Journal of Great Lakes Research 49 (2023) 506–514

Contents lists available at ScienceDirect

Journal of Great Lakes Research

journal homepage: www.elsevier.com/locate/ijglr

The influence of conditions in Lake Superior and the Bois Brule River, Wisconsin on returns of migratory rainbow trout

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ARTICLE INFO

Article history:
Received 26 September 2022
Accepted 13 January 2023
Available online 23 January 2023
Communicated by Brian Weidel

Keywords:
Lake Superior Steelhead
Bois Brule River
Potamadromous
Climate change

ABSTRACT

Rainbow trout were introduced to Lake Superior in the late 1800's and exhibit a potamodromous life history and exhibit high variability in reproductive success. We examined reproductive variability in the Bois Brule River, WI (Lake Superior), through analyses of returns of wild first spawning (hereafter "maiden" returning) adults. We used classification and regression tree analyses to identify in-stream and in-lake (western Lake Superior) sources of variability and to identify the environment (stream or lake) that was most influential to the returns to each location. Among in-stream influences, high discharge rates in the spring period (March – May) during a pre-smolt's first stream year were the strongest source of variability and were negatively correlated with returns. High discharge during the fall period from September to November in the pre-smolt first stream year was also negatively correlated with numbers of maiden returning steelhead from that year class. When variables associated with Lake Superior were considered, maiden returns were positively correlated with higher lake surface temperatures in Lake Superior. Returns were negatively correlated with the abundance of adult rainbow smelt and bloater suggesting a possible competitive interaction among those species. Finally, we also observed a conditional (minor) positive effect of age-0 smelt abundance indicating the importance of this prey for juveniles in colder years in western Lake Superior. Taken together, our findings indicate that both stream and lake conditions in their first lake year are important sources of variability and point to spates in the spring and fall as initial controlling variables.

Introduction

Rainbow trout (*Oncorhynchus mykiss*) provide valuable sport fisheries in the Laurentian Great Lakes and have become naturalized since the late 1800's, (Dubois and Pratt, 1994; Daugherty et al., 2003; Schreiner et al., 2006). They exhibit migratory and stream-resident life histories and are classified as partially anadromous in their native range (Hendry et al., 2004). Anadromy takes fish from freshwater streams to the ocean as juveniles grow and mature and back to freshwater to spawn. In the Great Lakes, rainbow trout exhibit similar behavior, but are considered potamodromous, as they migrate among bodies of freshwater (Negus, 2003; Negus et al., 2012). Both anadromous and potamodromous rainbow trout are commonly referred to as steelhead; a moniker we will adopt hereafter. In the Great Lakes, steelhead spend 1–3 stream years as juveniles before smolting and migrating to the lakes, followed by 1–3 lake years before their spawning migration (Hassinger et al., 1974; Biette et al., 1981; Seelbach, 1993; DuBois and Pratt, 1994; Ward, 2010). Such diversity in life history traits is considered to be adaptive and common under variable stream and lake environmental conditions (Hendry et al., 2004; Moore et al., 2014).

Steelhead from the Pacific coast were introduced to U.S. waters of the Lake Superior basin in the Bois Brule River, Wisconsin (hereafter called the Bois Brule River), in 1892 (Scholl et al., 1984). The Bois Brule River supports self-sustaining wild steelhead populations resulting from those initial introductions. While the Bois Brule River was one of the earliest locations to receive introductions, steelhead have become naturalized in all five Great Lakes (Biette et al., 1981). There is significant among-year variability in the number of steelhead that return to the Bois Brule River. This variability has largely been attributed to variability in limiting factors associated with in-river conditions prior to emigration and

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https://doi.org/10.1016/j.jglr.2023.01.009
0380-1330/

first-year lake conditions that influence the production and survival of juvenile steelhead because of their relatively small size at smolting. Understanding the factors in the stream and lake habitats that determine the returns of spawning adults will be valuable to the management of their populations and considerations of habitat quality for this species throughout the Great Lakes.

Factors associated with both open water habitat and stream conditions can strongly influence the production and survival of juvenile steelhead (DuBois and Schram, 1993; DuBois and Pratt, 1994; Power et al., 2015; Johnson and McKenna 2017). In open water environments, important factors include thermal conditions (Höök et al., 2004a; Höök et al., 2004b; Thalmann, 2020), prey resources (Thompson and Beauchamp, 2014) and predation (Naughton et al., 2011). General stream conditions that are associated with variability in steelhead juvenile success include flow rates, temperature and habitat characteristics (Keeley, 2001; Power et al., 2015; Mryold, 2019). Furthermore, growth during pre-smolt stages may also be associated with success in the open water environment (Catterson et al., 2019).

The Bois Brule River is somewhat unique in western Lake Superior, but not to other Lake Superior tributaries or the Great Lakes, in being generally characterized by seasonally stable flows and moderate temperatures, which contribute to it being relatively ice-free early in the spring and providing excellent rearing habitat for parr. DuBois and Pratt (1994) suggested that early season floods in the Bois Brule were deleterious for eggs and fry, whereas low spring river temperatures and flow instability in the lower river limited growth and survival of juveniles. Unlike the Bois Brule River, tributaries in other areas of Lake Superior often lack cobble and large boulder substrate to slow the current, which can limit young of the year (YOY) production (Close and Anderson, 1997). Close and Anderson (1997) also noted that low summer discharge, migration barriers and lack of woody debris habitat limited smolt production in bedrock dominated tributaries.

