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**Factors Regulating Walleye Early Survival and Cohort Strength
in Eastern South Dakota Glacial Lakes**

By

Richard D. Zweifel

A dissertation submitted in partial
fulfillment of the requirements for the degree

Doctor of Philosophy

Biological Sciences (Fisheries Science)

South Dakota State University

2006

**Factors Regulating Walleye Early Survival and Cohort Strength
in Eastern South Dakota Glacial Lakes**

This dissertation is approved as a creditable and independent investigation by a candidate for the Doctor of Philosophy degree and is acceptable for meeting the dissertation requirements for this degree. Acceptance of this dissertation does not imply that the conclusions reached by the candidate are necessarily the conclusions of the major department.

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Date

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I would like to dedicate this dissertation to the person who really made this study possible, my wife Karla. She has been the single biggest stabilizing force in my life throughout my career and has supported me, although grudgingly at times, in all my endeavors. Thank you.

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Abstract

Factors Regulating Walleye Early Survival and Cohort Strength in Eastern South Dakota Glacial Lakes

Richard D. Zweifel

16 November 2006

Walleye *Sander vitreus* is an important ecological component of glacial lake aquatic communities in eastern South Dakota, and the most popular sport fish in the region. Walleye populations in this region exhibit consistently poor or annually-variable reproductive success and are regularly stocked in an effort to maintain consistent recreational fisheries. However, current stocking programs are based on reproductive success from previous years rather than on expected reproductive success in the year which stocking occurs. Determination of walleye cohort strength at the larval life stage would provide a stocking prioritization system that would utilize the natural reproduction of in situ walleye populations, and maximize the potential benefits of stocked walleye by supplementing weak or failed cohorts. In consideration of these management issues, the objectives of this study were to: 1) evaluate the utility of three ichthyoplankton gears for estimating the strength of walleye cohorts at the larval life stage; 2) assess the interaction between yellow perch and walleye during their first year and 3) determine the factors influencing the reproductive success of South Dakota glacial lakes walleye populations.

Three cohorts of walleye were sampled from spring to fall in each of three years (2001 to 2003). Sampling was conducted in Clear (Marshall County), Madison

(Lake County), Parks (Day County), Sinai (Brookings County), and Thompson (Kingsbury County) lakes in the glacial lakes region of eastern South Dakota.

Concurrent larval walleye and yellow perch samples were collected weekly from 1 May through 15 June using a 0.5-m conical plankton net, a Miller high-speed fry sampler, and quatrefoil light traps. Juvenile walleye and yellow perch were collected bi-weekly from 1 July through 20 August with night-time seining; fall walleye collections consisted of a single night-time electrofishing trip during mid-September.

Light traps captured substantially more larval walleye than either of the other two active ichthyoplankton (IP) gears. In general, light traps captured walleye yolk-sac larvae shortly after hatching (third week in May) and the conical net and Miller sampler captured walleye two weeks later. Precision of larval walleye abundance estimates was poor for all three IP gears. However, significant positive correlations were found between peak larval walleye abundance estimates from all three IP gears, suggesting that catch rates from all three gears varied in accordance with larval walleye abundance. Mean lengths of walleye larvae captured by each of the three IP gears reflected the differences in catch timing. Walleye captured with light traps were less than 11 mm and were generally larger than 13 mm in the two active IP gears.

Peak larval walleye catch rates from all three IP gears showed highly significant ($P < 0.001$) positive linear correlations to estimates of relative abundance of juveniles from both summer seining and fall electrofishing. Although, prediction of walleye cohort strength from larval sampling is plausible using any of the three IP gears, light traps show the most promise as a predictive tool. Light traps captured walleye larvae from weak to

very strong cohorts, while the active gears only captured walleye larvae from strong to very strong cohorts. In addition, light traps capture newly-hatched yolk sac larvae during the same time of the year that state hatcheries are producing walleye fry for stocking. Predictions of cohort strength generated at this time could direct hatchery products to waters with weak or failed cohorts. That walleye cohort strength was correlated with larval abundance suggests that cohort strength was set before larval sampling occurred. Mortality of larvae to fall was likely high but occurred in a predictable manner. The absence of walleye larvae in IP samples from waters with failed cohorts suggests that cohort strength was determined by the number of walleye that hatch rather than catastrophic or episodic mortality occurring at the larval or juvenile life stages.

Agreement between trap-net and gill-net estimates of walleye population structure and function was assessed using historical standardized survey data collected by the South Dakota Department of Game, Fish, and Parks. Concurrent trap-net and experimental gill-net sets in eleven eastern South Dakota glacial lakes from 1994 to 2000 were used to generate paired estimates of population size structure (proportional stock density, PSD and relative stock density- preferred length, RSD-P), catch per unit effort (CPUE), and growth (mean length-at-age). Relative size selectivity of the two gears was also determined and was found to show a negative relationship with fish length. Estimates of size structure did not differ between the two gears for walleye PSD or RSD-P. Relative abundance estimates did not agree for any age-classes considered or for all ages combined. Trap-net estimates of walleye mean length-at-age were significantly higher than gill-net estimates for ages 1, 2, 3, and 5. Consideration should be given to

size selective biases associated with using multiple gears when catch data are being used for long-term monitoring purposes.

Standardized fish sampling (summer trap netting and gill netting and fall electrofishing) and climatological data from either 2000 or 2001 were compiled for 12 eastern South Dakota walleye populations to determine the factors that cause the variability observed in walleye cohort strength. The models that were evaluated included combinations of variables reflecting measures of parental stock (abundance, size structure, and energetic state), spring egg incubation conditions (temperature warming rate and stability), inter-specific competition with yellow perch, and cannibalism. Second-order Akaike's Information Criterion was used to evaluate the likelihood of the potential models. The five best models included combinations of three to seven of the following variables: mean winter temperature, CPUE of age-4+ walleye, walleye RSD-P, CPUE of yellow perch from the year prior to spawning, CPE of yellow perch during a walleye cohort's first growing season, CPUE of yellow perch <156 mm, CPUE of yellow perch >156 mm, and coefficient of variation for temperature during the incubation period. The best model included seven of the eight above explanatory variables, all except incubation temperature CV, and was by far the "best" of all the models evaluated, accounting for all of the variation in walleye cohort strength (adjusted $R^2=1.0$). These results suggest that walleye cohort strength is the product of a complex interaction of factors acting through parental stock to effect egg production, egg quality, and hatching success. There is some evidence to suggest that eastern South Dakota walleye populations may follow a stock-recruitment relationship. However, this relationship is

obscured by the variability arising from factors influencing first year survival, i.e. hatching success and prey availability. Management strategies implemented to improve walleye cohort strength should focus on maintaining moderate adult (age 4+) walleye population abundance and enhancing the reproductive success of yellow perch to provide a consistent prey base for walleye.

Table of Contents

Acknowledgements	iii
Abstract	iv
List of Tables.....	xi
List of Figures.....	xiv
Chapter 1. Evaluation of Three Ichthyoplankton Gears for Collection of Larval Percids in Shallow Glacial Lakes	
Introduction.....	1
Methods.....	2
<u>Larval collection and processing</u>	2
<u>Analyses</u>	4
Results and Discussion	5
Recommendations.....	10
Chapter 2. Relations Between Larval Abundance and Cohort Strength of Walleye in South Dakota Glacial Lakes	
Introduction.....	27
Methods.....	29
Results and Discussion	31
Chapter 3. Importance of age-0 Yellow Perch for Survival of age-0 Walleye: Implications for Walleye Cohort Strength	
Introduction.....	44
Methods.....	45
Results and Discussion	47

Management Implications.....	50
Chapter 4. Comparison of walleye population parameter estimates derived from concurrent trapnet and gillnet sets	
Introduction.....	59
Methods.....	60
<u>Fish Collections</u>	60
<u>Analyses</u>	62
Results.....	63
Discussion.....	65
Chapter 5. Factors Controlling Walleye Cohort Strength in Eastern South Dakota Glacial Lakes	
Introduction.....	81
Methods.....	83
<u>Study populations</u>	83
<u>Data collection / sources</u>	84
<u>Model development</u>	85
Results and Discussion	88
Chapter 6. Summary and Future Research Needs	
Summary.....	96
Research and Data Needs.....	97
References.....	99

List of Tables

Table 1-1. Characteristics of South Dakota glacial lakes sampled during 2001-2003. Taken in part from Stukel (2003).....	13
Table 1-2. Larval walleye abundance estimates generated from three ichthyoplankton gears in South Dakota glacial lakes from 1 May to 15 June, 2001-2003. Abundance estimates from 0.5-m and Miller nets are mean number / m ³ and light trap estimates are mean number per trap. Sampling week indicates the week the larval sample was collected, where week 1 is 1 May through 7 May and week 6 is 5 June through 11 June. Only sampling dates where walleye larvae were captured are shown. The number of samples required indicates the required effort necessary to obtain an abundance estimate with a coefficient of variation that is 20% of the mean.....	14
Table 1-3. Yellow perch abundance estimates (number / cm ³) from 0.5-m conical plankton net samples. Sampling week indicates the week of the year a sample was collected, where week 1 is 1 May through 7 May and week 6 is 5 June through 11 June. Only sampling dates where yellow perch larvae were captured are shown. The number of samples required indicates the effort necessary to obtain an abundance estimate with a coefficient of variation that is 20% of the mean.....	15
Table 1-4. Larval yellow perch abundance estimates (number / cm ³) from Miller net samples. Sampling week indicates the week of the year a sample was collected, where week 1 is 1 May through 7 May and week 6 is 5 June through 11 June. Only sampling dates where yellow perch larvae were captured are shown. The number of samples required indicates the effort necessary to obtain an abundance estimate with a coefficient of variation that is 20% of the mean.....	16
Table 1-5. Larval yellow perch abundance estimates (number / trap) from light trap samples. Sampling week indicates the week of the year a sample was collected, where week 1 is 1-May through 7-May and week 6 is 5-June through 11-June. Only sampling dates where yellow perch larvae were captured are shown. The number of samples required indicates the effort necessary to obtain an abundance estimate with a coefficient of variation that is 20% of the mean.....	17
Table 1-6. Mean length of larval walleye from 0.5-m conical net, Miller net, and light trap samples, collected from eastern South Dakota glacial lakes during 1 May to 15 June, 2001-2003.....	18

Table 1-7. Yellow perch mean length from 0.5-m conical plankton net, Miller net, and light trap samples collected from eastern South Dakota glacial lakes during 1 May to 15 June, 2001-2003.....	19
Table 1-8. Linear relations between estimates of peak larval abundance from 0.5-m conical plankton net, Miller net, and light trap samples for walleye and yellow perch collected from eastern South Dakota glacial lakes, 2001-2003.....	20
Table 2-1. Relative abundance of age-0 walleye generated from summer seine samples in South Dakota glacial lakes 2001-2003. CPUE is mean number of age-0 walleye per seine haul and SE is the standard error of the mean.....	37
Table 2-2. Estimates of age-0 walleye relative abundance from fall electrofishing samples in South Dakota glacial lakes 2001-2003. Catch per unit effort (CPUE) is the mean number of age-0 walleye collected per hour of electrofishing.....	38
Table 2-3. Linear relations between peak larval walleye abundance estimated with three ichthyoplankton gears and juvenile walleye abundance estimates from summer seine and fall electrofishing samples.....	39
Table 4-1. Annual effort (net nights) values for simultaneous trap-net and gill-net sets in eleven South Dakota lakes from 1994 through 2000.....	70
Table 4-2. Comparison of trap-net and gill-net proportional stock density (PSD) and relative stock density of preferred-length fish (RSD-P) relations for walleye in eleven South Dakota lakes. Confidence intervals are 95% intervals of regression model parameter estimates.....	71
Table 4-3. Least-squares relations between trap-net and gill-net catch rate ranks for walleye in eleven South Dakota lakes. Confidence intervals are joint 95% confidence intervals of regression model parameter estimates.....	72
Table 4-4. Comparisons of walleye mean length-at-age estimates calculated from catches in trap-nets and gill-nets. Confidence intervals are 95% confidence intervals of regression model parameter estimates.....	73
Table 4-5. Estimated efficiency of gill-nets and trap-nets for sampling age-1 and age-2 walleye in eastern South Dakota glacial lakes. Expected CPUE were calculated from extrapolation of catch curves based on mean catches of age-3 to age-5 walleye from the 1993-1997 cohorts.....	74

Table 5-1. Eastern South Dakota glacial lake walleye populations used to explain the variation observed in walleye cohort strength. CPH is fall electrofishing catch per hour.....	94
Table 5-2. Model selection criteria results for the five best models used to explain the variation in walleye recruitment from eastern South Dakota glacial lakes. K is the number of parameters in the model, AIC_C is the corrected Akaike's information criteria statistics, and Δ_i is the increase in AIC_C compared to the “best” model. Variables included in the models were: Trap-net catch per unit effort (CPE) of age-4+ walleye (4+WCPE), trap-net estimates of walleye RSD-P (WRSDP), gillnet CPE of yellow perch from the previous year (YPCPE-1), mean winter temperature (WIT), gillnet CPE of yellow perch (YPCPE), gillnet CPE of yellow perch >156mm (YP>156), gillnet CPE of yellow perch <156mm (YP<156), and the coefficient of variation of temperature during 15 April to 15 May (INCV).	95

List of Figures

- Figure 1-1. Weekly estimates of larval walleye abundance generated from a 0.5-m conical net (A), a Miller sampler (B), and light traps (C) in three eastern South Dakota glacial lakes during the spring of 2001. Larval abundance estimates were calculated as density (number / m³) for active gears and catch per trap for light traps. Error bars are ± 1 standard error.....21
- Figure 1-2. Weekly estimates of larval walleye abundance generated from a 0.5-m conical net (A), a Miller sampler (B), and light traps (C) in three eastern South Dakota glacial lakes during spring of 2002. Larval abundance estimates were calculated as density (number / m³) for active gears and catch per trap for light traps. Error bars are ± 1 standard error.....22
- Figure 1-3. Weekly estimates of larval walleye abundance generated from a 0.5-m conical net (A) and light traps (B) in three eastern South Dakota glacial lakes during spring of 2003. Larval abundance estimates were calculated as mean density (number / m³) for the 0.5-m net and mean catch per trap for light traps. Error bars are ± 1 standard error.....23
- Figure 1-4. Weekly estimates of larval yellow perch abundance (number / m³) generated from 0.5-m conical net samples in eastern South Dakota glacial lakes, 2001-2003. Larval abundance estimates were calculated as density (number / m³) for active gears and catch per trap for light traps. Error bars are ± 1 standard error.....24
- Figure 1-5. Weekly estimates of larval yellow perch abundance (number/m³) generated from Miller net samples in eastern South Dakota glacial lakes, 2001-2003. Larval abundance estimates were calculated as density (number / m³) for active gears and catch per trap for light traps. Error bars are ± 1 standard error.....25
- Figure 1-6. Weekly estimates of larval yellow perch abundance (number / trap) generated from light trap samples in eastern South Dakota glacial lakes, 2001-2003. Larval abundance estimates were calculated as density (number / m³) for active gears and catch per trap for light traps. Error bars are ± 1 standard error.....26
- Figure 2-1. Linear relations between peak larval walleye abundance (no./m³) from 0.5-m conical net samples and relative abundance of age-0 walleye from summer seining (number / haul) and fall electrofishing (number / h).....40
- Figure 2-2. Linear relationships between peak larval walleye abundance (number / m³) estimated from Miller net samples and relative abundance of

age-0 walleye from summer seining (number / haul) and fall electrofishing (number / h).....	41
Figure 2-3. Linear relationships between peak larval walleye abundance (number / trap) estimated from light trap samples and relative abundance of age-0 walleye from summer seining (number / haul) and fall electrofishing (number / h).....	42
Figure 2-4. Linear regressions between estimates of age-0 walleye cohort size and electrofishing catch rates from Wisconsin (Serns 1982; dashed line) and South Dakota lakes (solid line).....	43
Figure 3-1. Linear relations between age-0 walleye fall abundance and peak abundance of yellow perch larvae from three ichthyoplankton gears and from peak abundance of juveniles from summer seine samples. Abundance is catch per unit effort for light traps (number / trap) and seine (number / haul) and density (number / m ³) for Miller and plankton net estimates.....	54
Figure 3-2. Linear relations between age-0 walleye fall abundance and weekly estimates of larval yellow perch abundance from 0.5-m conical plankton net (number / m ³) and light trap (number / trap) samples.....	55
Figure 3-3. Relations between age-0 walleye fall abundance (catch / hour) and weekly estimates of larval yellow perch mean length from eastern South Dakota glacial lakes.....	56
Figure 3-4. Relations between age-0 walleye fall abundance and growth rate of age-0 yellow perch as larvae (open circles) and juveniles (filled circles). The relationship presented for yellow perch larval growth rate does not include the Parks Lake 2001 cohort.....	57
Figure 3-5. Yellow perch length distributions from July and August seine samples from four South Dakota glacial lakes. Grey boxes indicate the upper and lower quartiles, vertical bars represent the 10 th and 90 th percentiles, and points indicate the 5 th and 95 th percentiles. The lines represent estimated maximum gape of the smallest (lower broken line), median (solid line), and largest (upper broken line) age-0 walleye captured on each sampling date...58	58
Figure 4-1. Length distributions of walleye collected by gill-nets and trap-nets in eleven South Dakota glacial lakes 1994-2000.....	75
Figure 4-2. Relations between relative selectivity of trap-nets and experimental gillnets (trap-net CPUE / gill-net CPUE) to fish length for walleye in eastern South Dakota glacial lakes. The solid line is a least-squares regression line.....	76

- Figure 4-3. Relations between proportional stock density (PSD) and relative stock density of preferred-length fish (RSD-P) calculated from catches of walleye in trap-nets and experimental gill-nets in eleven South Dakota glacial lakes. Solid lines are least-squares regression lines and the dotted lines are 1:1 reference lines.....77
- Figure 4-4. Relations between trap-net and experimental gill-net CPUE (walleye / net night) ranks for eleven South Dakota walleye populations. The solid line is a least-squares regression line and the dotted line is a 1:1 reference line.....78
- Figure 4-5. Relations between trap-net and experimental gill-net CPUE (walleye / net night) ranks for age-1 through age-5 walleye in eleven South Dakota lakes. Solid lines are least-squares regression lines and the dotted lines are 1:1 reference lines.....79
- Figure 4.6. Relations between trap-net and gill-net mean length-at-age estimates from eleven South Dakota walleye populations. Solid lines are least-squares regression lines and the dotted lines are 1:1 reference lines.....80

Chapter 1

Evaluation of Three Ichthyoplankton Gears for Collection of Larval Percids in Shallow Glacial Lakes

Introduction

Interpretation of fisheries abundance data often relies on the assumption that catch of fishes at a given point in time is a representative sample of an entire population or cohort. However, this assumption is often not met for assessments of larval fishes as the composition of ichthyoplankton samples is determined by a complex interaction among behaviors and performance of the targeted fish(es), sampling environment, and the specific gear used (Kelso and Rutherford 1996). Species- and life-stage specific differences in size, visual acuity, swimming speed, and habitat use determine the susceptibility of larvae to sampling methods (Barkley 1964; Cada and Loar 1982). Environmental conditions such as water clarity or net clogging, as a result of high algal or zooplankton biomass, can reduce the efficiency of larval sampling gears (Smith et al. 1968; Williams and Deubler 1968). Net design, tow speed, mesh size, and specific sample site characteristics must be chosen carefully based on the objectives of the study (Smith et al. 1968; Noble 1970; Noble 1971).

Abundance estimates for larval fishes are often highly variable and difficult to interpret (Cyr et al. 1992). Studies exploring methods to reduce this variability and to develop an understanding of the biases associated with a particular sampling gear are numerous (Gregory and Powles 1988). These studies have often evaluated the specific

application (e.g., tow speed, mesh size) of a single gear for collection of a single species. Few studies have assessed the relative biases between concurrent catches from multiple larval gears. The purpose of this study was to compare size distributions, and estimates of abundance and associated precision from catches of three ichthyoplankton gears in multiple lakes with the intent of developing a practical protocol for sampling larval walleye *Sander vitreus* and yellow perch *Perca flavescens* in eastern South Dakota glacial lakes.

Methods

The percid populations sampled were characteristic of those throughout the glacial lakes region of eastern South Dakota. A thorough description of physical and chemical characteristics of all study lakes is given in Stukel (2002) and is summarized in Table 1-1. Lake Sinai was sampled in all three years of the study (2001-2003). Parks Lake (2001 and 2002) and Lake Thompson (2002 and 2003) were both sampled in two years. Lake Madison and Clear Lake were only sampled in 2001 and 2003, respectively.

Larval collection and processing

Ichthyoplankton (IP) samples were collected weekly in three eastern South Dakota glacial lakes each year using modified quatrefoil light traps and a conical IP net from 1-May to 15-June, in 2001, 2002 and 2003. A Miller high-speed fry sampler was also used to collect concurrent IP samples in 2001 and 2002 but was discontinued in 2003 because of its ineffectiveness at sampling larval fishes in these lakes. Ten conical IP net

and Miller samples were collected during the same day at the same sample sites, except at Parks Lake where only eight sites were sampled per week. Tow distance and volume filtered was determined for active gears using a General Oceanics mechanical flow meter. The conical net used was 2 m long, 0.5-m diameter mouth, with 1 mm bar-mesh. The net was towed just below the surface, 10-m behind the boat, at approximately 1 m/s, averaging 75 m³ of water filtered during a typical 5 minute tow. The net was towed in a circular pattern to prevent the net from encountering the boat wake and propeller cavitation. The rigid body of the Miller sampler was composed of a fiberglass tube 61 cm long and 15 cm wide, with a 10 cm aperture. The attached collection net was 61 cm long, with 1 mm bar-mesh. The Miller sampler was towed on the starboard side of the boat just below the surface at an average speed of 2 m/s, filtering 10 m³ of water during an average 10 min tow.

Light traps were constructed from four clear acrylic tubes (10 cm outside diameter x 28 cm long, 0.125 cm thick) attached (top and bottom) between two 23x23-cm acrylic panels, with a 3.8 L collection bucket attached underneath (Floyd et al. 1984). Collection buckets were equipped with 0.5-mm bar mesh. The light source used was a submersible lantern with a single incandescent bulb (23 lux at 10 cm) powered by four dry-cell batteries, which powered the lamp for approximately 4 h. Light traps were floated 25 cm below the surface at the same collection sites as the active gears. Light traps were set beginning at sunset and were retrieved the following morning, except at remote sampling locations (Clear Lake and Parks Lake) where light traps were retrieved after 4 h of submersion and loss of incandescence. Light trap and active gear samples were normally

collected on the same day, but were never collected more than 3 d apart during the same sampling week.

All samples were fixed in a 10% (by volume) formalin solution until they could be processed (1-7 d). Ichthyoplankton were stored in a 90% ethanol solution until they could be identified, enumerated, and measured. Total length was measured for up to 100 larval walleye and yellow perch collected in each gear on each sampling date. Many larvae captured in light trap samples were partially consumed by predacious invertebrates (Corixidae and Notonectidae), making further processing difficult. Partially-consumed individuals that could not be identified to species were assigned a species based on the species-proportions of the identifiable fishes in a sample.

Analyses

On each sampling date, larval walleye and yellow perch abundance was calculated as density (number / m³) for active gears and as number per trap for light traps. Determination of volumetric larval density estimates (number/L) for passive light trap samples was difficult because the effective range of this gear varies with water clarity, ambient light, and wind action or turbulence. Differences in units between larval abundance estimates prohibited direct comparisons between the three IP gears. However, association between larval abundance estimates was evaluated by testing for a positive linear relationship (H_0 : Slope = 0; $\alpha=0.05$) between peak abundance estimates calculated for all three gears.

Timing of peak catch was evaluated between years for each gear. To make direct comparisons across years, samples were grouped by the week of collection. Analysis of variance was used to test for significant differences between sampling weeks for each gear.

Precision of larval walleye and yellow perch abundance estimates was evaluated by determining the number of samples required to obtain a coefficient of variation that was 20% of the mean. Required sample size was estimated for each gear during each sampling week using the formula of Krebs (1999) for a Poisson distribution:

$$n = \left(\frac{100 \cdot CV \cdot t_{\alpha}}{r} \right)^2$$

where n is the number of samples required, CV is the coefficient of variation of the mean (standard deviation / mean), t_{α} is a tabulated t -value for large sample sizes and $\alpha = 0.05$, and r is the desired relative precision (20%).

