

Figure 4.

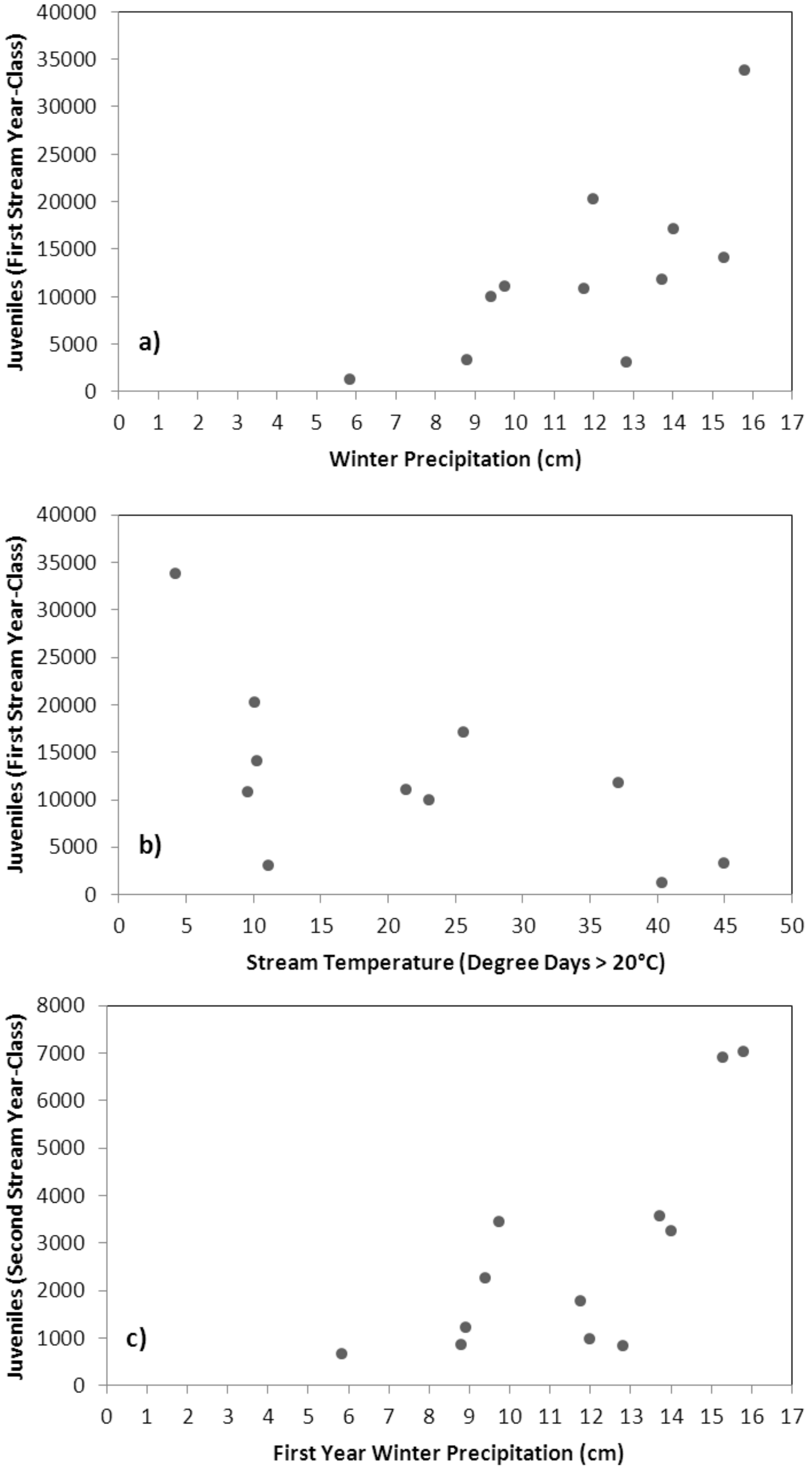

a)
Juveniles (First Stream Year-Class)
0
5000
10000
15000
20000
25000
30000
35000
40000
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17
Winter Precipitation (cm)
b)
Juveniles (First Stream Year-Class)
0
5000
10000
15000
20000
25000
30000
35000
40000
0 5 10 15 20 25 30 35 40 45 50
Stream Temperature (Degree Days > 20°C)
c)
Juveniles (Second Stream Year-Class)
0
1000
2000
3000
4000
5000
6000
7000
8000
0 1 2 3 4 5 6 7 8 9 10 11 12 13 14 15 16 17
First Year Winter Precipitation (cm)

Figure 5.

