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Genetic Variability of Leech and Woman Lake Walleye Populations

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Variation in Young Walleye Growth in Leech Lake

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Background

Minnesota's ten largest walleye lakes, which include Leech, account for nearly 40% of the annual statewide walleye *Sander vitreus* harvest and provide significant contributions to resource-based economies on both local and statewide scales (MNDNR 1997). As a result, the Minnesota Department of Natural Resources (MNDNR) recognizes the importance of these systems and collects robust data annually to effectively identify and evaluate trends in their fisheries, detect management needs, evaluate management actions, and enhance public outreach.

Leech Lake is renown among anglers as an exceptional multi-species fishery; however, most anglers target and harvest walleye. In 2009-2010, the MN DNR convened a citizen input committee (Leech Lake Advisory Committee; LLAC) comprised of stakeholders representing local and statewide interests in Leech Lake management. This group outlined walleye population management objectives and actions, including double-crested cormorant control, special regulations, and walleye fry stocking (LLAC 2010). These recommendations were incorporated into DNR's Leech Lake Management Plan, 2011-2015 (Schultz 2010a).

The City of Walker has been formally represented by a sub-committee since February 2006 (Leech Lake Fishing Task force). Concerns from this group were raised over the MN DNR's walleye management strategies on Leech Lake at the genetic level. The Woman Lake walleye population was determined to be the preferred brood source for Leech Lake walleye fry stockings given the genetic similarities between the two populations and the large quantities of fry programmed during 2011-2014 (Miller 2007). Walleye fry produced from Woman Lake brood stock have been stocked into Leech Lake annually since 2005, and continuation of this strategy as the primary brood source was recommended by the LLAC.

These reports address the specific concerns regarding the genetic diversity of the Leech and Woman Lake walleye populations within a broader statewide context, the diversity of the Leech Lake walleye population before and after stockings were initiated in 2005, and the growth rate of young walleye originating from stocked and naturally-produced sources.

Executive Summary

Genetic variability of Leech and Woman lake walleye populations (page 4)

- Small population size can lead to loss of genetic variation and inbreeding (the mating of close relatives) that can reduce survival, reproduction, growth, and condition. These reductions are called inbreeding depression.
- Genetic diversity of the Leech Lake walleye population was compared before (2002) and after (2011) fry stocking was initiated in 2005. The Woman Lake walleye population, which is the source population for fry stocking activities in Leech Lake, was also tested.
- No declining trends in genetic diversity in either population were observed using microsatellite (DNA) analysis.
- No indications of inbreeding (increases in relatedness or signatures of population bottlenecks) were detected in either population.
- Genetic diversity levels of both populations were similar compared to other Minnesota walleye populations.
- There is no genetic evidence that the Leech Lake walleye population or the source population for programmed fry stockings are inbred or in need more genetic diversity. Both of these populations were as diverse as others in Minnesota.

Variation in young walleye growth in Leech Lake (page-12)

- Reduced growth of young fish can be a physical manifestation of inbreeding depression.
- Walleye fry stockings initiated in 2005 used oxytetracycline (OTC), a chemical marker, to differentiate stocked (marked) walleye from naturally-produced (unmarked) fish.
- Growth rates of young walleye were compared between marked and unmarked individuals from 2005 through 2012. No meaningful differences in growth rates among groups were observed for either age-0 or age-1 fish.
- Growth rates of young walleye compared between pre-stocking (1987-2004) and post-stocking (2005-2012) periods. Growth rates of stocked year classes have expressed similar variability among years as those produced prior to stocking activities.
- There is no physical evidence that either the Leech Lake walleye population or the source population used for fry stocking suffer inbreeding depression.
- Historically, three of the five slowest growth observations for age-0 fish where observed during years of high fry stocking densities.
- Age-0 growth was strongly associated with warmer growing conditions and negatively associated with higher fry densities. Warmer summers can offset slower growth caused by high fry densities, but colder summers would worsen this condition.
- Future management decisions should consider managing for total fry densities having the optimum growth and recruitment potential.

Genetic Variation in the Leech Lake and Woman Lake Walleye Populations
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Key points:

- Isolated populations can maintain genetic diversity and minimize inbreeding so long as they remain large
- Conservation genetics guidelines often suggest a minimum effective population size of 50 to minimize inbreeding concerns
- Leech Lake (10s-100s of thousands) and Woman Lake (thousands) have high breeding population estimates
- No declining trends in genetic diversity were detected from pre-stocking (early 2000s) to now (2011)
- No increases in relatedness or signatures of population bottlenecks were detected
- Genetic diversity levels are typical for Minnesota walleye populations
- Demographic and genetic data together indicate no recent or historical population bottleneck of an extent that would have greatly increased inbreeding
- In short, there is no genetic evidence that Leech Lake or Woman Lake walleye populations are inbred or need more genetic diversity

Background

Low recruitment in some years and the perceived condition of walleyes in Leech Lake have led to public concerns that lack of genetic diversity and inbreeding may be affecting the population. This paper summarizes genetic evidence to address those concerns.

Both environmental and genetic factors will affect the fitness (survival and reproduction) and performance (growth and condition) of fish and other organisms but it can be difficult to disentangle the factors. Inbreeding is the mating of close relatives, which can result in expression of recessive deleterious mutations that reduces the fitness of inbred individuals (i.e., inbreeding depression) (Keller and Waller 2002). Because inbreeding depression results from the mating of close relatives, even an isolated population can maintain diversity and have minimal inbreeding if its size remains large because few close relatives will encounter each other during spawning. Conversely, when populations become small, many individuals will be related because they share the same few ancestors (i.e., eventually everyone becomes cousins). Population geneticists evaluate inbreeding using the effective population size (N_e), which is less than population size (N) because it includes only mature adults and incorporates differences in reproductive success among individuals (Ne/N averaged 0.11 in one review; Frankham 2007). Conservation geneticists recognize that inbreeding in unlikely to be a major concern unless populations get quite small, often using a minimum N_e = 50 as a guideline for avoiding inbreeding problems (Franklin 1980).

Leech Lake was estimated to have 10s to 100s of thousands of mature walleyes each year over the past two decades (D. Schultz, MNDNR, unpublished data). The Woman Lake egg collections during the years of fry stocking came from 1,100-2,800 spawners per year from a population estimated to have 3,700-11,700 adults (Shroyer and Logsdon 2013). These numbers alone suggest that inbreeding should not be prevalent but they may not reflect past declines that "bottlenecked" populations to low N_e. Populations that have bottlenecked may have high levels of inbreeding because all individuals are related descendents of the few ancestors that survived the bottleneck. Following a bottleneck, inbreeding is not alleviated and genetic diversity cannot recover without new inputs (migrants or mutations) even if population size increases.