Results and Discussion

In total there were 1,178 IP samples collected during the course of this study, 471 0.5-m net samples, 471 light trap samples, and 236 Miller net samples. Larval walleye were typically only captured from one population in each sampling year, corresponding to strong cohorts. Catches of larval walleye were highest in Parks Lake in 2001, Lake Sinai in 2002, and Clear Lake in 2003. During the course of this study 767 larval walleye were collected in the three ichthyoplankton gears. A majority of these fish were collected

in light traps (n=748) with relatively few fish captured in either conical ichthyoplankton (n=11) or Miller (n=8) net tows. A majority of the larval walleye captured with light traps were collected from Parks Lake in 2001 (n=394) and Clear Lake in 2003 (n=252). The remaining larval walleye were collected in Sinai 2001 (3), Sinai 2002 (15), Parks 2002 (47), and Thompson in 2002 (40).

Similarly, light traps captured substantially more yellow perch (n=22,390) than both the conical ichthyoplankton (n=3,242) and Miller (n=1,812) nets. Yellow perch were collected by all gears in all lakes each year, except Parks Lake in 2002 where no larval yellow perch were collected.

Timing of peak larval walleye catches differed between gears, resulting in little temporal overlap in the occurrence of walleye between gears. Light traps typically captured newly hatched (yolk-sac) walleye, while active gears collected larger, more advanced, larvae. Peak light trap catch generally occurred during the 15-21 May sampling period, while the occurrence of walleye in 0.5-m conical net samples occurred during the 29 May – 4 June period in all years (weeks 5 and 6; Table 1-2; Figures 1-1, 1-2, and 1-3). Larval walleye were only captured with the Miller sampler on two dates at Parks Lake in 2001, but peak abundance occurred during the 5-11 June sampling period. However, for a given gear no significant difference in estimates of abundance was found among sample weeks (ANOVA, $P>0.3$) as these estimates were highly variable on each sampling date. Timing of peak larval yellow perch catch rates was much more variable for all gears (Tables 1-3, 1-4, and 1-5). Peak abundance of yellow perch typically occurred between 29 May and 4 Jun in light trap samples, between 22 May and 28 May

in 0.5-m net samples, and between 5-11 June in Miller samples. No significant difference in larval abundance was found among sampling weeks for any gear (ANOVA, $P>0.4$).

Differences in timing of peak walleye catches between gears resulted in significant differences (ANOVA; $P<0.0001$; $df = 2, 327$) in mean lengths of walleye captured by the three gears (Table 1-4). Tukey's studentized range test indicated that the mean length of walleye from light trap samples were significantly smaller (8.3 mm) than those collected in conical ichthyoplankton-net (14.2 mm) and Miller-net samples (15.2 mm). Mean lengths of walleye captured in active gears were not significantly different. However, there was no difference in the mean length of yellow perch captured by the three gears (ANOVA $df=2, 897$; $P=0.61$; Table 1-5). Mean length of larval yellow perch captured by 0.5-m net, Miller, and light traps were 8.8, 9.0, and 8.6 mm, respectively.

Precision of both walleye and yellow perch abundance estimates was low for all gears. The mean number of samples required to obtain precise estimates of walleye abundance was 200 for the conical plankton net (range, 132-250), 100 for the Miller net (range: 86- 115), and 165 for light traps (range, 33-350). Mean required effort for precise yellow perch abundance estimates was 121 for the conical plankton net (range, 10-250), 97 for the Miller net (range, 26-250), and 134 for light traps (range, 30-325). An estimate of walleye abundance with the desired level of precision ($CV=20$) was never obtained and was achieved only once for yellow perch with the conical plankton net (Clear Lake 2003 week 4, required $N=10$).

The number of samples required to obtain precise estimates of abundance would have been logistically difficult to collect for either species. Cyr et al. (1992) found that estimates of larval abundance are typically highly variable and suggested that sampling precision can be improved for active gears by either increasing the volume filtered per sample, or by collecting more, smaller (less volume), samples. The pelagic algal and zooplankton biomasses found in South Dakota glacial lakes during larval sampling would prevent the efficient filtering of larger sample volumes. However, collection of more, lower-volume samples may improve the overall precision of larval density estimates in these waters. For light traps, increasing the number samples collected would, likewise, be the best option for increasing precision of larval abundance estimates.

Significant ($P < 0.001$) positive correlations ($r^2 = 0.88$ to 0.98) were found between peak larval walleye density estimates from all three ichthyoplankton gears, suggesting that abundance estimates of all gears were indicative of overall abundance. However, these relations were highly influenced by the high catch rates of larval walleye with all gears in Parks Lake in 2001. For larval yellow perch, significant ($P < 0.025$) positive correlations were found between peak catch rate estimates from Miller samples and catch rates from the 0.5-m net ($r = 0.87$) and light traps ($r = 0.87$). Yellow perch abundance estimates from light trap and conical plankton net samples were marginally correlated ($r = 0.65$, $P = 0.055$).

The vast difference in total catches of larval walleye between light traps and actively-towed nets is likely the result of an interaction between age-specific differences in larval walleye behavior / habitat use and net avoidance. A majority of walleye

collected in light trap samples were small (7.0 - 8.5 mm), newly hatched yolk-sac larvae (Colby et al. 1979). Houde (1968) and Houde and Forney (1970) observed little swimming activity of yolk sac larvae (<9 mm) in aquarium experiments. However, Bulkowski and Meade (1983) found that walleye showed a strong positive phototaxis for the first three weeks after hatching, orienting to the highest light intensities available. After hatching, walleye fry likely remained near the bottom until their yolk-sac was absorbed and did not encounter active gears towed through the upper 0.5-m of the water column, but their strong positive phototaxis made them highly susceptible to light traps.

Immediately after their yolk-sac is fully absorbed, swimming activity increases and walleye larvae become pelagic and begin feeding on zooplankton (Michaletz et al. 1984), therefore making them more susceptible to the active gears. However, swimming speed increases with larval size, improving their net avoidance capability. Thayer et al. (1983) reported that catch of larval spot *Leiostomus xanthurus* and Atlantic menhaden *Brevoortia tyrannus* increased with tow speed for Miller-net samples. Noble (1970) observed higher yellow perch catch rates with increasing speeds (range from 3.5 to 5 m/s) on all dates sampled with a Miller fry sampler, indicating net avoidance for fry 10 to 20 mm. The range of speeds tested by Noble (1970) and Thayer et al. (1983) was greater than 95% of the Miller tow samples collected during this study. A combination of the Miller sampler tow apparatus used and the rough water conditions frequently encountered during the spring sampling season limited tow speeds to a maximum of 2.5 m/s. Avoidance of the Miller sampler at these speeds was likely higher than that observed by Noble (1970), which may have accounted for the low numbers of walleye collected by

both active gears. Mitzner (2002) reported effectively capturing larval walleye up to 25 d post-hatch in a 1 m conical plankton net (0.8-mm bar mesh) towed at 2 m/s. Michaletz (1984) and Mitzner (2002) stratified larval walleye collections by depth, suggesting that vertical position of exogenous-feeding walleye larvae in the water column could also have played a significant role in the ineffectiveness of the surface-towed active gears observed during this study.

Recommendations

The amount of effort required to obtain precise estimates of larval walleye and yellow perch abundance limits the reliability of these estimates. However, concordance between peak abundance estimates among gears suggests that walleye and yellow perch larvae are sampled in proportion to their abundance by all three of these gears. Given the few walleye captured, the methods used for active gears during this study provide little utility for generation of walleye abundance, size distribution, or growth information. Any further investigation into the utility of active gears to assess larval walleye abundance should utilize larger nets (1-2 m) or faster tow speeds, and focus on sampling the entire water column, in accordance with the methodology of Michaletz (1984) and Mitzner (2002). Light traps deployed during the 15-21 May sampling period were the most effective strategy for assessment of larval walleye abundance. This short sampling window limits the number of populations that could be assessed during a given spring, as one field crew can only sample one water per night. In addition, the effectiveness of light traps is strongly linked to the sampling conditions, more so than the active gears. Any

environmental variables that act to diffuse light penetration, such as water clarity / turbidity, lunar or artificial illumination, and wave action, would be expected to reduce the effective range of light traps. Ideal conditions for optimal light trap effectiveness are high water clarity and moonless or overcast nights with little wind. The short sampling window provided by light traps limits the ability to repeatedly sample a single population when estimates of larval survival or growth are of interest. The greatest utility for the use of light traps is for targeting newly-hatched walleye larvae, such as for generating an annual index of larval hatch.

Since light traps are most effective at collecting newly-hatched walleye, variance of abundance estimates generated with this gear may be reduced by targeting likely spawning areas, as opposed to randomly selecting sample sites from an entire lake. Walleye yolk-sac larvae are most likely to be found near spawning areas. Focusing sampling efforts in a few discrete sites

Sufficient numbers of yellow perch were captured by all gears to generate estimates of abundance and size structure on most sampling dates. Furthermore, the sampling window for collection of yellow perch with all three gears (approximately 4 weeks) was considerably longer than that for walleye. Conical plankton nets have been shown to be an effective gear for the assessment of yellow perch abundance in South Dakota glacial lakes (Anderson et al. 1998; Isermann 2003), which is in agreement with the findings of this study. Active gears are deployed for shorter times (five minutes) relative to light traps (4 h) allowing for the collection of more samples during a given

period. Thus, continued assessments of yellow perch abundance via conical plankton net is recommended.

Table 1-1. Characteristics of South Dakota glacial lakes sampled during 2001-2003. Taken in part from Stukel (2003).

Lake	County	Surface area (ha)	Secchi Depth (m)	Maximum depth (m)	Years sampled
Clear	Marshall	474	1.8	6.7	2003
Madison	Lake	1,069	0.8	4.9	2001
Parks	Day	121	1.4	12.5	2001, 2002
Sinai	Brookings	696	2.5	10.1	2001-2003
Thompson	Kingsbury	5,041	1.8	7.9	2002, 2003

Table 1-2. Larval walleye abundance estimates generated from three ichthyoplankton gears in South Dakota glacial lakes from 1 May to 15 June, 2001-2003. Abundance estimates from 0.5-m and Miller nets are mean number / m³ and light trap estimates are mean number per trap. Sampling week indicates the week the larval sample was collected, where week 1 is 1 May through 7 May and week 6 is 5 June through 11 June. Only sampling dates where walleye larvae were captured are shown. The number of samples required indicates the required effort necessary to obtain an abundance estimate with a coefficient of variation that is 20% of the mean.

Lake	Year	Sampling week	CPUE		Number of samples collected	Number of samples required
			Mean	Standard error		
0.5-m Conical Net						
Parks	2001	5	0.008	0.007	8	132
Sinai	2001	5	0.001	0.001	10	250
	2002	5	0.001	0.001	10	250
Clear	2003	5	0.005	0.004	10	168
Light Trap						
Parks	2001	3	35.63	16.76	8	61
		6	0.2	0.2	8	250
Sinai	2001	6	0.1	0.1	10	250
Parks	2002	4	0.8	0.29	8	33
		5	3.08	2.46	8	192
		6	0.18	0.12	8	124
Sinai	2002	3	0.64	0.64	10	350
		4	0.45	0.31	10	130
Thompson	2002	6	3.33	2.91	11	156
Clear	2003	3	13.7	12.15	10	197
		4	6.05	2.18	10	62
Miller Sampler						
Parks	2001	3	0.064	0.04	8	86
		6	0.121	0.09	8	115

Table 1-3. Yellow perch abundance estimates (number / cm³) from 0.5-m conical plankton net samples. Sampling week indicates the week of the year a sample was collected, where week 1 is 1 May through 7 May and week 6 is 5 June through 11 June. Only sampling dates where yellow perch larvae were captured are shown. The number of samples required indicates the effort necessary to obtain an abundance estimate with a coefficient of variation that is 20% of the mean.

Lake	Week	CPUE		Number of samples collected	Number of samples required
		Mean	Standard Error		
2001					
Madison	2	0.287	0.287	10	250
	3	0.001	0.001	10	250
	4	0.155	0.138	20	200
	5	0.009	0.006	10	122
	6	0.002	0.001	10	111
Parks	2	0.002	0.002	6	150
	3	0.671	0.261	9	30
	5	0.188	0.078	8	35
	6	0.218	0.097	8	40
Sinai	3	0.049	0.019	10	38
	4	2.275	1.611	10	125
	5	0.466	0.305	10	107
	6	0.137	0.101	10	138
2002					
Sinai	5	0.003	0.002	10	135
	7	0.012	0.005	10	41
Thompson	6	0.009	0.005	14	110
	7	0.004	0.003	14	164
2003					
Clear		0.073	0.022	10	24
	3	0.014	0.007	10	63
	4	0.162	0.032	10	10
	5	0.176	0.093	10	70
	6	0.098	0.033	10	29
	7	0.008	0.003	10	38
Sinai	2	0.001	0.001	10	250
	3	0.000	0.000	10	250
	4	0.004	0.004	10	250
Thompson	5	0.004	0.004	10	250

Table 1-4. Larval yellow perch abundance estimates (number / cm³) from Miller net samples. Sampling week indicates the week of the year a sample was collected, where week 1 is 1 May through 7 May and week 6 is 5 June through 11 June. Only sampling dates where yellow perch larvae were captured are shown. The number of samples required indicates the effort necessary to obtain an abundance estimate with a coefficient of variation that is 20% of the mean.

Lake	Week	CPUE		Number of samples collected	Number of samples required
		Mean	Standard error		
2001					
Madison	3	0.287	0.167	20	84
	4	0.070	0.070	5	125
	6	0.027	0.027	10	250
Parks	3	1.046	0.399	8	29
	6	13.93	9.847	8	100
Sinai	3	0.252	0.114	10	51
	5	7.387	2.906	10	39
	6	17.11	7.999	10	55
2002					
Sinai	5	0.018	0.012	10	111
	7	0.153	0.049	10	26
Thompson	6	0.013	0.009	14	162
	7	0.048	0.029	14	127

Table 1-5. Larval yellow perch abundance estimates (number / trap) from light trap samples. Sampling week indicates the week of the year a sample was collected, where week 1 is 1-May through 7-May and week 6 is 5-June through 11-June. Only sampling dates where yellow perch larvae were captured are shown. The number of samples required indicates the effort necessary to obtain an abundance estimate with a coefficient of variation that is 20% of the mean.

Lake	Week	CPUE		Number of samples collected	Number of samples required
		Mean	Standard Error		
2001					
Madison	3	26.09	22.96	11	213
	4	6.90	3.97	10	83
	5	37.0	16.29	9	44
	6	3.83	2.67	6	73
Parks	3	172.6	116.4	11	125
	6	69.10	36.83	10	71
Sinai	4	3.10	2.07	10	112
	5	107.2	50.24	11	60
	6	615.0	512.9	10	174
2002					
Sinai	2	0.154	0.15	13	325
	4	4.0	3.90	11	262
	5	2.23	1.34	13	118
	7	5.67	1.87	12	33
Thompson	6	1.55	1.16	11	156
	7	28.75	17.86	12	116
2003					
Clear	2	0.2	0.20	10	250
	3	158.1	105.6	10	112
	4	295.6	120.7	9	38
	5	662.4	229.2	10	30
	6	29.40	15.26	10	67
	Sinai	3	0.60	0.60	10
4		0.50	0.50	10	250
5		0.77	0.57	9	122
6		1.0	0.78	10	156
Thompson	5	1.44	1.44	8	200
	6	0.70	0.33	10	57

Table 1-6. Mean length of larval walleye from 0.5-m conical net, Miller net, and light trap samples, collected from eastern South Dakota glacial lakes during 1 May to 15 June, 2001-2003.

Lake	Gear	Date	n	Length (mm)	
				Mean	Standard error
2001					
Parks	0.5-m net	1 June	3	12.7	0.33
	Light Trap	18 May	100	7.0	0.06
		6 June	1	19.0	
	Miller	18 May	2	7.5	0.50
		8 June	4	19.0	0.82
2002					
Sinai	Light Trap	20 May	9	9.0	0.29
		28 May	5	14.6	7.95
2003					
Clear	0.5-m net	4 June	7	14.9	0.83
	Light Trap	15 May	100	8.3	0.07
		22 May	69	9.0	0.08
		28 May	30	10.5	0.21

Table 1-7. Yellow perch mean length from 0.5-m conical plankton net, Miller net, and light trap samples collected from eastern South Dakota glacial lakes during 1 May to 15 June, 2001-2003.

Lake	Gear	Week	n	Total length (mm)	
				Mean	Standard error
2002					
Sinai	0.5-m	5	3	10.3	0.3
		7	10	9.2	0.7
	Light trap	2	1	6.0	
		4	45	5.3	0.1
		5	29	8.0	0.2
Miller	5	2	9.0	0.01	
2003					
Clear	0.5-m	2	52	5.3	0.1
		3	12	8.0	0.7
		4	198	8.6	0.1
		5	70	11.5	0.2
		7	7	15.7	0.7
	Light trap	2	2	4.5	0.5
		3	100	5.8	0.1
		4	205	7.0	0.1
		5	102	13.2	0.1
		7	10	19.7	0.8
Sinai	0.5-m	3	1	8.0	
		4	4	9.5	0.2
	Light trap	2	1	5.0	
		4	5	13.6	0.8
		5	7	16.2	0.6
Thompson	0.5-m	5	2	8.5	0.5
		5	25	13.8	0.5
		6	7	9.7	1.5

Table 1-8. Linear relations between estimates of peak larval abundance from 0.5-m conical plankton net, Miller net, and light trap samples for walleye and yellow perch collected from eastern South Dakota glacial lakes, 2001-2003.

Covariates		n	r	<i>P</i>
Walleye				
0.5-m	Miller	6	0.94	<0.0001
0.5-m	Light trap	9	0.98	0.0004
Miller	Light trap	6	0.99	<0.0001
Yellow perch				
0.5-m	Miller	6	0.87	0.021
0.5-m	Light trap	9	0.65	0.055
Miller	Light trap	6	0.87	0.021

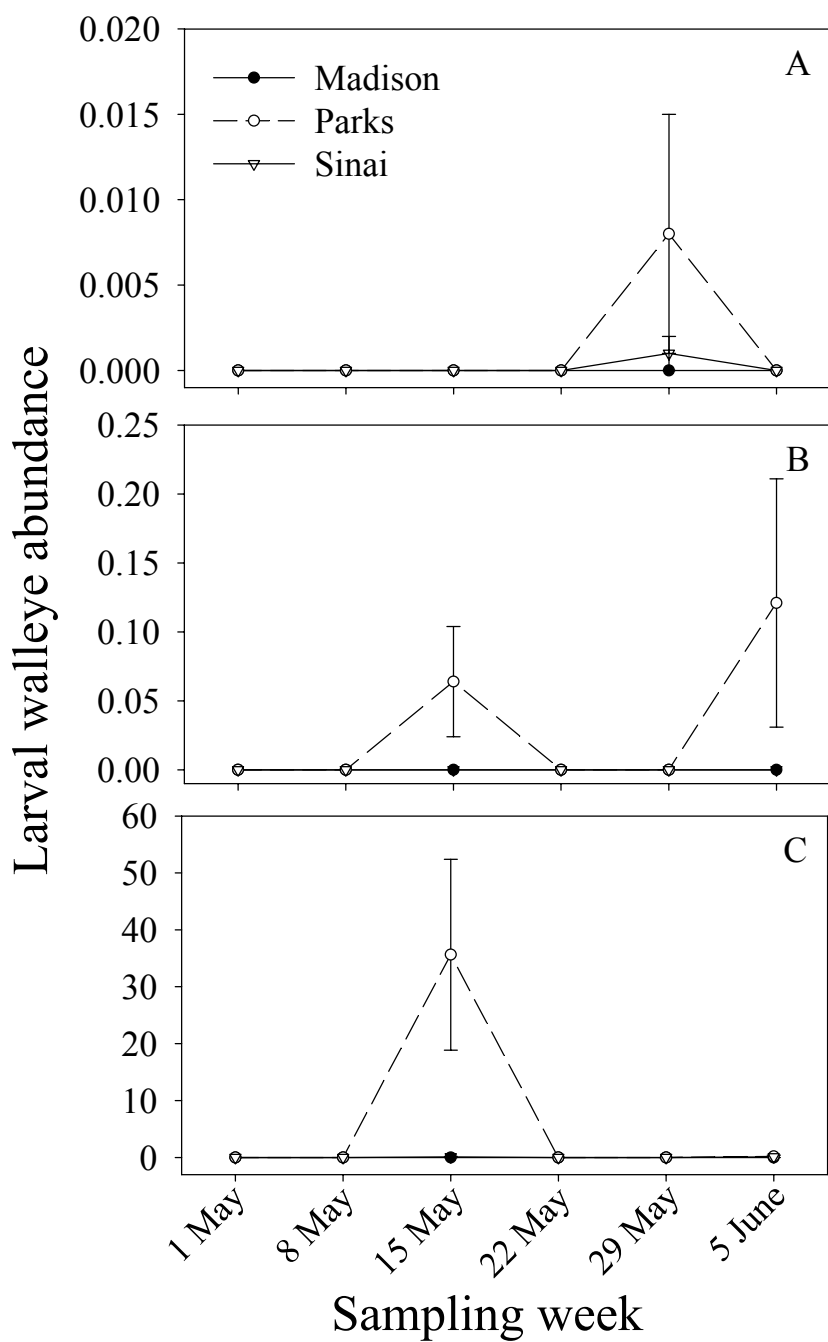


Figure 1-1. Weekly estimates of larval walleye abundance generated from a 0.5-m conical net (A), a Miller sampler (B), and light traps (C) in three eastern South Dakota glacial lakes during the spring of 2001. Larval abundance estimates were calculated as density (number / m^3) for active gears and catch per trap for light traps. Error bars are ± 1 standard error.

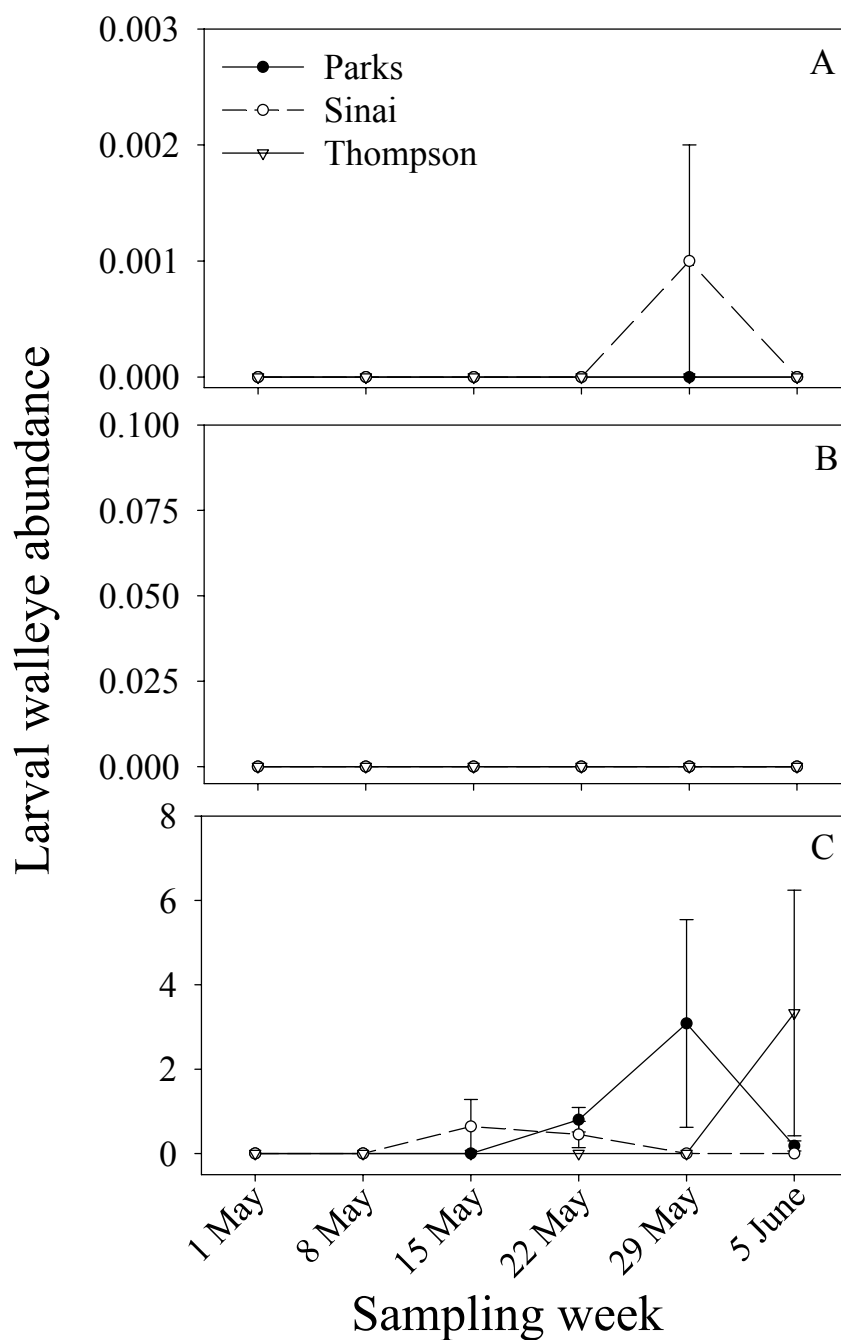


Figure 1-2. Weekly estimates of larval walleye abundance generated from a 0.5-m conical net (A), a Miller sampler (B), and light traps (C) in three eastern South Dakota glacial lakes during spring of 2002. Larval abundance estimates were calculated as density (number / m³) for active gears and catch per trap for light traps. Error bars are ± 1 standard error.