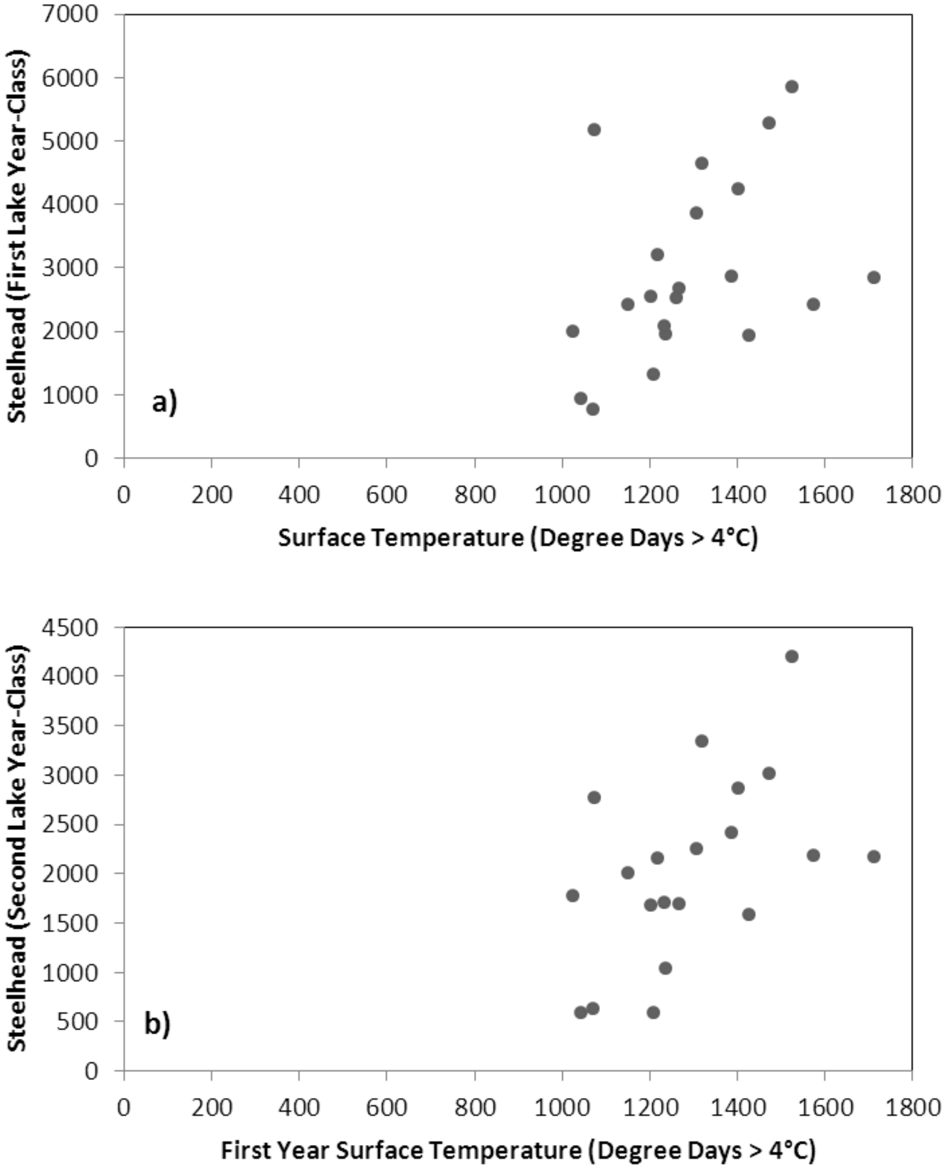

Steelhead (First Lake Year-Class)
7000
6000
5000
4000
3000
2000
1000
0
a)
0
200
400
600
800
1000
1200
1400
1600
1800
Surface Temperature (Degree Days > 4°C)
Steelhead (Second Lake Year-Class)
4500
4000
3500
3000
2500
2000
1500
1000
500
0
b)
0
200
400
600
800
1000
1200
1400
1600
1800
First Year Surface Temperature (Degree Days > 4°C)

Figure 6.

