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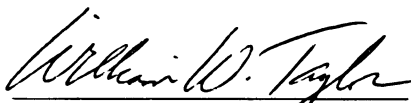
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Survival and Recruitment of Lake
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presented by

Russell W. Brown

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FACTORS INFLUENCING THE LARVAL SURVIVAL AND RECRUITMENT
OF LAKE WHITEFISH IN THE UPPER GREAT LAKES

By

Russell W. Brown

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ABSTRACT

FACTORS INFLUENCING THE LARVAL SURVIVAL AND RECRUITMENT OF LAKE WHITEFISH IN THE UPPER GREAT LAKES

By

Russell W. Brown

Eggs were collected from two stocks of lake whitefish in Lakes Michigan and Huron to assess the effect of egg composition and prey density on larval growth and survival. Larval fish hatched from six parental females in each stock were fed one of four rations (0, 18, 24, 50 brine shrimp/day) after yolk-sac absorption. Length at hatch, endogenous growth, exogenous growth, and survival were measured during a 42-day laboratory experiment. Length at hatch of larvae was positively related to egg caloric content ($R^2 = 0.780$). Endogenous growth for lake whitefish larvae was positively related to percent lipid content ($R^2 = 0.896$) and total egg lipid content ($R^2 = 0.876$) of parental females. These results indicate that egg composition has the potential to significantly influence the growth and survival dynamics of larval lake whitefish.

Spawning stock and climate-based recruitment models were developed for lake whitefish in northern Green Bay and the North Shore areas of Lake Michigan. Beverton-Holt and Ricker stock-recruitment functions, ice cover

concentrations, wind intensity data, and spring water and air temperature variables were used as model inputs in climate-based recruitment modelling. The climate-based model for northern Green Bay, modelled lake whitefish recruitment as a function of a Beverton-Holt stock-recruitment function, ice concentration, and wind intensity. The climate-based recruitment model ($R^2 = 0.65$) demonstrated improved hindcasting ability when compared to the Beverton-Holt stock-recruitment model ($R^2 = 0.37$) for the 1961-1985 cohorts. The climate-based model for the North Shore modelled lake whitefish recruitment as a function of a spring air temperatures, ice concentration, the Beverton-Holt stock-recruitment function, and wind intensity. The climate-based recruitment model ($R^2 = 0.57$) demonstrated improved hindcasting ability when compared with Ricker stock-recruitment model ($R^2 = 0.13$). Results of this study indicate that climate-based recruitment models have the potential to more accurately forecast lake whitefish cohort strength several years in advance of recruitment into the fishery.

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CHAPTER 1

Effects of Egg Composition and Prey Density on the Larval Growth and Survival of Lake Whitefish

ABSTRACT

Eggs were collected from two stocks of lake whitefish in Lakes Michigan and Huron to assess the effect of egg composition and prey density on larval growth and survival. Egg composition parameters including wet weight (mg/egg), dry weight (mg/egg), percent water, caloric content (cal/egg), caloric density (cal/mg), percent lipid content, and lipid content (mg/egg) were measured. Fish hatched from six parental females in each stock were fed one of four rations (0, 18, 24, 50 brine shrimp/larva/day) after yolk-sac absorption. Length at hatch, endogenous growth, exogenous growth, and survival were measured during a 42-day laboratory experiment. Length at hatch of larvae was positively related to egg caloric content ($R^2 = 0.780$). Endogenous growth of larvae was positively related to percent lipid content ($R^2 = 0.896$) and total egg lipid content ($R^2 = 0.876$) of parental females. Exogenous growth and survival of larval lake whitefish was positively related to prey availability. Larval growth was accurately modelled ($R^2 = 0.973$) as a function of prey ration using a threshold-corrected hyperbolic equation. These results indicate that egg composition has the potential to significantly influence the growth and survival dynamics of larval lake whitefish.

INTRODUCTION

Mortality rates experienced during the pelagic larval stages are important in determining year class strength in many fish species (Gulland 1965; Chenoweth 1970; May 1973). For many species, larval mortality is concentrated during a relatively short period during early development (Hjort 1914; May 1973). Because mortality experienced during the egg and larval stages is severe, strong year-to-year variations in recruitment may arise from relatively small fluctuations in egg and larval survival rates (Taylor and Freeberg 1984; Freeberg et al. 1990).

A number of abiotic factors (i.e. temperature, salinity, and currents) and biotic factors (i.e. starvation, competition, and predation) have been proposed as possible mechanisms controlling recruitment of larval and juvenile fishes. The ability of larval fish to cope with adverse biotic and abiotic factors is dependent upon a number of factors including body size, available energy resources, swimming ability, and reactive distance (Miller et al. 1988).

Body size is an important variable influencing many aspects of the physiology, ecology, and behavior of larval fish (McMahon and Bonner 1983; Peters 1983; Calder 1984; Miller et al. 1988). The ability of smaller larvae to feed successfully is constrained because they have shorter

reaction distances and restricted swimming abilities limiting their searching ability (Blaxter 1986; Webb and Weihs 1986). Body size also influences the susceptibility of larval fish to predation through differential encounter rates and escape ability (Blaxter 1986; Zaret 1980). Swimming ability, largely determined by body size (Webb and Weihs 1986; Miller et al. 1988), also influences the ability of larval fish to maintain their position in optimal areas for growth and survival.

During the period following hatching, initial feeding by larval fishes appears to be crucial for survival (Einsele 1963; O'Connell and Raymond 1970) as larvae switch from endogenous to exogenous food resources (Blaxter 1965; O'Connell and Raymond 1970; Blaxter 1971). Survival of larvae through the transitional period from endogenous to exogenous food resources is dependent upon a number of factors including the availability of suitable prey resources. Small increases in body size at hatching or available endogenous energy resources may result in large benefits in terms of the "window of opportunity" when first feeding can occur (Miller et al. 1988). Delayed initial feeding and subsequent mortality can occur if prey density is too low (Lasker et al. 1970; Beers and Stewart 1971), or if an inadequate prey species composition is present (Einsele 1963; Fluchter 1980).

The "starvation hypothesis" only focuses on the extreme

case when the energy balance remains negative long enough for the larval fish to die (Fritz et al. 1990). Smaller larvae within a species generally have less endogenous reserves and thus are more vulnerable to starvation (Hunter 1981). Delayed initial feeding reduces searching ability and increases larvae susceptibility to predation (Ivlev 1961; Blaxter 1969). Larvae exhibiting slow growth also remain in a size range more vulnerable to predators for a longer period of time.

The impact of exogenous prey resources on larval fish growth and survival depends upon the availability of endogenous energy resources. For example, a positive relationship between egg size and larval survival and growth has been demonstrated for arctic char, Salvelinus alpinus (Wallace and Aasjord 1984); brown trout, Salmo trutta (Brown 1946; Bagenal 1969); chinook salmon, Oncorhynchus tshawytscha (Fowler 1972); and rainbow trout, O. mykiss (Gall 1974). The ability of larvae to survive during starvation was positively related to the yolk content of eggs in trout (Gray 1928; Smith 1958) and herring (Blaxter and Hempel 1963; Schnack 1981). The relative amount of endogenous food reserves may be important in determining larval survival, especially if the production of initial food sources is mismatched in time with the initiation of exogenous feeding by larval fish (Cushing 1982).

Once initial feeding has occurred, the ability of

larval fish to grow rapidly largely influences their survival. Availability of prey resources (Einsele 1963; Lasker et al. 1970; Beers and Stewart 1971; Fluchter 1980) and water temperature (Miller et al. 1988) are the two ecological resources most important in determining the growth of larval fish once their endogenous food resources have been exhausted. In addition, as larvae grow they become better able to visually detect both food and predators resulting in higher survival rates (Miller et al. 1988). Thus, the quantity and quality of exogenous food resources can significantly effect survival of larval fish and ultimately their year class strength.

To evaluate the relative importance of endogenous versus exogenous energy resources on the population dynamics of lake whitefish, a laboratory study was designed to determine the influence of egg composition and prey density on the larval growth and survival of lake whitefish. Specific objectives of this study were to:

1. Evaluate the relationship between egg composition measures and the length of hatch of larvae hatching from individual female lake whitefish from two stocks in the upper Great Lakes.
2. Evaluate the relationship between egg composition measures and the endogenous growth of larval lake whitefish.

3. Determine the influence of zooplankton prey densities and egg composition on the larval survival and growth of lake whitefish.

METHODS

Egg Collection and Incubation

Eggs were collected from two stocks of lake whitefish, one in Lake Michigan and the other in Lake Huron (Figure 1). Eggs were collected from 14 ripe female fish at Naubinway (Lake Michigan) on November 6, 1989. Eggs were collected from 17 ripe female fish at Bayport (Lake Huron) on November 14, 1989. In each case, female fish were manually stripped into a dry bowl. The unfertilized eggs from each female were mixed and a random sample of the unfertilized eggs was collected and frozen for subsequent laboratory analysis of egg composition parameters. The remaining eggs from each female were fertilized with milt from one male fish using dry fertilization methods (Piper et al. 1985). The fertilized eggs were then rinsed in lake water, allowed to water harden, and transported back to the laboratory within six hours of fertilization.

Fertilized eggs from each female were incubated separately in a Heath-Tech 8-tray incubator. Eggs were treated with a 1:600 solution of formalin for thirty minutes on a weekly basis to control fungal growth. Fertilized eggs

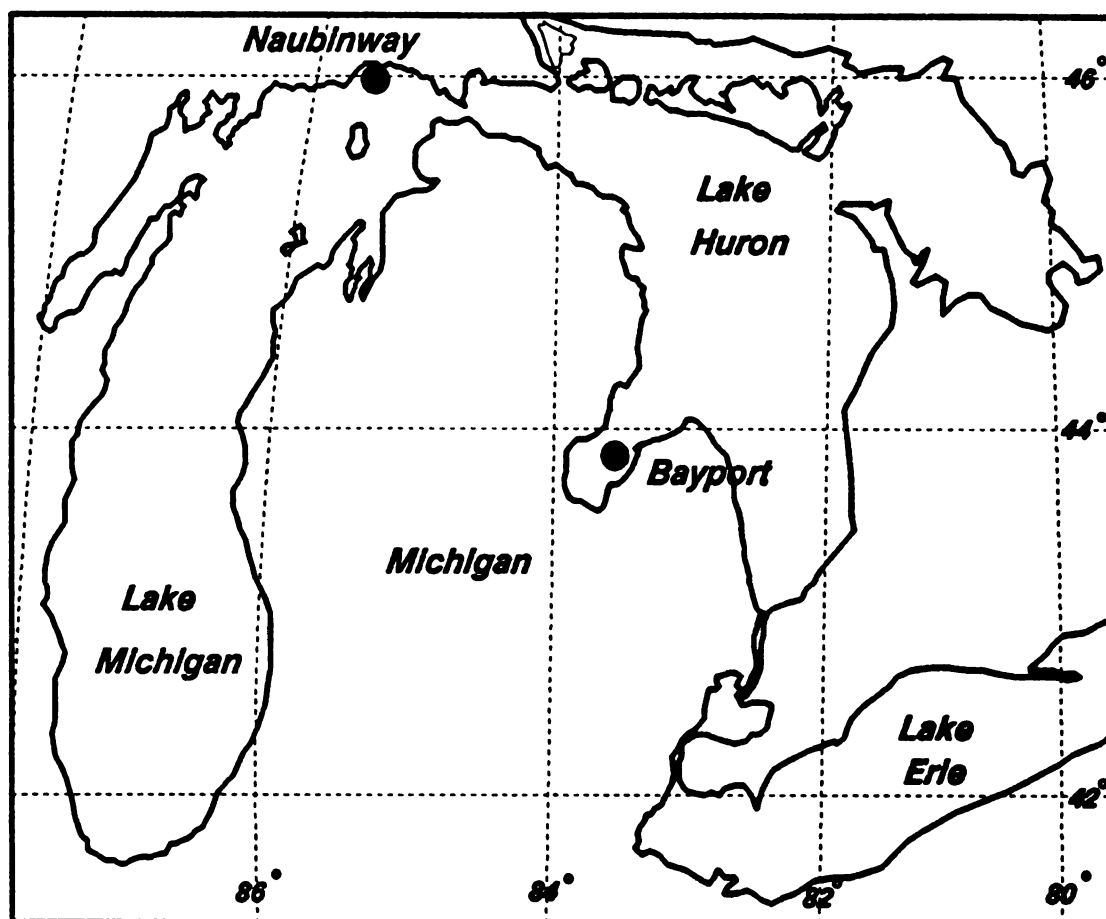


Figure 1. Map showing sampling locations of spawning lake whitefish in Lakes Michigan and Huron.

were incubated at an average temperature of 3.4°C ($\pm 0.3^{\circ}$) and hatching occurred between 84 and 101 days ($\bar{X} = 94$ days) after fertilization. Length at hatch was measured for a sample of 100 larvae hatching from each of the 31 parental females sampled during egg collection.

Laboratory Analysis of Egg Composition

To obtain measures of egg composition for each female, unfertilized eggs were analyzed in the laboratory to determine egg wet weight (mg/egg), egg dry weight (mg/egg), percent water, egg caloric content (cal/mg and cal/egg), and egg lipid content (percent composition and mg of lipid/egg). To determine mean egg wet weight, three replicate samples of 100 eggs were weighed from each female. Each of these samples was dried in a forced air oven at 60°C for 48 hours and reweighed to obtain dry weight measurements for each female. Percent water measurements were calculated using the following equation:

$$\text{Percent Water} = \frac{(\text{Wet Weight (mg)} - \text{Dry Weight (mg)})}{\text{Wet Weight (mg)}} * 100\%$$

The remaining egg sample from each female was dried in a forced air oven at 60°C for 48 hours in preparation for measures of energy content.