Molecular genetic markers provide a means of evaluating inbreeding in wild populations. The markers we used do not directly measure genetic traits potentially affected by inbreeding (e.g., survival, growth). Instead, they can detect genetic signatures of population decline (increased relatedness and loss of genetic diversity) that would indicate a risk of inbreeding depression. To evaluate whether the Leech Lake and Woman Lake walleye populations have increased inbreeding or lost genetic diversity over the period of recent fry stocking we compared genetic diversity between samples from the early 2000s and 2011. To infer whether these populations may have suffered historical losses of diversity we compared their genetic diversity to that in other upper Mississippi and statewide walleye populations. These other populations represent a range of genetic diversity found in other important Minnesota walleye populations.

Methods

Sampling and genotyping - Tissues samples for genetic analysis were obtained from archived collections of dried scales and fin rays from ongoing MNDNR sampling. Samples from 2011 came from fall gillnetting in Leech Lake and spawning run collections in Woman Lake/Little Boy River. Genetic data were available from previous analyses of 2002 Leech Lake gillnet and 2000 Woman Lake spawning samples, as well as samples from 13 other Minnesota walleye populations.

Genotypes were determined for eight microsatellite DNA loci (*Svi2, Svi4, Svi6, Svi16, Svi18, Svi20, Svi26, and Svi33)* that were previously described by Borer et al. (1999) and Eldridge et al. (2002). We genotyped 70-82 individuals per sample from Leech Lake and Woman Lake.

Data analysis - Conformance with Hardy-Weinberg and linkage equilibrium was evaluated for each sample using exact tests in Genepop v4.1.3 (Rousset 2008) to verify the suitability of the data for further analyses. Significance values were adjusted for multiple testing using sequential Bonferroni procedures (Rice 1989).

Several tests were used to determine if Leech or Woman Lake populations have low or declining genetic diversity or other evidence for inbreeding or population bottlenecks. Three direct measures of genetic variation were calculated, including heterozygosities and allelic richness. Heterozyosity is the average number of markers with two different alleles (observed heterozygosity; H_o) and that expected under Hardy-Weinberg equilibrium (expected heterozygosity; H_e). Allelic richness is the number of alleles standardized to a common sample size (Kalinowski 2005). Small population sizes accelerate loss of rare alleles, making allelic richness a more sensitive indicator of loss of genetic diversity than heterozygosity (Allendorf 1986). Potential for inbreeding was evaluated directly by estimating the relatedness (r) of each pair in a sample based on the number of identical alleles they shared (Queller and Goodnight 1989). For example, full-siblings (e.g., brothers) share on average half of the alleles from their parents and have an expected r = 0.5 while unrelated pairs have r = 0.0. We estimated relatedness for each pair in a sample using the software Coancestry (Wang 2011) and compared the average relatedness and percentage of pairs that were highly related (r > 0.5) between samples taken in the 2000s and 2011 to determine if inbreeding potential increased over the decade. We tested for molecular genetic evidence for population decline using the software Bottleneck (Cornuet and Luikart 1996). Two tests were employed, one to detect heterozygote excess expected after a bottleneck in population size and another to detect the expected loss of rare alleles (mode shift test). Finally, we compared the measures of genetic diversity between Leech Lake and Woman Lakes samples and samples from 13 other lakes determine if the Leech Lake or Woman Lake populations have uncharacteristically low diversity for Minnesota walleye populations.

Results and Discussion

Genetic equilibrium testing - The genetic data were consistent with expectations for Hardy-Weinberg and linkage equilibrium in all but one test. The locus Svi6 did not meet HW expectations using an exact test but it did after follow-up testing for a heterozygosity deficit. These results indicate the genetic data were suitable for subsequent data analysis.

Genetic diversity measures - The genetic diversity measures of heterozygosity and allelic richness showed no declining trend between the early 2000s and the 2011 samples from Leech Lake and Woman Lake (Table 1). Estimates for He and Ho changed little (< 0.03) and one increased slightly while the other decreased slightly over time in each lake. Allelic richness, the more sensitive indicator of small population effects, actually rose slightly in each population. Sampling error likely contributed to the higher richness estimates but the stocking of the Woman Lake strain into Leech Lake may also have altered allele frequencies or contributed new alleles, leading to an increase in richness. The Leech Lake sample from 2011 had 11 alleles that were not found in the 2002 Leech Lake sample but were in Woman Lake samples (they were at low frequencies, 0.007 to 0.028, so some may have just been missed in the 2002 sample).

Relatedness - Average pair-wise relatedness was low in both populations at both sampling periods (r = 0.00-0.04). The distribution of r-values broadly overlaps for samples from both lakes and over time within the same lake (Figure 1). A recent increase in inbreeding within a population or a large difference between lakes would have shifted some distributions to the right. Of particular concern would be pairs of individuals that are closely related, and if mated, would create highly inbred offspring that may suffer detrimental condition or fitness effects. Only 1.1-1.7% of potential pairs from each sampling period had r > 0.50 and the percentage declined slightly from the 2000s to the 2011. Relatedness estimates for single pairs are imprecise but because they are unbiased a large sample provides a good representation of what to expect across a population (Queller and Goodnight 1989). The rarity of high r values indicates that few closely related matings would be expected in these populations.

Bottleneck testing **-** The Leech and Woman populations did not show indications of a recent bottleneck using the heterozygosity excess (all p-values > 0.05) or mode shift tests in the software Bottleneck. Bottleneck tests have low power to detect small population declines with the moderate number of markers for which we had data. In contrast, simulations and real data sets have shown there is high power to detect large recent declines in population size (Cornuet and Luikart 1996). These tests, along with the stability of genetic diversity measures, indicate that the Woman or Leech populations have not undergone recent, severe bottlenecks.

Comparisons with other Minnesota walleye populations – To this point, only recent changes in genetic diversity in the Leech Lake and Woman Lake populations have been evaluated but past declines or bottlenecks can have long-lasting effects on genetic diversity. If genetic diversity declined in these populations prior to the 2000s then they should have lower values than other Minnesota populations, especially those within the same region. The Leech and Woman samples rank in the middle range of 18 Minnesota walleye populations for the three measures of genetic diversity (Table 2). Nearby populations with similar levels of genetic diversity include those in Lake Bemidji, Lake Andrusia and the Mississippi River near Grand Rapids.