There is evidence of coherent variation among steelhead populations in the Bois Brule and other rivers of the region that may be related to conditions in western Lake Superior (Schreiner et al., 2010). Conditions in the large waterbodies that harbor post-smolt steelhead may also be important for survival and the return of the adults for a number of reasons. In the Great Lakes, predation, forage, lake surface temperature, and angler harvest are considered possible sources of variability (Höök et al., 2004a; Höök et al., 2004b). In Lake Superior, the most abundant and likely predators for steelhead during their first year are lake trout, *Salvelinus namaycush* (Negus et al., 2007). Lake surface temperatures may also influence steelhead growth and survival, especially in their first lake year, as steelhead spend most of their time in the upper 20 m of the water column (Negus and Hoffman, 2013). There was also a positive correlation between mean summer lake temperature and returns of steelhead stocked in the Knife River and the nearby French River, which are also tributaries flowing into western Lake Superior from Minnesota (Negus et al., 2012) indicating temperature as an important condition for young steelhead.

The primary objectives of this study were to determine whether the stream conditions, which affect early life stages, or lake conditions, which affect post-smolt to adult stages, were associated with the abundance of maiden returning Bois Brule River steelhead from 1984 to 2007. Given the findings of DuBois and Pratt (1994), we hypothesized that in-stream variables would resolve a significant amount of variability in steelhead. Alternatively, if conditions in western Lake Superior, which is low in productivity and characterized by colder than optimal temperatures for steelhead, were most limiting, variability explained by in-lake variables would also explain variability in addition to those captured by in-stream variables. To test these hypotheses, we compiled data sets on the age structure of returning steelhead as well as in-stream and in-lake variables. Information associated with conditions in the Bois Brule River included variables related to precipitation (rain and snow cover), air and water temperatures and stream flow conditions. Variables associated with Lake Superior included lake surface temperatures, the abundance of predatory species and the abundance of prey species.

Methods

Study area

The Bois Brule River is located in Douglas County in northwestern Wisconsin, USA (Fig. 1), is approximately 76 km in length, drains a 306 km^2 watershed, and flows northward to Lake Superior. The upper and middle sections flow through glacial drift underlain by igneous rock, and the lower section flows through glacial lake deposits of red clay underlain by sandstone (Scholl et al., 1984). The Bois Brule River receives significant groundwater from springs in the upper river section, creating a moderate thermal regime and relatively stable flows (Sather and Johannes, 1973). In the middle section of the river near the town of Bois Brule, the average discharge (1943–2011) was 4.8 m^3 s^{-1} (169.6 ft^3 s^{-1}), with daily average flows ranging from 1.9 to 43.0 m^3 s^{-1} (67 to 1520 ft^3 s^{-1}) (USGS online: http://waterdata.usgs.gov/nwis).

Bois Brule River steelhead spawn during the spring, but the majority (>76 %) of returning adults ascend the river in autumn and overwinter. The remainder of the spawning adults ascend the river in a spring run (DuBois and Pratt, 1994). These two distinct runs are similar to the summer and winter runs typically found on the Pacific Coast (Behnke, 2002). Most adults outmigrate to the lake again after spawning with the majority of the adult population reaching the lake by mid-May.

Bois Brule River adult steelhead range in age from 3 to 10 years and vary in 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 %) years. Scale analysis revealed that the majority of returning adults had spent two stream years before smoltification (Scholl et al., 1984; DuBois and Pratt, 1994).

Steelhead population analyses

We used estimates of annual migratory steelhead runs from 1985 to 2010 provided by the Wisconsin Department of Natural Resources (WDNR), based on counts of fish that passed a viewing window at the Lamprey Barrier fishway approximately 9.7 km upstream from the river mouth (Fig. 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, the estimated numbers of years spent in the river and in the lake, and spawning status (maiden or repeat spawner) were determined from scales taken in the fall from approximately 250 fish sampled annually using electrofishing (1986–2010). Fall samples were used because they represent most of the adult run in any given year. Length, gender, and presence/absence of an adipose clip (stocked fish were clipped) were also recorded. In this case, stocking of Bois Brule fry reared in the Brule hatchery occurred in most years where fish were released into the upper portion of the river and were exposed to the same in-stream conditions as wild fish. Length-at-age data from those fish were applied to length-frequency data from the fishway to estimate the proportion of steelhead that were maiden spawners in any year. Maiden spawners were defined as fish that contained no spawning checks on scales. Using scale data from each year's sample of maiden spawn-