Two major types of measures of energy contained within eggs were utilized in this study. Egg caloric content (cal/egg) is a measure of the total amount of energy

contained within the egg, and is primarily a function of egg size and composition. Egg caloric density (cal/mg) measures energy content independently of egg size, and is primarily a function of the proportion of carbohydrate, lipid, and protein contained within the egg (Potts and Wooton 1984). Egg caloric density is most highly correlated with the lipid content, the most energy dense of the three major types of compounds normally found in fish eggs (Potts and Wooton 1984).

Caloric content was measured using a Parr adiabatic calorimeter. Three sub-samples of dried eggs weighing 1.0 g each were analyzed for each female. The following equation was used to calculate the caloric content of each sample:

$$H_g = \frac{\Delta t * W - e_1 - e_2}{m}$$

- H_g = gross heat of combustion (cal/mg);
- Δt = change in temperature;
- W = energy equivalent of calorimeter in cal per degree Celsius
- e_1 = nitric acid (HNO_3) formation correction;
- e_2 = wire heat of combustion correction;
- m = sample weight (mg).

Egg samples from individual females were pulverized with an electric grinder and the lipid content was

determined for three 1.0 g subsamples. Lipids were extracted by the diethyl ether extraction method using a Tecator Soxtec System HT 1043 Lipid Extraction Unit. Lipid content of each sample was calculated using the following formula:

$$\text{Percent Lipid} = \frac{(\text{Initial Wt (mg)} - \text{Extracted Wt (mg)})}{\text{Initial Weight (mg)}} * 100\%$$

Laboratory Experimental Design

Eggs from six female fish in each stock were selected to produce larval lake whitefish that were utilized in the laboratory growth experiments. Once hatching began, egg containers were examined and hatching larvae were removed daily. A sample of 100 newly hatched larvae from each female was measured to determine a mean length at hatch. Larvae hatched from each female were divided among four treatment groups of 100 larvae each (Figure 2). Larvae hatching after similar incubation times were selected to avoid the confounding effects of differential incubation times on the length at hatch and endogenous growth rates of larvae.

Each treatment group was assigned one of four brine shrimp feeding rations (0, 18, 24, and 50 brine shrimp/fish). Feeding was conducted on a prey/larvae basis

to maintain constant feeding levels while the number of remaining larvae changed through the course of the experiment (Taylor and Freeberg 1984). Each experimental unit was fed the corresponding prey ration twice daily, and prey rations were adjusted for changes in the number of larval fish on a daily basis. Dead brine shrimp were siphoned from the bottom of each tank on a daily basis.

A large recirculating water bath was used to maintain constant temperatures ($6.9^{\circ} \pm 0.6$) between experimental aquaria. Twenty liter aquaria initially containing 100 lake whitefish larvae were randomly assigned positions within this water bath. Water temperatures within individual aquaria were initially measured daily, and the maximum difference in water temperature between aquaria never exceeded 0.3° .

Yolk-sac absorption occurred between 23 and 25 days posthatch for all larval lake whitefish observed in this study. Larvae were not fed for a period of 21 days after hatching to obtain accurate measurements of growth based on endogenous energy resources. Beginning on day 21, larvae were fed 2-day old brine shrimp (Artemia sp.), which were cultured continuously in the laboratory. As such, growth of larval lake whitefish occurring between day 0 and day 21 of life represented the endogenous growth period, while growth occurring between days 21 and 42 of life represented the exogenous growth of the larvae.

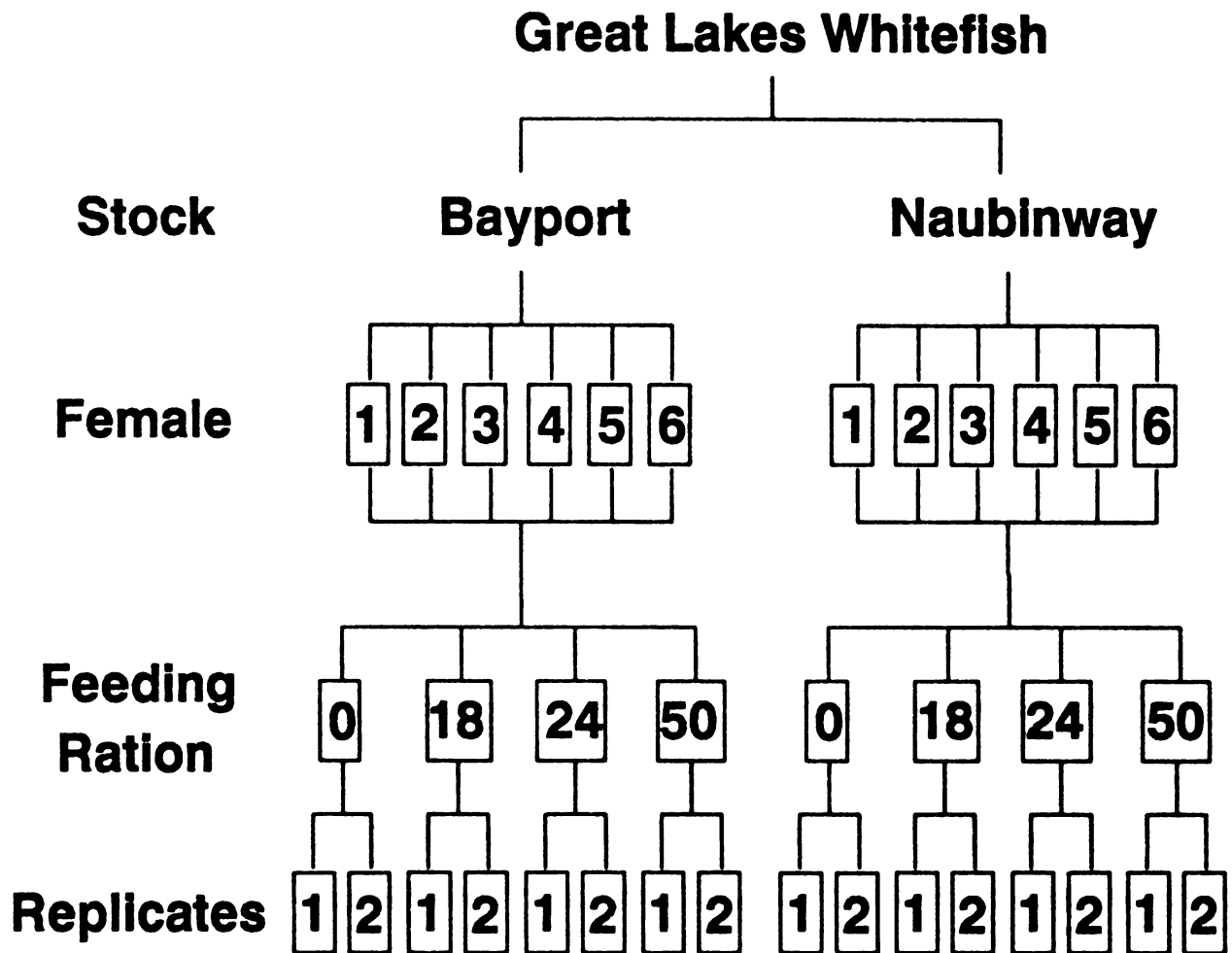


Figure 2. Diagram of the experimental design for the laboratory experiment.

Measurement of Survival and Growth

Survival of larvae was measured by removing and recording dead individuals from each tank on a daily basis. Larval growth of lake whitefish was measured by sampling and measuring the remaining individual larvae on a weekly basis.

Larval fish sampled for growth were photographed on the date of hatch and weekly thereafter using slide photography. The fish from each experimental unit were isolated in a grided petri dish and photographed using a standard focal distance on a light table to enhance the resulting image. Slide photographs were then projected onto a Summagraphics digitizing pad and the images of each larval fish were digitized to determine length. A BASIC computer program was written to calibrate the scaling of the digitizing pad with a known scale place on the bottom of each petri dish at the time of photographing. Initial evaluation of this procedure demonstrated that straight objects and curved objects with less than three curves could be accurately measured to within ± 0.02 mm. Images of larval fish which either were not horizontal in the photograph or were obscured by the edge of the petri fish were not measured using the digitizing program. This procedure allowed for the accurate measurement of large numbers of living larval fish (approximately 38,000 measurements) with little subsequent mortality (17 fish).

Data Analysis

Mean, variance, and standard error estimates were calculated for egg composition parameters measured for eggs from each spawning female. Mean egg composition estimates were tested to detect differences in these estimates between stocks using T-Test analysis. Because non-homogenous variances were detected between stocks for some parameters, an approximate T-statistic was calculated and used for hypothesis testing in these cases (Cochran and Cox 1950; Lee and Gurland 1975).

Mean lengths of larval lake whitefish were used to calculate instantaneous daily growth using the following equation (Ricker 1975):

$$\mu = \frac{(\log_e l_t - \log_e l_{t-1})}{T}$$

u = instantaneous daily growth;

l_t = mean length (mm) in week t;

l_{t-1} = mean length (mm) in week t-1;

T = time interval in days.

Regression analysis was used to test for significant differences between egg composition parameters, length at hatch, and endogenous growth of larval lake whitefish. Analysis of covariance was used to test for significant differences in the regression relationships between stocks.

For statistical analysis, survival rates of larval lake whitefish were calculate on a weekly basis. Mean weekly survival rates were calculated using the following equation (Ricker 1975):

$$S = \frac{N_t}{N_{t-1}}$$

S = mean weekly survival rate

N_t = number of larvae alive at week t

N_{t-1} = number of larvae alive at week t-1

Three stage analysis of variance was used to test for differences in exogenous growth and survival between feeding rations, progeny of females within stocks, and stocks of lake whitefish.

A threshold-corrected hyperbolic growth equation (Freeberg et al. 1990) was calculated as a function of zooplankton feeding rations to model specific growth rates of larval lake whitefish during the exogenous growth period (weeks 3-6). Instantaneous growth rates were plotted as a function of prey ration (zooplankton/larvae) using a Monod threshold-corrected hyperbolic equation for substrate-limited growth (Freeberg et al. 1990):

$$\mu = \frac{\mu_{\max} [(z/f) - (z/f)_q]}{[K_s - (z/f)_q] + [(z/f) - (z/f)_q]}$$

μ = instantaneous daily growth;

$\mu_{\max}$ = maximum instantaneous daily growth;

(z/f) = prey ration (zooplankton/fish);

$(z/f)_q$ = maintenance prey ration; and

K_s = prey ration producing one-half maximum growth.

Maintenance substrate level was estimated from the plot and calculated constants of $\mu_{\max}$ and K_s using the regression equation:

$$\frac{[(z/f) - (z/f)_q]}{\mu} = \left(\frac{K_s}{\mu_{\max}} \right) + \left(\frac{1}{\mu_{\max}} \right) [(z/f) - (z/f)_q]$$

RESULTS

Characteristics of Sampled Female Lake Whitefish

Length, weight, and age of sampled female lake whitefish are shown in Appendix 1. Female lake whitefish sampled from the Bayport stock were longer ($\bar{L}_B = 569$ mm vs. $\bar{L}_N = 537$ mm) and heavier ($\bar{W}_B = 1713$ g vs. $\bar{W}_N = 994$ g) than females sampled from the Naubinway stock (Table 1). I found no significant differences in the mean age of female lake whitefish between stocks (Randomization Test, $P = 0.1910$).

To eliminate differences in parental female size as a confounding factor during feeding trials, I selected eggs from a similar range of parental female sizes from each stock. As such, there were no significant differences between stocks in the mean length (Table 1, $P = 0.9859$) or age (Randomization Test, $P = 0.4328$) of the parental females of larvae used in the feeding trials.

Egg Composition

Mean values and variance estimates for egg composition parameters including wet weight, dry weight, percent water, cal/mg, cal/egg, percent lipid, and mg lipid/egg were calculated for eggs collected from each female spawner in each stock (Appendix 2). Mean values, standard error estimates, and ranges of egg composition parameters for each stock are shown in Table 2. With the exception of caloric density, the female fish sampled from the Naubinway stock

Table 1. Mean length, weight, and age data of all sampled parental females sampled from Bayport (Lake Huron) and Naubinway (Lake Michigan) in November 1989, and parental females of eggs used in the laboratory studies.

	Field	
	<u>Bayport</u>	<u>Naubinway</u>
Mean Length ($\pm$ SE)	569 $\pm$ 9.3	537 $\pm$ 13.0
Mean Weight ($\pm$ SE)	1713 $\pm$ 92	1341 $\pm$ 103
Mean Age	5.9	5.3

	Laboratory	
	<u>Bayport</u>	<u>Naubinway</u>
Mean Length ($\pm$ SE)	557 $\pm$ 19.7	557 $\pm$ 19.3
Mean Weight ($\pm$ SE)	1592 $\pm$ 184	1514 $\pm$ 180
Mean Age	5.8	5.8

Table 2. Mean values, standard errors, and ranges of egg composition parameters of female lake whitefish sampled from stocks at Naubinway (n = 14) and Bayport (n = 17) in November, 1989.