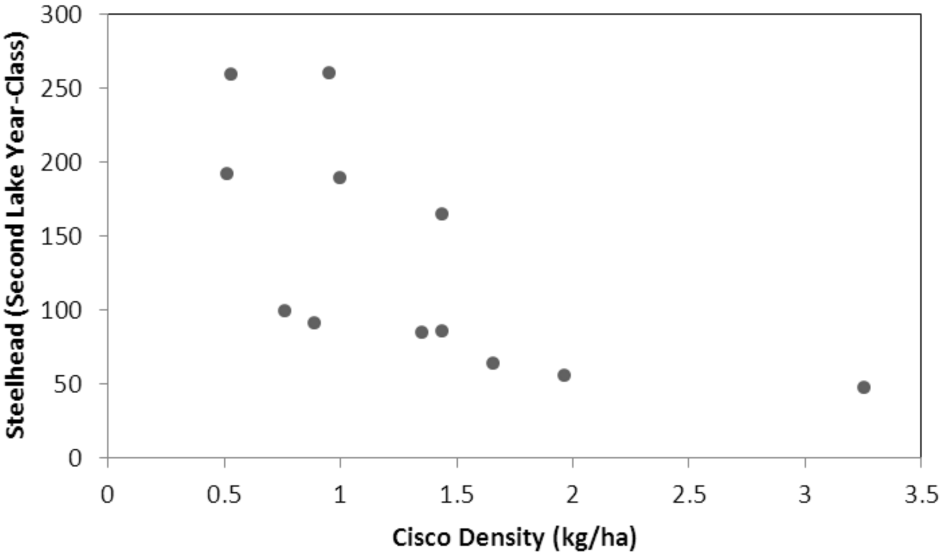

Steelhead (Second Lake Year-Class)
300
250
200
150
100
50
0
0
0.5
1
1.5
2
2.5
3
3.5
Cisco Density (kg/ha)

Figure 7.