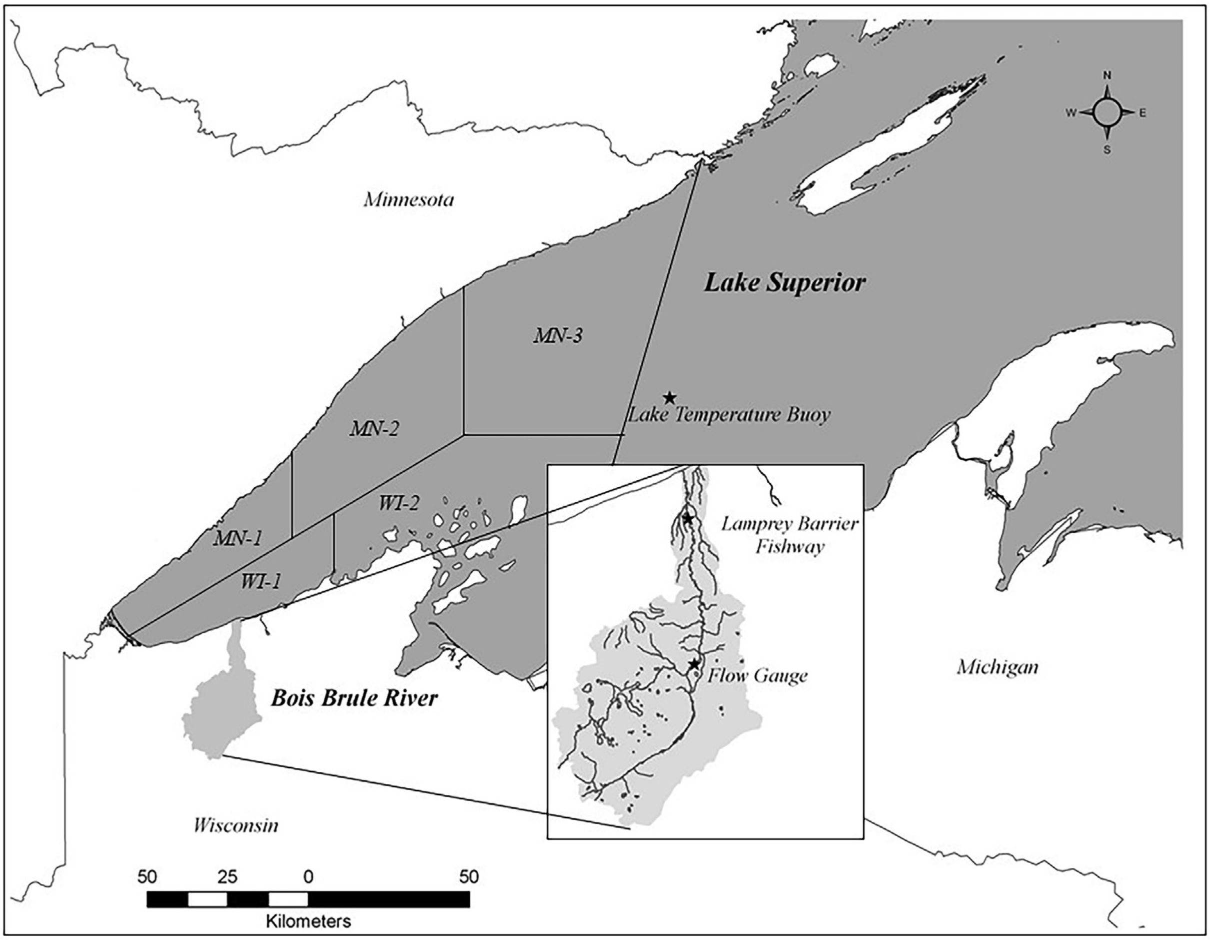

Fig. 1. Map of the Bois Brule River watershed including the location of the flow gauge in the town of Bois Brule, WI and location of the temperature buoy in Lake Superior.

ers, extent of stream and lake residence was used to determine which years the fish had spent in-stream as juveniles, and to match those years (and the strength of their maiden returns) with corresponding-year data on stream conditions. Similarly, the scale data were used to determine which years the fish had entered the lake as smolts, and to examine the effects of lake conditions in those years on strength of maiden returns. After an initial set of analyses, we restricted our consideration for this study to examining only maiden returns because the river is the primary location where fish are vulnerable to significant fishing exploitation, which would potentially bias subsequent returns. We also restricted our analyses to assessing conditions in the river during their first year of life and in the lake during their first lake year because all subsequent responses to independent variables would be dependent on the first year experiences.

Stream conditions

Discharge

Discharge data for the Bois Brule River were obtained from the USGS National Water Information System website (http://waterdata.usgs.gov/nwis). The Bois Brule River gage (Hydrologic Unit 04025500) is located at N46°32′16″, W91°35′43″ (Fig. 1). Daily discharge has been recorded on the Bois Brule River since January 1984. To characterize seasonal discharge, we calculated the average, peak, and lowest flows for spring (April 1 – May 31), summer (June 1 – September 15), and fall (September 16 – November 30). We also split flow rates into monthly averages for June and September individually to examine variability in these months specifically because they typically represent periods of low flow with yearly anomalies. Each time period was chosen arbitrarily to represent seasonal differences and for comparison of interannual variability in river conditions. We also calculated the average, peak, and lowest flows for June and September because these months were expected to be important for juvenile survival. June is important because young-of-year fry are fragile and require refuge from main current areas. Smolts begin migrating out of the stream in September, thus making them susceptible to impacts of extreme discharge during September.

Temperature and precipitation

Bois Brule River water temperatures were taken at the lamprey barrier fishway located in the lower section of the river (Fig. 1). Hourly data from thermographs were used to calculate daily averages for years 1987–1995 and 1999–2010. In years with missing data, daily points were estimated by averaging the values from the days before and after the missing day. Degree days above 20 °C, a temperature near the avoidance temperature for rainbow trout (Coutant, 1977, >19 °C; also see Wismer and Christie, 1987), were calculated from June 1-September 30 using daily averages, with temperatures below 20 °C given a zero value. Air temperature from 1995 to 1999 were used to estimate water temperature during those years based on a relationship between air temperature and water temperature (Kaspar, 2012). Winter severity at the Bois Brule River was calculated using daily minimum air temperatures from December 1 to March 30 or 31 (depending on leap years for a total of 121 days), obtained from the WDNR field station on the Bois Brule River during the study period. For the winter severity calculation, air temperature negative degree days were calculated for each station using an upper threshold temperature of 0 °C. Degree-day values above the threshold temperatures were given a zero value. Finally, total precipitation was calculated for each station for spring (April 1 – May 31), summer (June 1 – September 15), fall (September 16 – November 30), winter (December 1-March 31), June, and September.