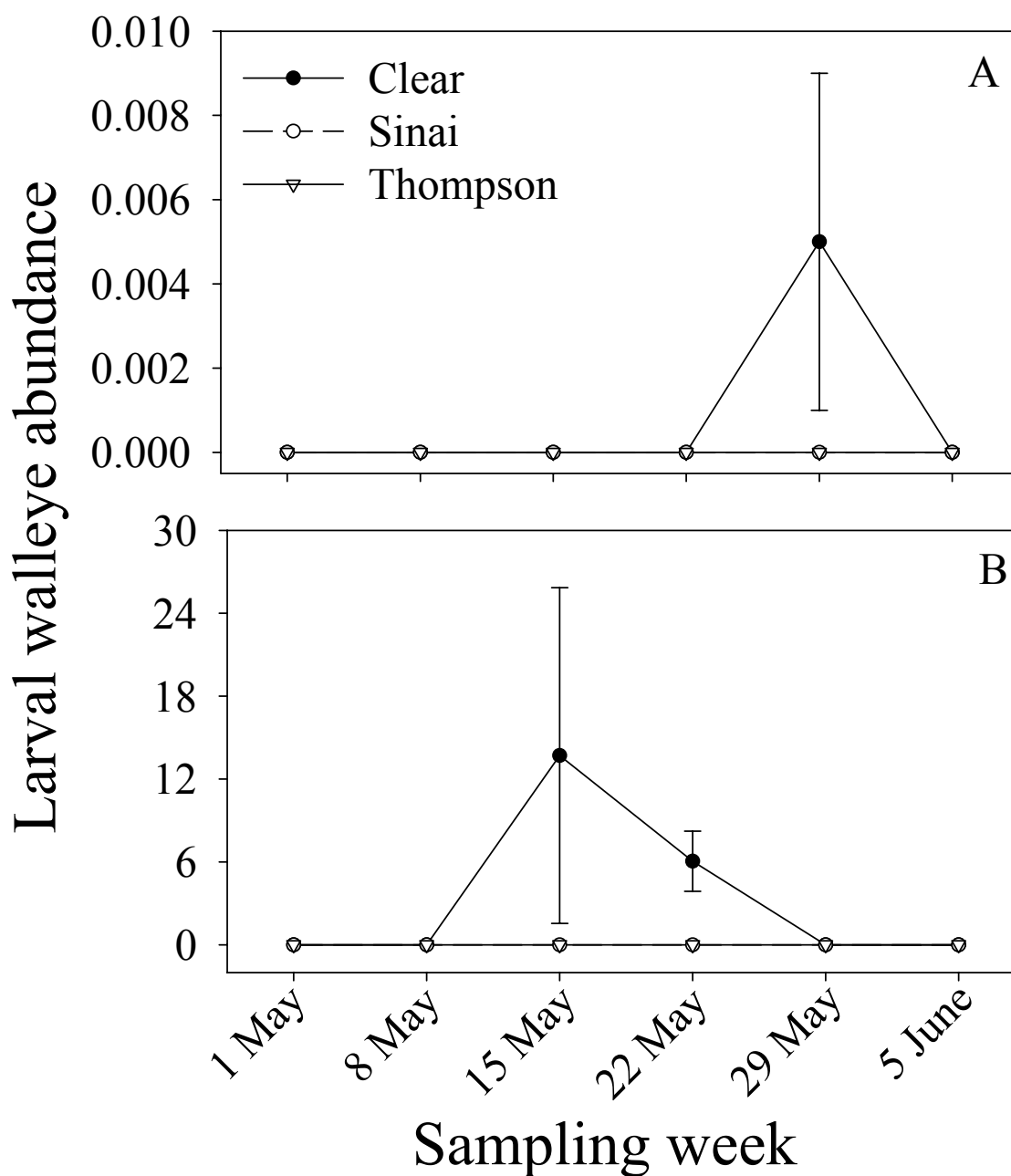


Figure 1-3. Weekly estimates of larval walleye abundance generated from a 0.5-m conical net (A) and light traps (B) in three eastern South Dakota glacial lakes during spring of 2003. Larval abundance estimates were calculated as mean density (number / m^3) for the 0.5-m net and mean catch per trap for light traps. Error bars are ± 1 standard error.

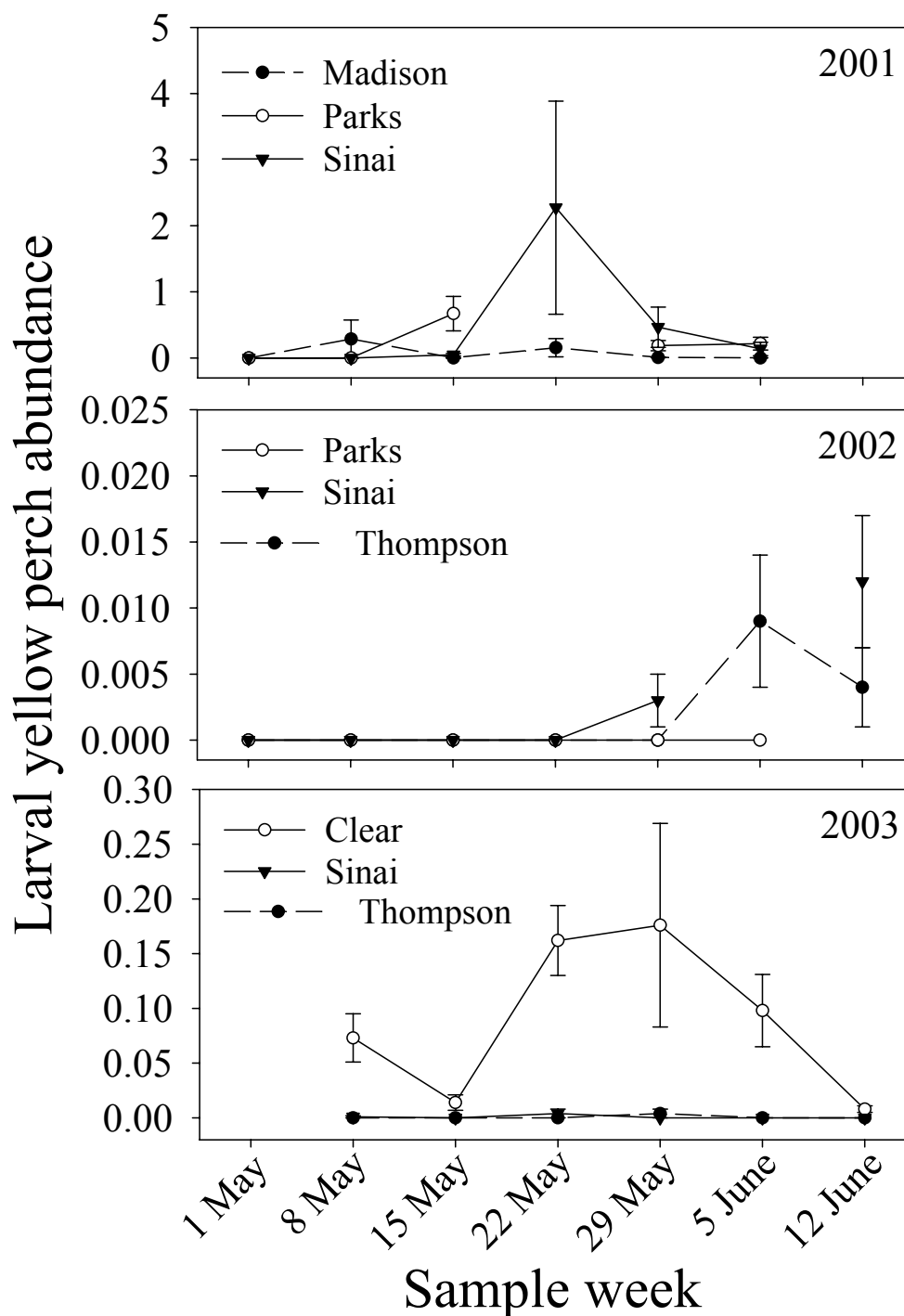


Figure 1-4. Weekly estimates of larval yellow perch abundance (number / m³) generated from 0.5-m conical net samples in eastern South Dakota glacial lakes, 2001-2003. Larval abundance estimates were calculated as density (number / m³) for active gears and catch per trap for light traps. Error bars are ± 1 standard error.

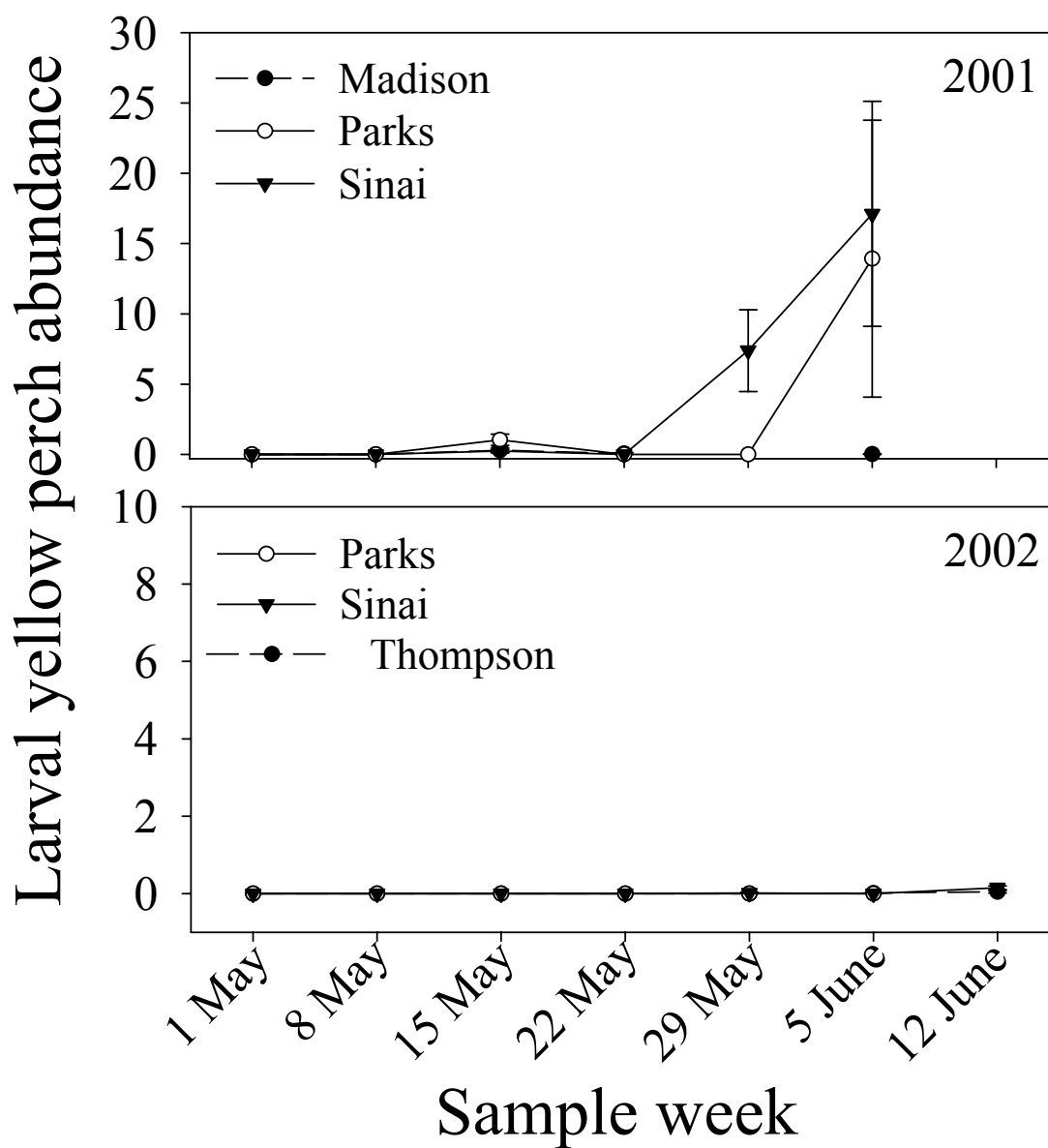


Figure 1-5. Weekly estimates of larval yellow perch abundance (number/m³) generated from Miller net samples in eastern South Dakota glacial lakes, 2001-2003. Larval abundance estimates were calculated as density (number / m³) for active gears and catch per trap for light traps. Error bars are ± 1 standard error.

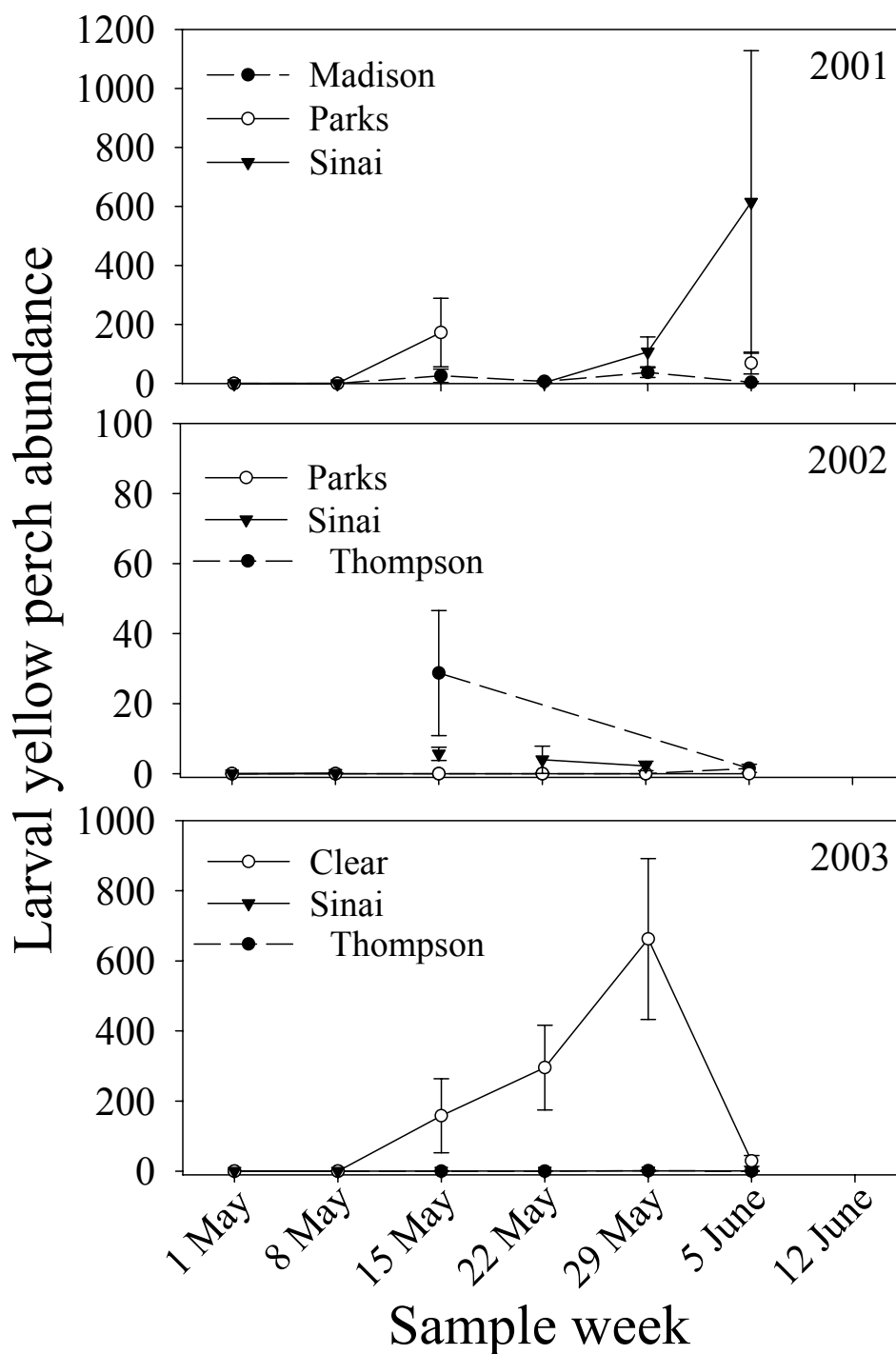


Figure 1-6. Weekly estimates of larval yellow perch abundance (number / trap) generated from light trap samples in eastern South Dakota glacial lakes, 2001-2003. Larval abundance estimates were calculated as density (number / m³) for active gears and catch per trap for light traps. Error bars are ± 1 standard error.

Chapter 2

Relations Between Larval Abundance and Cohort Strength of Walleye in South Dakota Glacial Lakes

Introduction

Reproductive success of walleye *Sander vitreus* populations in South Dakota glacial lakes has shown tremendous annual variability, which is characteristic of walleye populations throughout its native range (Ellison and Franzin 1992). Consequently, these populations often receive regular fry or fingerling stockings intended to maintain quality recreational fisheries by preventing the occurrence of consecutive weak cohorts. The South Dakota Department of Game, Fish and Parks (SDGFP) formulates stocking recommendations on fall catch rates of age-0 cohorts from previous years, rather than expected cohort strength for the year the lake is stocked. This strategy frequently results in stockings that overlap with strong naturally produced cohorts with possible negative influences on overall walleye growth through density-dependent competition for prey resources, and potential consequences for recruitment of these fish to a harvestable size (Jonas and Wahl 1998).

Assessments of age-0 cohort strength during September and October occur well after the peak of hatchery production, restricting the implementation of immediate remedial stockings to supplement weak or missing cohorts. The production of large fingerlings for fall stocking can be expensive and problematic, limiting the production of adequate numbers of these fish in most years. Furthermore, the success of these

stockings can be erratic (Larscheid 1995; Brooks et al. 2002) as these fish are often smaller at the time of stocking than naturally-produced fish, which may have negative consequences for survival and subsequent recruitment of stocked fish (Olson et al. 2000).

Houde (1987) and Houde (1989) suggested that catastrophic mortality events incurred by fishes during a critical period determines first-year survival and eventual cohort strength. Several studies have investigated the timing of critical periods of walleye mortality during their first year. However, there is little agreement among these studies as to when the critical period occurs. The three prevailing paradigms suggest that walleye cohort strength can result from mortality at the egg (Smith and Krefting 1953; Busch et al. 1975; Kallemeyn 1987), larval (Li and Mathias 1982; Johnston and Mathias 1993, 1994, 1996; Jonas and Wahl 1998), or juvenile (Chevalier 1973; Forney 1976) life stages.

The timing of the critical period dictates when year-class strength is set and can be assessed. Larval abundance has shown potential as an index of age-0 cohort strength during early life. Sammons and Bettoli (1998) found that abundance of white bass *Morone chrysops* and white crappie *Pomoxis annularis* larvae was strongly correlated to the fall abundance of those species in a Tennessee reservoir. Similarly, Anderson et al. (1998) and Isermann (2003) found positive correlations between larval yellow perch *Perca flavescens* density and catch rates of juveniles in summer seine samples. These studies suggest that cohort strength of these fishes show consistent survival between the larval and juvenile life stages. While substantial cohort mortality may occur between

sampling periods, these fishes are not prone to catastrophic mortality resulting in cohort failure following the larval period. The ability to assess walleye year-class strength shortly after hatching could provide a stocking prioritization system that would coincide with the peak of hatchery production. Thus, hatchery products could be directed toward waters where natural reproduction is low or allow for the manipulation of stocking rates to maximize walleye production. The objective of this study was to evaluate the utility of three ichthyoplankton gears for indexing walleye cohort strength at the larval life stage.

Methods

Relations between peak larval walleye abundance estimates from three ichthyoplankton (IP) gears (Chapter 1) and relative abundance of juvenile walleye in the summer and fall were investigated. Summer samples consisted of night-time shoreline seining (15.2 m, 6.4-mm bar mesh) at fixed sites every 14 d from 1 July through 31 August. Each seine sample consisted of a single 177 m² area, or a one-quarter arc haul. The number of seine sites varied from 8 to 20 per lake. A target number of 20 sites per lake were identified, but lake size, morphometry, substrate, receding water levels, and growth of submergent vegetation limited the number of sites that could be effectively sampled. All juvenile fishes captured were placed on ice for transport back to the laboratory and then frozen until samples could be processed. All fish from each sample were identified to species and counted. For yellow perch and walleye, length and weight of up to 100 individuals of each species were measured on each sampling date. Relative abundance was calculated as mean number of age-0 walleye per seine haul.

Fall abundance of age-0 walleye cohorts in each lake was determined in September by electrofishing using a Smith-Root pulsed-DC electrofishing boat (150-250 V, 10-12 A). Sampling protocols were the same as those used by SDGFP during fall walleye recruitment surveys. Electrofishing surveys consisted of six, 20-min transects, where fish netting was restricted to only age-0 and age-1 walleye. Length and weight of the first 50 fish collected were measured and scale samples were taken from five fish per centimeter group for age determinations. Relative abundance was calculated as mean age-0 walleye per hour (CPH) of electrofishing. Sampling sites at Clear, Madison, Sinai, and Thompson were fixed sites surveyed annually or semi-annually by SDGFP. Six 20-min samples encompassed the entire shoreline of Parks Lake during 2001 and 2002. Relations between larval walleye abundance from the three ichthyoplankton gears and cohort size were determined with linear regression.

In addition to CPH estimates, fall age-0 walleye cohort size was estimated using the Peterson population estimate procedure (Van Den Avyle 1993) for mark-recapture data collected from Parks Lake in 2001 and Lake Sinai in 2001 and 2002. Three electrofishing trips were made over a 14-d period. The first two trips were intended to mark age-0 walleye, with a single recapture trip. Age-0 fish were marked (removal of left pelvic fin) or checked for a mark, and immediately released. Linear relations between cohort size and electrofishing CPH were calculated to determine the overall effectiveness of fall electrofishing for assessing cohort strength.

Results and Discussion

Summer and fall estimates of abundance are presented in Tables 2-1 and 2-2, respectively. Linear relations between estimates of larval walleye peak abundance and juvenile abundance were highly significant (Table 2-3) for all three IP gears. Larval abundance explained 94-99% of the variance in seine CPUE and 82-95% of the variation in electrofishing CPH. Larval and juvenile walleye catch rates in Parks Lake in 2001 were the highest observed during the course of this study, causing a strong influence on all regressions (Figures 2-1 and 2-2). Removing 2001 Parks Lake data from regressions had a dramatic influence on the significance of all linear relations and the amount of variation explained by larval abundance indices. Larval abundance estimates from Miller net samples showed no positive correlation to either seine CPUE or fall electrofishing CPH in the absence of the Parks Lake 2001 data, and the amount of variation explained by 0.5-m net and light trap larval abundance estimates dropped to 90 and 92% for seine CPUE and to 56 and 37% for fall electrofishing CPH, respectively. However, these data were accurate indices of the 2001 walleye cohort in Parks Lake, and should be considered in these analyses. Further investigation of these associations could improve the overall confidence in these relations, particularly by the addition of larval, seine and electrofishing abundance data for year-classes intermediate to the abundances observed during this study.