Conclusions - The relatively high genetic diversity in Leech Lake and Woman Lake walleye populations, which has not declined over the past decade and is similar to that in other walleye populations, indicates no recent or historical population bottleneck of an extent that would have greatly increased inbreeding. A typical spawning pair, either in Leech Lake or in the Woman Lake spawning collection, will have low relatedness and thus low inbreeding in their offspring. Small changes in diversity may have been missed with the modest sample sizes and number of genetic markers we used but none of the analytical approaches suggested substantial inbreeding or losses of diversity, which is further supported by the demographic data indicating relatively large breeding populations. Furthermore, there is now the opportunity to form many unrelated pairs of Leech Lake x Woman Lake spawners in Leech Lake so long as stocking does not overwhelm the resident Leech population. These matings should enhance diversity because the Woman Lake population is slightly differentiated from the Leech lake population (Fst, a measure of population differentiation = 0.02); however, there is no reason to think artificially enhancing genetic diversity in Leech Lake is necessary or beneficial.

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Table 1. Sample sizes (N) and genetic diversity measures based on eight microsatellite DNA loci for 18 samples from Minnesota walleye populations. Diversity measures include expected heterozygosity (H_e), observed heterozygosity (H_o), and allelic richness A_r based on standardized sample of 80 genes (40 individuals).

Population	N	H_e	H_o	A_r (80)
Leech 2002	82	0.73	0.74	7.8
Leech 2011	70	0.74	0.71	8.4
Woman 2000	71	0.75	0.74	8.1
Woman 2011	79	0.74	0.76	8.3
Bemidji	30	0.74	0.73	7.9
Andrusia	44	0.74	0.74	8.1
Cutfoot	182	0.71	0.69	7.0
Miss- Grand Rapids	59	0.73	0.73	7.9
Miss- St. Paul	47	0.79	0.76	10.1
Miss- Red Wing	48	0.79	0.80	10.6
Miss- Brainerd	34	0.72	0.71	6.8
Pike	178	0.68	0.68	7.5
St. Louis	171	0.76	0.74	9.1
Pine	91	0.76	0.74	8.1
Ottertail	96	0.72	0.71	7.8
Red	169	0.73	0.70	7.7
Sallie	72	0.71	0.73	7.9
Average		0.73	0.73	8.10

Table 2. Genetic diversity measures as reported in Table 1 sorted from highest to lowest. Leech Lake and Woman Lake estimates are in the middle range of 13 other Minnnesota walleye populations.

Population	H_e	Population	H_o	Population	A_r (80)
Miss- Red Wing	0.79	Miss- Red Wing	0.80	Miss- Red Wing	10.6
Miss- St. Paul	0.79	Miss- St. Paul	0.76	Miss- St. Paul	10.1
St. Louis	0.76	Woman 2011	0.76	St. Louis	9.1
Pine	0.76	St. Louis	0.74	Leech 2011	8.4
Woman 2000	0.75	Pine	0.74	Woman 2011	8.3
Woman 2011	0.74	Woman 2000	0.74	Woman 2000	8.1
Leech 2011	0.74	Andrusia	0.74	Andrusia	8.1
Bemidji	0.74	Leech 2002	0.74	Pine	8.1
Andrusia	0.74	Bemidji	0.73	Sallie	7.9
Miss- Gr Rapids	0.73	Miss- Gr Rapids	0.73	Bemidji	7.9
Leech 2002	0.73	Sallie	0.73	Miss- Gr Rapids	7.9
Red	0.73	Miss- Brainerd	0.71	Ottertail	7.8
Miss- Brainerd	0.72	Leech 2011	0.71	Leech 2002	7.8
Ottertail	0.72	Ottertail	0.71	Red	7.7
Sallie	0.71	Red	0.70	Pike	7.5
Cutfoot	0.71	Cutfoot	0.69	Cutfoot	7.0
Pike	0.68	Pike	0.68	Miss- Brainerd	6.8

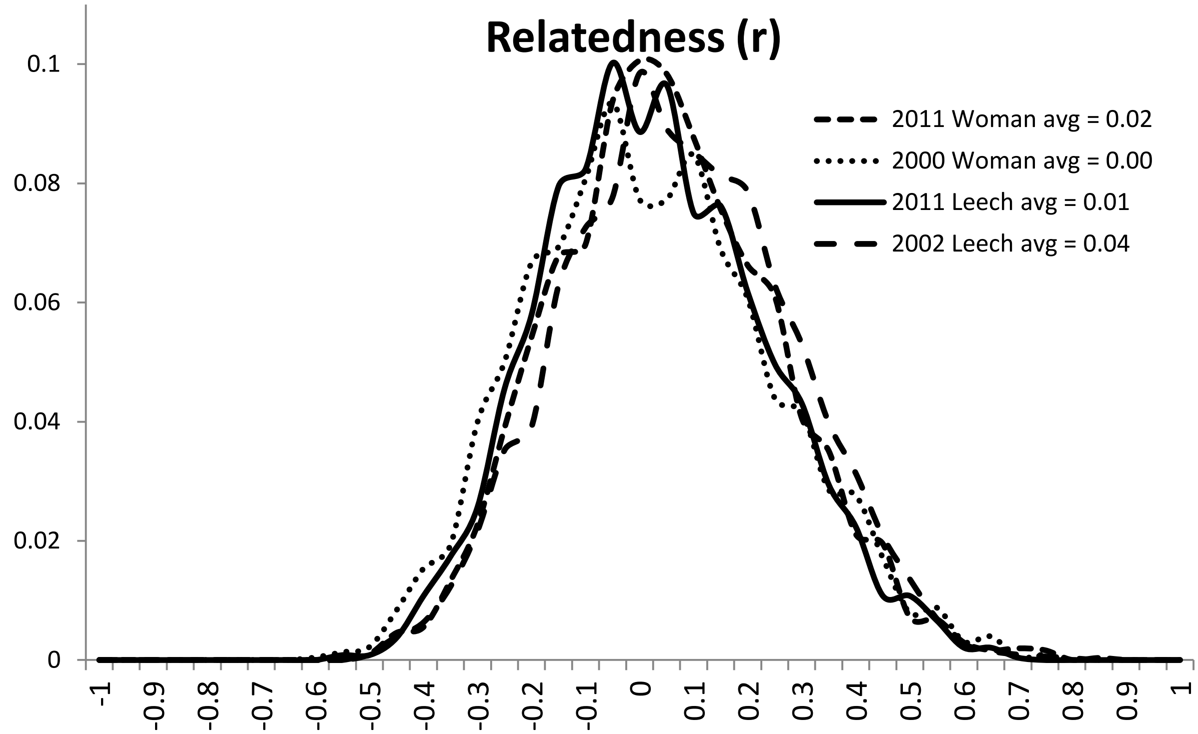

Figure 1. Relatedness estimates for all pairs of individuals in samples from Leech Lake in 2002 and 2011 and Woman Lake in 2000 and 2012. If a population had higher relatedness, which would lead to greater potential for inbreeding, its distribution would have shifted to the right. True values of r for unrelated pairs are 0.0 but this estimator can be negative when a pair shares fewer alleles than expected by chance.