Conditions in Western Lake Superior

Surface temperature

To evaluate the temperature conditions in western Lake Superior that would be conducive to steelhead survival, we estimated surface temperatures from data collected at NOAA Buoy #45006 (N47°20′5″ W89°47′34″) located north of Ironwood, MI (Fig. 1). This buoy had the only long-term data for surface temperatures in western Lake Superior and recorded temperatures hourly at 0.6 m below the surface. We calculated degree days (DD4) from June 1 to October 15 for each year (1980–1983, 1987–2010), with hourly temperatures above 4 °C (the annual average surface temperature in Lake Superior) summed and divided by 24, and temperatures at or below 4 °C given a zero value. We used the period 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. Any missing days were estimated for years 1980, 1981, 1984–1987, 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) using a predictive relationship between temperature at buoy 45,006 and 45001. Linear regression analyses showed significant and predictive positive linear correlation between the buoys (R^2 = 0.91, $p < 0.001$).

Predator abundance

Lake trout are the most abundant piscivore in Lake Superior (Bronte et al., 2003). We used spring (May-June) estimates of their abundance in the Minnesota and Wisconsin waters of western Lake Superior, the habitat that young steelhead encounter during their first year in the lake, provided by MNDNR and WDNR, to assess the potential for predation to limit young steelhead survival. We used MNDNR data from management zones MN1, MN2, and MN3 collected with 11.4–14 cm stretch mesh gill nets (Halpern and Schreiner, 2003), and WDNR data from management units WI1 and WI2, also collected with 11.4–14 cm stretch mesh gill nets (Seider, 2011). Abundance was expressed in standard units (catch per 1000 m net per night). Geometric means were estimated from all MN and WI units each year (1986–2007) to express overall annual abundance trends in western Lake Superior. In 1996 and 2001, no lake trout assessments were made in the Wisconsin units; for those years we used Minnesota data alone to estimate lake trout abundance.

Prey fish abundance and biomass

We based estimates of prey fish abundance on annual spring sampling by USGS personnel in western Lake Superior that occurred from April-June in each year from 1986 to 2007. Samples were taken during daylight hours using a Yankee bottom trawl with a 12 m head rope (Hoff and Bronte, 1999) at 16 nearshore (<80 m) stations (Table 1). Trawls crossed contours from depths < 15 m to approximately 100 m. Each species was counted, measured, and then weighed in aggregate to estimate relative density (fish ha^{-1}) and biomass (kg ha^{-1}). Density for the forage species in each was expressed as geometric means across sampling stations. 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*). Age-1 biomass estimates were also used for rainbow smelt, cisco, and bloater, to determine whether early life stage biomass of those major species was an influential factor. Because age-0 fishes are not readily captured by the trawl, we also used the abundance of age-1 fish the following year as a measure of age-0 fish abundance the previous year. Specifically, the age-1 biomass trends were used to represent available young of year prey during the first lake-year and were thus offset by one year (e.g., age-1 catches in 1989 were used to predict returns from 1988). Finally, we also created a general prey availability variable by summing density across prey species and age-1 biomass to approximate total availability of forage fish and YOY forage fish (Table 2).

Table 1
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.

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

Steelhead diets in Lake Superior are comprised of invertebrates and small fish, with analyses by Negus and Hoffman (2013) indicating the use of fish was higher (44 %) than other prey categories (aquatic insects 39 %, terrestrial insects 9 %, Mysis 7 %) (also see Negus et al., 2007, 2008). No metric of the other prey categories was available for the time period examined.

Statistical analyses

We used two classification regression tree (CART) models to predict steelhead returns using: 1) in-stream variables and 2) lake variables. We chose CART models in this case because of their ability to handle many predictor variables. CART models do not suffer the same issues of overfitting as do linear regression techniques and node selection and pruning criteria select models of the appropriate size (Goldstein et al., 2017). For the in-stream analysis, stream conditions during the first year of life were used to predict the number of maiden steelhead returns from a given cohort. The model included 21 variables representing flow, temperature, and precipitation (described above). For the lake analysis, lake conditions in a given year were used to predict the number of maiden returning steelhead that migrated to Lake Superior in the same year. The model of lake effects included 13 variables representing lake temperature, predator and forage density (described above). Models were run in Program R version 3.4.0 (R Core Team 2017) using the Rpart package (Therneau and Atkinson, 2018).

Table 2
Independent variables used in the tree-based analyses of in-stream and in-lake variability in steelhead maiden returns to the Bois Brule River, WI. **Bold** text indicates variables selected as primary (1st) splits, ***bold and italicized*** text indicates splits conditional on other variables.

Model	Variable	Description
Stream	Stream temperature	Degree days relative to 20℃
	Spring discharge	Average discharge for April-May
	June discharge	Average discharge for June (cM/s)
	Summer flow	Average discharge for June-September (cM/s)
	September flow	Average discharge for September (cM/s)
	Fall flow	Average discharge for September-Nov. (cM/s)
	Spring peak flow	Highest daily discharge (cM/s) from April-May
	June peak flow	Highest daily discharge (cM/s) in June
	Summer peak flow	Highest daily discharge (cM/s) from June-August
	Summer lowest flow	Lowest daily discharge (cM/s) from June-August
	September peak flow	Highest daily discharge (cM/s) in September
	September lowest flow	Lowest daily discharge (cM/s) in September
	Fall peak flow	Highest daily discharge (cM/s) from Sept.-Nov.
	Fall lowest flow	Lowest daily discharge (cM/s) from Sept.-Nov.
	Spring precipitation	Total precipitation (cm) from April-May
	June precipitation	Total precipitation (cm) in June
	Summer precipitation	Total precipitation (cm) from June-August
	September precipitation	Total precipitation (cm) in Sept.
	Fall precipitation	Total precipitation (cm) from Sept.-Nov.
	Winter precipitation	Total snowfall (cm) from Dec.-March
	Winter temperature	Degree days below 0℃ from De.-March
Lake	***Surface temperature***	Sea surface degree days relative to 4℃
	Lake Trout abundance	Abundance (#/1000 m/night) of the top predator
	Rainbow Smelt abundance	Density (kg/Ha) of a prey/competitor
	Ninespine Stickleback abundance	Density (kg/Ha) of a prey species
	Lake Cisco abundance	Density (kg /Ha) of a prey/competitor
	Bloater abundance	Density (kg /Ha) of a prey/competitor
	Kiyi abundance	Density (kg /Ha) of a prey/competitor
	Sculpin abundance	Density (kg /Ha) of a prey species
	Troutperch abundance	Density (kg /Ha) of a prey species
	Age-1 Cisco abundance	Density (kg /Ha) of a prey species
	Age-1 Bloater abundance	Density (kg /Ha) of a prey species
	Age-1 Rainbow Smelt abundance	Density (kg /Ha) of a prey species
	Total abundance of all prey	Density (kg /Ha) of all prey species (all ages)
	Total abundance of age-1 fish	Density (kg /Ha) of age-1 smelt, cisco, bloater, kiyi combined