	<u>Bayport</u>	<u>Naubinway</u>
Wet Weight (mg/egg)		
Mean	9.32	8.24
SE	0.24	0.34
Range	7.49-11.03	5.11-10.83
Dry Weight (mg/egg)		
Mean	2.66	2.61
SE	0.10	0.55
Range	2.19-2.98	1.68-3.19
Percent Water		
Mean	71.27	68.15
SE	0.44	0.82
Range	66.92-75.20	63.67-75.85
Caloric Content (cal/egg)		
Mean	17.23	17.13
SE	0.39	0.69
Range	14.02-19.68	10.78-21.27
Caloric Density (cal/mg)		
Mean	6.47	6.56
SE	0.03	0.03
Range	6.21-6.74	6.40-6.73
Percent Lipid		
Mean	19.58	19.09
SE	0.63	0.70
Range	15.44-23.43	13.80-23.98
Lipid Content (mg/egg)		
Mean	0.524	0.503
SE	0.024	0.033
Range	0.372-0.697	0.285-0.732

had larger ranges and standard errors for measured egg composition parameters.

Results of T-Tests and Cochran's T-Tests for non-homogenous variance to test for significant differences in egg composition parameters are shown in Table 3. Eggs sampled from Bayport female lake whitefish had a significantly higher mean wet weight ($\bar{W}_B = 9.32$ mg) than eggs sampled from Naubinway females ($\bar{W}_N = 8.24$ mg, Table 3, $P = 0.016$). However, I found no significant differences in the average dry weight of eggs sampled from female lake whitefish in these two stocks, indicating that the stock differences in wet weight were a function of the significantly higher water content of eggs sampled from Bayport lake whitefish (Table 3, $P = 0.006$).

Eggs sampled from Naubinway lake whitefish had a significantly higher caloric density ($\bar{X}_N = 6.56$ cal/mg) than eggs sampled from Bayport lake whitefish ($\bar{X}_B = 6.47$, Table 3). However, there were no significant differences in the caloric content of eggs (cal/egg) or the lipid content (%) of eggs from lake whitefish sampled from the Bayport and Naubinway stocks.

Length at Hatch of Larval Lake Whitefish

Least squares regression was used to test for significant relationships between egg composition parameters and length at hatch of larval lake whitefish. When significant relationships were indicated, analysis of

Table 3. Results of T-Tests and approximate T-Tests to evaluate differences in egg composition parameters between lake whitefish sampled from Bayport and Naubinway.

<u>Egg Composition Parameter</u>	<u>Test</u>	<u>T Value</u>	<u>P Value</u>
Wet Weight (mg/egg)	T-Test	2.55	0.016
Dry Weight (mg/egg)	Cochran's T	0.50	0.627
Water Content (%)	Cochran's T	3.23	0.006
Caloric Content (cal/egg)	Cochran's T	0.13	0.898
Caloric Density (cal/mg)	T-Test	-2.13	0.042
Lipid Content (%)	T-Test	0.51	0.612
Lipid Content (mg/egg)	T-Test	0.64	0.513

covariance was used to test for significant differences in the regression equations between stocks. Separate regression equations are reported for parameters when there were significant differences in the regression equations between stocks (Table 4).

I found a significant positive relationship between egg caloric content (cal/egg) and the length at hatch of larval lake whitefish (Figure 3). I also found a significant positive relationship between egg lipid content (mg/egg) and the length of hatch of larval lake whitefish (Figure 4). There were also positive relationships between the length at hatch of larval lake whitefish and other egg composition parameters (i.e. lipid content and caloric density) that were highly correlated with egg caloric content (Table 4). No significant relationship between the egg incubation times and the length at hatch of larval lake whitefish was noted ($R^2 = 0.087$, $P = 0.759$).

Endogenous Growth Rates

The relationship between stock egg source, parental female, and endogenous growth of hatching larvae was tested using two-stage analysis of variance. I found no significant relationship between parental stock and the endogenous growth rate of hatching larvae (Table 5, $P = 0.4555$). However, there was a significant relationship between parental females and the endogenous growth rate of hatching larvae (Table 5, $P < 0.0001$). I also found a

Table 4. Results of regressions between length at hatch of lake whitefish larvae and egg composition parameters of eggs sampled from Bayport and Naubinway. Analysis of covariance was used to determine whether combined or separate regression equations for each stock were used.

<u>Egg Composition Parameter</u>	<u>Stock(s)</u>	<u>R²</u>	<u>P</u>
Caloric Content (cal/egg)	Combined	0.780	< 0.0001
Egg Lipid Content (%)	Combined	0.579	< 0.0001
Lipid Content (mg/egg)	Combined	0.228	0.0038
Caloric Density (cal/mg)	Naubinway	0.186	0.0296
	Bayport	0.146	0.0468

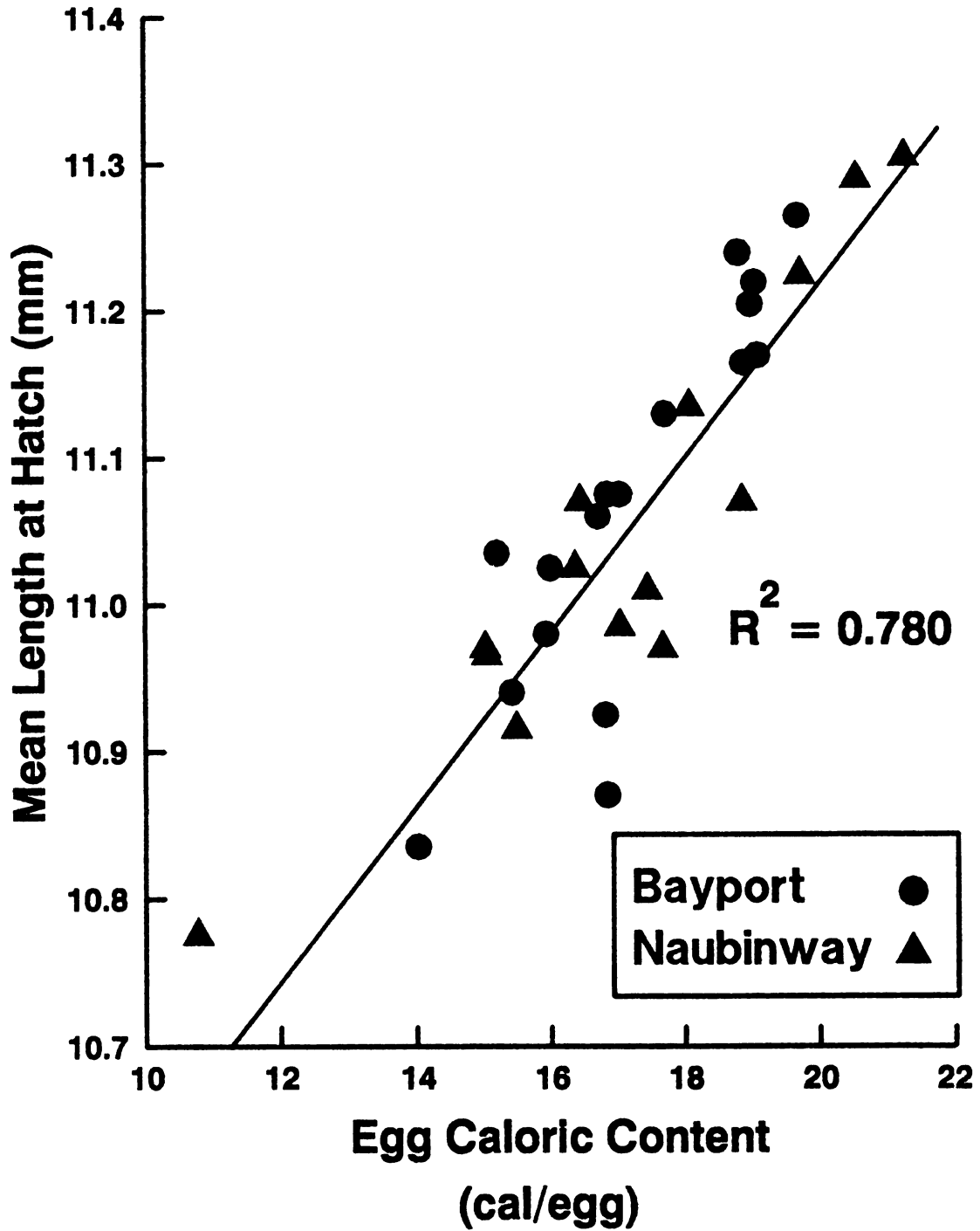


Figure 3. Mean length of hatching larval lake whitefish as a function of their egg caloric content (cal/egg).

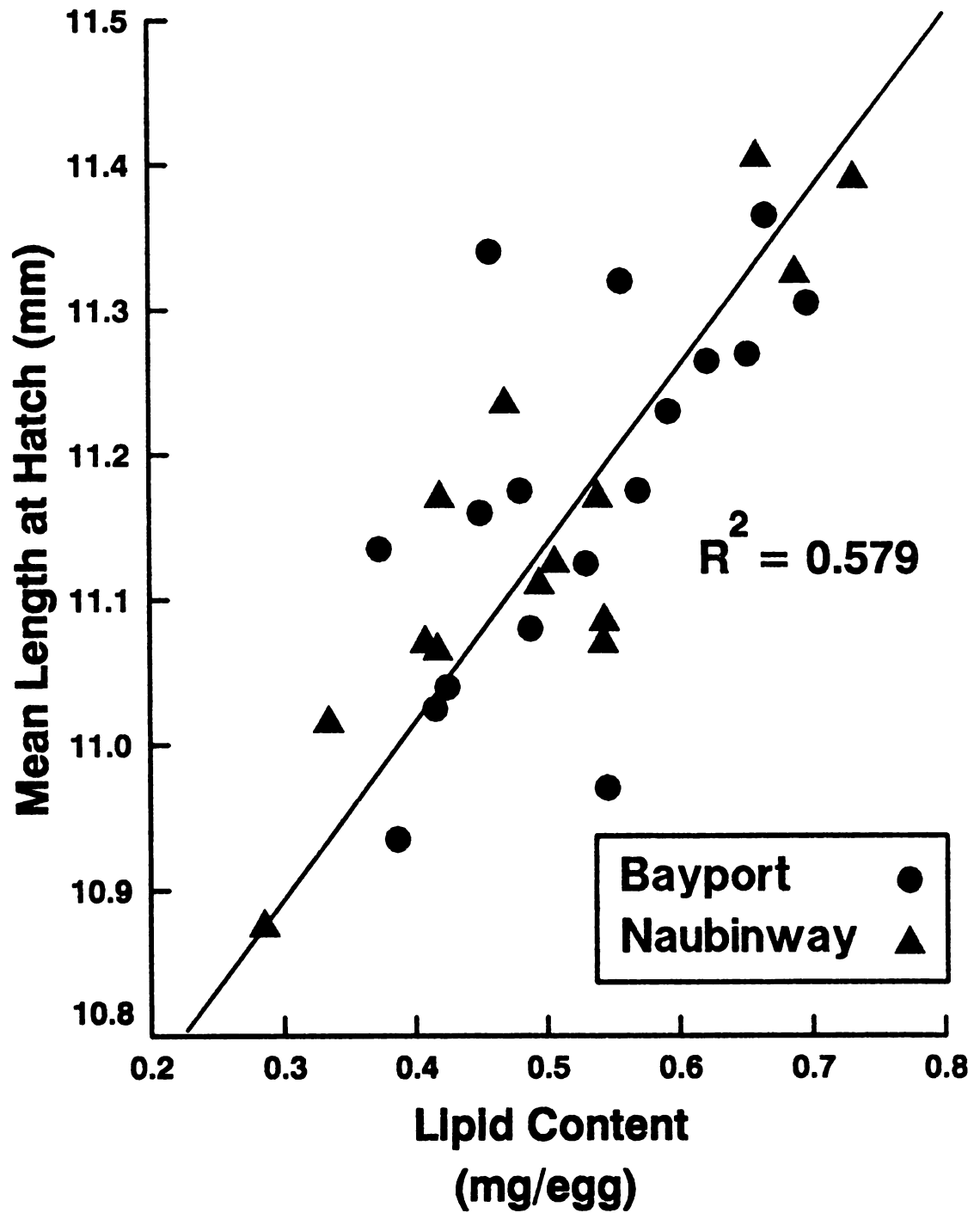


Figure 4. Mean length of hatching larval lake whitefish as a function of their lipid content (mg/egg).

Table 5. Results of analysis of variance to test for differences between stocks, females, and feeding rations in the endogenous growth, exogenous growth, and survival of larval lake whitefish under laboratory conditions.

Endogenous Growth Rate			
<u>Source</u>	<u>Degrees of Freedom</u>	<u>F-Value</u>	<u>P-Value</u>
Stock	1	0.56	0.4555
Female	5	9.70	0.0001

Exogenous Growth Rate			
<u>Source</u>	<u>Degrees of Freedom</u>	<u>F-Value</u>	<u>P-Value</u>
Stock	1	0.74	0.3945
Female	5	3.48	0.0065
Ration	3	95.01	0.0001

Exogenous Survival			
<u>Source</u>	<u>Degrees of Freedom</u>	<u>F-Value</u>	<u>P-Value</u>
Stock	1	1.66	0.2014
Female	5	0.45	0.8102
Ration	3	170.11	0.0001

significant relationship between parental females nested within stocks and the endogenous growth rate of their offspring during the first three weeks of the experiment (Nested ANOVA, $F = 31.21$, $P < 0.0001$).

The relationship between parental females and endogenous growth rates of their larvae was related to egg composition (Table 6). I found a significant relationship between the endogenous growth rate of larvae and egg percent lipid content (Figure 5). Additionally, there was also a significant relationship between endogenous growth rate and egg lipid content (Figure 6).