The positive linear relationship between larval and juvenile abundance suggests that all three gears provide some insight into year-class strength. However, the overall utility of the active gears used in this study as an early index of cohort strength was

limited. Lucchesi (2001) suggested that walleye cohort strength should be considered strong and very strong when fall electrofishing CPH is 101-250 and greater than 250, respectively. Walleye larvae were captured with the conical plankton net only when fall electrofishing CPH exceeded 120 (strong cohorts), and with the Miller net only when fall CPH exceeded 500 (very strong). Thus, the resolution for indexing year-class strength is limited to qualitatively categorizing a cohort as either weak (fall CPH < 120) or strong (fall CPH > 120) with the conical plankton net, or for detection of very strong cohorts with the Miller net. The year-class strength indices provided by these gears provides little utility as a management tool as the critical abundance used by SDGFP for stocking the following spring occurs when fall electrofishing CPH is less than 50.

Light traps show the most promise for indexing walleye cohort strength at the larval life stage. In contrast to active gears, light traps captured walleye larvae over the entire range of cohort strength categories proposed by Lucchesi (2001), allowing for a more precise quantification of age-0 walleye cohort strength. Furthermore, light traps are most effective at capturing newly-hatched walleye fry during 15-21 May (Chapter 1) which coincides with the timing of peak walleye production in South Dakota hatcheries. Thus, quantification of cohort strength during this time would allow for fry-stocking waters when missing, or weak, cohorts are detected from larval catches.

The absence of larval walleye in light traps samples in lakes with weak cohorts suggests that the critical period for walleye cohort formation likely occurs before the third week of May, during the incubation period. Walleye spawning in South Dakota waters typically occurs 18 - 25 April, peaking approximately 20 April, and hatching

occurs between 14-23 May, peaking on approximately 18 May (Michaletz 1984). If larval starvation or predation/cannibalism influenced cohort strength at the larval or juvenile life stage, walleye yolk-sac larvae should have been abundant in light trap samples from all lakes every year. The success of SDGFP's fry-stocking program supports this contention, as the timing of fry stockings typically coincide with the peak of walleye hatching and peak light trap catches in these waters. Weak cohorts (fall electrofishing CPH<50) occurred in only 4 of 21 (19%) fry-stocked lakes between 1996 and 2002, and 62% (13) of these fry-stockings produced strong or very strong cohorts (Lucchesi 2001; D. Lucchesi and B. Blackwell, SDGFP, unpublished data). Thus, formation of cohort strength for naturally-produced cohorts likely occurs before the time these waters are stocked with fry (typically 2,500 fry/ha) in mid- to late May.

The lack of abundant yolk-sac walleye in light traps from all lakes suggests that annual variations in cohort strength observed for glacial lake walleye populations are most likely the result of differences in the number of walleye that hatch in a given year, rather than variations in mortality at the larval or post-larval life stages. The number of walleye that hatch in a given year is a product of the interaction between the total number of eggs spawned, egg quality, and the suitability of ambient environmental conditions for incubation and development. Parental stock size (Hansen et al. 1998), energetic condition of females (Henderson and Nepsy 1994; Henderson et al. 1996), or shifts in fecundity (Baccante and Reid 1988) could account for variations in the number of eggs produced, and egg quality has been shown to influence both hatching success and viability (Moodie et al. 1989). Suitability of the environment for incubation of walleye

eggs depends on the availability of substrate suitable for egg deposition (Johnson 1961), water temperatures during incubation (Oseid and Smith 1971; Smith and Koenst 1975), parasitism (Smith and Kramer 1963), and predation (Carlander et al. 1960; Erickson and Stevenson 1967; Wolfert et al. 1975). Future studies investigating walleye recruitment in eastern South Dakota glacial lakes should focus on the relative importance of these factors in determining walleye cohort strength, as it is likely that walleye year-class strength is the product of a combination of these regional- and local-scale influences on hatching success.

Fall age-0 cohort size was estimated in Parks and Sinai lakes in 2001 and in Sinai Lake in 2002. Peterson estimates of age-0 walleye cohort size showed a positive relationship to fall electrofishing CPE (Figure 2-4). This relationship was not statistically significant ($P > 0.1$) but fall electrofishing CPE explained approximately 90% of the variation in cohort size estimates. The small sample size ($n=3$) limits the application of this relation to walleye management or research, but the positive relationship observed does indicate that fall electrofishing should be reflective of overall cohort size.

Larval abundance explained more of the variation in juvenile abundance from summer seine estimates than from fall electrofishing. While mortality during the larval life stage is often substantial (Houde 1987; Houde 1989) the rate of mortality at this time may be more predictable across populations than during late summer and fall when mortality may arise from other sources occurring at the lake-scale. For example, prey limitation (Knight et al. 1984; Jonas and Wahl 1998), thermal stress (Clapp et al. 1997), or rates of predation (Santucci and Wahl 1993) or cannibalism (Chevalier 1973; Forney

1976) may all be important sources of first-year walleye mortality. The relative importance of each of these factors varies both annually and among populations. Mortality during the late summer likely does not have as profound of an impact on year-class strength as during early life but may account for the additional variation observed between summer and fall abundance estimates.

It is unlikely that gear-related biases would account for the observed difference in predictive accuracy of larval abundance between summer and fall. Catch rates of age-0 walleye in fall electrofishing surveys have shown a significant positive relationship to estimates of cohort size in both South Dakota and Wisconsin (Serns 1982c) lakes. In addition, relative abundance estimates from fall electrofishing surveys were less variable (Coefficient of variation = 14 - 126) than estimates derived from summer seining (Coefficient of variation = 67-333). Thus, the statistical confidence in fall estimates of abundance showed improvements over those determined from summer samples. Fall estimates of age-0 abundance have proven to be a reliable index of expected recruitment of a cohort to the fishery in subsequent years. Willis (1987) found a strong correlation between catch rates of age-0 and age-1 walleye the following year from fall gill net surveys in Kansas reservoirs. Likewise, Serns (1981) found a positive relationship between walleye cohort abundance at age-0 and age-1 from fall electrofishing surveys in northern Wisconsin lakes. The results of these studies suggest that significant mortality events have occurred before the first fall, as walleye mortality must remain relatively consistent between the first and second fall for these relationships to be manifested.

Larval walleye abundance provided a reasonable index of age-0 walleye cohort strength at the juvenile life stage. Estimates of yolk-sac larvae abundance provided the best potential for predicting cohort strength, suggesting that the critical period for walleye populations in South Dakota glacial lakes occurs before hatching. However, there is likely some irregular mortality occurring at the lake-level during the larval and juvenile life stages that varies between populations. Assessment of walleye cohort strength at the larval life stage should provide a useful tool that would allow fisheries managers to maximize the overall benefit of hatchery-produced walleye to naturally reproducing populations.

Table 2-1. Relative abundance of age-0 walleye generated from summer seine samples in South Dakota glacial lakes 2001-2003. CPUE is mean number of age-0 walleye per seine haul and SE is the standard error of the mean.

Lake	Date	n	CPUE	
			Mean	SE
2001				
Madison	5 Jul	13	0.2	0.6
	19 Jul	15	0.5	1.6
	2 Aug	15	0.0	
	14 Aug	15	0.4	0.7
Parks	6 Jul	10	24.8	25.8
	18 Jul	10	39.6	40.4
	31 Jul	10	19.1	12.8
	15 Aug	8	7.1	5.7
Sinai	3 Jul	17	0.2	0.4
	17 Jul	15	0.5	0.6
	30 Jul	15	0.8	1.4
	13 Aug	14	0.6	0.7
2002				
Parks	11 Jul	10	1.6	2.8
	28 Jul	9	0.7	1.0
	6 Aug	7	0.3	0.3
	17 Aug	8	0.3	0.3
Sinai	8 Jul	10	0.0	
	22 Jul	14	0.4	0.8
	14 Aug	15	0.5	0.3
Thompson	10 Jul	17	0	
	25 Jul	20	0	
	5 Aug	17	0	
	16 Aug	17	0	
2003				
Clear	1 Jul	7	18.1	14.7
	16 Jul	7	5.7	4.9
	30 Jul	11	1.8	2.4
	11 Aug	10	5.4	4.7
Sinai	2 Jul	20	0	
	14 Jul	17	0	
	27 Jul	17	0	
Thompson	3 Jul	10	0	
	15 Jul	10	0	
	28 Jul	10	0	

Table 2-2. Estimates of age-0 walleye relative abundance from fall electrofishing samples in South Dakota glacial lakes 2001-2003. Catch per unit effort (CPUE) is the mean number of age-0 walleye collected per hour of electrofishing.

Lake	Number of samples	CPUE	
		Mean	SE
2001			
Madison	6	3.5	1.80
Parks	6	569.0	33.35
Sinai	6	58.5	13.99
2002			
Parks	6	9.5	0.92
Sinai	6	121.6	14.55
Thompson	6	78.0	24.43
2003			
Clear	6	131.6	27.4
Sinai	6	19.0	4.87
Thompson	6	15.5	6.8

Table 2-3. Linear relations between peak larval walleye abundance estimated with three ichthyoplankton gears and juvenile walleye abundance estimates from summer seine and fall electrofishing samples.

Larval Gear	Degrees of freedom	Intercept	Slope	r^2	P
Seine CPUE					
0.5-m	8	-1.158	4305.13	0.95	<0.0001
Miller	5	0.626	321.94	0.99	<0.0001
Light trap	8	-0.401	1.14	0.98	<0.0001
Electrofishing CPH					
0.5-m	8	16.863	50739.00	0.82	0.0008
Miller	5	54.4	4118.62	0.96	0.0008
Light trap	8	22.766	13.93	0.91	<0.0001

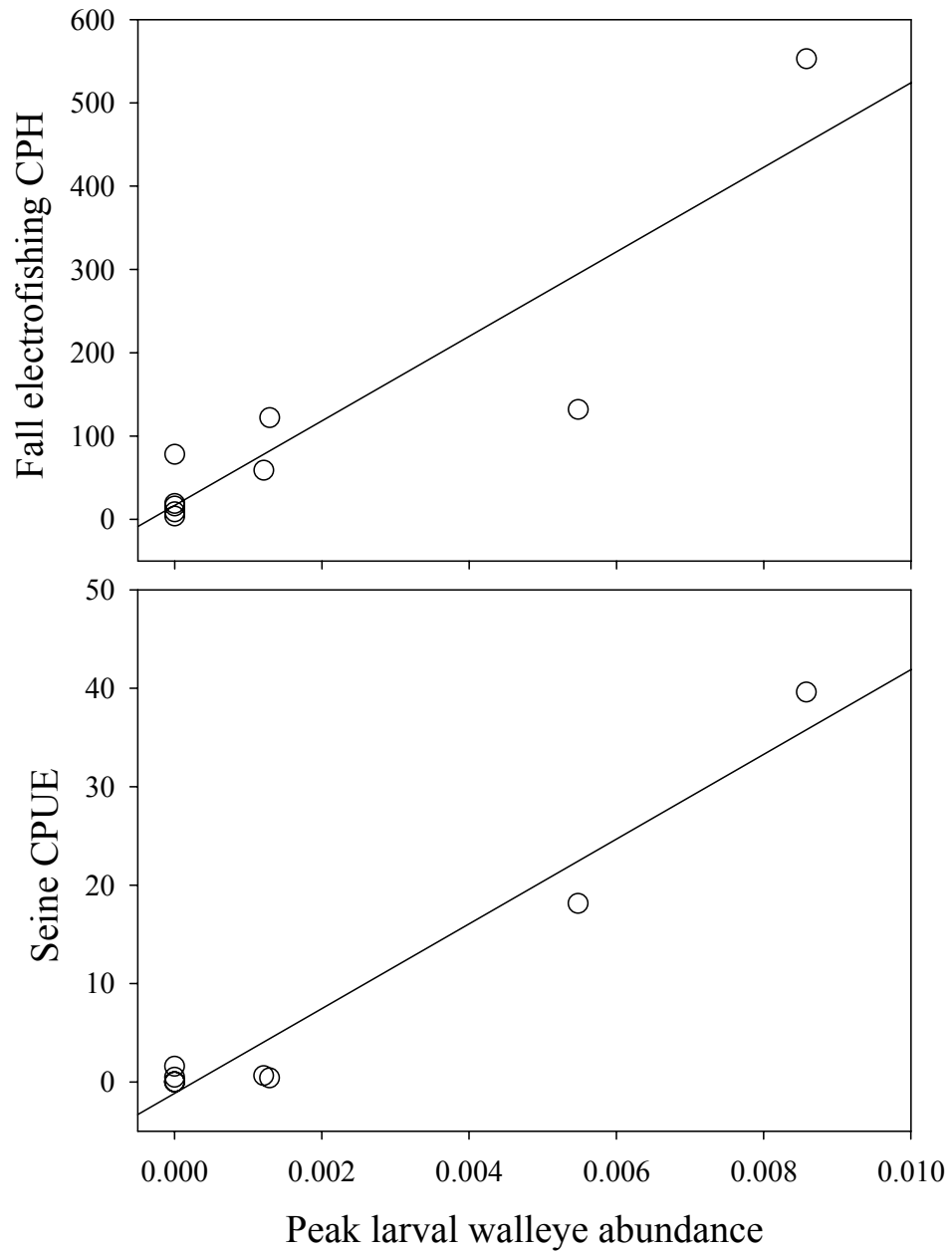


Figure 2-1. Linear relations between peak larval walleye abundance (no./m³) from 0.5-m conical net samples and relative abundance of age-0 walleye from summer seining (number / haul) and fall electrofishing (number / h).

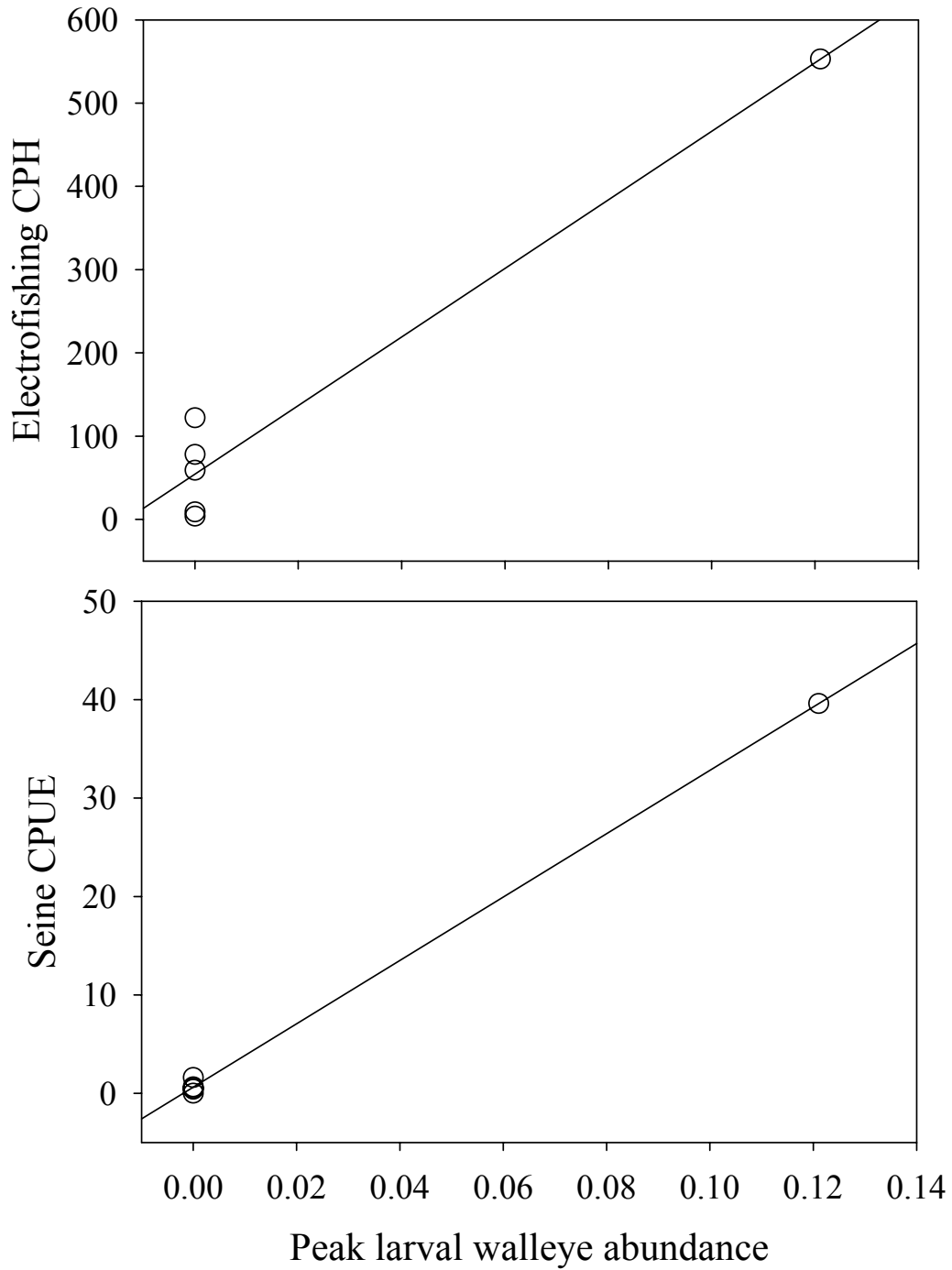


Figure 2-2. Linear relationships between peak larval walleye abundance (number / m³) estimated from Miller net samples and relative abundance of age-0 walleye from summer seining (number / haul) and fall electrofishing (number / h).

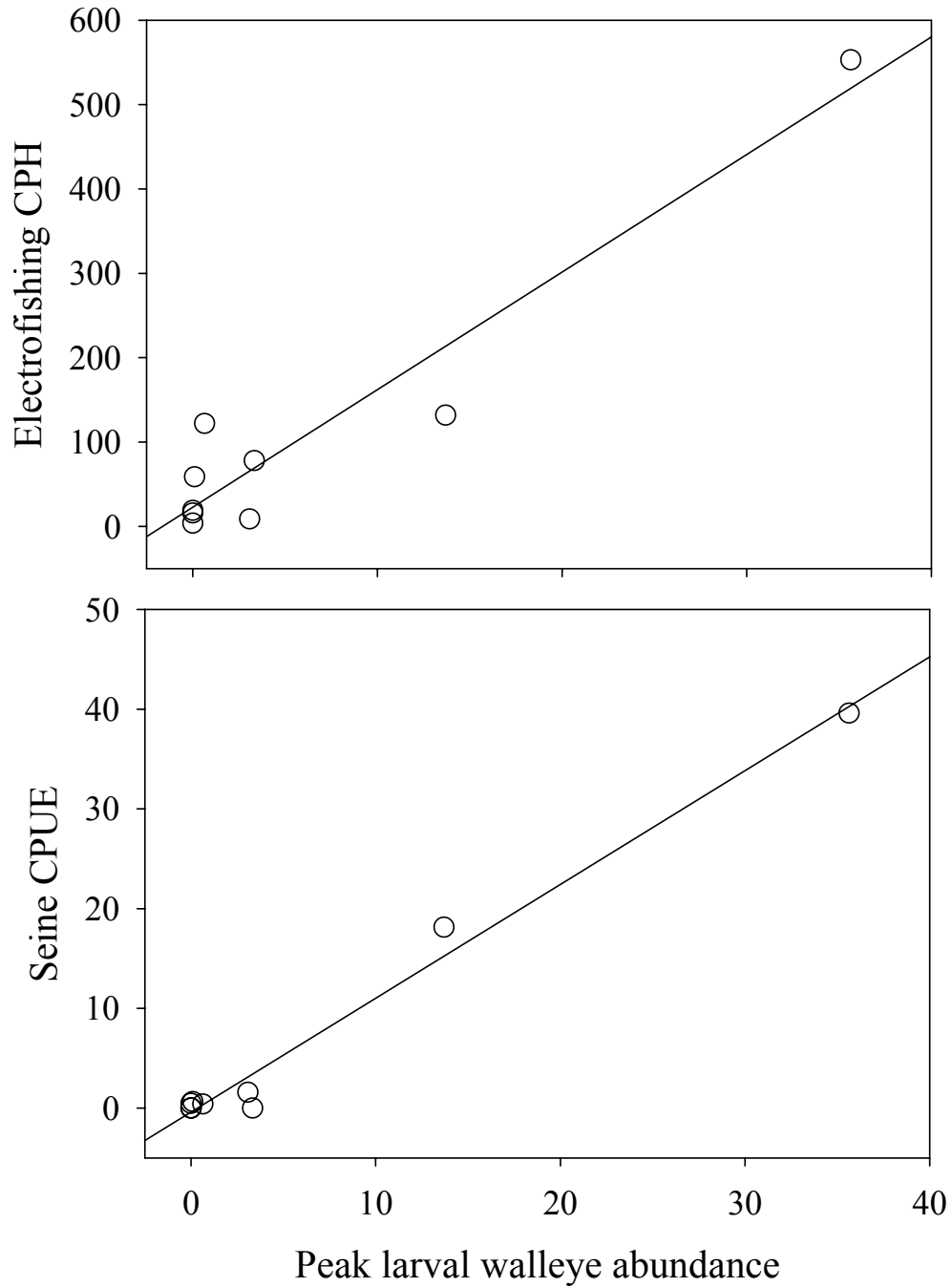


Figure 2-3. Linear relationships between peak larval walleye abundance (number / trap) estimated from light trap samples and relative abundance of age-0 walleye from summer seining (number / haul) and fall electrofishing (number / h).

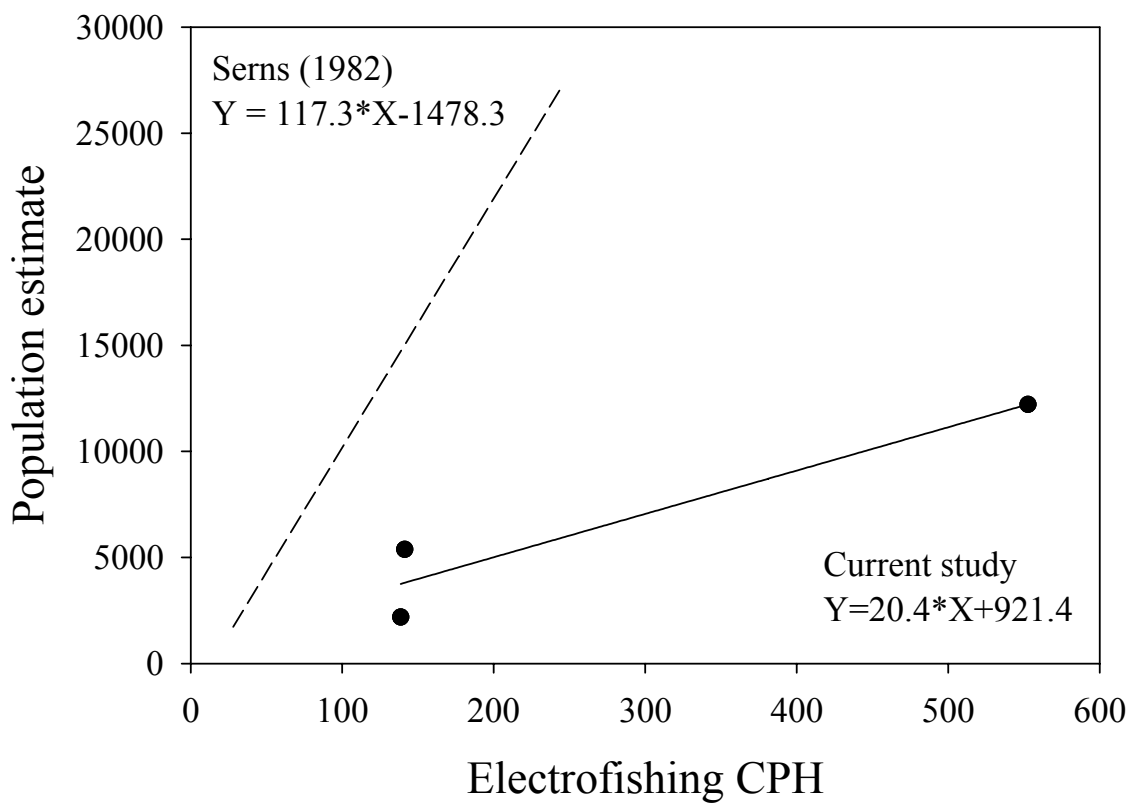


Figure 2-4. Linear regressions between estimates of age-0 walleye cohort size and electrofishing catch rates from Wisconsin (Serns 1982; dashed line) and South Dakota lakes (solid line).