CART models provide several benefits over traditional linear regression techniques (Goldstein et al., 2017). One of the benefits of using CART models in this analysis is that we can provide the model with many predictor variables and let the model select the top few variables that are most associated with the response variable, which in this case is steelhead maiden returns (Goldstein et al., 2017). Traditional regression models estimate regression coefficients for each variable that we would theoretically provide (i.e., n = 21 in the stream model and n = 13 in the lake model), which would have led to overparameterized models given the number of observations available. The CART model selects only the single most influential variable at each node which provides a robust selection process and can entertain more predictor variables than response variables (Goldstein et al., 2017). Additionally, by using the CART model, we did not have to a priori choose which predictor variables to include or exclude in the model. Finally, CART models are flexible in their ability to capture non-linear relationships and complex interactions, are robust to outliers and do not require transformation of explanatory variables (Moisen, 2008).

It should be noted, however, both that overfitting and underfitting are concerns when using CART models. To address overfitting, we applied cross-validation and pruning procedures during the model fitting procedure. The Rpart package fitting procedure a priori removes splits that do not decrease the model R^2 by 0.01 to 'pre-prune' trees (Therneau and Atkinson, 2018). Additionally, we used cross-validation procedures (n = 100) to identify additional nodes that should be pruned. The Rpart cross-validation procedures are used to identify the risk of miss-classification associated with different model complexities (i.e., number of splits) and splits that did not increase the overall R^2 of the classification model by 1 % were pruned. This cross-validation procedure is an alternative to dividing the dataset into a training and validation datasets and was chosen because of the small size of our dataset (see Moisen, 2008). To reduce concerns with model underfitting, we used a minimum node size of three observations. Combined, these procedures should minimize the risk of both under and overfitting the model.

Results

In-stream factors

The number of maiden steelhead returns from each cohort ranged from 713 to 6,850 (mean = 2,850) fish during the study period. With the exception of the 1987 cohort (which had the second highest return numbers at 5,627 fish), steelhead returns from each cohort showed an increasing trend over the study period (Fig. 2A). Fitting CART models to the in-stream variables indicated that spring, September, and fall peak flows were the best predictors for steelhead maiden returns. The largest steelhead returns occurred when spring peak flow was <9.3 m^3s^{-1} (mean returns of 5,567 fish; Figs. 3 and 4A). The smallest returns occurred when both spring and September peak flows were high, $\geq$9.3 m^3s^{-1} and $\geq$8.6 m^3s^{-1}, respectively (Figs. 3 and 4B). Intermediate steelhead returns were observed when high spring and low September peak flows occurred (Figs. 3 and 4C). These intermediate returns were further split into high and low fall peak flows by the model and suggested a negative relationship between return size and peak flow (mean returns of 2,368 and 3,362 fish respectively; Figs. 3 and 4C).

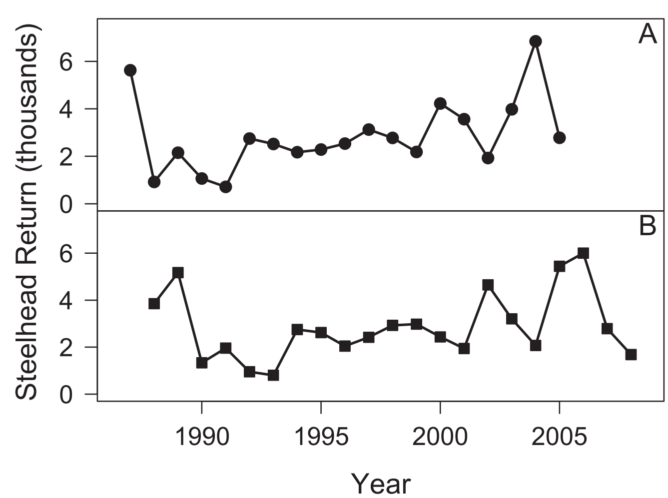

Fig. 2. Steelhead maiden returns from each cohort between 1987 and 2005 (A) and from each first lake-year between 1988 and 2008 (B) from the Bois Brule River, WI.