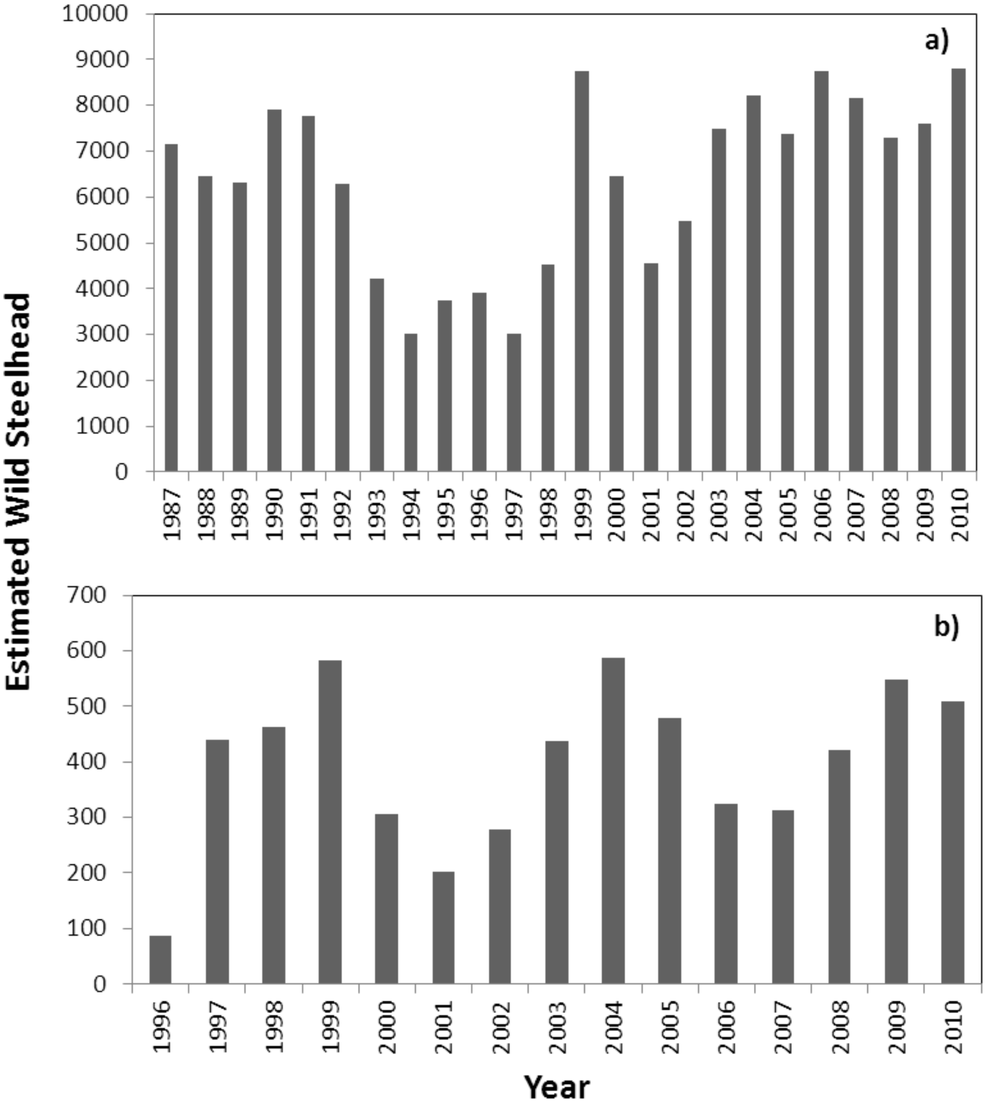

Estimated Wild Steelhead
a)
10000
9000
8000
7000
6000
5000
4000
3000
2000
1000
0
1987
1988
1989
1990
1991
1992
1993
1994
1995
1996
1997
1998
1999
2000
2001
2002
2003
2004
2005
2006
2007
2008
2009
2010
b)
700
600
500
400
300
200
100
0
1996
1997
1998
1999
2000
2001
2002
2003
2004
2005
2006
2007
2008
2009
2010
Year

Figure 8.

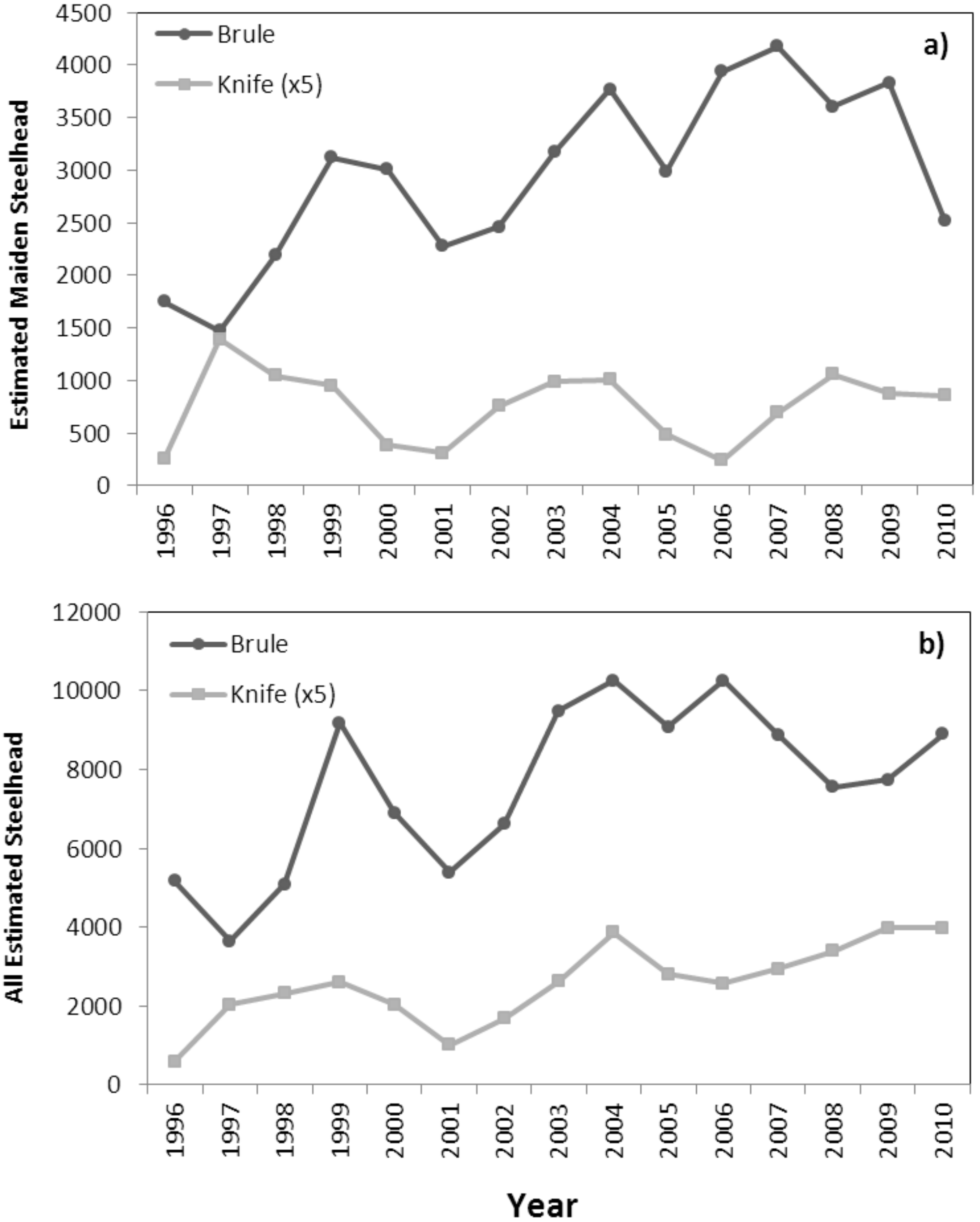
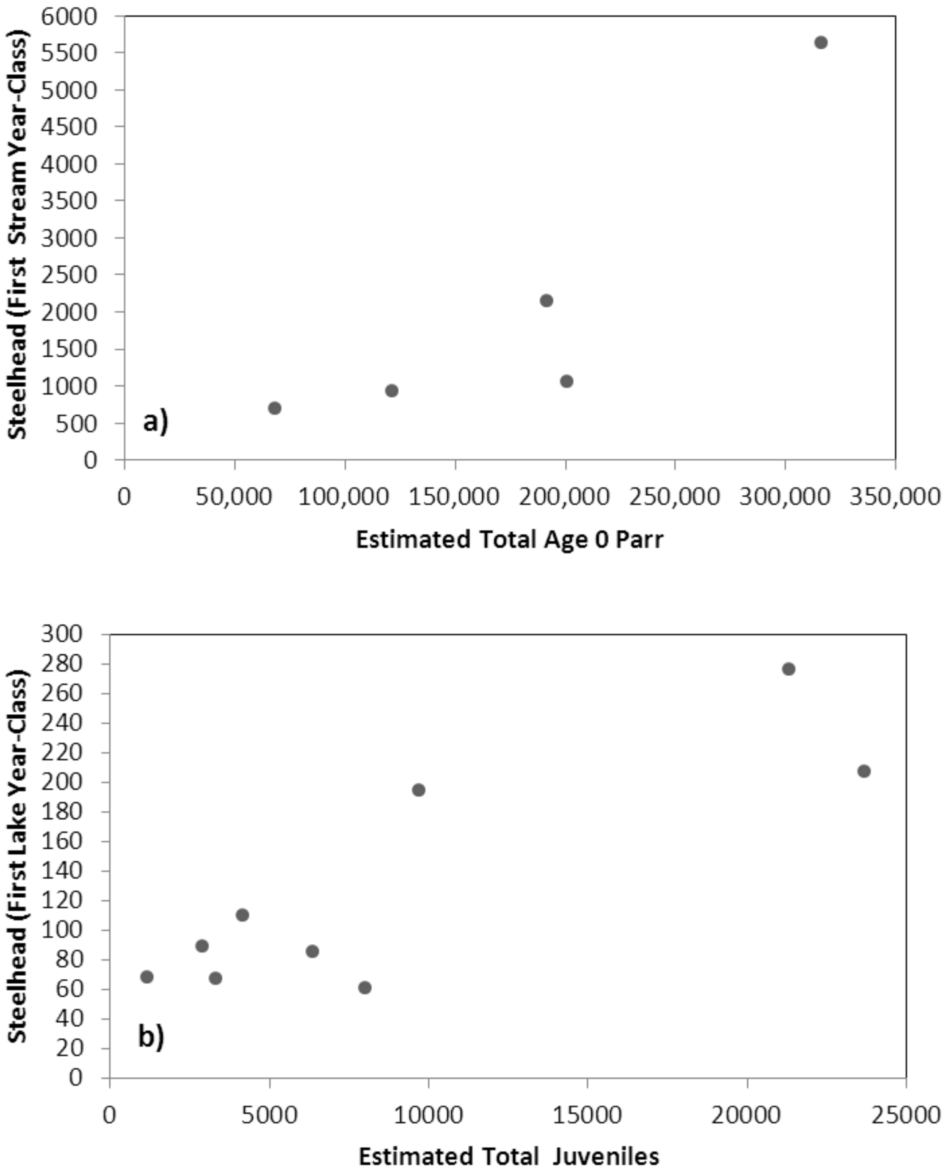

4500
4000
3500
3000
2500
2000
1500
1000
500
0
Estimated Maiden Steelhead
Brule
Knife (x5)
a)
1996
1997
1998
1999
2000
2001
2002
2003
2004
2005
2006
2007
2008
2009
2010
12000
10000
8000
6000
4000
2000
0
All Estimated Steelhead
Brule
Knife (x5)
b)
1996
1997
1998
1999
2000
2001
2002
2003
2004
2005
2006
2007
2008
2009
2010
Year

Figure 9.


Steelhead (First Stream Year-Class)
6000
5500
5000
4500
4000
3500
3000
2500
2000
1500
1000
500
0
a)
0
50,000
100,000
150,000
200,000
250,000
300,000
350,000
Estimated Total Age 0 Parr
Steelhead (First Lake Year-Class)
300
280
260
240
220
200
180
160
140
120
100
80
60
40
20
0
b)
0
5000
10000
15000
20000
25000
Estimated Total Juveniles

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