Chapter 3

Importance of age-0 Yellow Perch for Survival of age-0

Walleye: Implications for Walleye Cohort Strength

Introduction

Predation by piscivorous fishes can alter the population dynamics of prey fishes by reducing their overall abundance or growth (Werner et al. 1983; Werner and Hall 1988), possibly resulting in alterations of production and recruitment dynamics (Knight and Vondracek 1993; Olson et al. 2001; Irwin et al. 2003). The rapid growth often exhibited by age-0 prey fishes can limit the duration of time they are vulnerable to predation by exceeding the gape limitations of sympatric predators. Michaletz (1998) found that growth of age-0 gizzard shad was negatively related to predation by piscivorous sport fishes in Missouri reservoirs, with the most intense limitations in age-0 gizzard shad availability observed for the youngest sport fish cohorts. Age-0 fishes are gape-limited predators throughout their first year, with gape limitation reducing the biomass of available prey most acutely at the larval and juvenile life stages (DeVries et al. 1998). Larvae and juveniles often show strong selection for the largest prey items they can consume (Graham and Sprules 1992; Campbell 1998), presumably to maximize net energy gain (Mills 1984; Graeb et al. 2004). Annual variations in the abundance and growth of age-0 prey fishes can have significant consequences for growth, and potentially recruitment, of age-0 sport fishes (Garvey and Stein 1998).

Yellow perch is an important component of the aquatic communities of northern Great Plains glacial lakes, in that it is a popular sport fish (Isermann 2003), but also the primary prey species for adult walleye in these systems and throughout northern North America (Arnold 1960; Seaburg and Moyle 1964; Swenson and Smith 1976; Johnson 1977). However, the relative importance of yellow perch as a prey resource for age-0 walleye in northern Great Plains glacial lakes is not well understood. Pelham et al. (2001) noted that while age-1 and older walleye consumed predominantly age-0 yellow perch, the rapid growth of yellow perch made them unavailable to age-0 walleye as prey in Spirit Lake, Iowa during 1997-1998. However, consumption of yellow perch by age-0 walleye has been documented in a number of systems (see references in Colby et al. 1979). The objective of this study was to investigate the importance of age-0 yellow perch as a prey resource for age-0 walleye indirectly, by examining the relations between walleye year-class strength and yellow perch abundance and growth.

Methods

The importance of age-0 yellow perch as a prey resource for age-0 walleye was determined using the spring larval, summer seine, and fall electrofishing samples collected from Parks Lake (2001, 2002 cohorts), Lake Sinai (2001-2003 cohorts), Lake Madison (2001 cohort), and Lake Thompson (2002, 2003 cohorts) described in the two previous chapters. Fall electrofishing catch rates were used as the measure of walleye cohort strength, as catches from the first and second fall are often strongly correlated (Serns 1981; Willis 1987). Relations between walleye cohort strength and yellow perch

abundance and growth were determined separately for larval (1 May – 15 June) and juvenile (1 July – 31 Aug) life stages. Although abundance of yellow perch at the larval and juvenile life stages are not independent (Anderson et al 1998; Isermann 2003) both walleye and yellow perch undergo marked shifts in diet and habitat use during these life stages. Both fishes are limnetic as larvae (Houde and Forney 1970), but during the summer months walleye become demersal (Forney 1976; Ryder 1977) and yellow perch either remain pelagic or move into littoral areas (Post et al. 1997). Spatial overlap of these fishes and the importance of yellow perch as a prey item for age-0 walleye were expected to differ between these two life stages. Therefore, these two periods were considered separately in these analyses.

Bivariate correlations were determined between age-0 walleye fall abundance and peak abundance of larval yellow perch from light trap, conical plankton net, and Miller sampler (see chapter 1 for a description of gears) collections; weekly larval yellow perch abundance estimates generated from each ichthyoplankton gear; peak abundance of juvenile yellow perch from summer seine collections; weekly estimates of larval yellow perch size (from all ichthyoplankton gears combined); and growth rate (mm/d) of yellow perch during both the larval and juvenile life stages.

In addition, the temporal availability of age-0 yellow perch to age-0 walleye predation was determined by comparing walleye gape limitation to age-0 yellow perch length distributions from summer seine samples. The range of yellow perch lengths that could be consumed by age-0 walleye was calculated based on walleye length distributions observed from summer seine samples. Age-0 walleye prefer prey that are

approximately 33% of their total length (TL) (Einfalt and Wahl 1997) but are physiologically able to consume spinous prey fishes of approximately 40% of their TL (Knight et al. 1984). Maximum walleye gape was calculated as 40% of walleye TL for the smallest, largest, and median walleye sizes captured on each sampling date, encompassing the entire range of walleye maximum gape. No age-0 walleye were captured in seine samples in Lake Thompson in either 2002 or 2003, or in Lake Sinai in 2003, and no age-0 yellow perch were collected in Parks Lake in 2002, therefore, these lake-year combinations were not included in these analyses.

Results and Discussion

Little of the variance in fall walleye abundance (electrofishing CPH) was explained by peak larval yellow perch abundance estimates generated from any of the three ichthyoplankton gears ($r = 0.14, 0.52, \text{ and } 0.14$ for conical plankton net, Miller sampler, and light traps, respectively). However, fall walleye abundance showed significant positive correlations with conical plankton net estimates of larval yellow perch density collected 15 - 21 May ($r = 0.96, P < 0.0001$) and 5 - 11 June ($r = 0.81, P = 0.007$), light trap estimates of yellow perch abundance collected during 15 - 21 May ($r = 0.77, P = 0.01$), and peak juvenile abundance ($r = 0.88; P = 0.001$). The very strong walleye cohort observed in Parks Lake in 2001 (569 fish/h electrofishing) had a strong influence on all of these relations. However, the strength of this cohort is within the range observed for naturally-produced walleye cohorts (0-921 fish/h fall electrofishing;

D. Lucchesi and B. Blackwell, SDGFP, unpublished data) from populations throughout this region of South Dakota, and should not be dismissed as being an extreme case.

That fall walleye abundance was not correlated to peak larval yellow perch abundance from any of the three ichthyoplankton gears but was correlated to estimates of larval yellow perch abundance during the week of peak walleye hatching (i.e. 15-21 May period) suggests that timing of larval yellow perch hatching is an important influence on larval walleye survival, more so than absolute abundance alone. The timing of peak yellow perch abundance varied among lakes and among years. Peak larval yellow perch abundance occurred after 21 May for all yellow perch populations, except Parks Lake and Lake Madison in 2001 (peak abundance prior to 21 May). However, larval yellow perch had been observed in conical plankton net and light trap samples during the 15-21 May period in five of the nine lake years studied. The presence of at least some larval yellow perch during this period, indicating an early onset of yellow perch hatching, may be an important determinant of larval walleye survival. Stahl et al. (1996) found that timing of stocking, in relation to the occurrence of peak larval gizzard shad abundance, was an important determinant of saugeye survival in Ohio reservoirs. In general, larval yellow perch densities of at least $0.1 / \text{m}^3$ from conical plankton net samples during the 15-21 May period corresponded to strong or very strong walleye cohorts. Li and Mathias (1982) demonstrated that daphnid densities of at least $0.1 / \text{m}^3$ optimized survival of walleye larvae. Similar densities of larval yellow perch would be expected to provide comparable benefits for walleye survival and improved growth over walleye larvae consuming zooplankton prey.

Yellow perch growth rates ranged from 0.11 to 0.56 mm/d as larvae and from 0.16 to 0.94 mm/d as juveniles. Fall walleye abundance was negatively correlated with larval yellow perch TL from the 22-28 May ($r = -0.94$, $P = 0.01$) and 29 May – 4 June ($r = -0.96$, $P = 0.008$) sampling weeks, but was not correlated to larval growth rate ($r = 0.18$, $P = 0.68$). However, fall walleye abundance was negatively related to yellow perch growth rate during the summer months ($r = -0.90$, $P = 0.005$; Figure 3-3). These results suggest that walleye survival is linked to the availability of yellow perch as prey through the first fall in glacial lake populations.

Age-0 yellow perch mean length exceeded 40% of age-0 walleye mean length on all sampling dates in every lake except Parks Lake in 2001, where all but the smallest age-0 walleye in Parks Lake were able to consume age-0 yellow perch throughout the summer of 2001. In all other lakes, the entire range of age-0 yellow perch lengths exceeded gape limitations of age-0 walleye on most sampling dates (Figure 3-5). On dates when yellow perch length distributions and walleye gape potential overlapped, only the largest walleye were able to consume the smallest yellow perch. Although we did not document similar relations between walleye gape and yellow perch length distributions as planktivorous larvae, size limitation is likely important at this stage as well, as piscivorous walleye fry show active selection for the smallest individuals available (Forney 1965; Wolfert 1966; Hoffamn 1972).

Starvation and predation of larvae and juveniles are arguably the most important sources of mortality acting to shape cohort strength of walleye after hatching (Houde 1967). Forney (1974) and Forney (1976) noted synchrony between cohort strength of

walleye and yellow perch in Oneida Lake, New York, concluding that strong yellow perch cohorts provided an alternate prey for adult walleye, reducing the significance of cannibalism. A reduction in cannibalism may also have contributed to the increased survival observed for age-0 walleye to fall, but as predation rates were not determined during this study, the significance of this effect is unknown. That walleye cohort strength was negatively correlated to yellow perch growth suggests that concordance between walleye and yellow perch cohort strength was a result of improved walleye survival from abundant yellow perch prey, rather than from a reduction in cannibalism by older walleye. Years in which yellow perch exhibit density-dependent growth likely prevents age-0 yellow perch from exceeding the gape limitations of age-0 walleye throughout the summer months, providing a high-energy prey for walleye throughout their first year. Furthermore, if the importance of age-0 yellow perch to age-0 walleye was not as a prey item, relations between yellow perch and walleye abundances would be expected to be negative as these fishes would be competing for the same prey resources, particularly at the larval life stage.

Management Implications

The Clear Lake 2003 walleye cohort was the only cohort sampled during this study that was not entirely a product of natural reproduction. Clear lake was stocked with 1-2 d old fry at approximately the same time that peak hatching of naturally-produced walleye occurs. Because age-0 yellow perch are not important as a prey until after walleye begin exogenous feeding, the source of the walleye cohort (natural or stocked)

likely had little importance in determining their survival, as survival of stocked fry was likely influenced by the same factors as naturally-produced fry. Thus the source of walleye in Clear Lake likely added little variation to these relations and are valid predator-prey interactions for both fry-stocked and naturally-produced cohorts.

The abundance of small, slow-growing age-0 yellow perch likely contributed to the very strong 2001 walleye cohort (fall electrofishing CPH = 563 fish/h) observed in Parks Lake. The 2001 yellow perch cohort was among the strongest observed during this study and showed slower summer growth (0.16 mm/d) than any of the other yellow perch cohorts documented during this study (range: 0.55-0.94 mm/d). The 2001 cohort of walleye in Parks Lake likely began consuming abundant yellow perch as larvae and were able to consume yellow perch as prey throughout their first year. However, the ability to consume yellow perch throughout their first year did not improve age-0 walleye growth. In general, low density walleye cohorts showed the most rapid growth (Madison 2001 and Parks 2002). Age-0 walleye from the 2001 Parks Lake cohort were among the largest age-0 walleye observed, but mean length did not differ from that observed from the Parks 2002 or Sinai 2002 cohorts (ANOVA, $df = 8, 887, P < 0.0001$).

Abundance of larval yellow perch shows limited potential as a predictor of walleye cohort strength, as the availability of yellow perch as a prey item is not the sole factor contributing to walleye cohort strength. The availability of yellow perch as a prey for larval and juvenile may enhance the survival of age-0 walleye to fall, but overall cohort strength is likely set prior to hatching (Chapter 2). Therefore, age-0 yellow perch abundance may provide some insight into walleye cohort strength for walleye

populations that show consistent natural reproduction, but little potential for populations with little or infrequent natural reproduction. For example, peak abundance of larval yellow perch (conical plankton net or light trap samples) occurred during the 15-21 May sampling period in both Lake Madison and Parks Lake in 2001, suggesting that fish prey were available for newly-hatched walleye in both lakes. However, the strength of those walleye cohorts were markedly different. The 2001 walleye cohort in Lake Madison was weak (3.5 fish/h) but was very strong in Parks Lake (569 fish/h). Larval walleye catch rates in Parks Lake 2001 were the highest observed during this study, but no larval walleye were captured in Lake Madison, suggesting that the weak 2001 walleye cohort observed in Lake Madison was a result of few larval walleye hatching, rather than poor survival of larval walleye. In addition, no larval yellow perch were captured in Lake Thompson before 29 May in either 2002 or 2003, but walleye cohort strength was fair in 2002 (78 fish/h). Thus, the utility of age-0 yellow perch abundance and growth as a predictor of walleye cohort strength is limited.

Manipulation of prey fish populations is a common management practice that has been used to enhance sport fish production in lakes and reservoirs (DeVries and Stein 1990). Management strategies to boost reproductive success and/or reduce growth of yellow perch may provide improvements for first-year survival of walleye in waters where natural reproduction is expected. The implementation of regulations to maintain high-density adult yellow perch densities may reduce some of the annual variability in cohort strength exhibited by yellow perch populations in eastern South Dakota lakes.

The installation of in-lake spawning structures has shown some potential for enhancing yellow perch reproductive success in South Dakota glacial lakes (Hanchin 2002).

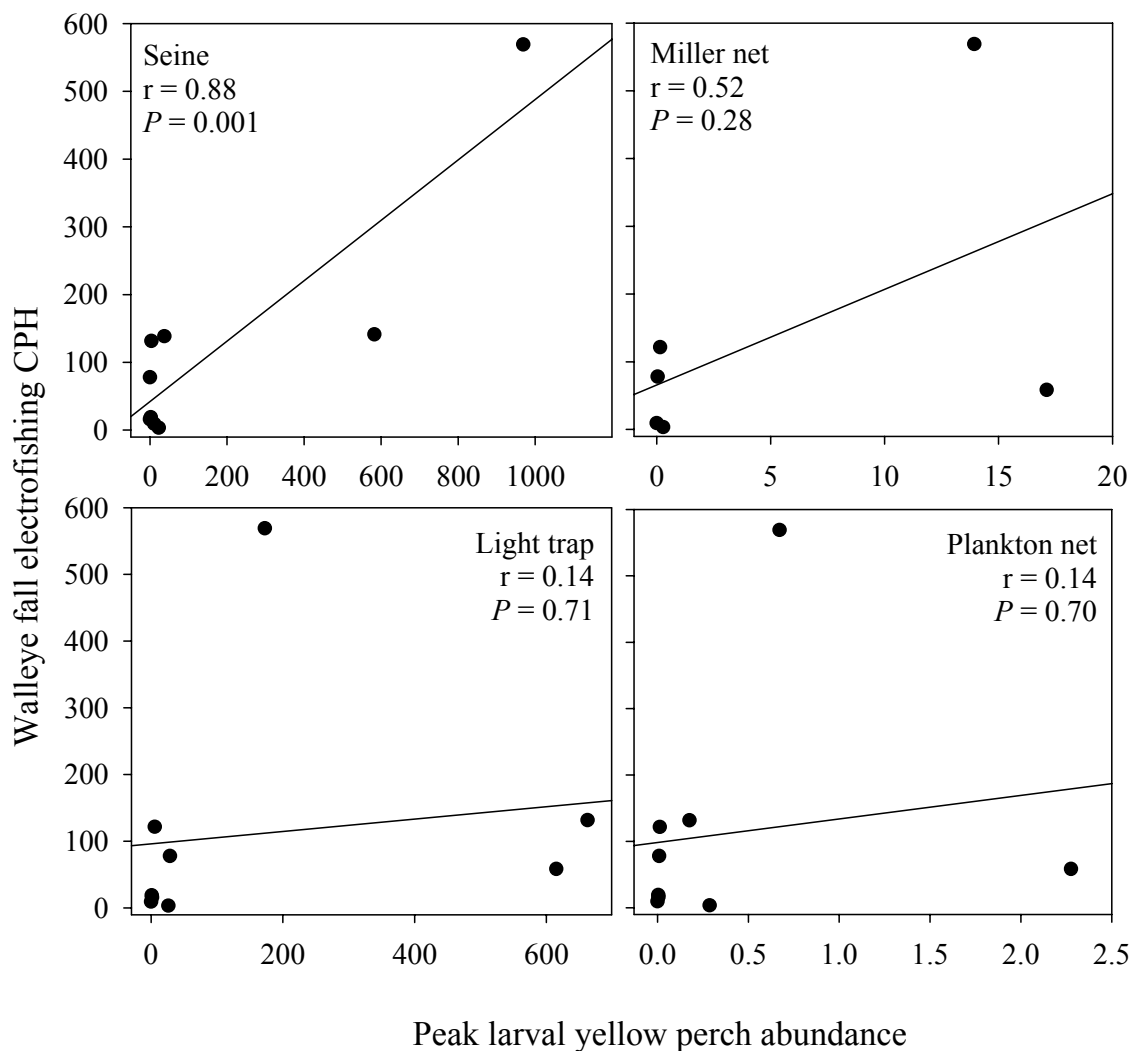


Figure 3-1. Linear relations between age-0 walleye fall abundance and peak abundance of yellow perch larvae from three ichthyoplankton gears and from peak abundance of juveniles from summer seine samples. Abundance is catch per unit effort for light traps (number / trap) and seine (number / haul) and density (number / m^3) for Miller and plankton net estimates.

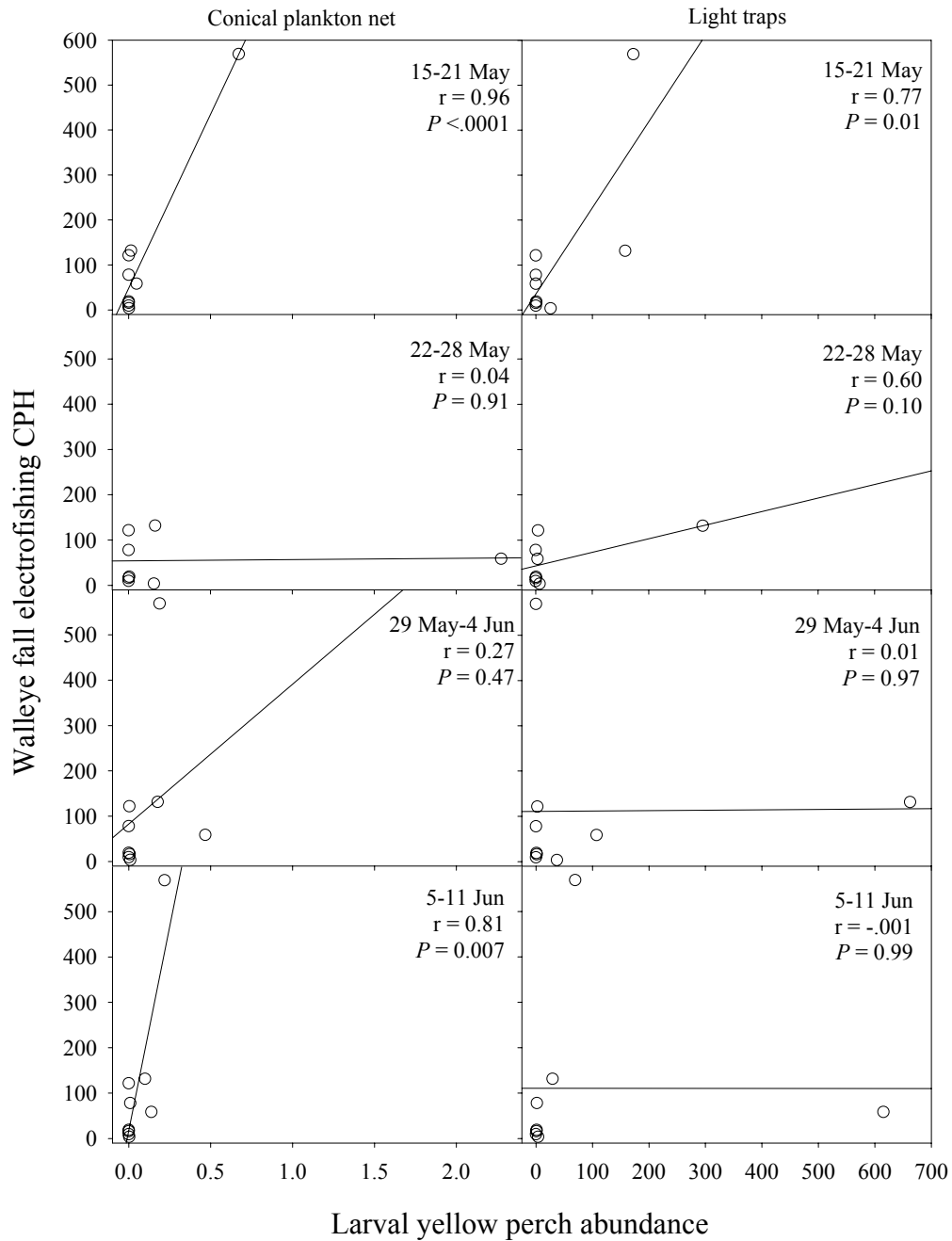


Figure 3-2. Linear relations between age-0 walleye fall abundance and weekly estimates of larval yellow perch abundance from 0.5-m conical plankton net (number / m³) and light trap (number / trap) samples.

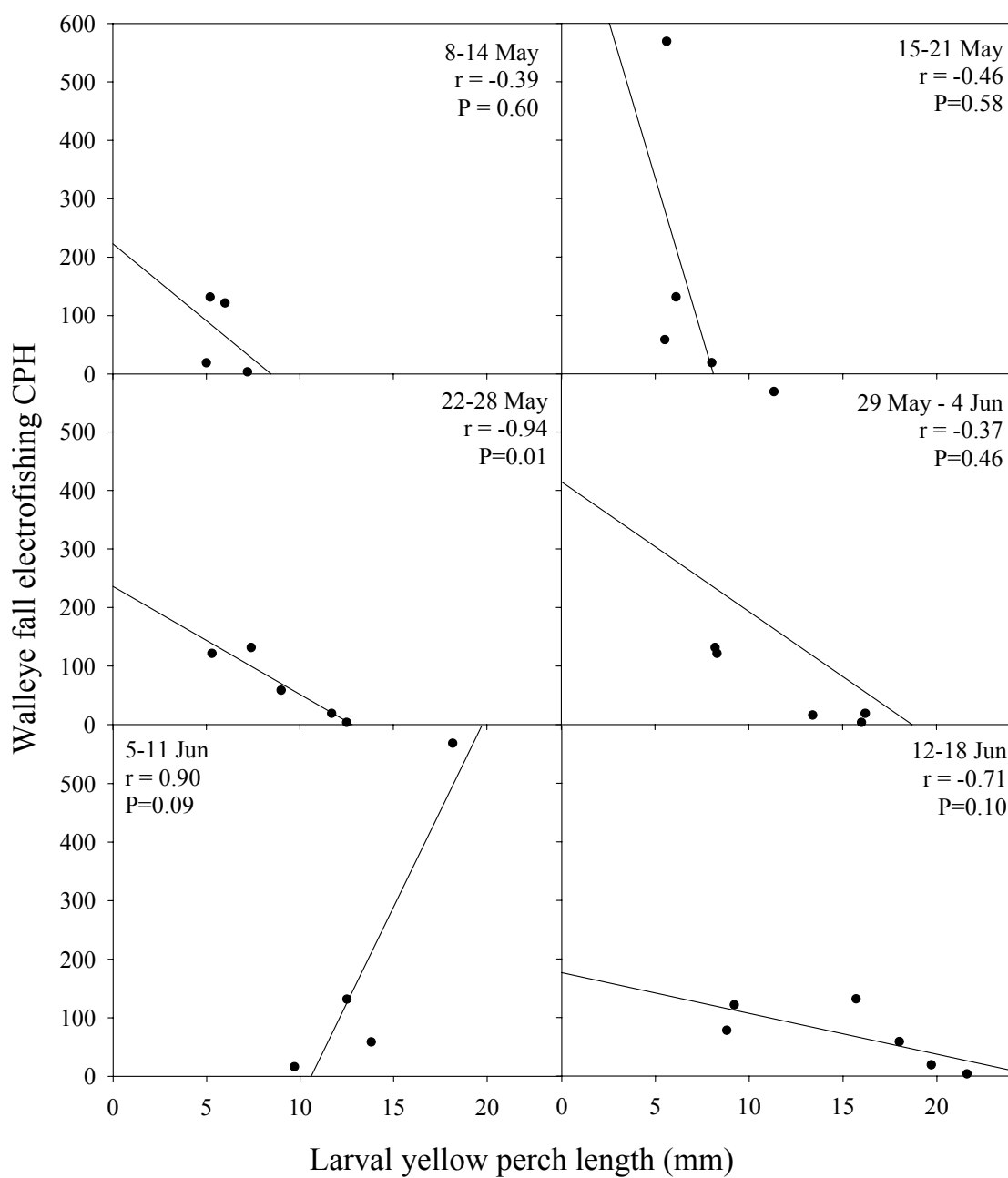


Figure 3-3. Relations between age-0 walleye fall abundance (catch / hour) and weekly estimates of larval yellow perch mean length from eastern South Dakota glacial lakes.