Positive relationships between endogenous growth and other egg composition parameters (i.e. egg caloric content, egg caloric density) that were highly correlated with egg percent lipid content were also observed (Table 6). No significant relationship between egg incubation time and endogenous growth rate was found ($R^2 = 0.052$, $P = 0.856$).

Exogenous Growth Rates

The relationships between exogenous growth rates of larval lake whitefish and parental stock, parental female, and feeding ration were tested using three-stage analysis of covariance. There was a significant relationship between parental females and the exogenous growth rate of their offspring during weeks 4-6 post-hatch (Table 5, $P = 0.0065$). However, there was not a significant relationship between parental stock and the exogenous growth of larval lake

Table 6. Results of regressions between endogenous growth rate of lake whitefish larvae and egg composition parameters of eggs sampled from Bayport and Naubinway. Analysis of covariance was used to determine whether combined or separate regression equations for each stock were used.

<u>Egg Composition Parameter</u>	<u>Stock(s)</u>	<u>R²</u>	<u>P</u>
Lipid Content (%)	Combined	0.896	< 0.0001
Lipid Content (mg/egg)	Combined	0.876	< 0.0001
Caloric Content (cal/egg)	Naubinway	0.649	0.0019
	Bayport	0.562	0.0042
Caloric Density (cal/mg)	Naubinway	0.187	0.1153
	Bayport	0.115	0.1639

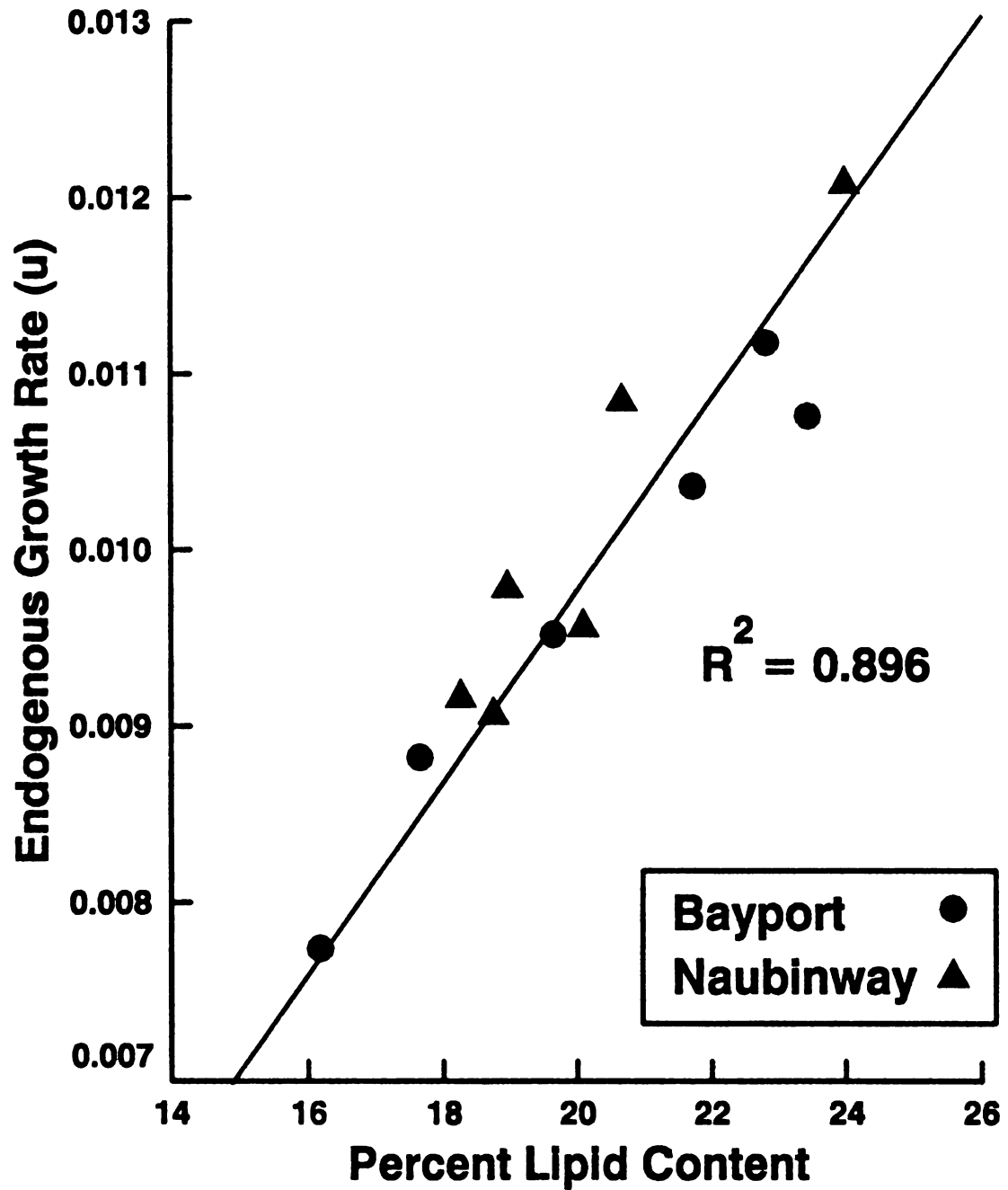


Figure 5. Endogenous growth rates (u) of larval lake whitefish during the first 21 days of the laboratory experiment as a function of percent lipid content.

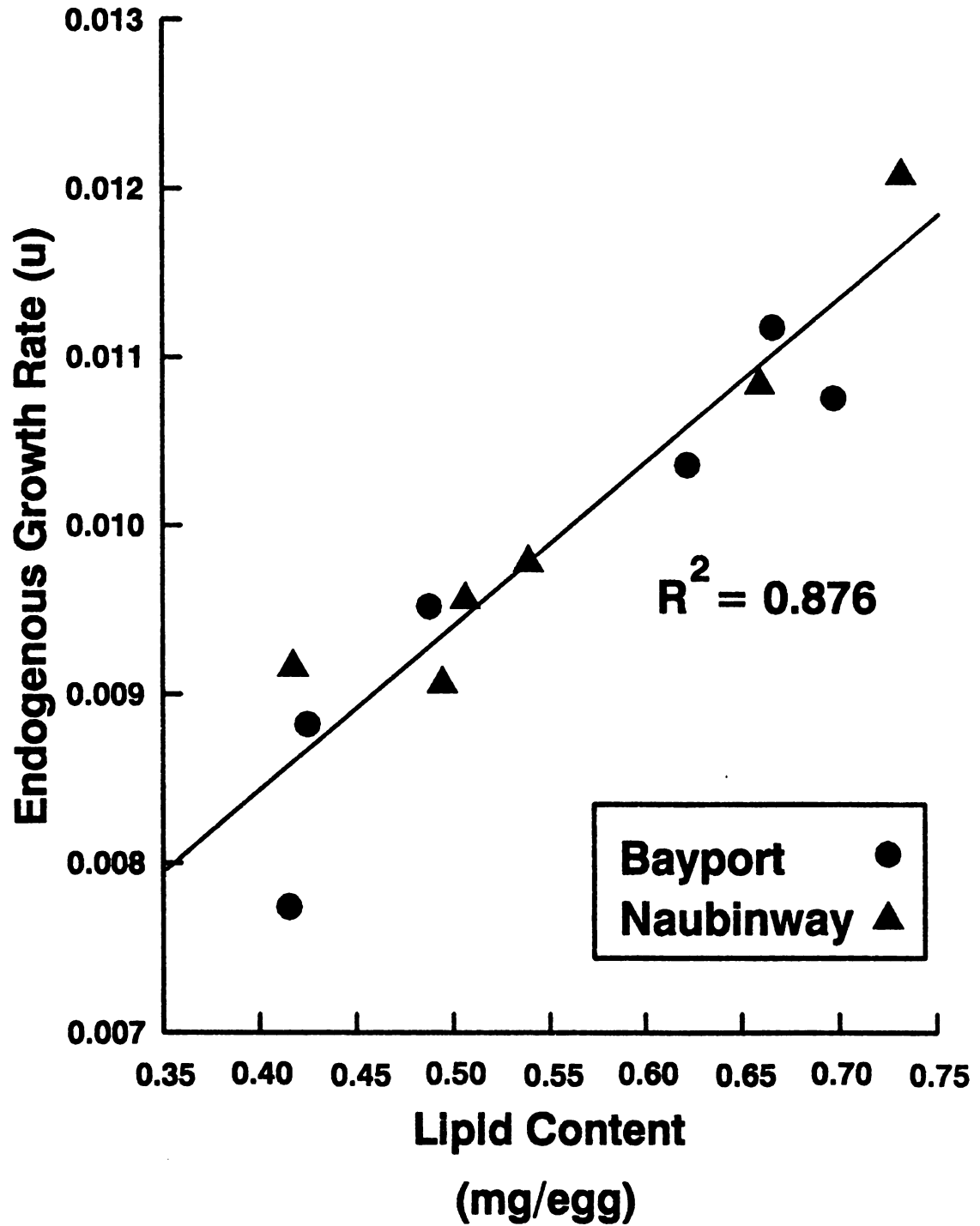


Figure 6. Endogenous growth rates (u) of larval lake whitefish during the first 21 days of the laboratory experiment as a function of lipid content (mg/egg).

whitefish (Table 5, $P = 0.3935$).

I found a significant positive relationship between feeding ration and exogenous growth of larval lake whitefish (Table 5, $P < 0.0001$), with higher feeding rations resulting in higher exogenous growth rates of larval lake whitefish (Figure 7).

Larval Survival Rates

There were no significant differences in survival rates between any of the treatment groups during the three week period of endogenous growth. Therefore, analysis of survival rates concentrated on the period during weeks 4-6, when larval lake whitefish made the transition from endogenous to exogenous food resources.

The relationships between survival rates during weeks 4-6 and parental stock, parental female, and feeding ration were tested using three-stage analysis of variance. There was a significant relationship between feeding ration (zooplankton/larvae) and larval survival during exogenous feeding (Table 5, $P < 0.0001$). Higher feeding rations resulted in higher larval survival rates throughout the 21-day exogenous feeding period (Figure 8). There were no significant relationships between exogenous survival rate of larval lake whitefish and parental stock (Table 5, $P = 0.2067$) or parental females (Table 5, $P = 0.8102$).

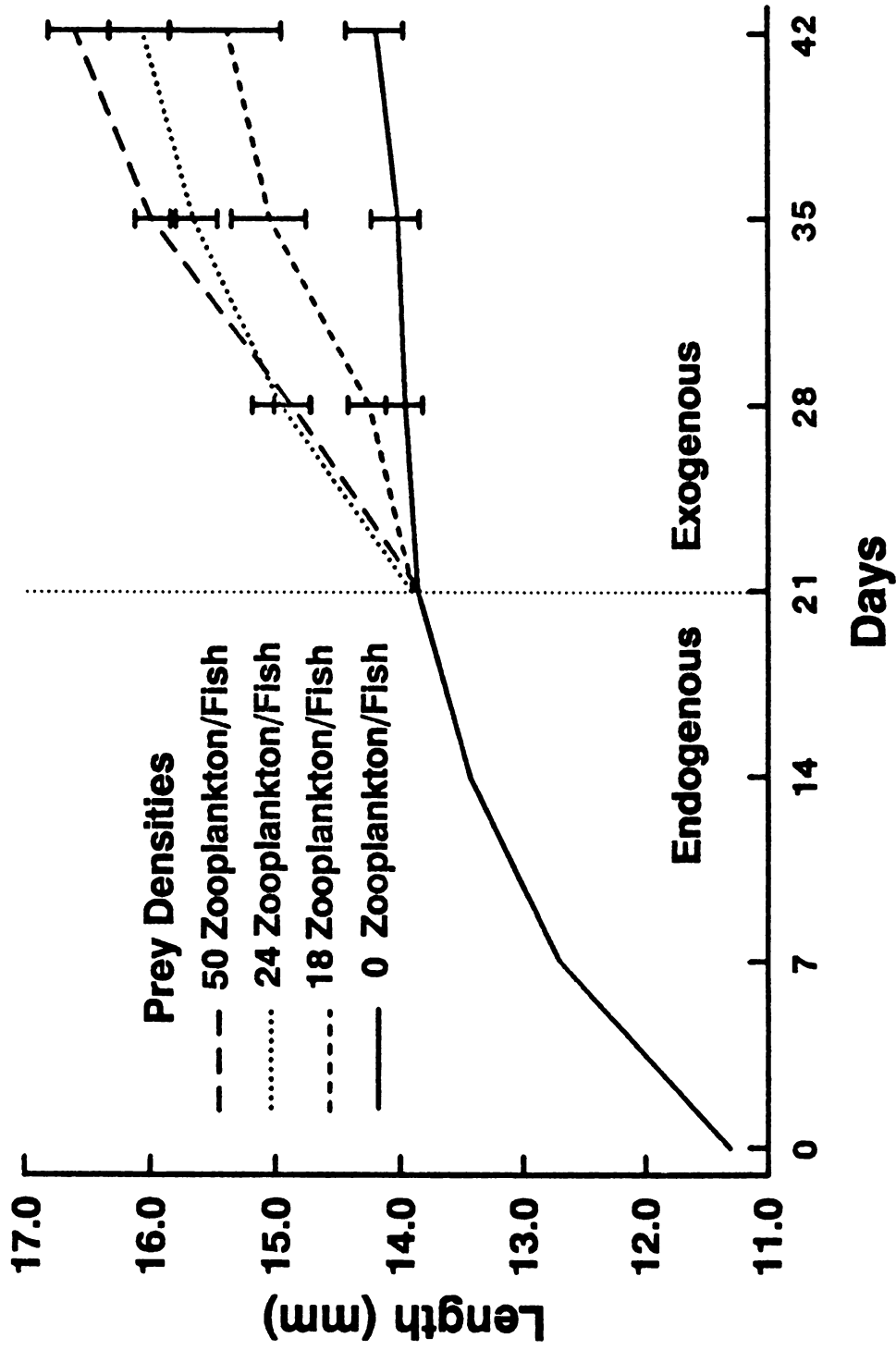


Figure 7. Endogenous and exogenous growth rates of larval lake whitefish during the 42 day laboratory experiment. Endogenous growth rates were not significantly different from each other, and exogenous growth rates are expressed as a function of prey rations. Error bars represent $\pm$ one standard error.