Variability in young walleye growth in Leech Lake
Ward, M., D. Staples, and D. Schultz. 2013. Staff Report. Minnesota Department of Natural Resources, Walker Area Fisheries Office, Walker, MN.

Key points:

- Growth of age-0 walleye was tested for differences between naturally produced (wild) and stocked (OTC-marked) fish from the 2005 through 2012 year-classes sampled via seining (July), trawling (August), and electrofishing (September).
- No significant difference in growth rates were detected for age-0 walleye in 2005, 2006, 2008, 2010, 2011, and 2012. Statistically, OTC-marked fish were larger in 2007 by 0.1 inches ($p = 0.01$) but smaller by 0.1 inches ($p = 0.05$) in 2009. Although growth rates in 2007 and 2009 were statistically different, these do not represent effects that result in meaningful biological outcomes, such as survival of age-0 fish through their first winter.
- Growth of age-1 walleye was tested for differences between naturally produced and stocked fish from the 2005, 2006, and 2011 year-classes. These fish were collected via trawling, electrofishing, and gillnetting.
- Growth rates of age-1 walleye were similar among stocked and naturally-produced groups through the second summer of life.
- Growth rates of age-0 walleye sampled in trawl hauls from 1987 through 2012 were compared within the context of pre-stocking (1987-2004) and post-stocking (2005-2012) levels.
- Growth rates have varied considerably among years. Median lengths of age-0 walleye sampled by trawling were the second (2009), third (2008), and fourth (2011) poorest on record; these corresponded with fry stockings of 22.7, 22.2, and 22.0 million, respectively.
- A more detailed review of influences on age-0 growth determined a negative relationship between first-year growth and total fry density, whereas growth was positively associated with cumulative temperature units; this relationship has been well-documented elsewhere. A relationship between total fry density and temperature units was not detected, suggesting these two factors were acting independently on growth.
- In conclusion, stocked and naturally-produced fish are growing at similar rates that are within the range observed in the pre-stocked population, providing no evidence that inbreeding depression is occurring. Higher fry densities, whether occurring naturally or inflated by stocking activities, have had an adverse effect on growth of age-0 walleye, and this could impact recruitment. Poor growth resulting from high fry densities could be offset by warmer summers but exacerbated during cooler growing seasons. Future management decisions should consider managing for total fry densities having the optimum growth and recruitment potential.

Background

Recently, stakeholders have expressed concerns over the genetic diversity of the Leech Lake, Minnesota walleye population as well as the diversity of the brood source used for experimental fry stockings during 2005-2012. Tools used to measure loss of genetic diversity and its possible impacts (inbreeding depression) include molecular genetic testing (see Miller 2012) and comparing growth rates of young fish. Cena et al. (2006) found that early growth of walleye (mm/y) was the only one of three major life history categories (growth, reproductive investment, and mortality) that was strongly associated with genetic diversity of a walleye population. That is, as genetic diversity of a population declined and inbreeding increased, early growth rates of fish was the only physical trait where effects were readily manifested and detectable. One of the concerns explicitly expressed was declining growth rates of young fish in Leech Lake as the result of management activities by the Minnesota DNR. Therefore, our objectives were to test the growth rates of age-0 and age-1 walleye for differences among source (stocked versus wild) during years stocking occurred and among years, which included sampling conducted from 1987-2004 before stocking was initiated.

Methods

Field sampling

Seining - Five long-term seining stations (Figure 1) were sampled weekly throughout July using the parallel-to-shore method. Two hauls were made at each station using a bag seine (100-ft. long, 5-ft. deep, 0.25-in. untreated mesh). The area seined was determined by assuming the actual lakeward distance covered by the seine was 90 feet, which compensated for the bow in the seine created by water resistance during pulling. This figure was then multiplied by the distance of the pull (150 feet) and resulted in an area of 13,500 ft^2 (0.310 acres) per seine haul. Up to 20 age-0 walleye were collected from each haul when possible. These fish were retained for individual measurement (total length (TL), mm; weight (W), g) and otolith removal no later than the following day.

Trawling- Trawling was conducted at the three long-term stations, Figure 1, in mid-August using a semi-balloon bottom trawl (25-ft. headrope, 0.25-in. mesh cod end liner) from 1987 through 2012. Eight trawls were conducted at Five Mile Point (TR-1), seven at Goose Island (TR-2), and five at Whipholt Beach (TR-s), for a total of 20 hauls, annually. Hauls at the three long-term stations consisted of five-minute tow times at a speed of 3.5 mph for a total effort of 100 minutes of trawl time. Up to 20 age-0 walleye were collected per haul for individual measurement (TL, mm; W, g) and otolith removal no later than the following day.

Electrofishing - Fall nighttime electrofishing targeting YOY walleye was initiated in 2005 and stations were standardized in 2007 (Figure 1). Sampling was conducted during mid-September using a Coffelt pulsed-DC electrofishing boat (VVP 2E; single array anode). Standardized stations consist of four clusters of three 20-minute transects of continuous on-time from the starting point (Figure 1). Transects were approximately 3-5 feet deep on sand/gravel/cobble shorelines. Up to 25 age-0 walleye per transect were kept for individual measurement (TL, mm; W, g) and otolith removal no later than the following day. All age-1 walleye sampled were kept in 2012 for measurement and otolith removal.

Gill netting - Standard experimental gillnet sets were lifted at 36 different locations throughout the lake from early to mid-September (Figure 2). Four sets were made in each of 9 different areas (Figure 2). All age-

1 walleye captured were measured (TL, mm; W, g) and otoliths removed per standard methods for gill net surveys on Leech Lake.

Data analysis

An analysis of covariance model (ANCOVA) with Gaussian errors was used to test if the lengths of stocked and wild fish were different while accounting for fish growth during the sampling period:

$$\text{Length} = b_0 + b_1 * W + OTC + e,$$

where b_0 and b_1 are linear regression parameters denoting how fish length changes throughout the sampling period, W is the week of the year in which the walleye was sampled, OTC is a dichotomous variable denoting the fish's marking status, and *e* is random error assumed to be normally distributed. A likelihood ratio test was used to determine if the OTC parameter significantly improved the model; if so, it would infer a difference in average length between stocked and wild walleye. Length differences were tested for each individual year for age-0 walleye from 2005 through 2012. Growth differences were tested by year for age-1 walleye sampled in 2006, 2007, and 2012.