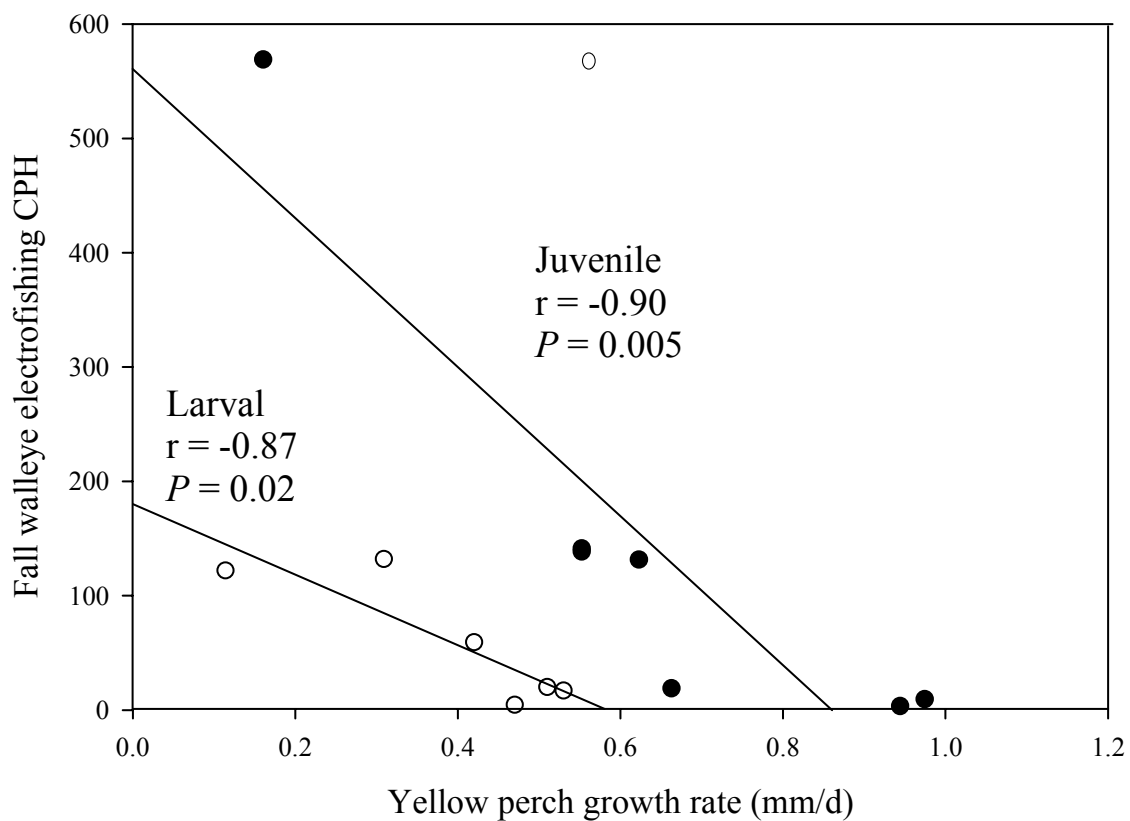


Figure 3-4. Relations between age-0 walleye fall abundance and growth rate of age-0 yellow perch as larvae (open circles) and juveniles (filled circles). The relationship presented for yellow perch larval growth rate does not include the Parks Lake 2001 cohort.

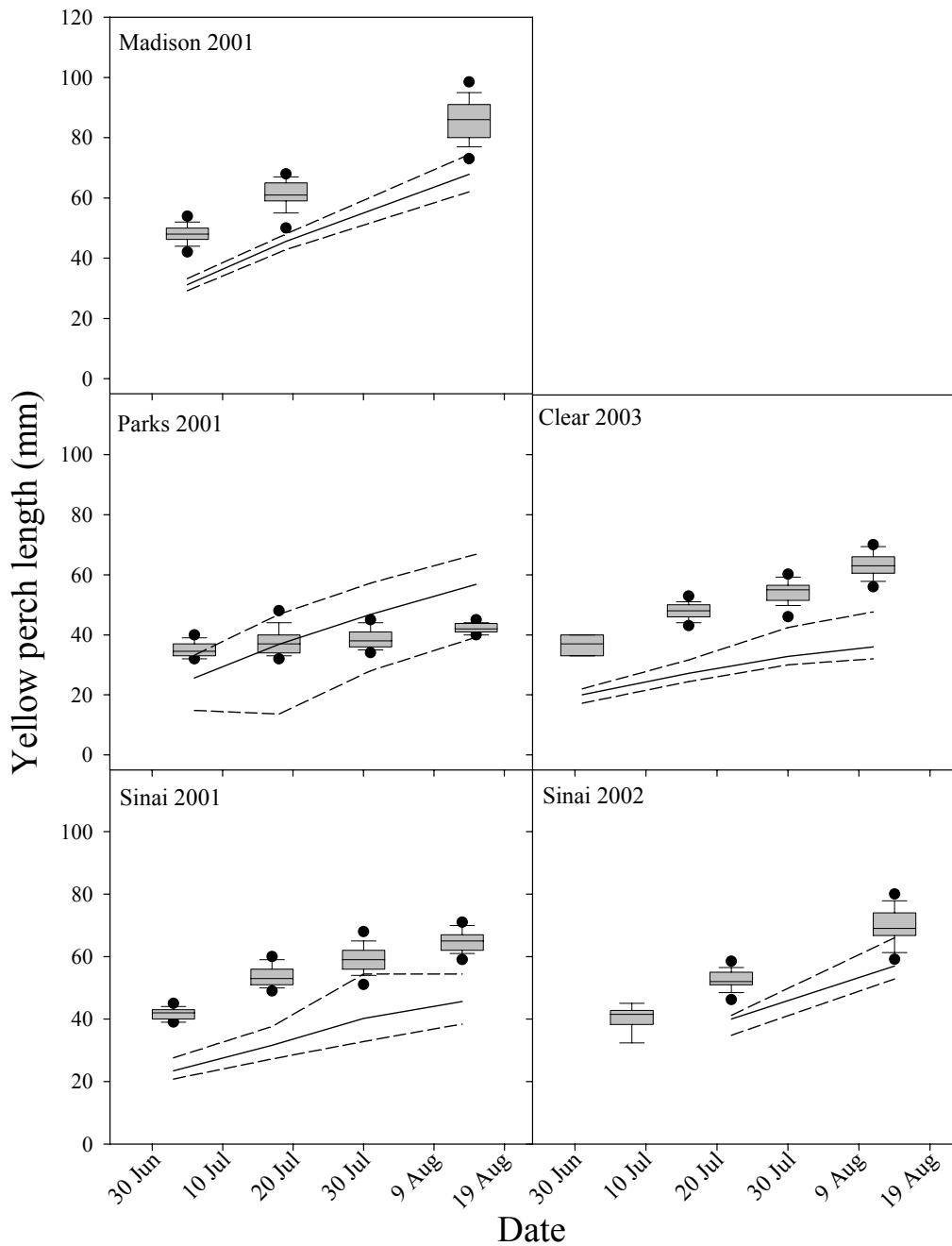


Figure 3-5. Yellow perch length distributions from July and August seine samples from four South Dakota glacial lakes. Grey boxes indicate the upper and lower quartiles, vertical bars represent the 10th and 90th percentiles, and points indicate the 5th and 95th percentiles. The lines represent estimated maximum gape of the smallest (lower broken line), median (solid line), and largest (upper broken line) age-0 walleye captured on each sampling date.

Chapter 4

Comparison of walleye population parameter estimates derived from concurrent trap-net and gill-net sets

Introduction

Interpretation of catch data for the purpose of population management or monitoring relies on two assumptions: 1) a particular gear collects a representative sample from the population and 2) catch rates are reflective of overall population abundance. However, the first of these assumptions is often not met because catches of all sampling gears show some size selective bias (Hayes et al. 1996; Hubert 1996; Reynolds 1996). The size of fish that is effectively retained by passive capture gears such as trap nets and gill nets is largely dependent upon the body morphometry of the targeted species and net mesh size, so neither gill-net or trap-net samples can be considered truly random, but if biases are known and constant, corrections can be made (Willis et al. 1985).

If catch per unit effort (CPUE) of two sampling gears reflects actual population abundance, a strong positive correlation would be expected between the two gears. Mean CPUE comparisons of multiple gears have shown both seasonal and size-selective differences associated with agreement of abundance estimates. Colvin (2002) found no correlation between relative abundance of white bass *Morone chrysops* collected by gill-nets and electrofishing. McNerny (1993) and Miranda et al. (1990) found positive correlations between abundance estimates of crappies *Pomoxis spp.*, but Guy et al. (1996)

reported that estimates of white crappie *P. annularis* abundance collected with trap-nets and gill-nets were not positively correlated in Kansas reservoirs. Agreement of CPUE and population size structure from multiple gear types have not been reported for walleye, *Sander vitreus*.

Most resource agencies employ some combination of gears to perform annual standardized assessments of fish populations. South Dakota Department of Game, Fish, and Parks biologists uses gill nets and trap nets to annually assess relative abundance, growth, and size structure of fish populations in the glacial lakes region of eastern South Dakota. The purpose of this study was to evaluate the agreement between population parameter estimates generated from trap-nets and gill-nets for walleye populations.

Methods

Fish Collections

Simultaneous trap-net and experimental monofilament gill-net sets were used to collect walleye in 11 glacial lakes in eastern South Dakota. Trap nets consisted of a single 16 m lead, two 0.91 x 1.52 m frames, with 19 mm mesh (bar measure). Gill-nets were 45.7 x 1.8 m, with 7.6 m panels of 13, 19, 25, 32, 38, and 51 mm mesh (bar measure) arranged by ascending mesh size. Simultaneous sets were conducted annually in Brant Lake, Clear Lake, Enemy Swim Lake, Madison Lake, Poinsett Lake, Roy Lake, South Buffalo Lake, and Thompson Lake from 1994 through 2000. Annual samples were conducted from 1994 – 1999 in Herman Lake, 1994 through 1997 in Sinai Lake and from 1997 through 2000 in Waubay Lake. Blackwell (2001) and Stukel (2003) provided

thorough descriptions of the physical and chemical characteristics of all study lakes. Sampling was conducted between 3 July and 15 August each year, and the sets for a particular lake occurred within the same week of the year in each year (i.e. Brant Lake was sampled between 23 July and 1 August, during each year).

Effort (net nights) was not equal between gears for any lake-year combination (Table 4.1). Typically trapnet effort was two to four times that of gill-nets. Gill net effort was low (2-8 net nights) compared to trap nets (4-32 net nights) because of the high walleye mortality associated with using gill nets that result from warm water temperatures.

Length and weight of walleye were measured in all lakes. Typically, all walleye collected in each gear were measured. However, if catch rates were excessively high, at least 100 fish of each species captured in each gear were measured and the remaining fish were counted and assigned to 1 cm length groups based on the length distribution of the measured sample.

Age determinations were typically conducted annually in all lakes, however, no age determinations were made for Lake Thompson in 1996, or Lake Herman in 1995, 1997, and 2000. Scales were used to age a sample of fish from each 1 cm length group in each lake in each year. Any fish that was not aged was assigned an age based on an age-length key produced from the aged sample from each gear. Because fish older than age-5 accounted for only a small proportion of the walleye captured and the accuracy of aging walleye with scales declines for fish over age-5 (Isermann et al. 2003), age-specific analyses were restricted to walleye less than or equal to age-5.

Analyses

Simultaneous sets of the two gears generated paired estimates of population parameters for each lake-year combination. Differences in population parameter estimates between the two gears were determined using a two-tiered analysis. First, differences in means were evaluated using Wilcoxon signed ranks test, which is a non-parametric equivalent of a paired t-test. Then, overall agreement between estimates generated from the two gears was evaluated using linear regression and testing for a 1:1 relationship (intercept = 0 and slope = 1), which would indicate perfect agreement.

Relative size-selectivity (S_R) of the two survey gears was assessed for the entire range of walleye sizes captured. For each lake-year combination S_R was calculated for each 1-cm length group using an adaptation of the selectivity index used by Kraft and Johnson (1992):

$$S_R = CPUE_T / CPUE_G$$

where $CPUE_G$ is gill-net CPUE and $CPUE_T$ is trap-net CPUE. In this index, length-specific gill-net CPUE serves as a reference population and trap-net CPUE of each length group is assessed against this reference population. It is important to note that this index is not a direct estimate of selectivity for either gear. Rather, it provides insight into the overall trends of size composition between gears. Mean S_R was only calculated for length groups that were observed in at least two lakes ($n \geq 2$), and those means were regressed against length group to determine overall trends in the selectivity relations.

Proportional stock density (PSD) and relative stock density (RSD-P) size structure indices (Gablehouse 1984) were calculated separately for each gear-lake-year combination. Size structure comparisons were limited to those lake-year combinations where at least 10 stock-length fish were captured by both gears.

Mean CPUE were compared between trap nets and gill nets using linear regression on catch rate ranks. Wilcoxon signed ranks test was not used to compare means of paired catch rate estimates because effort units were not equal. Therefore, ranks were assigned to catch rates of each gear in ascending order (1-7) for each lake and linear regression was then used to test for deviations from a 1:1 relationship over all lakes combined. Thus, if catches of both gears reflect population abundance, catch rate ranks should correspond for a given year and follow a 1:1 relationship. Linear regression was used only to test for deviations from a 1:1 relationship in catch rate pairs, not to develop predictive models. Catch rates of age 1-5 walleye were also assessed in the same manner for each age-class separately over all lakes combined. Differential in walleye growth was compared between gears using mean length-at-age (growth rate) of each age-class separately.

Results

During the course of this study 56,596 walleye were collected, but only 4.2% of these fish were captured in trap-nets despite the considerably higher effort allocated to this gear. The range of fish lengths captured was comparable between gears, but the length distributions were markedly different (Figure 4.1). Relative selectivity showed a

significant ($P < 0.01$) negative trend with fish length (Figure 4.3), and showed a regular oscillating pattern over the entire range of lengths, resulting in a relatively low correlation coefficient for this relationship ($r^2=0.15$).

Estimates of PSD ranged from 2 to 94 for gill-nets and 0 to 94 for trap nets. RSD-P estimates ranged from 0 to 51 in gill nets and from 0 to 49 in trap nets. Wilcoxon signed ranks tests indicated that there was no difference between gears for estimates of PSD or RSD-P (Table 4.2). There was a significant positive correlation ($P < 0.0001$) between both size structure indices (Figure 4.1). These relationships were highly variable for both PSD ($r^2 = 0.69$) and RSD-P ($r^2 = 0.31$), but did not differ significantly from a 1:1 line for either PSD or RSD-P.

Mean CPUE ranged from 0 to 71 for gill nets and from 0 to 21 for trap nets. Catch rate assessments for individual lakes revealed that there was poor agreement between gears for a majority of lakes. Perfect agreement of catch rate ranks between gears (a 1:1 relationship) was only observed for Clear Lake ($n = 7$). Trap-net and gill-net catch rate ranks were not significantly correlated for walleye when all age groups were combined (Table 4-3). Overall, catch rate ranks were highly variable and did not follow a 1:1 relationship. Age-specific catches did not agree between gears when age 1-5 walleye were considered separately (Table 4-4; Figure 4-5). The relationships between trap-net and gill-net catch rate ranks were significantly different from a 1:1 line for all walleye age groups (Table 4-4). Intercepts were always significantly higher than zero and slopes were always significantly less than one for overall CPUE and comparisons of CPUE for all walleye age groups.

Lengths of age 1, 2, 3, 4, and 5 walleye ranged from 120 to 350 mm, 190 to 460 mm, 240-520 mm, 270-610 mm, and 340-610 mm, respectively. Relations between trap-net and gill-net mean length at age estimates showed a significant positive correlation for all ages of walleye considered (Figure 4-6). For all age groups the range of lengths captured by both gears was comparable, but the proportions of specific length groups differed between gears. Wilcoxon signed ranks tests indicated that estimates of gill-net mean length-at-age were significantly lower ($P < 0.007$) than trap-net estimates for all ages, except age-4, but relationships between trap-net and gill-net estimates of mean length-at-age differed from a 1:1 line only for age-1 fish (Table 4-5).

Discussion

Hamley (1975) demonstrated that gill-net mesh selectivity determines the length distribution of fishes captured. Thus, the sample drawn from a population depends entirely on the selectivity of the mesh sizes employed. Selectivity of both gill-nets and trap-nets varies with fish length (Hamley and Reiger 1973; Kraft and Johnson 1992), but the relationship between selectivity and fish length for gill-nets and trap-nets are markedly different. Trap net selectivity shows a sigmoidal relationship with fish length, wherein maximum selectivity is skewed towards the upper tail of the length distribution (Hamley and Reiger 1973; Kraft and Johnson 1992). Gill-net selectivity for a particular mesh size follows a normal, or bell-shaped, distribution (Hamley 1975; Spangler and Collins 1992), where selectivity is low for the largest and smallest sizes captured and is highest for intermediate-sized individuals. Consideration should be given to such

species-specific biases of size-selectivity when interpreting catches from either gear, size-specific adjustments may be made when necessary (Willis et al. 1985; Spangler and Collins 1992).

Differences in size selectivity between trap nets and gill nets account for a majority of the differences in estimates of population structure and function observed in this study. Hamley and Reiger (1973) found that overall gill-net selectivity increases with both mesh size and fish size for adult walleye between 20 and 75 cm. When an experimental gill-net has been encountered, the probability of retaining larger fish is higher than for smaller individuals, but trap-net selectivity remains stable for larger fish once maximum selectivity has been obtained. The decline in S_R observed over the range of fish lengths captured is likely a result of this increase in selectivity of gill-nets, rather than changes in size selectivity of trap-net catches.

Oscillations in S_R relations is also a result of gill-net selectivity. Peaks in S_R to length relations correspond to the fish lengths between the optimal lengths retained by gill-net meshes. Trap-net selectivity peaks relative to gill nets because the gill-net mesh sizes used are least effective at retaining fish of those length intervals. Likewise, troughs in S_R relations corresponded closely to the reported optimal lengths of fish retained (both wedged and tangled) by the gill-net mesh sizes used (Hamley and Reiger 1973; Willis et al. 1985). Estimates of walleye size structure did not differ between gears. Agreement between size structure estimates of trap-nets and gill-nets has also been reported for white crappie (Guy et al. 1995).

Selectivity of trap nets would be expected to remain consistently high for all walleye over stock-length (Hamley and Reiger 1973), but the gill-net meshes used in this study were insufficient to sample the entire size range of these walleye populations, a large portion of preferred-length fish in particular may be under-represented. Over the 7 years of this study 95% of the walleye captured in gill-nets ranged from 123 to 531mm, which is consistent with the length range reported by Willis et al. (1985) for equivalent gill-net meshes. Willis et al. (1985) also found that fish over 550 mm were most effectively sampled with 64-mm mesh, which was not used during this study. A large portion of preferred-length walleye would not be represented in gill-net catches so estimates of gill-net size structure may be biased low as a result of mesh-size inefficiencies.

Assuming that encounter rates are equal for both gears, trap-net estimates of size structure may be more representative of population size structure than gill-net estimates. However, this assumption is likely not met for either species during the summer sampling period. Size structure estimates showed positive covariance between the two gears, but size structure estimates of the two gears are not necessarily interchangeable.

Overall catch rate trends should be similar if catch rates from both gears are reflective of actual population abundance. Studies comparing mean CPUE of multiple gear types often use a positive correlation between gears as the criterion for assessing agreement between gears (Schorr and Miranda 1991; McInerny et al. 1993; Guy et al. 1995). The lack of a positive correlation does indicate disagreement between catch rates, but this criterion may not always indicate agreement when a significant positive

correlation is found. Comparisons of CPUE estimate ranks of separate walleye age-classes showed highly significant correlations ($P < 0.0001$) for all age groups, but all relations were significantly different from a 1:1 relationship. Using regressions of catch rate ranks to test for deviations from a 1:1 relationship is a more robust method of assessing agreement between abundance estimates. As gill-net catch rates increased, trap-net catch rates did not increase proportionately, suggesting that trap-nets are not as sensitive to changes in walleye population abundance. The higher number of walleye captured in gill-nets despite the lower overall effort allocated to that gear and the greater sensitivity of gill-nets to fluctuations in population abundance suggests that gill-net CPUE may more closely reflect actual population abundance during the summer months. A seasonal effect on trap-net catch rates has been demonstrated for crappies, *Pomoxis spp.*, (Miranda et al. 1990; Guy and Willis 1991). Forney (1961) found a seasonal effect on trap-net catches of walleye, but no seasonal effect was observed for gill-nets.

The range of walleye lengths captured by both gears were comparable for all age classes, but gill-net catches were always comprised of a higher proportion of smaller fish. It is unclear why trap-net estimates of mean length at age were larger than gill-net catches. One possible explanation would be that the marked differences in growth rates of individual walleye within an age class observed in this study resulted in differences in habitat use among individuals. Blackwell (2001) observed that larger walleye remained significantly closer to shore than smaller individuals during the summer months (June through August) in two South Dakota glacial lakes, and Anderson (1998) found that gill-net encounter rates decreased with walleye size in eleven lakes. The discrepancy in size

between the smallest and largest walleye of an age class may result in size-specific behavioral differences, influencing encounter rates between the two gears. For example, smaller age-1 walleye would be vulnerable to predation by common littoral piscivores like northern pike *Esox lucious* and smallmouth bass *Micropterus dolomieu* which may reduce the use of those areas by those smaller individuals, decreasing the probability they would encounter littoral-set trap-nets. Differences in habitat use between males and females (Blackwell 2001) or between juvenile and mature individuals of an age group may also contribute to differences in encounter rates. However, neither sex or maturity data were obtained during this study.

Gill-net meshes of 12.7, 19, and 25 mm should retain age-1 and age-2 walleye, but the selectivity of these meshes is low. The difference in catch rate trends observed between the two gears for ages 3, 4, and 5 should also be realized in catch curves as well. Because relative abundance estimates of these two gears did not agree for any age group, mortality rate estimates generated from these gears would consequently be expected to differ as well.

Table 4-1 Annual effort (net nights) values for simultaneous trap-net and gill-net sets in eleven South Dakota lakes from 1994 through 2000.

Lake	Year						
	1994	1995	1996	1997	1998	1999	2000
Gill-net							
Brant	4	4	4	4	5	4	6
Clear	6	6	6	6	6	6	6
Enemy Swim	6	6	6	6	6	6	6
Herman	3	2	4	3	4	5	-
Madison	4	3	3	3	3	3	3
Poinsett	8	8	6	6	6	6	6
Roy	2	6	6	6	6	6	6
Sinai	4	3	3	2	-	-	-
South Buffalo	6	4	5	6	6	6	6
Thompson	2	2	3	3	4	3	3
Waubay	-	-	-	6	8	8	8
Trap-net							
Brant	12	12	4	12	12	12	12
Clear	20	18	18	18	20	18	18
Enemy Swim	21	18	15	13	11	4	8
Herman	11	5	10	10	-	10	-
Madison	10	10	9	8	10	10	10
Poinsett	20	21	21	10	10	7	13
Roy	21	23	24	20	21	13	10
Sinai	8	10	10	10	-	-	-
South Buffalo	21	20	19	15	18	11	10
Thompson	13	10	11	14	14	14	10
Waubay	-	-	-	29	32	23	32

Table 4-2. Comparison of trap-net and gill-net proportional stock density (PSD) and relative stock density of preferred-length fish (RSD-P) relations for walleye in eleven South Dakota lakes. Confidence intervals are 95% intervals of regression model parameter estimates.