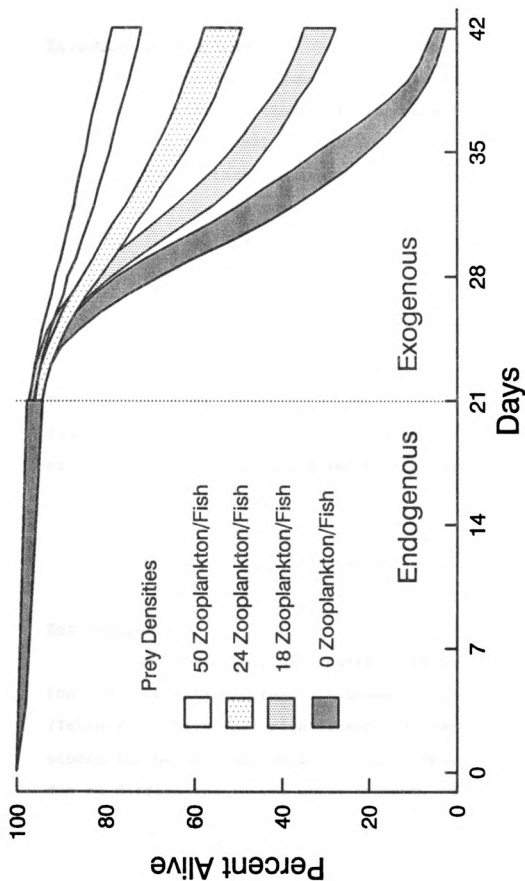


Figure 8. Endogenous and exogenous survival rates of larval lake whitefish during the 42 day laboratory experiment. Endogenous survival rates were not significantly different from each other, and exogenous survival rates are expressed as a function of prey rations. Daily error bounds represent $\pm$ one standard deviation.

Exogenous Growth Model

A plot of instantaneous growth rate (u) versus zooplankton feeding ration (z/f) is shown in Figure 9. Larval growth of larval lake whitefish was accurately modelled using a threshold-corrected hyperbolic equation:

$$\mu = 0.104138 * \left[\frac{(z/f) - 0.277623}{(z/f) + 12.032211 - (2 * (0.277623))} \right]$$

$$R^2 = 0.973.$$

The instantaneous growth rate associated with each of the four zooplankton feeding rations was within one standard deviation of the curve predicted by the threshold-corrected hyperbolic equation.

DISCUSSION

Egg Composition

I found few significant differences between stocks in the egg composition parameters measured for sampled fish (Table 1). There were significant differences between stocks in the mean wet weight of eggs, which were primarily due to differences in the water content. There were no significant differences in the egg dry weight, egg caloric content, or egg lipid content between stocks.

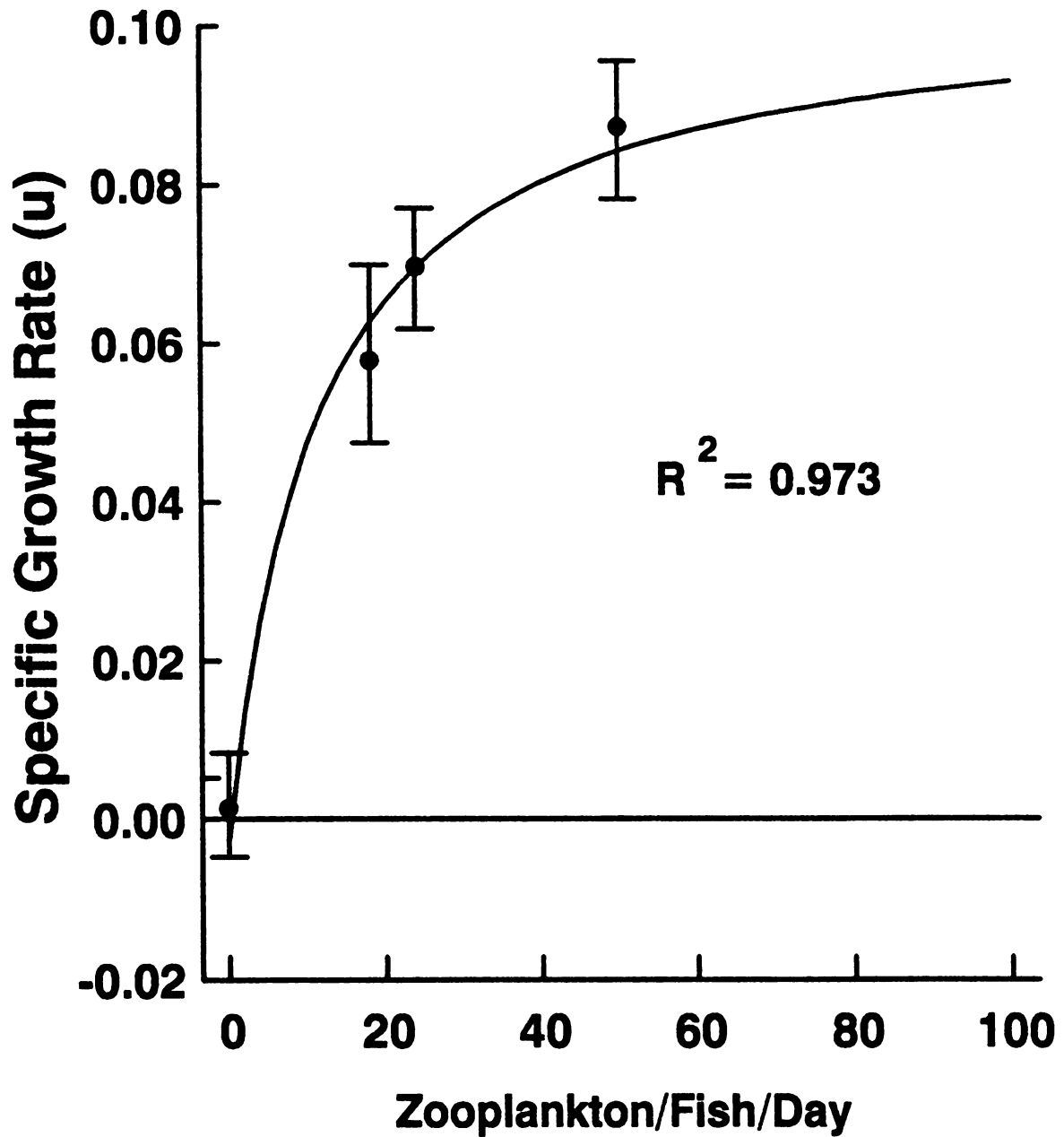


Figure 9. Specific exogenous growth rate (u) of larval lake whitefish during weeks 4-6 of the laboratory experiment as a function of prey ration. Solid line represents the fit of the Monod threshold-corrected equation to predict specific growth rates as a function of prey ration.

One of the principal responses of lake whitefish populations to commercial exploitation is a shift in the age and size structure from older, larger individuals to younger, smaller individuals (Smale 1988). Another population level response to exploitation commonly observed is that somatic growth rates of lake whitefish increase (Ebener and Copes 1985; Smale 1988). Although the age at maturation may decline in response to exploitation, the size at maturation of lake whitefish populations is fairly constant over different levels of exploitation (Smale 1988; Taylor et al. 1991). In response to exploitation, lake whitefish populations would therefore tend to have a higher proportion of younger and smaller female spawners.

In this study, the Naubinway stock is a relatively heavily exploited stock comprised of primarily younger, smaller sized fish. The Bayport stock is a relatively lightly exploited stock dominated by older, larger-sized individuals. One of my predictions regarding average egg composition of these two stocks was that the larger and older female spawners in the Naubinway stock would have higher egg quality, as measured by egg composition parameters. Although this study was not designed to assess population responses to exploitation, data were collected from female lake whitefish with sufficient age and size ranges to allow for preliminary conclusions. Based on the analysis of a limited sample size of two stocks, there is no

evidence to suggest that exploitation influences the egg quality parameters of lake whitefish measured in this study.

Tradeoffs Between Egg Size, Egg Number, and Egg Composition

In allocating available energy for reproductive products, spawning female fish face two major tradeoffs. First, available reproductive energy must be allocated between egg size and egg number (Svårdson 1949). Second, energy reserves must be allocated between carbohydrate, protein, and lipid components within individual eggs. Life history theory suggests that natural selection will select for females that allocate reproductive energy in a manner to maximize fitness return per unit of ovarian resource invested (Smith and Fretwell 1974; Lloyd 1987; McGinley et al. 1987; Sargent et al. 1987; Winkler et al. 1987; Fleming and Gross 1990). Thus, egg number should vary in response to selection upon egg size, egg composition, and total investment in egg production (Fleming and Gross 1990).

Caloric Content versus Caloric Density

In evaluating egg composition of lake whitefish, there appears to be a tradeoff between the caloric content (cal/egg) and the caloric density (cal/mg) in eggs when examined independently of egg size. Parental females having a high egg caloric density (cal/mg) also have a higher percent lipid content. These eggs in turn produce larvae having more endogenous energy reserves. Larvae hatching from eggs with higher lipid contents hatched at a slightly

smaller average size, but were able to compensate for this size disadvantage through higher levels of endogenous growth.

Larvae with greater endogenous energy reserves may have a number of abilities enhancing survival and growth of these larvae, despite their smaller initial size. Greater endogenous energy reserves would enhance the ability of larvae to delay initial feeding for longer periods of time compared to larvae with less lipid energy reserves. During this time, larvae could also expend larger amounts of energy to actively seek and capture prey resources.

Parental females having high egg caloric content (cal/egg) but lower caloric densities had higher levels of protein and carbohydrate. These larvae hatched at a slightly larger size, but had lower levels of endogenous growth. These larvae may have size-related advantages such as enhanced feeding (Hunter 1981; Blaxter 1986; Webb and Weihs 1986) and predator escapement abilities (Zaret 1980; Blaxter 1986), but their limited endogenous energy resources limit the time available to initiate feeding on exogenous prey resources. However, relatively small size differences may translate into substantial differences in survival and subsequent recruitment (Adams and DeAngelis 1987), and thus may be significant in lake whitefish recruitment dynamics.

Point of No Return

The presence or absence of a "point of no return" in fish, a point beyond when fish are no longer capable of feeding, has been the point of conflicting reports in the literature (Lasker et al. 1970; Miller et al. 1988; Fritz et al. 1990). The point of no return is defined as the time after which the effects of starvation are irreversible due to destruction of the digestive system (Miller et al. 1988). The point of no return is defined for each individual larva, but can only be measured for a group of larvae. The presence of a point of no return has been reported by Lasker et al. (1970) for anchovy (Engraulis mordax).

During the present research, larval lake whitefish not utilized in the experimental design were held at a temperature of 4.0° C for as long as 86 days without feeding. Survival of these larvae ranged from 25 to 86 days after hatching. Repeated attempts to feed larvae after 28 days resulted in no evidence of feeding, despite the fact that larvae were able to survive for weeks beyond this point. This clearly indicates that lake whitefish larvae are capable of surviving beyond the point that they are capable of feeding. If starvation is an important source of mortality under field conditions, these results could have serious implications for the estimation of densities and average size of larval lake whitefish collected during ichthyoplankton sampling. Presence of starving fish could

lead to an overestimation of effective larval density or an underestimation of average size of non-starving larval fish. Considering the current emphasis on the analysis of the characteristics of surviving larvae (Fritz et al. 1990), this prolonged survival could be a confounding factor in the identification of characteristics allowing larval fish to survive.

Relative Influence of Temperature

Endogenous and exogenous growth observed during this study were lower than those reported from previous laboratory experiments using larval lake whitefish (Taylor and Freeberg 1984). There were two causes for the apparent slow growth during this experiment. First, larval lake whitefish in this experiment were not fed for a period of 21 days to allow for the measurement of endogenous growth. Under natural conditions, larval lake whitefish began feeding within 48 hours after hatching (Freeberg et al. 1990). Second, water temperatures in this experiment were maintained at relatively cold temperatures (6.9° C) to simulate temperatures normally encountered in the Great Lakes, while the earlier study (Taylor and Freeberg 1984) was conducted at 12° C. At this warmer temperature, larval lake whitefish exhausted their endogenous energy reserves between 12 and 15 days post hatch (Taylor and Freeberg 1984) compared to 23 to 25 days post-hatch in the present experiment.

Under natural conditions, larval lake whitefish emerge (late March and April) when open water temperatures in the Great Lakes are cold (2° - 4° C) and areas of warmer water (4° - 8° C) are located only at the surface and in near-shore areas. Larval lake whitefish located in nearshore areas with warmer water temperatures would be able to achieve growth rates commonly observed under field conditions. At this time of the year, warm water is probably an important ecological resource because it determines the bioenergetic potential for larval growth.