With no meaningful differences between lengths of stocked and naturally-produced fish observed, these groups were combined for the following analyses. A linear model was used to standardize annual age-0 lengths the 34^{th} week of the year, or approximately August 15. The standardized lengths were then used as the response variable in a series of regression models and model fits that were compared with AIC statistics. Independent variables tested included fry stocking density (StockedDen; fry/LA), total fry density (TotalDen; fry/LA), and growing degree days (GDD5). Since fish activity and metabolism in temperate zones can be determined by water temperature, growing degree days above 5 °C were calculated from air temperature data to characterize growing conditions among years. The linear relationship between air and lake surface temperature during ice-free months supports the use of GDD5 as a robust surrogate for lake temperature.

Results and Discussion

No significant differences in growth rates for marked and unmarked age-0 walleye were detected for the 2005, 2006, 2008, 2010, 2011, and 2012 year classes. An example of no significant difference is presented in Figure 3. In 2007, OTC-marked fish were significantly larger throughout the year by 0.1 inches ($p = 0.01$; Figure 4). In 2009, OTC-marked fish were significantly smaller throughout the year by 0.1 inches ($p = 0.05$; Figure 5). Although growth rates in 2007 and 2009 were statistically different, the small differences in length (0.1 inches) are not sufficient enough to infer biological implications, such as influencing first-winter survival, or evidence of inbreeding depression. The infrequency and contrast in the two observed differences further indicate that first-year growth rates are, for all practical purposes, similar among sources (stocked versus wild). No differences in growth rates for age-1 walleye in sampled 2006, 2007 or 2012 were found, and support other findings indicating that stocked and naturally-produced walleye are growing at similar rates in Leech Lake.

Growth differences of age-0 walleye sampled via trawling (August) from 1987 through 2012 were compared to determine if growth rates have changed overall relative to pre-stocking (1987-2004) years. Growth rates continue to be variable, similar to the pre-stocking time series (Figure 6). However, three of the five poorest growth observations occurred during years stocked with 20 million or more walleye fry. This prompted further questions on the influence of total walleye fry density on first- year growth which, in turn, could reduce winter survival.

First-winter survival of age-0 fish is a significant bottleneck affecting eventual recruitment of young fish to a fishery; this survival is positively associated with early growth and size entering winter. Consequently, management activities that have an adverse effect on growth could negatively impact recruitment. First-year growth was not strongly associated with stocked fry density but was negatively related to total fry density (Figure 7). As expected, increased temperatures resulted in faster growth. There was no strong relationship between total fry density and temperature, suggesting each factor acted independently on age-0 walleye growth.

Conclusions

Early walleye growth in Leech Lake is similar among stocked and natural sources and provides no indication that inbreeding depression is occurring or a management concern. Growth rates of stocked year classes have expressed similar variability among years as those produced prior to stocking activities initiated in 2005 and they are correlated with environmental factors. As observed in other systems, growth of age-0 walleye is strongly associated with temperature. However, higher fry densities, whether occurring naturally or inflated by stocking activities, have an adverse effect on growth of age-0 walleye, and this could adversely affect recruitment. A non-linear negative relationship between fry density and recruitment has been documented in Leech Lake (Schultz and Ward 2012); thus, it is highly probable that density-dependent growth is influencing walleye recruitment. Growing seasons with above-average temperatures could offset poor growth resulting from high fry densities. Conversely, poor growth would be exacerbated during cooler growing seasons, and recruitment would be expected to decline accordingly. As walleye recruitment is strongly associated with first-year growth in many lakes, future management decisions should consider managing for total fry densities with the optimum growth and recruitment potential.

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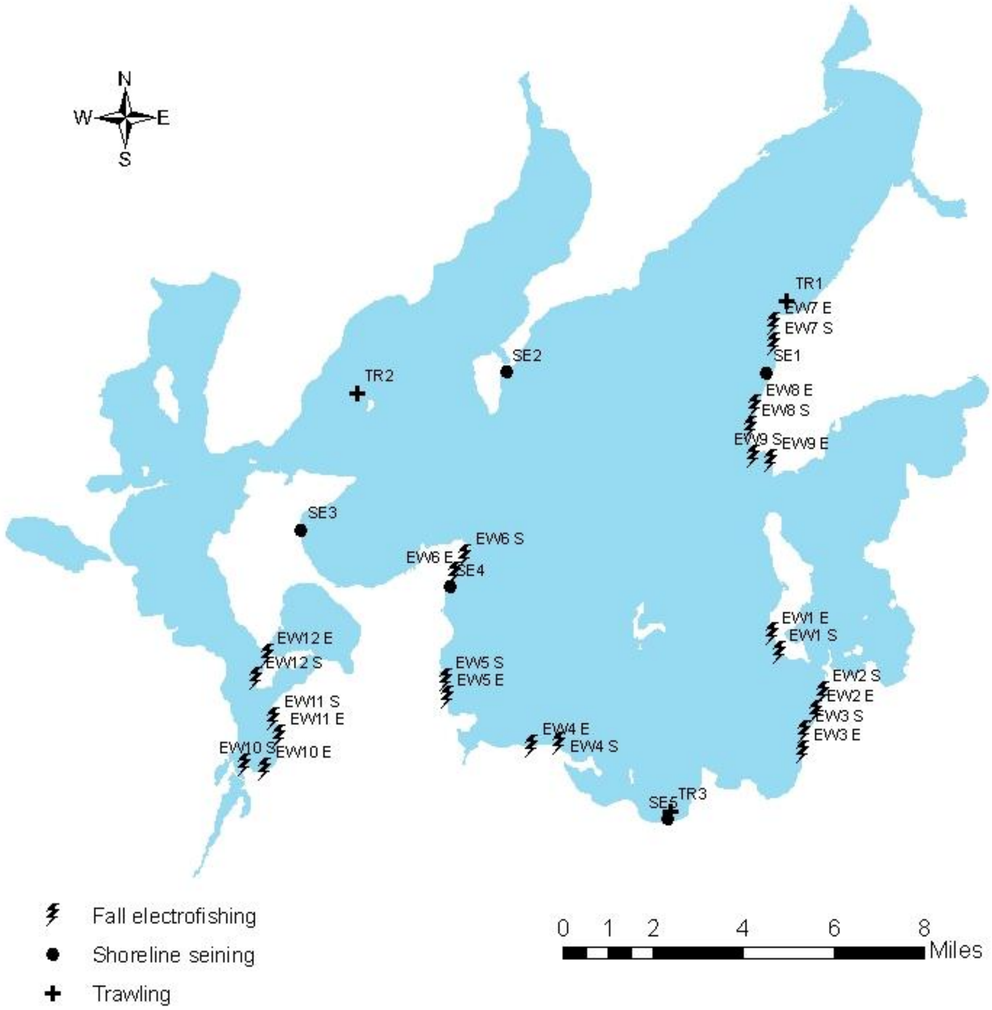

Figure 1. Long-term sampling stations targeting age-0 walleye in Leech Lake.