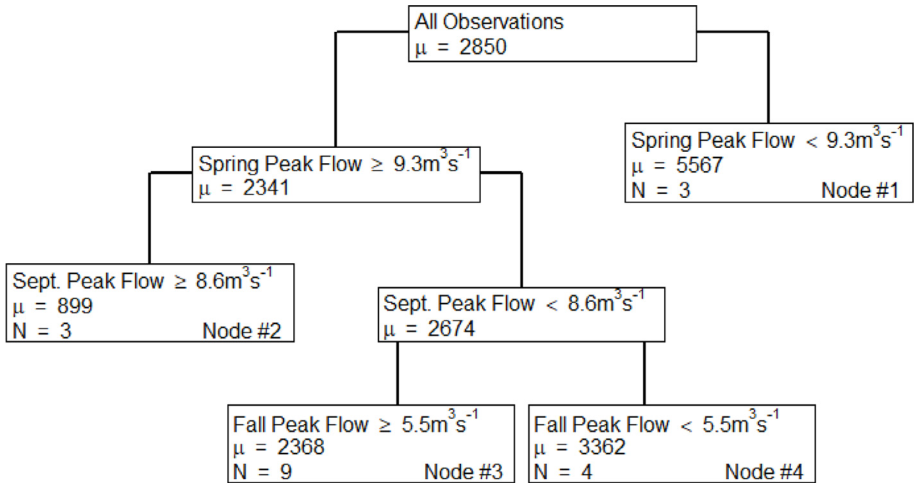

Fig. 3. Classification model for predicting maiden steelhead returns from a given cohort using in-stream variables during the first year of life with means (μ) for each step in the model, terminal node size (N), and classification node number.

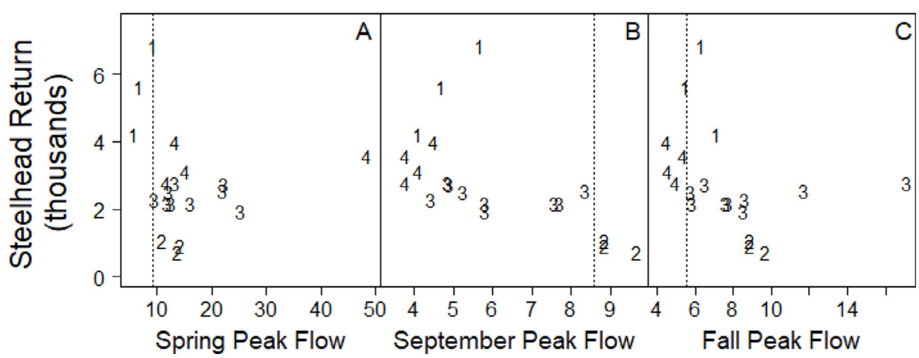

Fig. 4. Steelhead returns from each cohort from 1987 to 2005 plotted against peak flow in spring (A), September (B), and fall (C). Vertical dotted lines represent the breaks for each fork in the classification model and point number represents the classification nodes represented in Fig. 3.

Lake factors

Mean maiden steelhead return for a given lake-year was 2,859 and ranged from 803 to 6,001 fish and differed from the in-stream group because of lags related to years between smolting and returns. The number of steelhead returns in each lake-year tended to increase over the study period, except for 1988 and 1989 lake-years, which were among the highest returns (>3,800 fish for both years; Fig. 2B). The best predictors for return size from a given lake-year were indices for smelt (both total and Age-1) and Age-1 bloater along with surface degree days above 4 °C (Fig. 5). The largest lake-year returns were in years with low smelt densities (mean returns of 4,541 fish with smelt per ha < 0.22; Figs. 5 and 6A). With high smelt densities during cold years (surface DD4 < 1,265), the model predicted low returns (mean returns of 1,246 and 2,535 with Age-1 bloater kg/ha $\geq$ 0.25 and <0.25 respectively; Figs. 5, 6B, and 6C). Finally, moderate returns were predicted when smelt densities were high during warm years (mean returns of 2,582 and 3,666 with Age-1 smelt kg/ha $\geq$ 0.25 and < 0.25 respectively; Figs. 5, 6B and 6D).

Relative effects of stream and lake conditions on steelhead returns

Both the in-stream and lake CART models had R^2 values > 0.6 (Fig. 7). The in-stream CART model performed better at predicting the number of maiden steelhead returns, with R^2 = 0.88 versus 0.63 for the in-stream and lake models, respectively (Fig. 7).

Discussion

While overall success of diadromous fish populations is the product of success in stream and open water habitats, one location is often disproportionally influential in population dynamics (Hendry and Stearns, 2004). In many cases, in-stream variables have strong influence on migratory salmonid survival and may have primacy over those in adult habitats (Scarnecchia, 1981). Our results are consistent with the tenet that in-stream factors are primary sources of variability in steelhead population dynamics, with in-stream conditions explaining more variability than in-lake conditions (R^2 = 0.88 vs R^2 = 0.63). In our analyses, flow rates in the spring and fall were important for young steelhead survival in the Bois Brule River. However, prey resources and temperature within western Lake Superior are also important for juvenile steelhead survival during their first year in the lake. Taken together, our findings indicate that, among the parameters we measured, in-stream conditions had a greater influence than lake conditions in determining steelhead maiden return numbers to the Bois Brule River. However, prey availability and thermal conditions in western Lake Superior are critical to in-lake growth and survival. High water events were negatively associated with returns of steelhead in the Bois Brule, with apparent impacts on juvenile stages of steelhead. Our findings are consistent with other studies documenting natal stream habitat is important in dictating population success. In-lake conditions also provide meaningful predictors of variability in steelhead success. However, virtually all lake variables are likely

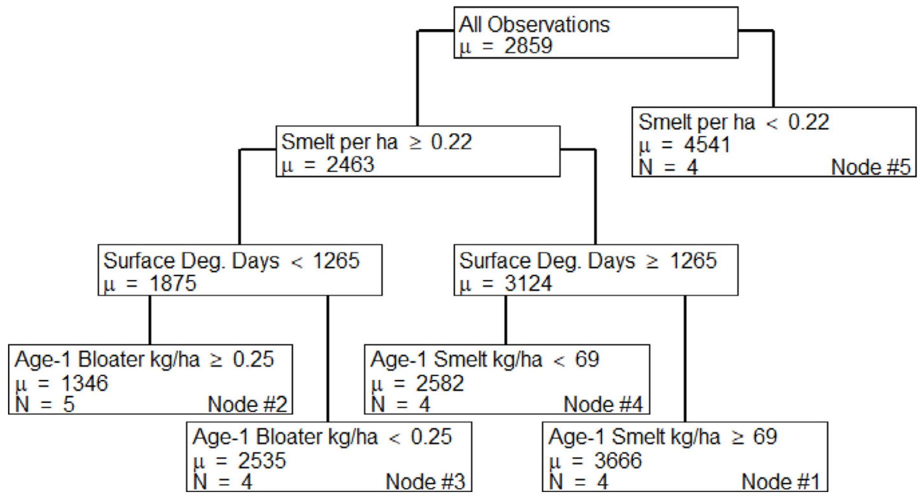

Fig. 5. Classification model for predicting maiden steelhead returns from a given lake-year using variables representing temperature and prey availability the first lake-year with means (μ) for each step in the model, terminal node size (N), and classification node number.