In this experiment, starvation was the only source of mortality experienced by larval lake whitefish. Other factors influencing larval survival under field conditions (i.e. predation) were not evaluated. However, if predation is important, I noted that larvae fed lower prey rations during this experiment demonstrated slow growth and impaired swimming ability which may result in higher mortality under natural conditions.

Conclusions

There were no apparent differences in the egg composition, larval growth, and larval survival dynamics of lake whitefish sampled from the Naubinway stock (Lake Michigan) and the Bayport stock (Lake Huron). Length at hatch of larval lake whitefish was primarily a function of egg size, as measured by the overall egg caloric content. Endogenous growth of larval lake whitefish was highly dependent on the egg lipid content, as measured by the percent lipid content and the mg lipid per egg. Exogenous growth and survival of larval lake whitefish were positively related to prey resource availability and both were sensitive to small changes in the availability of zooplankton prey resources. Variation in egg composition has the potential to be important in determining larval growth and survival and eventual recruitment of lake whitefish.

Chapter 2:
Climate-Based Recruitment Models of Lake Whitefish
in Two Areas of Northern Lake Michigan

Abstract

Spawning stock and climate-based recruitment models were developed for lake whitefish in northern Green Bay and the North Shore areas of Lake Michigan. Abundance and cohort strength indices were calculated for the 1961-1985 year classes based on catch and effort data from the commercial fishery for the 1958-1989 year classes of lake whitefish in each area. Beverton-Holt and Ricker stock-recruitment functions, ice cover concentrations, wind intensity data, and spring water and air temperature variables were used as model inputs in climate-based recruitment modelling. The climate-based model for northern Green Bay modelled lake whitefish recruitment as a function of a Beverton-Holt stock-recruitment function, ice concentration, and wind intensity. The climate-based recruitment model ($R^2 = 0.65$) demonstrated improved hindcasting ability when compared to the Beverton-Holt stock-recruitment model ($R^2 = 0.37$) for the 1961-1985 cohorts. The climate-based model for the North Shore modelled lake whitefish recruitment as a function of a spring air temperatures, ice concentration, the Beverton-Holt stock-recruitment function, and wind intensity. The

climate-based recruitment model ($R^2 = 0.57$) demonstrated improved hindcasting ability when compared with Ricker stock-recruitment model ($R^2 = 0.13$). Results of this study indicate that climate-based recruitment models have the potential to more accurately forecast lake whitefish cohort strength several years in advance of recruitment into the fishery.

Introduction

The lake whitefish is an important component of the commercial fishery of the upper Great Lakes, and currently comprises over 50% of the commercial landings in Michigan waters (Kinnunen 1990). Over the past century, there have been large fluctuations in the commercial landings and catch-per unit effort (CPUE) of lake whitefish (Figure 10) that have been primarily caused by variable levels of population abundance (Christie 1963; Taylor et al. 1987). Several potential causes for the observed variation in abundance of lake whitefish include overfishing (Patriarche 1977), habitat degradation (Christie 1963), sea lamprey (Petromyzon marinus) depredation (Smith and Tibbles 1980), competition with exotic species of fish (Christie 1974), and variable recruitment (Christie 1963; Lawler 1965; Patriarche 1977; Smale 1988).

Correlative studies of lake whitefish recruitment

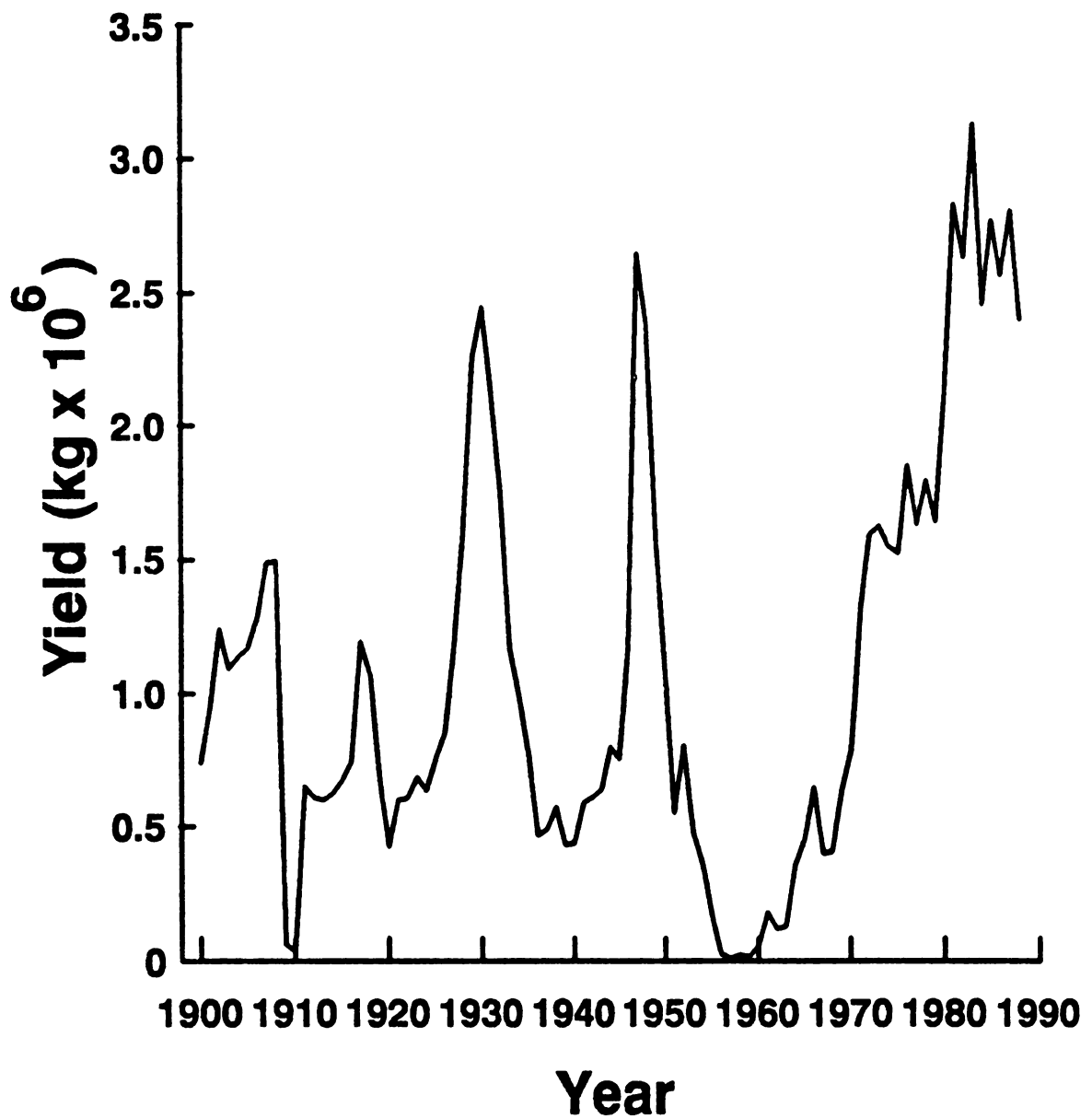


Figure 10. Commercial fishery landings of lake whitefish in Lake Michigan, 1900-1989.

suggest that much of the variability in the cohort strength and recruitment may be caused by variation in climatic influences, such as water temperatures and wind. Christie (1963) found a relationship between lake whitefish recruitment and winter and spring temperatures in Lake Ontario, with cold Novembers followed by warm Aprils providing conditions associated with the production of strong year classes. Strong year classes in Lake Erie resulted only when an optimal set of water temperatures for spawning, incubation, and development was observed (Lawler 1965). Strong year classes in Lake Erie occurred when fall temperatures fell below 6.1 C prior to spawning; the fall and winter temperature decline was steady with few fluctuations; and spring temperatures increased slowly and late, providing a long incubation period at optimal temperatures of 2.0 to 4.0 C. Miller (1952) found an inverse relationship between fall wind intensity and lake whitefish year class strengths in seven Alberta Lakes. These correlations between fall and winter weather conditions and year class strength of lake whitefish suggest that weather related variables significantly influence egg and larval survival.

In Grand Traverse Bay, Lake Michigan, ice cover over lake whitefish spawning grounds appears to reduce the intensity of wind generated waves and currents, directly influencing egg survival (Taylor et al. 1987; Freeberg et

al. 1990). Egg survival in Grand Traverse Bay during an ice covered winter (1983-84) was approximately 3.4 times greater than during an ice free year (1982-83). Additionally, the recruit per stock ratios for a lake whitefish stock along the North Shore of Lake Michigan were positively related to the maximum extent of ice cover on a lake wide basis ($R^2 = 0.56$), and historical trends in winter severity were positively associated with lake whitefish catch by the North Shore commercial fishery (Smale 1988).

In addition to late fall and winter climatic conditions influencing spawning and egg survival, spring climatic conditions appear to be important in determining survival of emerging lake whitefish larvae. Freeberg et al. (1990) found that the abundance of copepod zooplankton between 0.7 and 1.1 mm in total length significantly influenced the growth and survival of larval lake whitefish in Grand Traverse Bay, Lake Michigan. Spring climatic conditions, including the timing of ice dissipation and the warming of shallow water areas, appear to influence the timing of the initiation of production of copepod zooplankton, which in turn impacts larval survival of lake whitefish.

Identification and quantification of the factors influencing cohort strength of lake whitefish would enhance the management of the fishery by enabling forecasts of lake whitefish abundance several years in advance of their recruitment to the fishery. The goal of this study was to

identify key biotic and abiotic variables determining cohort strength and to incorporate these variables into recruitment models for lake whitefish in two areas of northern Lake Michigan. The specific objectives of this study were to:

1. Identify the biotic and abiotic variables important in determining the egg and larval survival of lake whitefish.
2. Incorporate these variables into a quantitative recruitment model to hindcast cohort strength of lake whitefish in two areas of northern Lake Michigan.

Hypotheses

Four hypotheses about the effects of biotic and abiotic variables were used as a basis for developing climate-based recruitment models during this study.

1. In the absence of climatic variables, the cohort strength and recruitment of lake whitefish is primarily a function of the size of the spawning stock, and that the relationship between stock size and recruitment can be approximated by a Ricker or a Beverton-Holt stock-recruitment relationship (Ricker 1975).

2. Wind generated currents and waves during and after spawning are important in determining egg survival of lake whitefish.
3. Ice cover over lake whitefish spawning areas protects eggs from wind generated currents and waves, thereby enhancing the survival of lake whitefish eggs.
4. Spring water temperatures are important in determining the production of zooplankton food resources, which in turn influence the growth and survival rates of hatching lake whitefish larvae.

Methods

Model Construction Overview

Analysis of commercial fishery and climatic data produced three models for each area modelled, two traditional stock-recruitment models and a climate-based recruitment model. A flow chart of the modelling process is shown in Figure 11. Commercial catch and effort data were used to calculate abundance and cohort strength indices, which were in turn used to calculate Ricker and Beverton-Holt stock-recruitment models for each area. Freezing degree day data and ice cover observations were used to construct ice cover models for each area. Outputs from ice

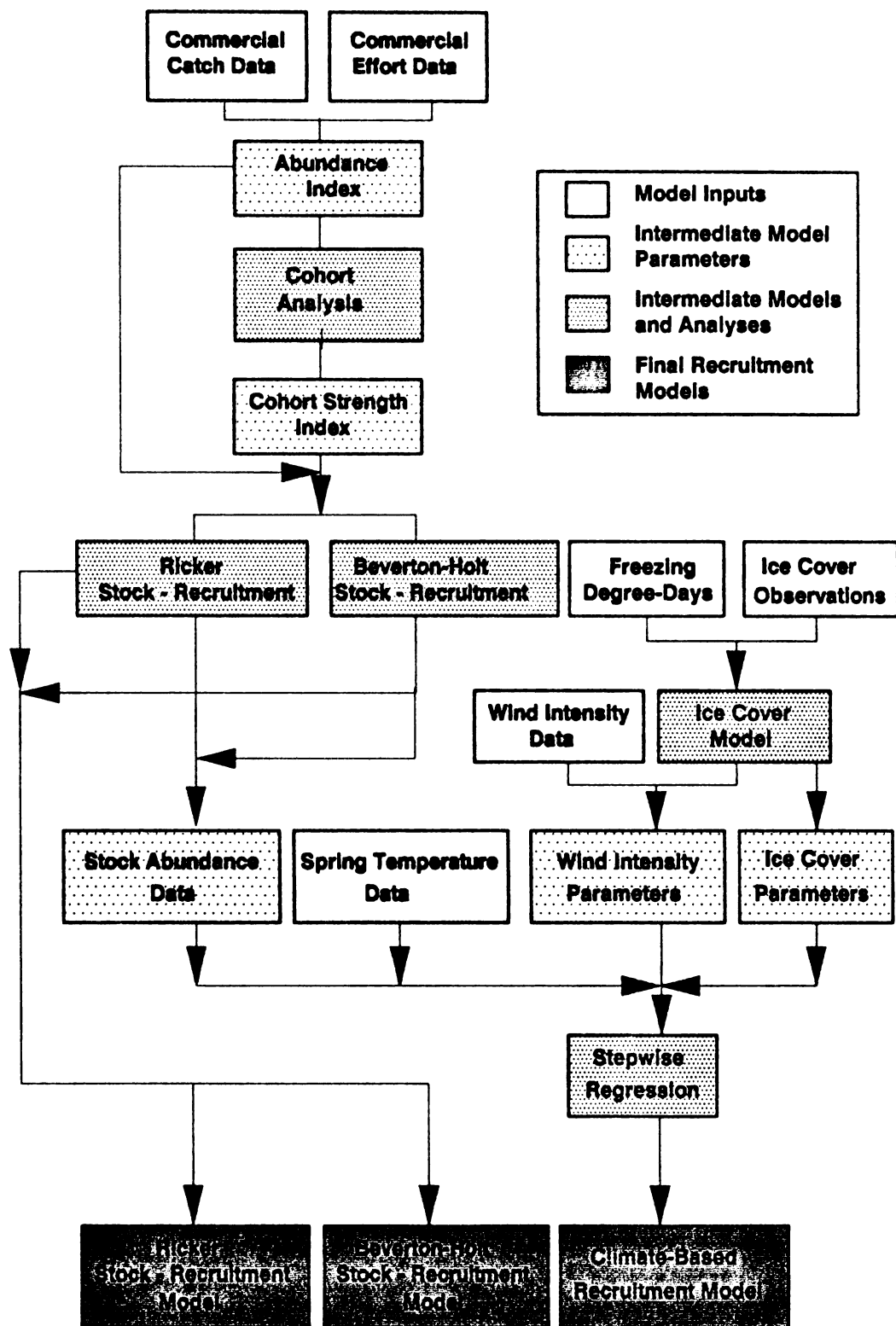


Figure 11.