Size structure	Wilcoxon signed ranks		r^2	Least squares regression			
	S	P		Intercept		Slope	
				Estimate	Confidence interval	Estimate	Confidence interval
PSD	-26.5	0.73	0.69	3.58	-3.72–10.90	0.88	0.69 – 1.07
RSD-P	-46.5	0.34	0.31	3.05	-0.26–6.36	0.73	0.38 – 1.08

Table 4-3. Least-squares relations between trap-net and gill-net catch rate ranks for walleye in eleven South Dakota lakes. Confidence intervals are joint 95% confidence intervals of regression model parameter estimates.

Age	n	P	Intercept		Slope	
			Estimate	Confidence interval	Estimate	Confidence interval
1	66	<0.0001	15.39	7.40 – 23.38	0.54	0.33 – 0.74
2	65	0.0012	12.04	4.75 – 19.34	0.63	0.44 – 0.82
3	64	<0.0001	11.82	4.55 – 19.09	0.63	0.44 – 0.83
4	57	<0.0001	14.95	7.30 – 22.61	0.48	0.25 – 0.71
5	41	0.005	11.76	5.05 – 18.48	0.43	0.16 – 0.71
All	69	0.1996	3.16	2.15 – 4.18	0.15	-0.08 – 0.39

Table 4-4. Comparisons of walleye mean length-at-age estimates calculated from catches in trap-nets and gill-nets. Confidence intervals are 95% confidence intervals of regression model parameter estimates.

Age	n	Wilcoxon signed rank		Intercept		Slope	
		S	P	Estimate	Confidence interval	Estimate	Confidence interval
1	32	189	0.0001	4.91	1.65 – 8.16	0.83	0.68 – 0.96
2	39	189	0.0066	0.14	-3.20 – 3.48	1.01	0.90 – 1.12
3	39	258	<.0001	0.93	-2.70 – 4.56	1.00	0.89 – 1.10
4	19	24	0.3525	4.85	-7.70 – 17.40	0.89	0.57 – 1.19
5	10	19.5	0.0488	-3.79	-18.83 – 11.26	1.11	0.78 – 1.44

Table 4-5. Estimated efficiency of gill-nets and trap-nets for sampling age-1 and age-2 walleye in eastern South Dakota glacial lakes. Expected CPUE were calculated from extrapolation of catch curves based on mean catches of age-3 to age-5 walleye from the 1993-1997 cohorts.

Lake	Age-1			Age-2		
	Catch Rate		Percent efficiency	Catch Rate		Percent efficiency
	Observed	Expected		Observed	Expected	
Gill-nets						
Brant	1.73	18.54	9.3	4.74	9.83	48.2
Clear	2.9	13.26	21.9	2.26	8	28.3
Enemy Swim	4.03	77.16	5.2	3.3	30.41	10.9
Madison	8.23	84.69	9.70	8.66	28.64	30.2
Poinsett	3.17	89.56	3.5	6.0	30.05	20.0
Sinai	1.28	5.20	24.6	5.16	3.56	144.9
South Buffalo	3.0	470.12	0.6	2.80	54.27	5.2
Waubay	5.6	55.20	10.1	4.81	18.57	25.9
Trap-nets						
Brant	0.36	2.82	12.8	0.81	1.05	77.1
Clear	0.11	0.233	47.2	0.09	0.23	39.1
Poinsett	0.48	3.86	12.4	0.43	1.4	30.7
Roy	0.07	2.23	3.1	0.65	0.99	65.7
South Buffalo	0.14	2.0	7.0	0.11	0.64	17.2
Waubay	0.1	1.49	6.7	0.28	0.67	41.8

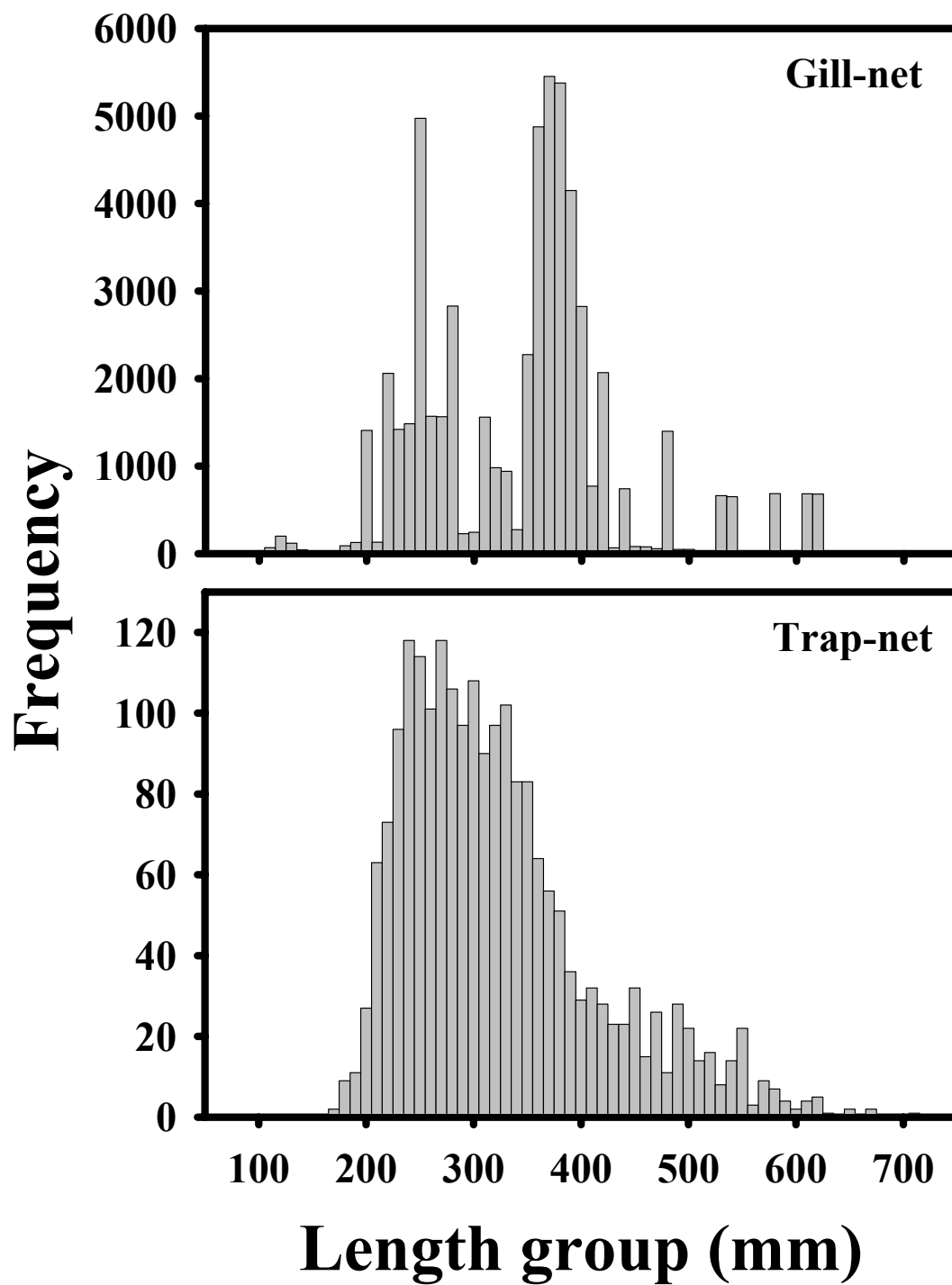


Figure 4-1. Length distributions of walleye collected by gill-nets and trap-nets in eleven South Dakota glacial lakes 1994-2000.

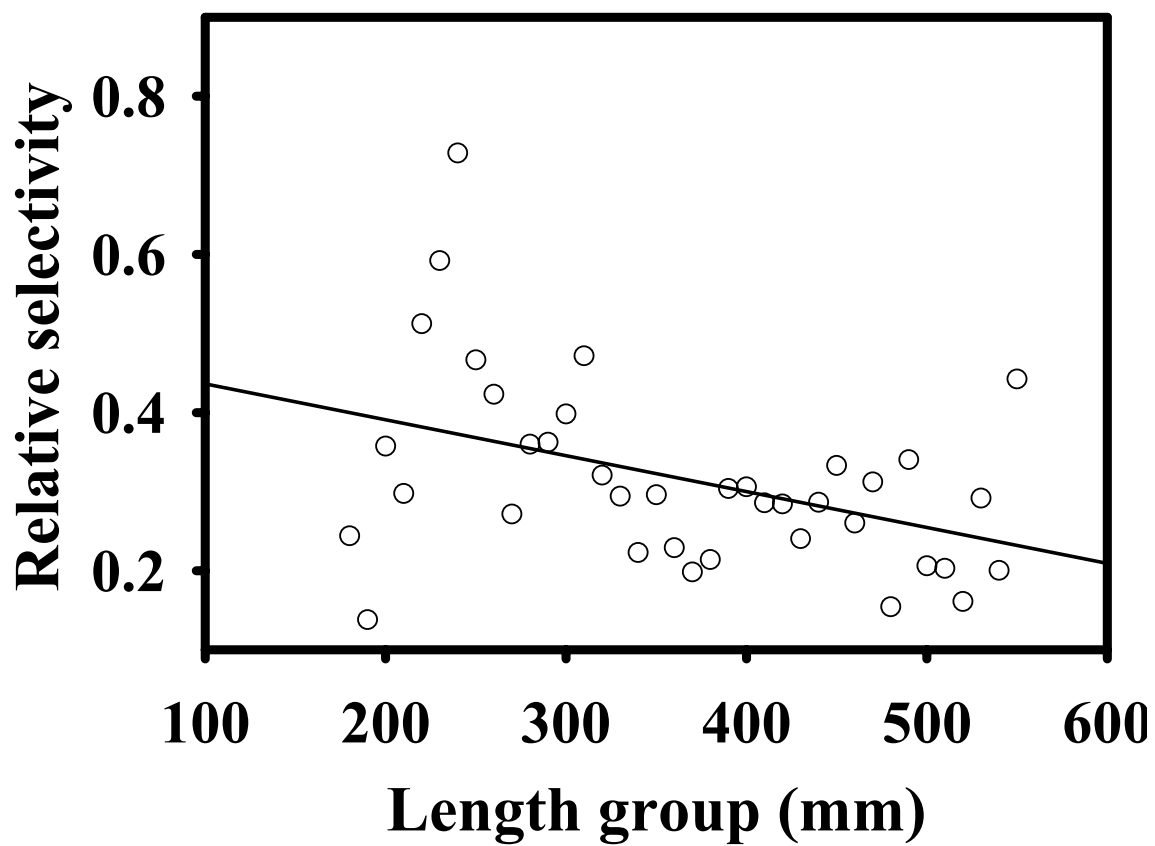


Figure 4-2. Relations between relative selectivity of trap-nets and experimental gillnets (trap-net CPUE / gill-net CPUE) to fish length for walleye in eastern South Dakota glacial lakes. The solid line is a least-squares regression line.

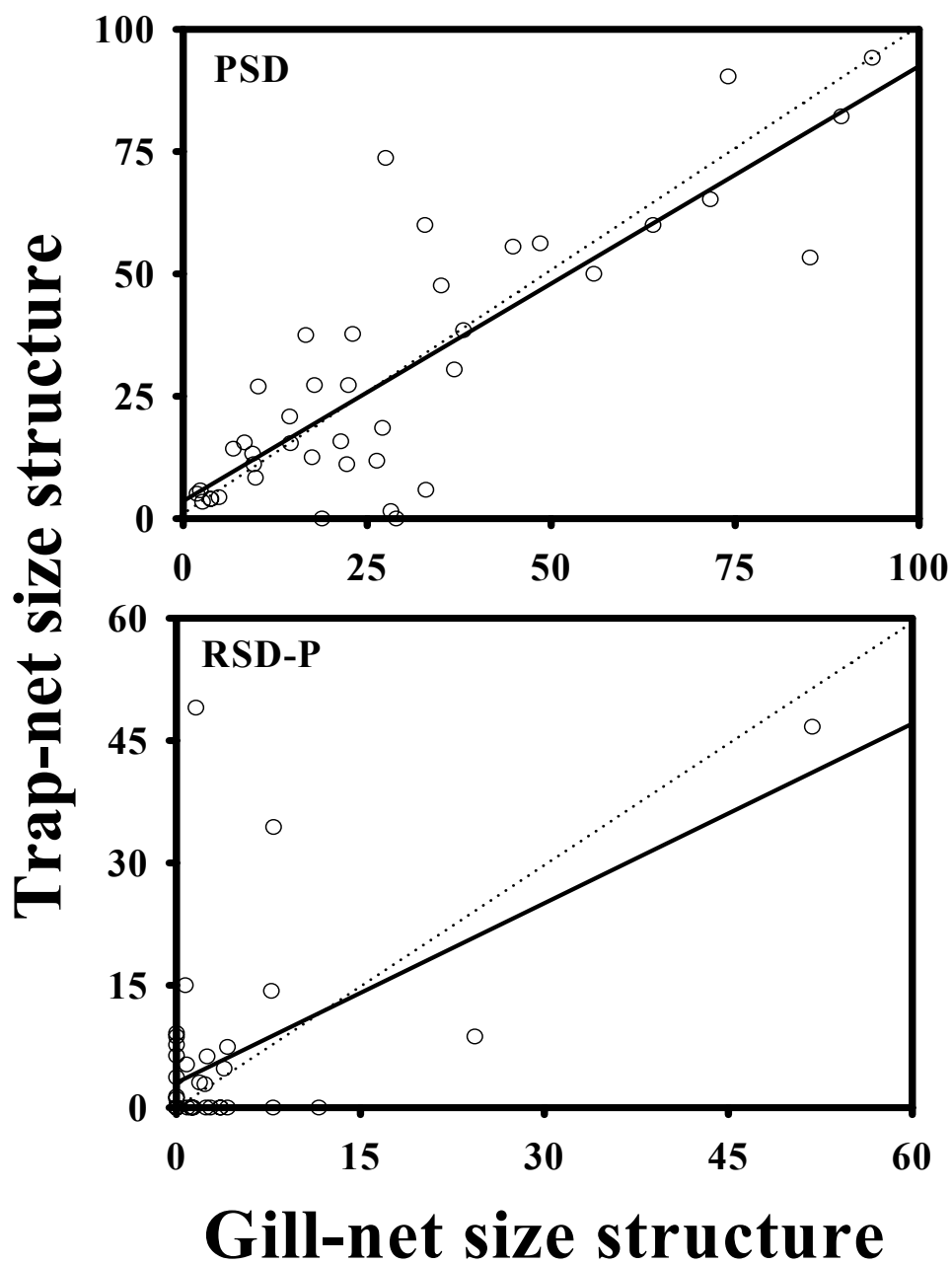


Figure 4-3. Relations between proportional stock density (PSD) and relative stock density of preferred-length fish (RSD-P) calculated from catches of walleye in trap-nets and experimental gill-nets in eleven South Dakota glacial lakes. Solid lines are least-squares regression lines and the dotted lines are 1:1 reference lines.

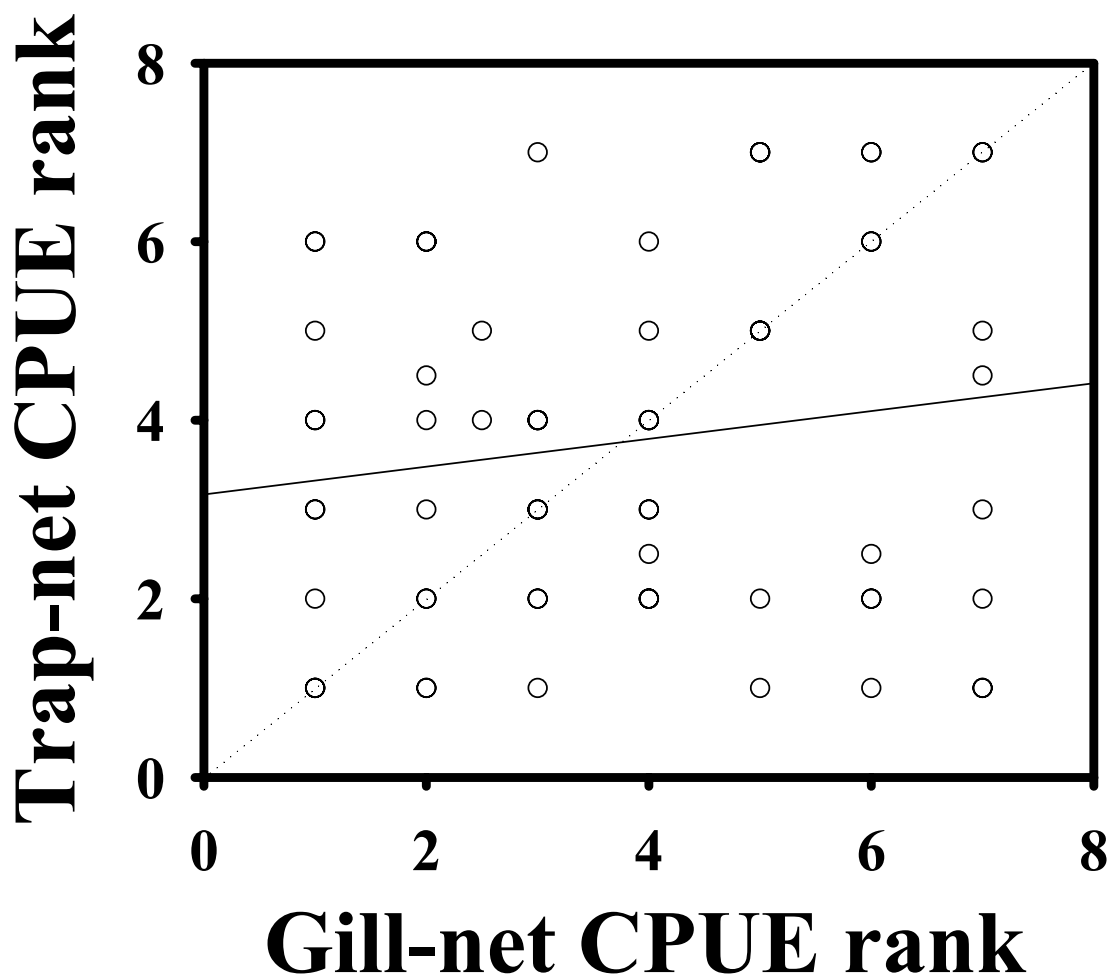


Figure 4-4. Relations between trap-net and experimental gill-net CPUE (walleye / net night) ranks for eleven South Dakota walleye populations. The solid line is a least-squares regression line and the dotted line is a 1:1 reference line.

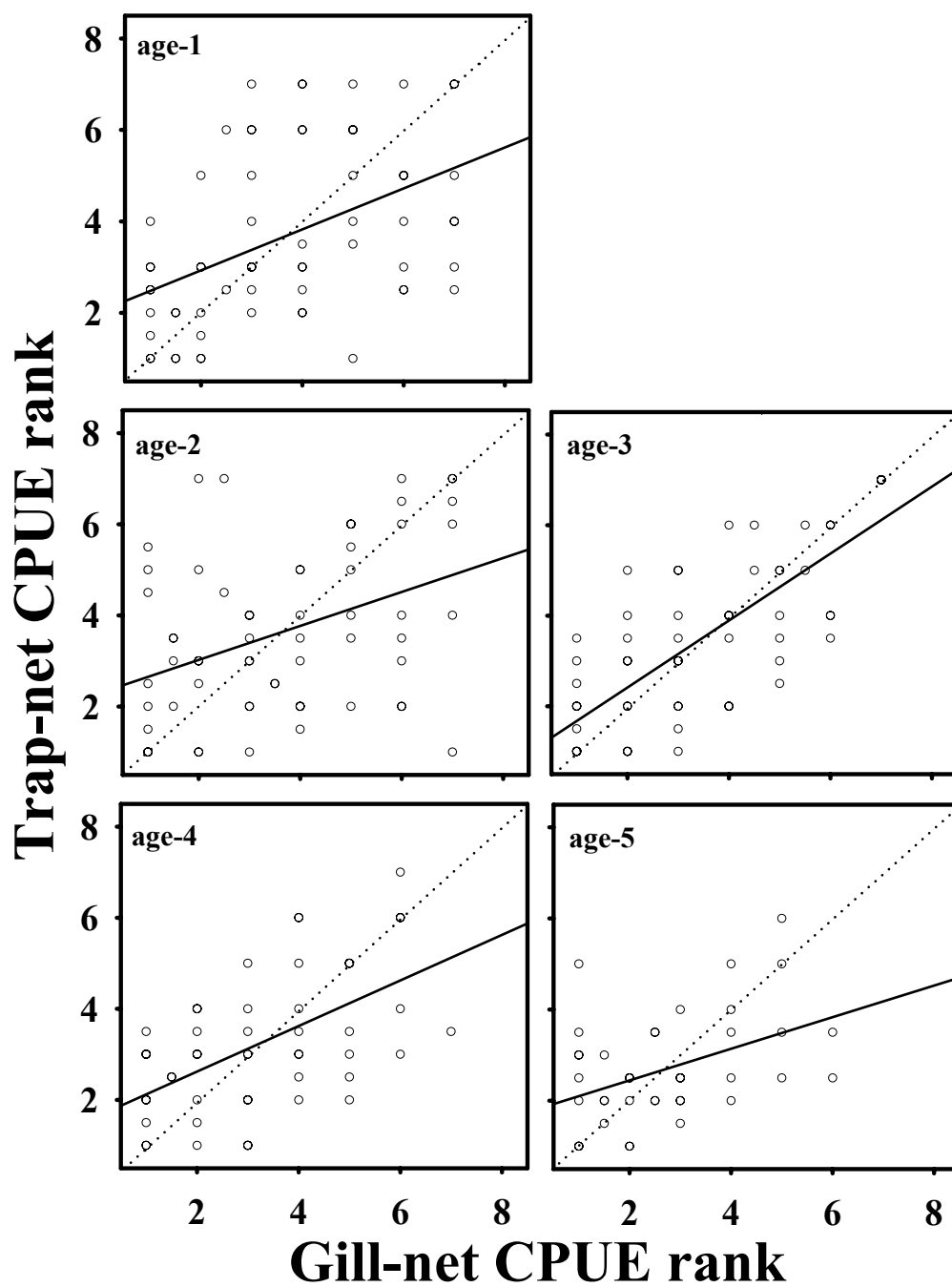


Figure 4-5. Relations between trap-net and experimental gill-net CPUE (walleye / net night) ranks for age-1 through age-5 walleye in eleven South Dakota lakes. Solid lines are least-squares regression lines and the dotted lines are 1:1 reference lines.