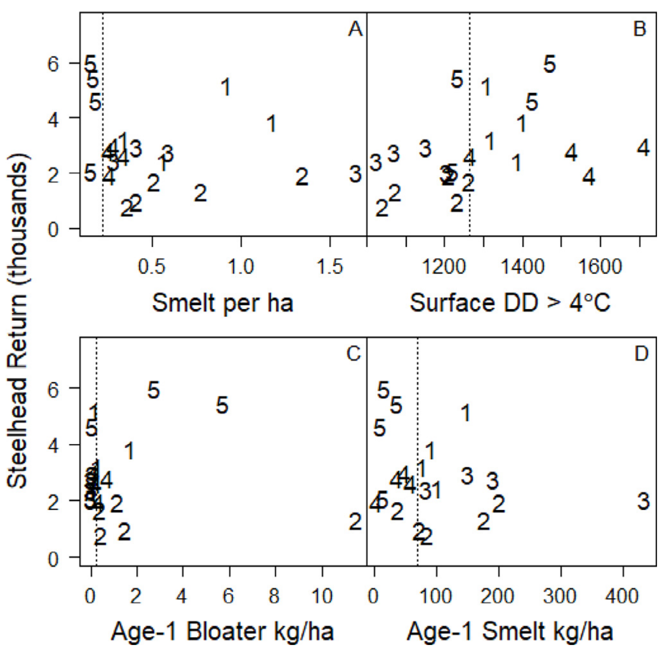

Fig. 6. Steelhead returns from a given lake-year between 1988 and 2008 plotted against Smelt per ha (A), surface degree days above 4 °C (B), Age-1 Bloater kg/ha (C), and Age-1 Smelt kg/ha (D). Vertical dotted lines represent the breaks for each fork in the classification model and point number represents the classification nodes represented in Fig. 5.

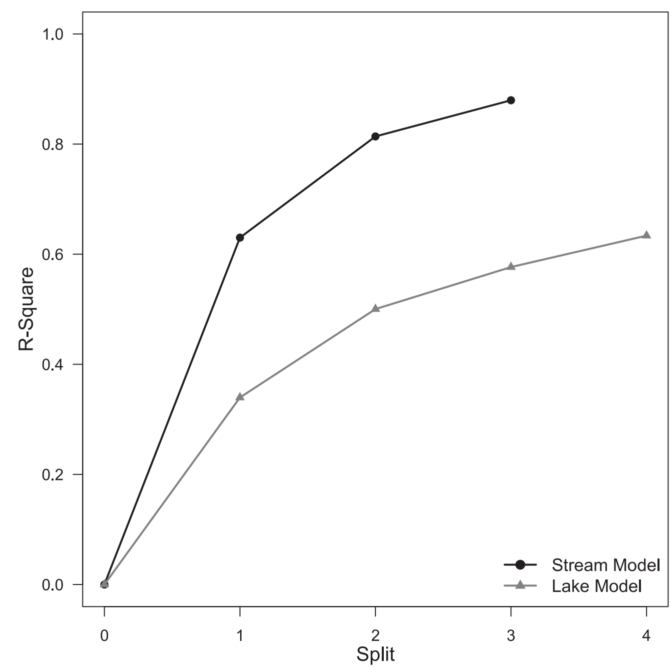

Fig. 7. Classification model performance (R^2) for the stream and lake CART models at each predicted model split.

outside the control of managing agencies outside of fishery harvest. Management efforts focused on preserving natural stream flow conditions and reducing overland runoff within the watershed should be the focus of forestry and construction practices in the watershed.

Flooding conditions alter refuge habitat, foraging opportunities and physiologic conditions for juvenile salmonids (Fausch et al., 2001; Hendry and Stearns, 2004). While higher water levels promote spawning immigration by adult salmonids, flooding often lowers juvenile success (He, 2017). For example, in California central coastal streams with highly variable seasonal temperature and flow regimes, juvenile steelhead had an order of magnitude greater growth rates under moderated conditions, presumably due to seasonally consistent food availability delivered by consistent flow regimes (Sogard et al., 2012). Conditions in natal streams also often dictate whether fry or parr emigrate at a given stage of development (Keeley, 2001). Wet years are often associated with higher outmigration of fry or parr, which under certain circumstances may contribute to returning adult salmonids in subsequent years where ocean conditions allow fry and parr survival (Sturrock et al., 2015). Furthermore, flow conditions are often associated with emigration of juvenile salmonids that use low flow areas in flood plains as refuge prior to outmigration (Takata et al., 2017). While the Bois Brule River has a relatively pristine flood plain system, the lower 25 miles of river, which run through glacial lake clay deposits, has a confined floodplain and limited off-channel habitat. High water events likely cause stress to juveniles in their first year of life. In the Manistee River, MI, increased discharge negatively affected numbers and growth of steelhead parr (Tyler and Rutherford, 2007). Spring high water events likely cause increased egg and parr mortality in a channel system exemplified by the Bois Brule River. Increases in flow rates during the spring and fall are likely to lead to declines in steelhead returns if the frequency and magnitude increase.