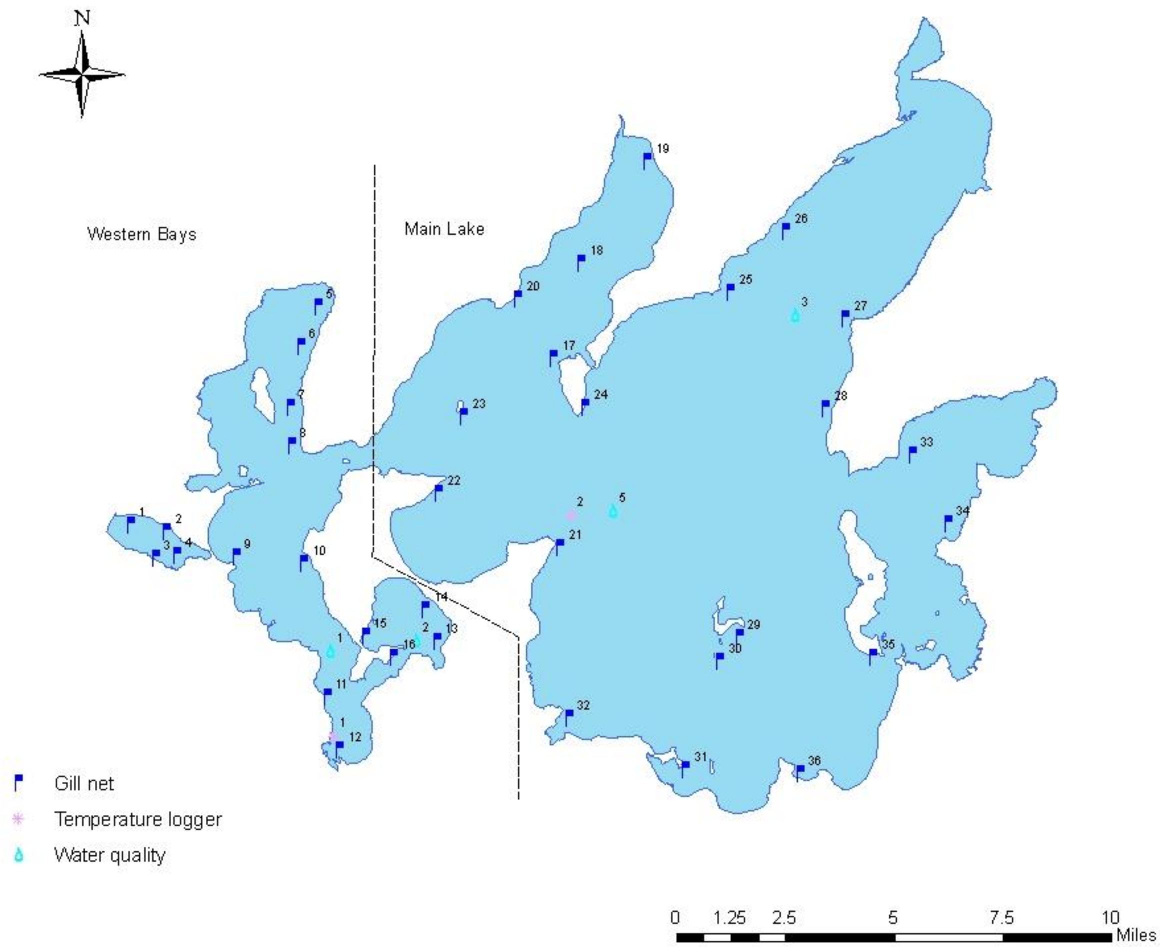

Figure 2. Gillnet (flags), temperature loggers (dots) and water quality (droplets) sampling locations on Leech Lake.

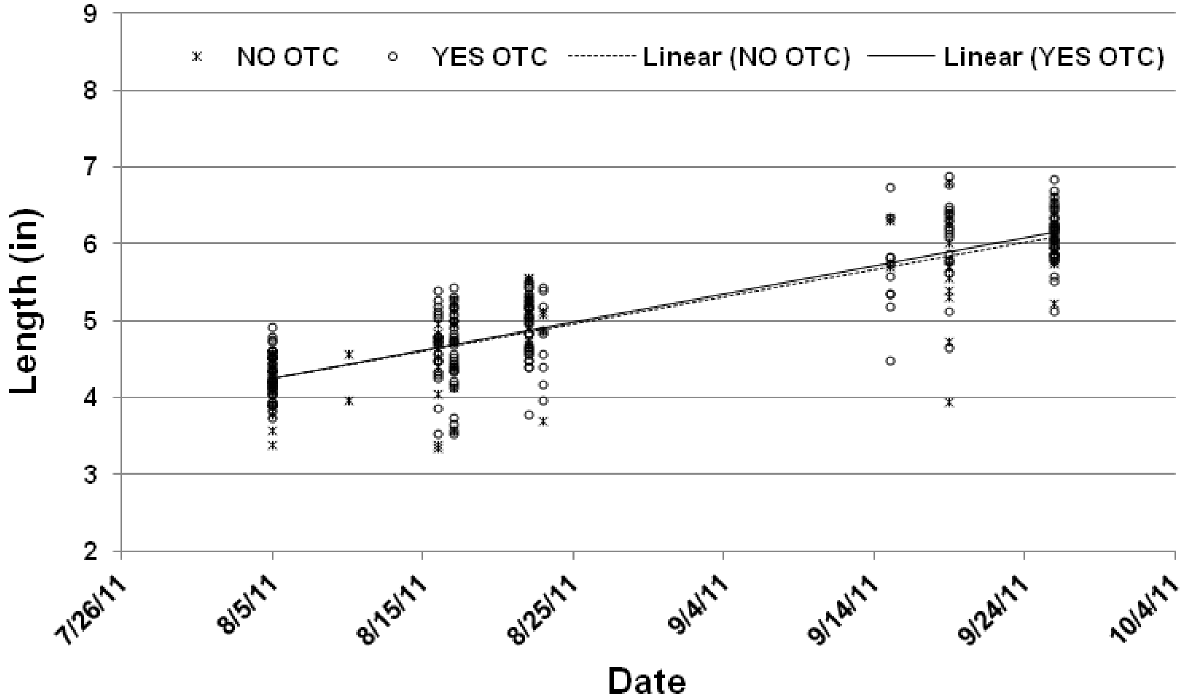

Figure 3. Growth rates of naturally produced (NO OTC) and stocked (YES OTC) age-0 walleye sampled throughout 2011. Growth rates were similar among the two groups.