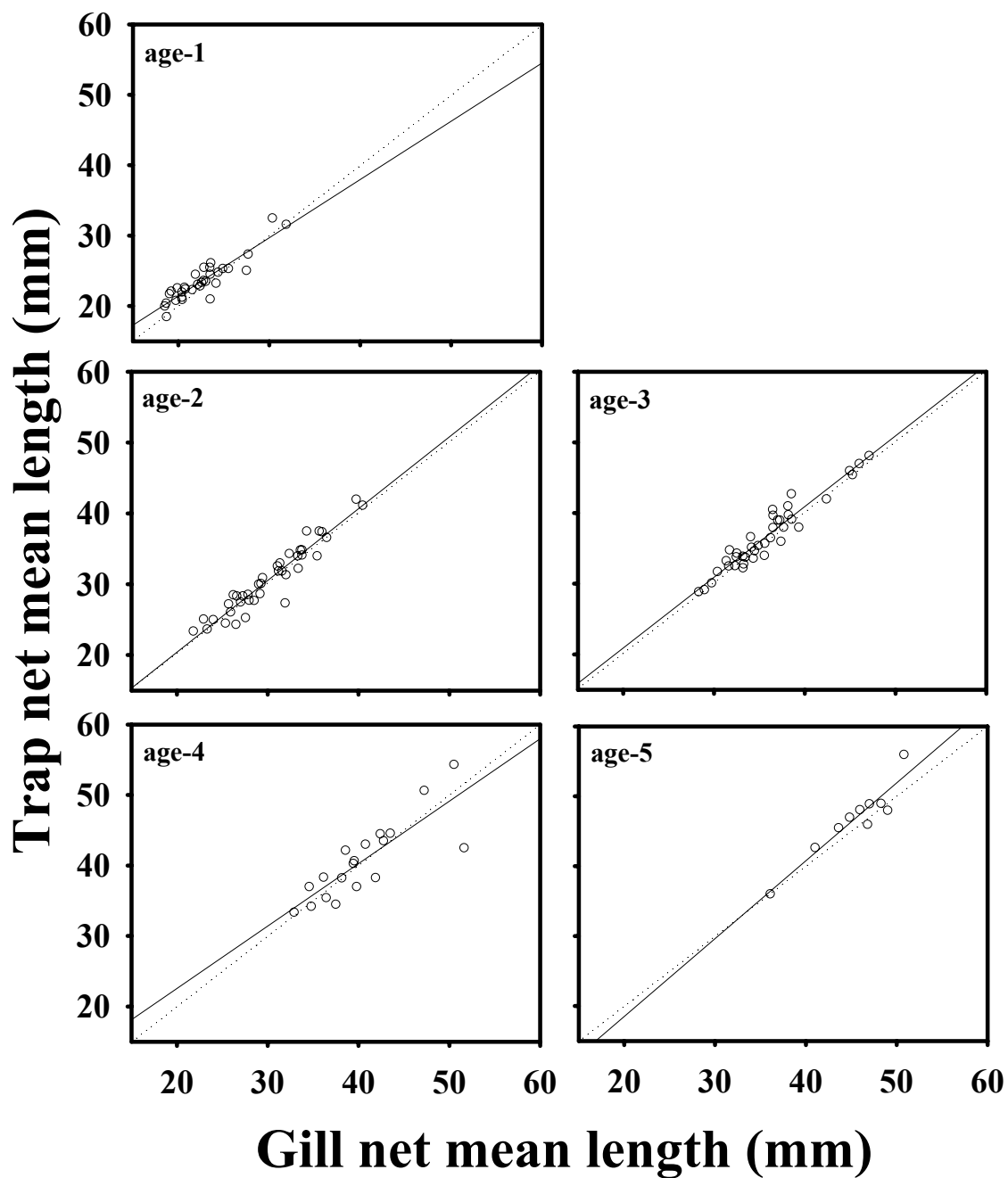


Figure 4-6. Relations between trap-net and gill-net mean length-at-age estimates from eleven South Dakota walleye populations. Solid lines are least-squares regression lines and the dotted lines are 1:1 reference lines.

Chapter 5

Factors Controlling Walleye Cohort Strength in Eastern South Dakota Glacial Lakes

Introduction

Survival of fishes through their first year of life has an important influence on cohort strength (Houde 1987; Houde 1989). Annual differences in first-year growth and survival can lead to erratic rates of recruitment into a fishery. Marked annual variations in cohort strength are characteristic of walleye populations throughout its native range and have been attributed to variations arising from four sources: 1) parental stock attributes; 2) favorability of environmental conditions during incubation; 3) starvation of larvae / juveniles; and 4) predation / cannibalism of age-0 walleye by sympatric piscivores.

Parental stock influences on walleye cohort strength have been attributed to the density of adults and maternal effects arising from fecundity and egg quality. Hansen et al. (1998) and Beard et al. (2003) found that walleye cohort strength followed a stock-recruitment relationship, in that the largest walleye cohorts were produced from intermediate densities of adult walleyes in northern Wisconsin lakes. Serns (1982a) found that significant annual variations in the total number of eggs spawned by walleye in Escanaba Lake, Wisconsin, could be related to annual variations in fecundity and attributed these annual differences to prey abundance during the previous year. Madenjian et al. (1996) found similar associations between cohort strength and prey

abundance from the previous year for walleye in western Lake Erie, where gizzard shad abundance from the previous fall explained 42% of the variation in walleye cohort strength. These relations presumably relate to the energy stores of females during ovary deposition which may have indirect effects on cohort success, as the size and energetic condition of female walleye has been related to the quality of eggs and larvae produced (Moodie et al. 1989; Johnston 1997; Henderson and Morgan 2002).

Favorability of environmental conditions for egg development has also been suggested to influence walleye cohort strength. Years with rapidly warming spring water temperatures has been shown to favor walleye reproductive success in Lake Erie (Busch et al. 1975; Madenjian et al. 1996), and Serns (1982b) and Hansen et al. (1998) both found a significant negative correlation between fall age-0 walleye density and the variation of May water temperatures in Escanaba Lake. Similar relations between cohort strength and water temperatures during the incubation period have been found for northern Minnesota populations (Kallemeyn 1987). In general, stable, warm or rapidly-warming water temperatures favor walleye hatching success.

The availability of prey for larval and juvenile walleye can influence cohort strength, as walleye survival can be reduced by even brief periods of starvation (Johnston and Mathias 1996; Jonas and Wahl 1998). Densities of zooplankton favorable to larval walleye feeding success has been shown to reduce mortality of walleye in production ponds (Johnston and Mathias 1993; Johnston and Mathias 1994; Fox 1989) and similar associations have been suggested to regulate the survival of *in situ* larval (Johnson and Goettl 1999) and juvenile (Ritchie and Colby 1988; Chapter 3) walleye as well.

A large percentage of first year mortality was found to result from cannibalism by older walleyes in Oneida Lake, New York (Chevalier 1973), but the rate of cannibalism in Oneida Lake was reduced in years when abundance of alternative prey (yellow perch) was high (Forney 1976). Predation of age-0 walleye by high-density sympatric piscivorous fish populations can also be a significant source of mortality. Swenson and Smith (1976) reported that consumption of age-0 walleye by adult sauger *S. canadense* can be an important source of first-year mortality in Lake of the Woods, Minnesota. Likewise, consumption of stocked walleye by abundant centrarchids has been shown to reduce walleye cohort strength in Illinois (Santucci and Wahl 1993) and Kansas (Quist et al. 2003) reservoirs.

There is less agreement among studies conducted on walleye populations from different regions in regard to local factors controlling cohort strength. The relative importance of local controls understandably varies by region and is likely related to differences in factors such as trophic dynamics, species composition, and prey assemblages. The objective of this study was to identify the factors that influence the strength of walleye cohorts in eastern South Dakota glacial lake populations and to develop a model to explain regional trends in walleye recruitment.

Methods

Study Populations

Walleye populations were selected based on their spatial distribution throughout the glacial lakes region of South Dakota and by the history of reproductive success

exhibited by these populations. The patterns of reproductive success exhibited by the 12 walleye populations chosen for this investigation (Table 5-1) are representative of the range observed throughout the glacial lakes region. Walleye populations in Madison and Pickerel lakes exhibit consistently poor natural reproduction and must be maintained by stocking. The Campbell, Enemy Swim, and Waubay populations show moderate reproductive success. The Brant, Herman, and Kampeska populations show annually variable cohort strength but do produce strong cohorts in some years. The Poinsett, Roy, and Thompson populations produce strong cohorts in most years.

Data collection/sources

Fall catch per unit effort of age-0 walleye provided reliable indices of cohort strength and eventual recruitment for both Wisconsin (Serns 1982c) and Kansas (Willis 1987) populations. Walleye cohort strength was quantified as catch per hour of age-0 walleye during fall electrofishing surveys. Electrofishing surveys were conducted by South Dakota Department of Game, Fish, and Parks (SDGFP) personnel and consisted of six, 20-minute transects, where fish netting was restricted to only age-0 and age-1 walleye. Ages were determined for five fish per centimeter group and used to develop an age-length key for each cohort to assist in the assignment of ages to non-aged fish.

Data used to quantify yellow perch and age-1+ walleye population abundance and structure were collected by SDGFP personnel as a part of annual or semi-annual standardized surveys of glacial lakes fish communities (Hubers and Pyle 1998; Hubers and Blackwell 1999; Meester 1999; Meester 2000; Hubers 2002; Knapp et al. 2000; St.

Sauver et al. 2001; St. Sauver et al. 2004a; St. Sauver et al. 2004b; Ermer et al. 2005; St. Sauver et al. 2005; St. Sauver et al. 2006). Sampling consisted of concurrent trapnet and gill net samples collected between 1-July and 31-August. A thorough description of these sampling methods was presented in Chapter 4.

Climactic data were obtained for the weather monitoring station closest to each lake from a National Climactic Data Center long-term monitoring database. Mean daily air temperature was used as a surrogate for water temperatures. Mean daily water temperature, collected with on-site data loggers at three glacial lakes (133-1,134 hectares) in 2001, showed strong positive correlations ($r^2 = 0.59-0.75$; $P < 0.0001$) to mean daily air temperature from nearby weather monitoring stations (R. D. Zweifel; unpublished data). Thus, mean daily air temperature was assumed to reflect both the trends and variability in water temperatures over time.

Model Development

A single year of data pertaining to each population was used to determine the factors influencing cohort strength of walleye populations at the regional scale. Biological and climatological data were compiled for Brant, Campbell, Clear, Kampeska, Pickerel Thompson, and Waubay lakes in 2000 and for Enemy Swim, Herman, Madison, Poinsett, and Roy lakes in 2001. None of these walleye populations received supplemental stockings in the year they were sampled. Thus, all age-0 walleye cohorts considered in this study were the product of natural reproduction.

Previous studies of walleye reproductive success have provided numerous insights into the factors that produce annual variations in cohort strength of other populations. The performance of models including combinations of similar explanatory variables were evaluated for South Dakota glacial lakes walleye populations using second order Akaike's information criteria (AIC_C).

There is growing evidence to suggest that many walleye populations exhibit a stock-recruitment relationship, in that the strongest walleye cohorts are produced from intermediate adult densities (Hansen et al. 1998; Beard et al. 2003). Low adult densities may only produce enough eggs to generate weak or moderate cohorts under ideal conditions (Serns 1982a), and the incidence of cannibalism may be greatest in high-density, slow-growing walleye populations (Chevalier 1973). Furthermore, maternal size has been shown to influence the quality of walleye eggs and larvae (Johnston and Leggett 2002). Relative stock density of walleye >51cm (RSD-P) from summer collections was used to index spawning stock size structure.

Estimates of walleye abundance and population size structure from summer surveys were used to evaluate the effect of stock density and stock structure on cohort strength. In general, female walleye are mature at age 4 in South Dakota glacial lakes populations (Zweifel; unpublished data). Trap nets produce more reliable indices of for larger (>38 cm) walleyes, while gill nets tend to catch smaller and juvenile walleye (Chapter 4). Trap-net CPUE of age-4+ walleye was assumed to be representative indices of parental stock size from the previous spring. Relative abundance of all walleye from

summer gillnetting was assumed to be indicative of overall population abundance and was used to assess the potential significance of cannibalism.

Prey abundance has been shown to positively influence cohort strength for a number of walleye populations. Yellow perch are the primary prey species of walleyes in South Dakota glacial lakes and throughout much of the northern portion of their range. Abundant prey during the year prior to spawning presumably enhances the energetic state of females during ovary deposition (Madenjian et al. 1996), while abundant prey during a cohort's first growing season may reduce the incidence of cannibalism by providing alternate prey for older walleye (Forney 1976). Although, there is some evidence to suggest that the abundance of larger (>15 cm) yellow perch can have a negative influence on walleye cohort strength by potentially competing with young walleyes for the same prey resources (Hansen et al. 1998). Estimates of yellow perch abundance from summer gill-net collections corresponding to a cohort's first summer and the abundance of yellow perch from the previous summer were used to test the influence of cannibalism and female walleye energetic condition on walleye cohort strength, respectively.

Gape limitation may exclude age-1 and age-2 walleye from consuming yellow perch >15 cm (Knight et al. 1984), so overall abundance of yellow perch from summer samples may not be indicative of the prey available to age-1+ walleye. Thus, catch rate of yellow perch <15 cm from gill-net collections was used to evaluate the potential role of yellow perch in reducing the incidence of cannibalism. Relative abundance rates of all yellow perch and those larger than 15 cm were both used to explore the possible effect of competition between yellow perch and age-0 walleye for prey resources.

Measures of both water temperature stability (Serns 1982a; Hansen et al 1998) and warming rates (Busch et al. 1975; Madenjian et al. 1996) during the incubation period have been shown to influence cohort strength. The incubation period for walleye in South Dakota waters typically occurs between mid-April and mid-May (Michaletz 1984). Mean daily temperature, temperature stability (coefficient of variation), and warming rate during this period (15 April to 15 May) were used to evaluate the effect of ambient environmental conditions.

South Dakota Department of Game, Fish, and Parks biologists have suggested that walleye populations with annually-variable reproductive success often produce strong cohorts in the years following harsh winters (D. Lucchesi, T. St. Sauver, B. Blackwell; personal communication), although the specific mechanism of this effect is unknown. Mean daily temperature and total snowfall from 1 Dec to 31 March were calculated to evaluate the influence of winter severity on cohort strength.

Results and Discussion

The five models that best explained the variation in walleye cohort strength involved combinations of the same eight explanatory variables, relating to all four paradigms of walleye reproductive success (Table 5-2). Models included combinations of three to seven of the following variables: mean winter temperature, CPE of age-4+ walleye, walleye RSD-P, CPE of yellow perch from the year prior to spawning, CPE of yellow perch during a walleye cohort's first growing season, CPE of yellow perch <156mm, CPE of yellow perch >156mm, and coefficient of variation of temperature

during the incubation period. Model 1 (Table 5-2) included seven of the eight above explanatory variables, except incubation temperature CV, and was by far the “best” of all the models evaluated, accounting for all of the variation in walleye cohort strength (adjusted $r^2=1.0$). The variability in walleye cohort strength explained by models 2 through 5 ranged from 95 to 84 percent, however these models showed markedly poorer fits to the data than model 1. The second best model (Model 2; Table 5-2) again included seven of the eight above variables (all except CPE of age-4+ walleye), but showed a marked drop in performance, as indicated by the change in AIC_C scores ($\Delta_i=65.5$).

Three of the eight variables included in the five best models were indices of parental stock abundance (age-4 walleye CPE), size structure (walleye RSD-P), or energetic state (abundance of yellow perch during the previous year). At least one of these variables was included in all of the five best models, and the “best” model (Model 1) included all three of these variables, implying the importance of maternal population size and quality.

The number of mature (age-4+) female walleye determines the reproductive potential (number of eggs spawned) of a population. However, walleye fecundity, egg quality, and larval survival has been shown to be strongly tied to maternal size and energetic condition, in that larger females produce more (Serns 1982a; Henderson and Morgan 2002) and larger eggs (Johnston 1997; Johnston and Leggett 2002), which likely has subsequent consequences for larval size and survival (Moodie et al. 1989). A higher proportion of the female population comprised of larger (>51 cm) individuals would similarly be expected to produce more and higher quality eggs.

In addition, the abundance of yellow perch from the previous year presumably relates to the importance of abundant prey for female walleye during ovarian development. The importance of abundant prey for female walleye during the year prior to spawning has also been suggested to be an important influence on cohort strength of the Lake Erie population (Busch et al. 1975; Madenjian et al. 1996). Abundant prey during the year prior to spawning is thought to enhance the amount of surplus energy that female walleye have available to invest in egg development, increasing egg quality and hatching success.

Coefficient of variation in temperature during the incubation period (Table 5-2, models 2, 4, and 5) was included in three of the five best models. The importance of stable water temperatures during the incubation period has been demonstrated for Wisconsin populations (Hansen et al. 1998; Beard et al. 2003). Unstable or fluctuating water temperatures can impact the percent of eggs that hatch. Walleye embryos show the lowest temperature tolerance of all percids (Hokanson 1977), and although brief deviations from fertilization temperature may not impact hatching success (Albaugh and Maraz 1964), prolonged exposure to large deviations from fertilization temperatures has been shown to reduce egg development and survival (Smith and Koenst 1975). In addition, departures from optimal developmental temperatures will extend the incubation period (Colby et al. 1979), exposing eggs to predation or mechanical destruction from wind / wave action for longer periods.

The inclusion of either overall yellow perch CPE and/or CPE of yellow perch <156 mm in four of the five best models suggests that cannibalism may play an important

role in determining cohort strength. Forney (1976) showed that the incidence of cannibalism by walleye in Oneida Lake is reduced during years when yellow perch are abundant, by providing an “alternative” prey for walleye. Yellow perch are also the primary prey fish species for walleye in eastern South Dakota glacial lakes, but reproductive success of yellow perch is variable both among populations and years (Isermann 2003). Variations in yellow perch abundance would be expected to have similar consequences for rates of cannibalism and cohort strength in eastern South Dakota walleye populations. The incidence of cannibalism should be highest in populations with relatively large walleye standing stocks during years in which yellow perch abundance is low. However, during years in which yellow perch abundance is high cannibalism should be greatly reduced even with a large walleye standing stock.

Mean winter temperature was the only explanatory variable included in all of the five best models. However, the specific mechanism by which winter temperatures acts to influence the reproductive success of walleye during the following spring is unclear. Cold winters may enhance ovarian development by increasing the likelihood that essential amino acids are incorporated fully into egg membranes improving egg viability (Konrad Dabrowski; Ohio State University, School of Environment and Natural Resources; personal communication). However, the specific temperature and exposure time necessary to enhance ovarian development is still being investigated.

The combination of both yellow perch and adult walleye abundance in the five-best models suggests that eastern South Dakota glacial lakes populations may follow a stock-recruit relationship (Ricker 1975), in that the greatest numbers of recruits are

produced at intermediate adult densities. With a low adult density, an insufficient number of eggs are spawned to produce a strong year class, and at high adult densities, rates of cannibalism may significantly reduce the number age-0 walleye (Chevalier 1973). However, a prey base abundant enough to meet the predatory demand of a high-density adult population, may mitigate the effect of cannibalism (Forney 1976). Many South Dakota glacial lake walleye populations may fall on the descending leg of the stock-recruit curve. Adult densities may be sufficient to produce strong cohorts however the success of those cohorts is dependent on the abundance of prey relative to adult predatory demand. Years with low yellow perch densities influence survival of young walleye by increasing the incidence of cannibalism.

The inclusion of variables pertaining to all four paradigms of walleye reproductive success reinforces that cohort strength is the product of a complex interaction among a number of factors controlling survival at the egg, larval, and juvenile life stages. Parental stock density, size structure, and energetic condition represent the potential of the population to generate a strong cohort. However, the variability inherent in spring conditions may override any stock-recruit relations that may exist. Cool spring water temperatures, unfavorable for egg development, may result in the mortality of all, or a large percentage of, viable eggs. In these years intermediate adult densities likely would not produce enough gametes to generate a strong cohort. However, in those years where spring conditions are favorable for egg incubation and development, cohort strength is likely to be more strongly influenced by parental stock size, and the number of eggs spawned. In these years, intermediate adult densities would be expected to produce

the largest cohorts, as cannibalism may become an issue when stock densities are high (Chevalier 1973).

Management strategies adopted to enhance walleye reproductive success should act to improve the favorability of conditions for age-0 walleye survival. Manipulating either walleye or yellow perch population structure could increase first-year walleye survival. Harvest strategies that would serve to bolster the adult abundance of low-density walleye populations and maintain a balanced age structure (RSD-P ~ 25) would be expected to reduce the annual variability in egg production and decrease the predatory demand of the walleye standing stock. In addition, enhancing yellow perch reproductive success in an attempt to reduce the year-to-year variability in yellow perch production could also improve first year walleye survival. Consistent yellow perch abundance would be expected to reduce the significance of predation/cannibalism even with high adult walleye densities.

Table 5-1. Eastern South Dakota glacial lake walleye populations used to explain the variation observed in walleye cohort strength. CPH is fall electrofishing catch per hour.

Lake	County	Surface area (ha)	Sample year	Fall age-0 walleye CPH
Brant	Lake	1,037	2000	24
Campbell	Brookings	910	2000	5
Clear	Marshall	1,170	2000	11
Enemy Swim	Day	2,150	2001	15
Herman	Lake	1,287	2001	133
Kampeska	Codington	4,820	2000	0
Madison	Lake	2,842	2001	4
Pickerel	Day	961	2000	11
Poinsett	Hamlin	7,903	2001	568
Roy	Marshall	2,054	2001	920
Thompson	Kingsbury	12,455	2000	231
Waubay	Day	12,841	2000	27

Table 5-2. Model selection criteria results for the five best models used to explain the variation in walleye recruitment from eastern South Dakota glacial lakes. K is the number of parameters in the model, AIC_C is the corrected Akaike's information criteria statistics, and Δ_i is the increase in AIC_C compared to the "best" model. Variables included in the models were: Trap-net catch per unit effort (CPE) of age-4+ walleye (4+WCPE), trap-net estimates of walleye RSD-P (WRSDP), gillnet CPE of yellow perch from the previous year (YPCPE-1), mean winter temperature (WIT), gillnet CPE of yellow perch (YPCPE), gillnet CPE of yellow perch >156mm (YP>156), gillnet CPE of yellow perch <156mm (YP<156), and the coefficient of variation of temperature during 15 April to 15 May (INCV).

Model	Explanatory variables	K	AIC_C	Δ_i	Adjusted R^2
1	4+WCPE, WRSDP, YPCPE-1, WIT, YP>156, YPCPE, YP<156	7	10.77		1.0
2	WRSDP, YPCPE-1, WIT, YEP>156, YPCPE, YP<156, INCV	7	76.29	65.52	0.95
3	WRSDP, YPCPE-1, WIT, YEP>156, YPCPE, YP<156	6	87.94	77.17	0.88
4	4+WCPE, WIT, INCV	3	88.15	77.38	0.85
5	4+WCPE, WIT, YPCPE, INCV	4	89.52	78.74	0.84

Chapter 6

Summary and Future Research Needs

Summary

The results of this study suggests that the strength of walleye cohorts in eastern South Dakota glacial lakes populations is determined by annual variations in the number of walleye that hatch, as opposed to variations in survival at the larval or juvenile life stages. The number of walleye that hatch in a given year is likely dependent upon both the density of the parental stock and the quality of the eggs produced. The density of mature females determines a population's reproductive potential, or the number of eggs that are produced. Maternal effects (particularly female size and energetic condition) influence the viability of eggs and subsequent larvae; larger females generally produce larger, more energy-rich eggs. The relative importance of parental stock density and egg quality requires further investigation.

In addition, yellow perch likely play an important role in shaping walleye cohort strength both directly, as the availability of age-0 yellow perch as a prey item for age-0 walleye may enhance first-year survival, and indirectly, as the abundance of yellow perch as prey for older walleye may influence rates of cannibalism and provide an important source of energy for ovarian development.

Future research efforts directed towards further understanding of the processes regulating walleye cohort strength should focus on the role of parental stock dynamics and the importance of yellow perch as a prey item for walleye.

Research and Data Need

- Increase sample sizes of larval to juvenile abundance relations, particularly between light trap and fall abundance estimates. A majority (7 of 9) of data points of the current relationship are clustered near the origin (larval CPUE <10, fall electrofishing CPH<100) with two observations distributed over the remaining range of larval and juvenile CPUE's observed (larval CPUE 10-40; fall electrofishing CPH>100). Addition of expected strong cohorts will likely improve the statistical confidence of these relations.
- Seasonal diet composition of age-0 walleye from spring to fall should be assessed to determine the effect of prey abundance / diet composition on first-year survival.
- Collection of other population / cohort data to increase sample size of regional data set to both 1) increase the statistical confidence of model selection results and 2) to test the applicability of model results to other glacial lakes populations over time.
- Determine the relative importance of parental stock density and egg quality to cohort strength. Model selection results indicated the importance of both parental stock density and maternal effects for cohort strength. The number of eggs spawned determines the potential strength of a cohort, but egg quality likely influences viability and subsequent larval survival. How important are annual variations in egg quality in determining the ultimate strength of a cohort?

- Determine the influence of prey abundance on adult female walleye seasonal energy density (somatic and reproductive tissues) and the relation between maternal attributes and egg quality.

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