Flow chart of lake whitefish recruitment modelling showing the model inputs, intermediate model parameters, intermediate models and analyses, and final recruitment models produced for each area.

cover modelling including the timing and duration of ice cover, wind intensity data, spring temperature data, and lake whitefish stock abundance were analyzed using stepwise regression to produce a climate-based recruitment model for each area. In summary, a Ricker stock-recruitment model, a Beverton-Holt stock-recruitment model, and a climate-based recruitment model were constructed for each area.

Commercial Catch Data and Study Areas

Records of commercial landings and standardized effort of the commercial fishery have been recorded since 1931 by state agencies and are currently maintained by the United States Fish and Wildlife Service at the National Fisheries Research Center - Great Lakes. Because of the difficulty of partitioning the effects of lamprey mortality from those of variable recruitment prior to 1958, commercial catch data from 1958 to 1989 were used to develop abundance and cohort strength indices for the 1961-1985 cohorts in this study.

Two areas in northern Lake Michigan were selected for recruitment modelling based on the consistent availability of commercial catch and age structure data. These areas were Great Lakes Fisheries Commission (GLFC) statistical district MM-1 including the Michigan waters of northern Green Bay and GLFC statistical district MM-3 including the north-central and northeastern areas of Lake Michigan (Figure 12). Because important spawning areas for lake whitefish are located in the northern portion of area MM-3,

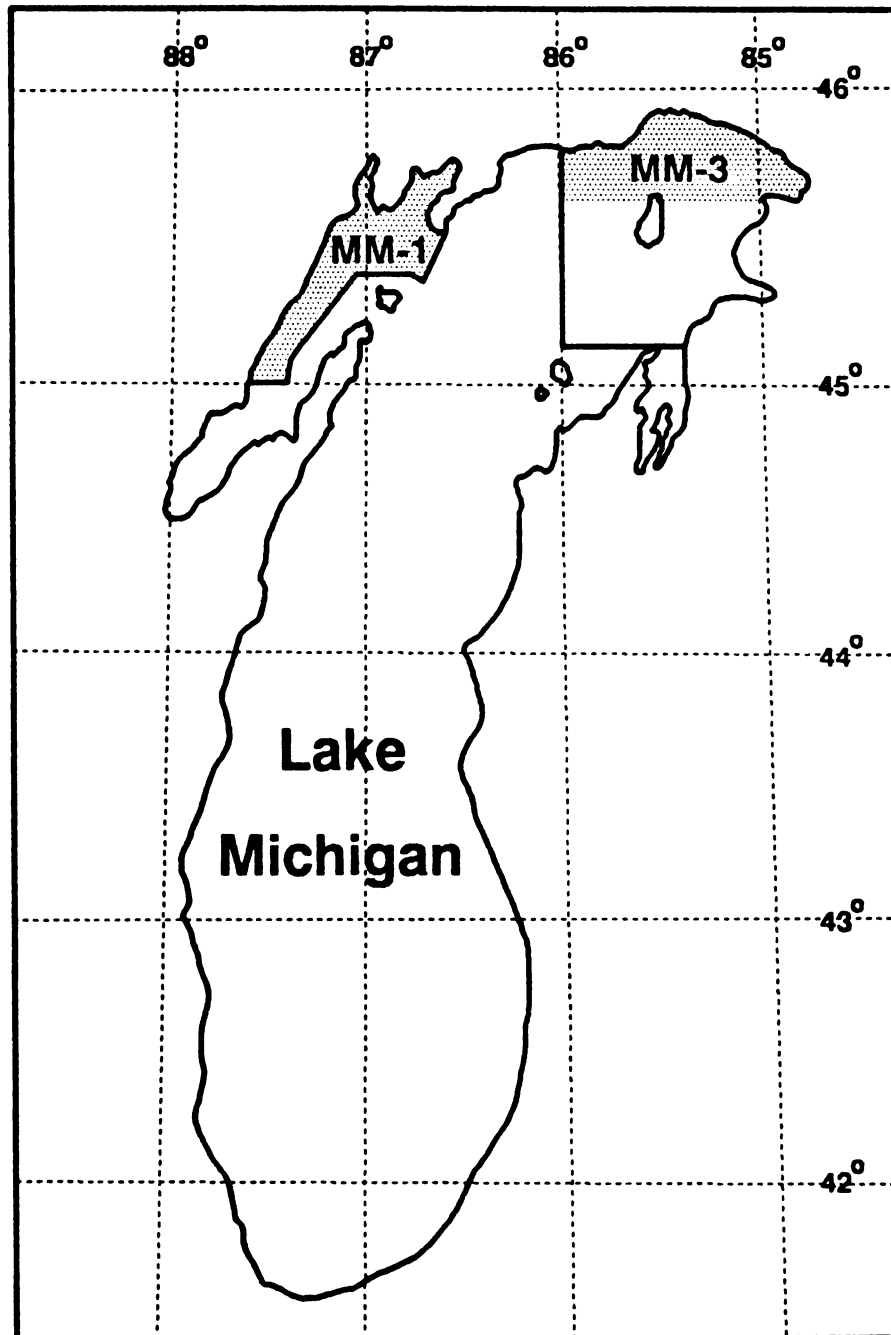


Figure 12.

Location map of Lake Michigan showing the two areas for which recruitment models were developed. The recruitment model for northern Green Bay included the entire area within GLFC statistical district MM-1. The recruitment model for the North Shore included the shaded region in the northern portion of GLFC statistical district MM-3.

a recruitment model was developed for the northern half of this area.

The commercial catch of lake whitefish over the past 30 years has fluctuated, but catch data suggests that similar recruitment mechanisms may be operating in each area (Figure 13). Each of these areas has multiple stocks of lake whitefish which contribute to the commercial landings within each district (Ebener and Copes 1985). Because of the nature of the data set and the limited data available from previous studies, modelling of individual stocks was not attempted.

Commercial Fishery Gear and Effort

Six types of gears have been used to fish for lake whitefish in area MM-1 since 1958 including 2-inch gill nets, 4-inch gill nets, shallow water trap nets, deep water trap nets, pound nets, and otter trawls. Seven types of gears have been used to fish for lake whitefish in area MM-3 including 2-inch gill nets, 4-inch gill nets, shallow water trap nets, deep water trap nets, pound nets, otter trawls, and seines. Catch and effort data from 2-inch gill nets, deep water trap nets, otter trawls, and seines were not used to index abundance or cohort strength because of the limited catch or time frame that these gears were fished. Catch and effort data from three principal gears, 4-inch gill nets, shallow water trap nets, and pound nets, were used to index abundance and cohort strength of lake whitefish in each

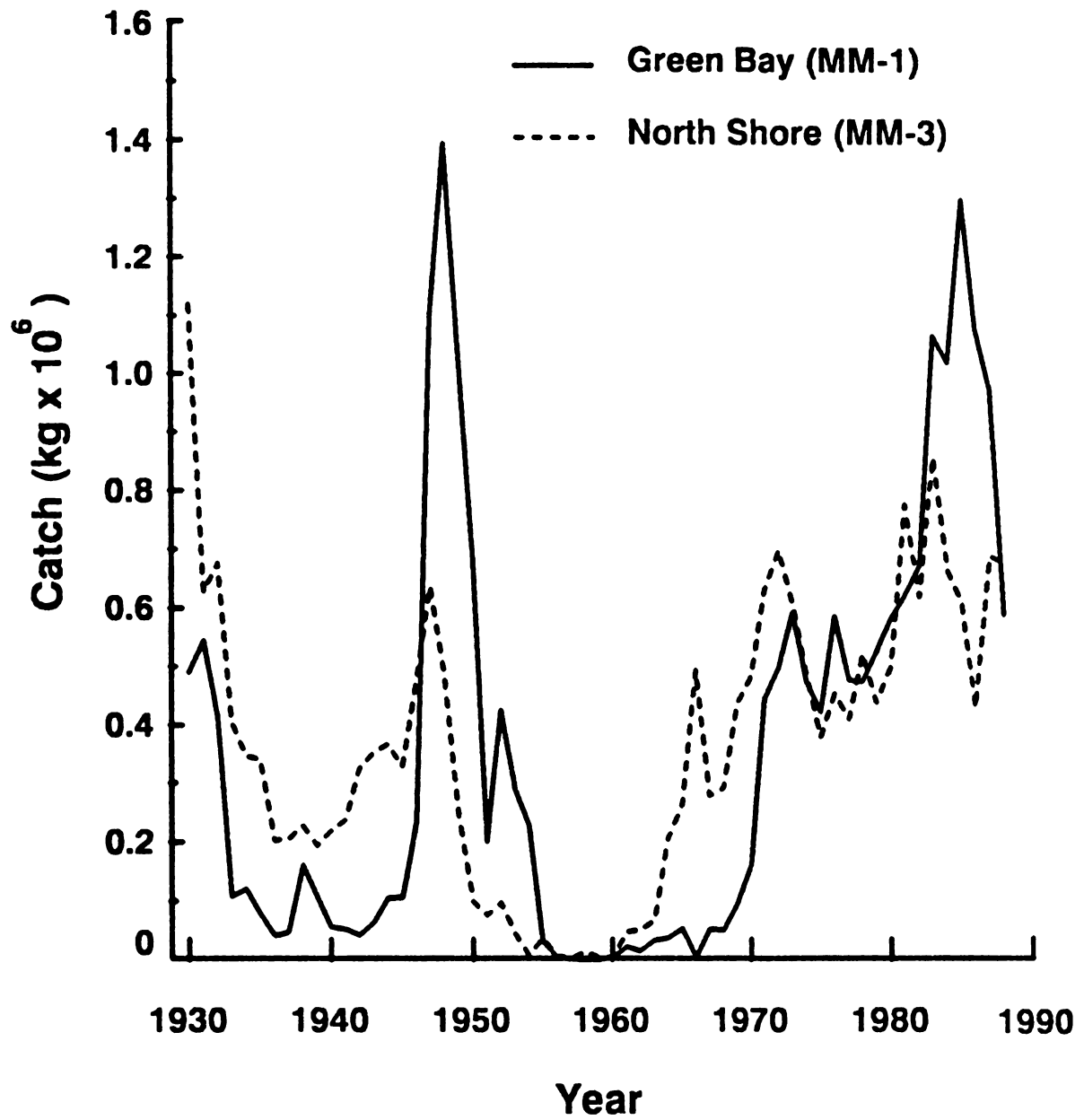


Figure 13. Commercial fisheries landings of lake whitefish in GLFC districts MM-1 and MM-3 in Lake Michigan from 1930-1989.

Indices of Spawning Stock and Recruitment

$$Abd_i = \frac{\sum_{j=1}^{\text{all gears}} C_{ji}}{\sum_{j=1}^{\text{all gears}} \frac{CPUE_j}{E_{1j}}}$$

ABD_i = abundance index in year i;

C_{ji} = lake whitefish catch in pounds by gear j
in year i;

CPUE_j = mean catch per unit effort of gear j for
the years 1960-1987;

E_{ji} = total effort using gear j in year i.

Table 7. Standardized units of effort for the commercial fishery in the Great Lakes as defined by the Great Lakes Fishery Commission (Hile 1962).

<u>Gear Type</u>	<u>Standardized Unit of Effort</u>
Shallow Water Trap Net	one lift of one net
Pound Net	one lift of one net
4-Inch Gill Net	one lift of 1000 linear feet of gill net

Several factors confounded efforts to partition abundance indices into cohorts and to estimate indices of cohort abundance. Recruitment age was not constant in either stock over the time period considered in this study. As the northern Green Bay and North Shore stocks gradually recovered from extremely low levels of abundance in the early 1960's, somatic growth rates declined and the mean age at recruitment increased by nearly two years (Smale 1988). In addition, the age at first recruitment was delayed in larger cohorts because of reduced somatic growth rates resulting from intraspecific competition within the cohort (Ebener and Copes 1985; Smale 1988).