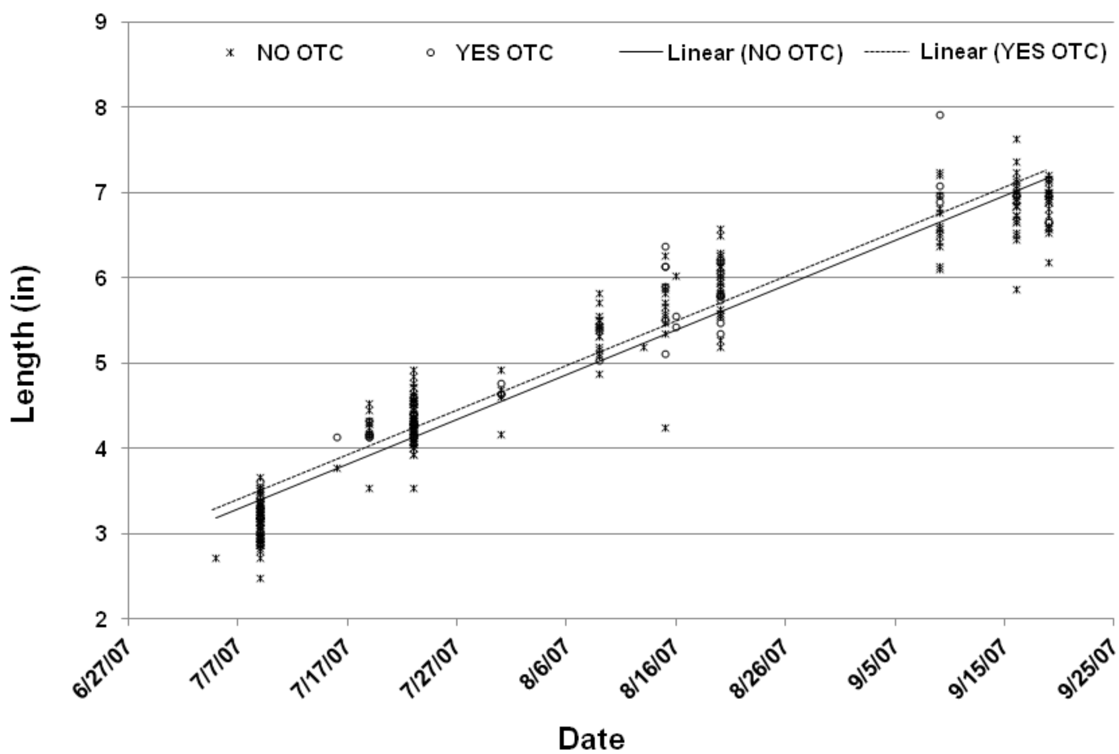

Figure 4. Growth rates of naturally produced (NO OTC) and stocked (YES OTC) age-0 walleye sampled throughout 2007. Stocked fish were 0.1 inches longer than naturally produced fish.

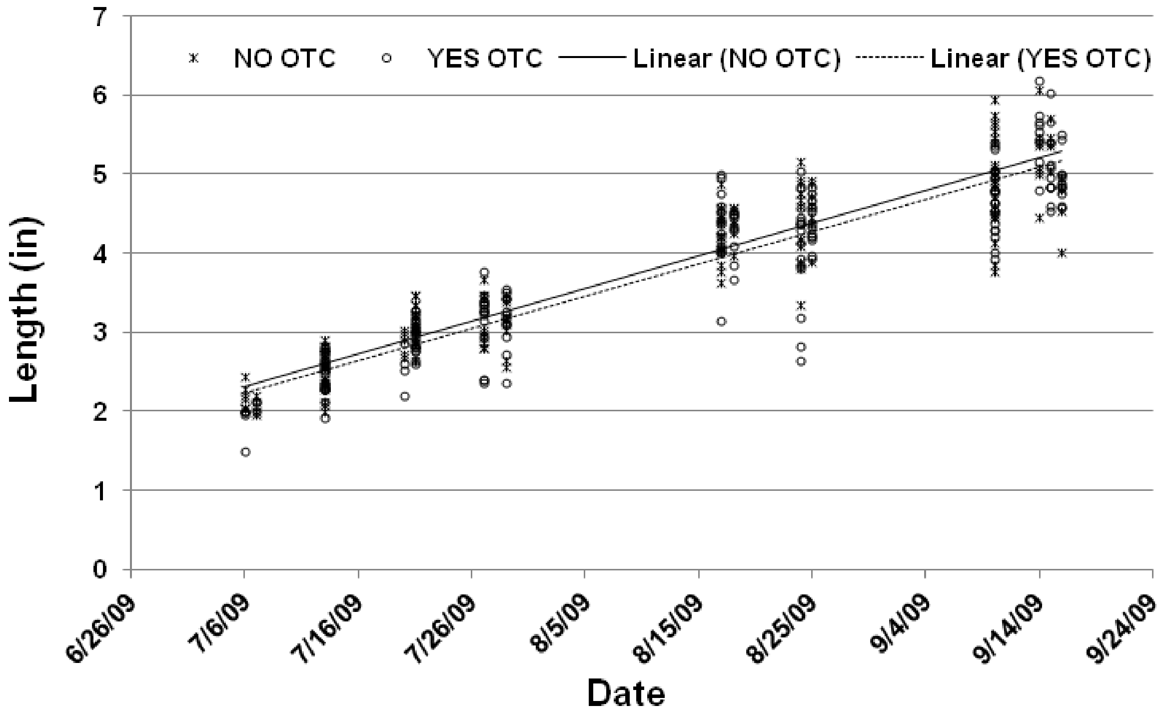

Figure 5. Growth rates of naturally produced (NO OTC) and stocked (YES OTC) age-0 walleye sampled throughout 2009. Stocked fish were 0.1 inches shorter than naturally produced fish.