Size at emigration has a strong influence on foraging success and avoiding predation (Sturrock et al., 2015). In the Laurentian Great Lakes, lake conditions likely do not favor young steelhead emigrants. Given the harsh conditions in Lake Superior characterized by cold thermal conditions, low food resources and risk to predation, small size at outmigration may reduce overall survival of a given year class. Our results are consistent with the contention that high-water events in both spring and fall can cause reduced success in Bois Brule River steelhead. Early outmigration or higher mortality in this case appears to be associated with the lower maiden returns.

A secondary peak of down migrating juveniles occurs in autumn (late August to November) that consists mainly of age 0 parr with some age 1 parr in the Bois Brule River (DuBois, 2001). The downstream movement of parr in fall may be associated with outmigration 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 rainfall events leading to high discharge during migration, this may have a negative effect on survival due to stressful conditions in the river or by initiating early outmigration by pre-smolt juveniles. High rainfall events can lead to unstable hydrological conditions in the lower Bois Brule River, resulting in high turbidity and siltation (DuBois and Pratt, 1994; DuBois, 2001).

Variability in open water conditions is often associated with variability in performance of maturing salmonids (Hendry et al., 2004). In the Great Lakes environment, Lake Superior is unique in that thermal stratification occurs later in the summer (mid to late August) and can be variable in offshore (>80 m) areas (Finchot et al., 2019). The thermal optimum of steelhead (~15 °C; Railsback, 1999) dictates use of warmer water layers and growth is undoubtedly enhanced during warm years. Prey resource availability is also likely associated with better conditions for steelhead in Lake Superior (Negus et al., 2004). Our results highlight the importance of food web relationships and thermal conditions on steelhead survival in their first year in Lake Superior. Lake conditions that led to steelhead success manifested as enhanced maiden returns included lower smelt abundance (both total and age-1) and lower age-1 bloater abundance. These results are consistent with competitive interactions because both smelt and bloater feed to a large extent on *Mysis diluviana* (Gamble et al., 2011a; Gamble et al., 2011b; Sierszen et al., 2014), as do steelhead (Negus et al., 2004). Thermal resources measured by surface degree days above 4 °C in their first lake year were associated with higher maiden returns and indicate that warmer conditions enhance young steelhead survival. We observed the largest lake-year returns in years with low smelt densities, the smallest returns with high smelt densities during cold years (surface DD4 < 1,265), with additional variability explained by the abundance of bloater. Each condition in this case was apparently associated with better foraging opportunities in warmer years. While we entertained a large number of variables in the lake analyses, an alternative interpretation includes the possibility that each of these fish species were responding to another external variable that was not included in the analyses and accept that possibility.

When we assessed overall impacts of both stream and lake variables, it was clear that processes in both environments were important sets of conditions for returning steelhead. Our findings are most consistent with the premise that return number is initially set by stream conditions for 1st year pre-smolt steelhead, and further shaped by post-smolt success in the lake. We note, however, that conditions in the lake may have dominant effects on fish population parameters we have not analyzed, such as condition of returning steelhead. Given that high summer stream temperatures may limit parr production, especially during periods of low flow (Close and Anderson, 1997; Mathews and Berg, 1997; Godby et al., 2007), the positive effects of warm temperatures on fish in the lake seem to be contradicted by potential impacts in the river. However, lake temperatures are often low relative to thermal tolerances for rainbow trout (Schreiner et al., 2010), whereas the Bois Brule River has baseflow conditions which contribute to good thermal rearing habitat for juvenile steelhead, particularly upstream from the town of Bois Brule. The river below the town of Bois Brule, in contrast, is susceptible to higher temperatures, turbidity and flooding (DuBois and Pratt, 1994). Godby et al. (2007) found high mortality of parr associated with high temperatures (>21 °C) in the Muskegon River, Michigan. A combination of flooding and possibly elevated temperatures in the lower river has the potential to drastically decreases the survival of juveniles in this area, thereby reducing the overall number of surviving smolts from those years (DuBois and Pratt, 1984).

River conditions associated with good survival of juvenile trout are often associated with land use, riparian buffers and pristine channel structure, which in many cases are a product of conservative land management strategies. The Bois Brule River watershed, particularly in the upper portion of the watershed, is relatively pristine, remains carefully managed for watershed and stream habitat quality (e.g., see https://Bois Bruleriversportsmensclub.com/habitat-management/overview/), and provides excellent rearing habitat for juvenile steelhead. The lower river, however, has conditions that are less conducive to juvenile trout survival. Furthermore, lake conditions are far less predictable and influenced by large scale food web dynamics as well as global and regional weather patterns, making them less amenable to management actions. Our findings are consistent with the premise that stream conditions, which to a certain extent are within the control of watershed managers, are among the most important factors. Consideration of factors that may be associated with low water quality and action monitoring temperatures, flooding and floodplain alteration in the lower portion of the river, should receive the highest management priority. We suggest strategies including protection of tributary streams, promoting refuge habitats including side channels and woody debris dams that may improve contribution of lower river areas to successful smolt production.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We thank Dennis Pratt and Bill Blust, WDNR (Retired), for initiating and supporting this project. We also appreciated Brad Ray and Paul Piszczek (WDNR) for their continued support in data corrections along with manuscript development. Many thanks to all technicians that spent innumerable hours analyzing video that resulted in data used in this project. We thank the Bois Brule River Sportsmen's Club, the Wisconsin DNR, the Department of Biology and the Swenson College of Science and Engineering at the University of Minnesota-Duluth for financial support associated with Mr. Kaspar's thesis work.

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