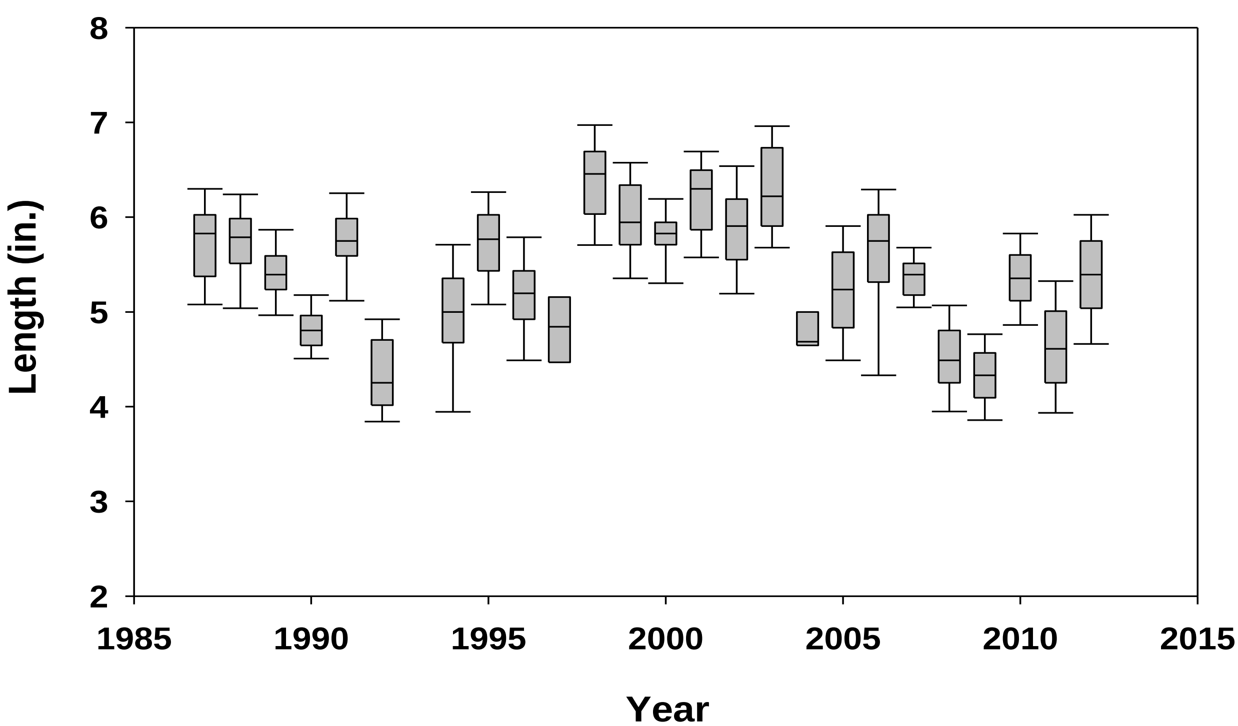

Figure 6. Length (inches) of age-0 walleye sampled via trawling in mid-August from 1987 through 2012. Median length (center line), 25th and 75th percentiles (grey box), and 10th and 90th percentiles (error bars) are represented.

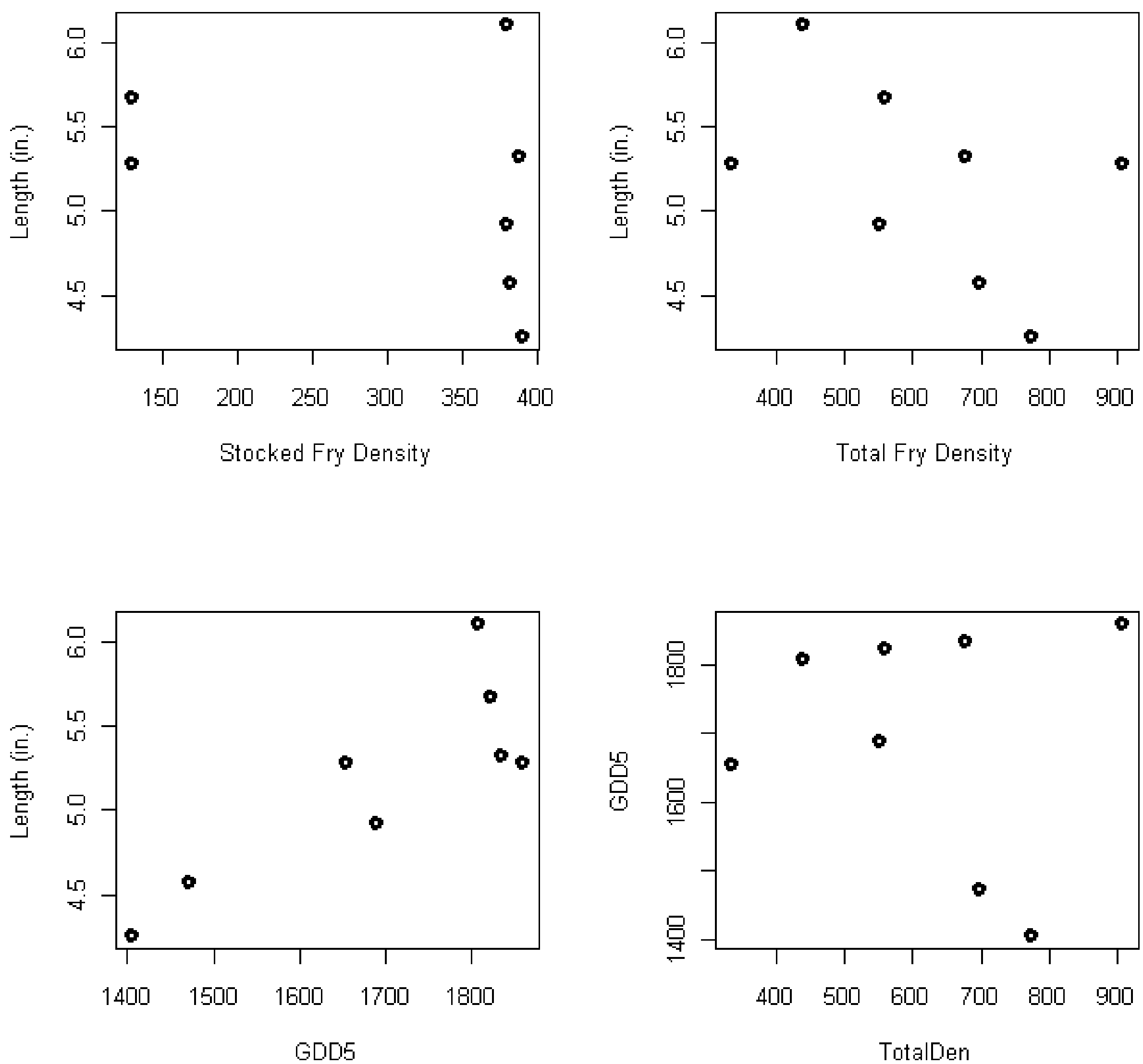

Figure 7. Relationships between mean total length of age-0 walleye during the 34th week of the year, stocked fry density, total fry density, and growing degree days (GDD5) at Leech Lake, Minnesota.