In order to account for variable age of recruitment, cohort analysis procedures were used to partition abundance indices into indices of cohort abundance. Percent age composition data were available for northern Green Bay (area MM-1) including Piehler (1967), NcComb (1989), and unpublished data from the Michigan Department of Natural Resources (Table 8). Percent age composition data for the North Shore (area MM-3) were available from Piehler (1967), Brown (1968), Patriarche (1977), Rybicki (1980), and Scheerer and Taylor (1985) and unpublished data from the Michigan Department of Natural Resources and the tribal management sources (Table 9).

The abundance index value for each year was partitioned into the cohorts contributing to the abundance index in each

Table 8. Percent age composition of lake whitefish sampled in area MM-1 during the period 1960-1987. Data sources are shown for each year.

<u>Year</u>	<u>II</u>	<u>III</u>	<u>IV</u>	<u>V</u>	<u>VI</u>	<u>VII</u>	<u>Source</u>
1958	58	33	9	0	0	0	MDNR, Unpublished
1959	84	14	2	0	0	0	MDNR, Unpublished
1960	74	16	10	0	0	0	MDNR, Unpublished
1963	62	31	7	0	0	0	MDNR, Unpublished
1964	88	8	4	0	0	0	MDNR, Unpublished
1966	94	6	0	0	0	0	Piehler 1967
1968	38	38	20	1	2	0	MDNR, Unpublished
1969	28	31	25	4	10	0	MDNR, Unpublished
1970	12	48	36	3	0	0	MDNR, Unpublished
1971	0	91	8	1	0	0	MDNR, Unpublished
1972	2	73	22	2	0	0	MDNR, Unpublished
1973	3	58	34	1	0	0	MDNR, Unpublished
1979	0	53	39	6	1	0	NcComb 1989
1980	0	29	61	8	1	0	NcComb 1989
1981	1	41	53	5	0	0	NcComb 1989
1982	1	33	52	10	3	1	NcComb 1989
1983	0	54	31	12	2	0	NcComb 1989
1984	0	44	53	3	0	0	NcComb 1989
1985	0	3	81	16	0	0	NcComb 1989

Table 9. Percent age composition of lake whitefish sampled in area MM-3 (North Shore) during the period 1960-1987. Data sources are shown for each year.

<u>Year</u>	<u>II</u>	<u>III</u>	<u>IV</u>	<u>V</u>	<u>VI</u>	<u>N</u>	<u>Source</u>
1960	84	14	1	1	0	151	Brown 1968
1961	82	13	2	0	0	153	Brown 1968
1962	55	40	4	0	0	109	Brown 1968
1965	100	0	0	0	0	72	Piebler 1967
1966	25	68	4	0	0	681	Piebler 1967
1967	29	31	35	2	0	1232	Brown 1968
1968	9	74	8	8	0	611	Patriarche 1977
1969	25	58	16	1	0	96	Patriarche 1977
1970	44	54	2	1	0	169	Patriarche 1977
1971	8	81	10	1	0	296	Patriarche 1977
1972	28	68	2	2	0	141	Patriarche 1977
1973	1	65	30	1	0	141	Patriarche 1977
1974	0	15	69	8	0	113	Patriarche 1977
1975	2	92	4	1	0	133	Rybicki 1980
1976	1	60	38	0	0	339	Rybicki 1980
1977	4	36	36	1	0	133	Rybicki 1980
1978	0	44	36	7	0	586	Rybicki 1980
1979	2	63	31	0	0	399	Rybicki 1980
1980	0	78	21	1	0	513	Scheerer & Taylor 1985
1981	0	12	83	5	0	738	Scheerer & Taylor 1985
1982	0	4	37	55	4	452	Scheerer & Taylor 1985
1983	0	14	37	33	16	606	Smale 1988
1984	0	8	52	26	14	361	Smale 1988

year based on the age composition data available in each area. The partitioned abundances were summed for all years that a cohort contributed to the commercial catch to calculate a cohort abundance index value for each year class. Commercial catch and age composition data were used to calculate cohort abundance index values for the 1961-1985 cohorts within each area.

Stock-Recruitment Relationships

Abundance and cohort strength indices were used to calculate a Beverton-Holt (Beverton and Holt 1957) and a Ricker (Ricker 1954; Ricker 1985) stock-recruitment relationship for each area. The Beverton-Holt stock-recruitment relationship for each area was based on the following form:

$$R = \frac{1}{\alpha + \frac{\beta}{P}}$$

R	=	Recruitment Index Value
P	=	Abundance Index Value
α, β	=	dimensionless fitting parameters

Parameters for the Beverton-Holt stock-recruitment relationship were estimated by regressing 1/R on 1/P to estimate β , and α was estimated by substitution.

The Ricker stock-recruitment relationship for each area

was based on the following formula:

$$R = \alpha P e^{-\beta P}$$

The Ricker stock-recruitment relationship was determined by regressing $(\log_e R - \log_e P)$ against P to estimate β , and α was estimated through substitution.

Ice Cover Models

Ice cover models based on mean daily temperatures were developed by Raymond Assel of the Great Lakes Environmental Research Laboratory (National Oceanic and Atmospheric Administration). Air temperatures collected at Escanaba, Michigan were used to calculate mean daily temperatures and freezing degree days. Weighted average daily temperatures for various averaging periods were used to estimate spatially averaged ice concentrations for each study area. The following model was a representative of the general form of the ice cover models.

$$I_t = C_0 + \sum_{i=1}^n \left[\left(\frac{C_i}{Del} \int_{Del}^t T_t dt \right) \right]$$

I_t	=	ice concentration on day t
Co, C_i, i	=	$1, 2, \dots, j \dots n, t$ empirical coefficients
Del	=	$(t - L_i), i = 1, 2, \dots, j \dots n, t > L_i$
L_j	=	a given date before day y , for $i = j$
n	=	number of terms in the summation
T_t	=	average temperature ($^{\circ}C$) on day t

The model given in the above illustration contains "n" terms and some models also have a significant intercept term "Co". The C's are temperature weighting factors (coefficients of regression) for the integrated daily temperature for averaging periods of 5, 10, 30, 60, 90, 120, 150, and 180 days. The ice cover data used to calibrate the models were divided into three parts, based on the winter severity classes of above normal, normal, and below normal. Seasonal maximal freezing degree-day accumulations were used for the winter severity classification analysis.

Averaging periods for each winter classification within each lake area were determined from a R^2 analysis using the SAS statistical package RSQUARE. The "Del" term in the models defines the averaging periods. The model was calibrated for each lake area using the observed spatially averaged ice cover data in the Great Lakes Environmental Research Laboratory's 20-year (1960-1979) computerized digital ice concentration data base. The averaging periods,

R^2 , root mean square errors (RMSE) and number of observations used in model calibration each winter classification within each area are given in Table 10.

Each set of models was used to produce mean daily ice cover concentrations for each area for the winters of 1960-1987. Because the critical level of ice cover concentration necessary to protect lake whitefish eggs was not known, the number of days with ice cover exceeding several levels were used as recruitment model inputs. Ice concentrations of 0, 10, 20, 30, 40, 50, 60, and 70 % were chosen to produce seven ice cover variables for each area. The number of days of ice concentration exceeding each of these ice concentration levels was calculated for each area.

Wind Speed Data

Wind speed data collected at Green Bay, Wisconsin and Sault St. Marie, Michigan were used as model inputs in areas MM-1 and MM-3, respectively. Two-day average wind speeds (knots) were calculated on a daily basis during November, December, and January for the years 1960-1987. Average wind speed levels above 8, 10, and 12 knots were selected to define days of intense wind activity. The number of days above these wind speed levels was tabulated for each ice cover level within each area.

Ice cover data were used to define the period when intense wind events could impact survival of lake whitefish eggs. I hypothesized that intense wind events would only

Table 10. Results of ice cover modelling for areas MM-1 (northern Green Bay) and MM-3 (North Shore). Asterisks indicate regression models containing an intercept term. The averaging periods used to produce each model, R^2 , root mean square errors (RMSE) and number of observations used in model calibration each winter classification within each area.

Northern Green Bay, Area MM-1

<u>Winter Severity</u>	<u>Averaging Periods (Days)</u>	<u>R^2</u>	<u>RMSE</u>	<u>NUM</u>
Above Normal *	10, 60, 120, 150	0.62	13.9	55
Normal *	5, 30, 60, 120, 180	0.73	12.2	117
Below Normal	10, 90, 120	0.94	16.7	26

North Shore, Area MM-3

<u>Winter Severity</u>	<u>Averaging Periods (Days)</u>	<u>R^2</u>	<u>RMSE</u>	<u>NUM</u>
Above Normal	10, 60, 90, 180	0.97	13.6	60
Normal	5, 60, 90, 180	0.96	13.9	163
Below Normal *	5, 10, 30, 120, 150	0.70	18.8	33

influence egg survival of lake whitefish prior to the formation of some critical concentration of ice cover over spawning areas. To define biologically meaningful wind variables, I only considered wind events occurring between the earliest possible spawning date and the formation of various levels of ice cover.

The starting date for tabulating intense wind events was November 1 in all cases, because this date corresponds with the earliest date of lake whitefish spawning in each area. Because no data were available to define a critical level of ice concentration necessary to protect major spawning areas, several ice concentration levels were selected to define the period of vulnerability of lake whitefish eggs to wind events. Ice concentration levels above 0, 20, 40, and 60 % ice cover were selected as ice concentration levels to determine the ending date for wind speed tabulation. The date when ice cover concentration first exceeded a given critical ice concentration was used as the end date for tabulated intense wind events. For example, the number of days between November 1 and the date when ice cover first exceeded 20 % in a given year was tabulated to create a single wind speed variable. In this way, the three wind speed levels (8, 10, and 12 knots) and the four ice cover concentration levels (0, 20, 40, 60 %) were used to calculate 12 wind speed variables for each lake area.

Spring Water and Air Temperatures

Mean monthly spring water temperatures for March, April, and May were available from a municipal water intake at Menominee, Michigan for the period 1960-1987. These temperature data were used to produce three spring temperature variables used as inputs in recruitment modelling in area MM-1.

Water temperature data could not be located for area MM-3. Mean monthly spring air temperatures taken at Sault St. Marie, Michigan were used to produce three monthly mean spring temperature variables used as inputs in recruitment modelling in area MM-3.

Climate-Based Recruitment Model Construction

All variables including stock-recruitment values, ice cover data, wind intensity data, and spring temperature data were used to predict year class strength index values using a least squares multiple regression approach. Stepwise multiple regression analysis was conducted using the SAS statistical software package and the variable selection model STEPWISE. Additional variables were added to each model until none of the variables outside had a significant F statistic ($\alpha = 0.15$), and every variable in the model has a significant F statistic. Each resulting model was tested for autocorrelation using a Durbin-Watson d statistic (Durbin and Watson 1951) and heteroscedasticity using analysis of the covariance matrix (White 1980).

RESULTS

Stock-Recruitment Relationships

Stock-recruitment parameter estimates for both areas are shown in Table 11. Both stock-recruitment relationships indicated a significant relationship between the abundance and cohort strength indices for the northern Green Bay area. The Beverton-Holt stock-recruitment relationship ($R^2 = 0.373$, $P = 0.0007$) provided a slightly better fit than the Ricker stock-recruitment relationship ($R^2 = 0.330$, $P = 0.0016$) for the northern Green Bay area.

In the North Shore area, the Ricker stock-recruitment relationship indicated a significant relationship between abundance and cohort strength indices (Table 11). Although these stock-recruitment models each explained less than 15% of the variation in recruitment, the Ricker stock-recruitment function ($R^2 = 0.126$, $P = 0.0458$) provided a slightly better fit than the Beverton-Holt stock-recruitment relationship ($R^2 = 0.091$, $P = 0.0786$) for the North Shore area.

Northern Green Bay Climate-Based Recruitment Models

Lake whitefish recruitment in northern Green Bay was best modelled as a function of the Beverton-Holt stock-recruitment function, the number of days of ice cover exceeding 40%, and the number of days of average wind speeds above 10 knots prior to the onset of 40% ice cover:

Table 11. Results of Beverton-Holt and Ricker stock-recruitment relationships for lake whitefish in northern Green Bay and the North Shore, Lake Michigan using abundance and year class indices from 1961-1985.

<u>Northern Green Bay</u>				
<u>Model</u>	<u>Alpha</u>	<u>Beta</u>	<u>Adjusted R²</u>	<u>P-Value</u>
Beverton-Holt	0.0035091	0.50842096	0.373	0.0007
Ricker	2.4132768	-0.00604602	0.330	0.0016

<u>North Shore</u>				
<u>Model</u>	<u>Alpha</u>	<u>Beta</u>	<u>Adjusted R²</u>	<u>P-Value</u>
Beverton-Holt	0.0066245	0.2153229	0.091	0.0786
Ricker	3.0296718	-0.0091653	0.126	0.0458

$$R_i = \beta_0 + \beta_1 \frac{1}{\alpha + \frac{\beta}{A_i}} + \beta_2 I_{40\%} + \beta_3 W_{10,40\%}$$

R_i	=	recruitment index value of lake whitefish year class i ;
A_i	=	abundance index value for year i ;
α, β	=	Beverton-Holt stock-recruitment constants
$\beta_0, \beta_1, \beta_2, \beta_3$	=	recruitment model regression constants;
$I_{40\%}$	=	number of days of ice cover exceeding 40%;
$W_{10,40\%}$	=	number of days of 2-day average wind speed above 10 knots prior to the formation of 40% ice cover.

The partial R^2 's for each parameter in this model are listed in Table 12.

This recruitment model was used to hindcast recruitment index values for the years 1961-1985, and these values were plotted against actual recruitment index values calculated from catch, effort, and age composition data (Figure 14). Model hindcasts for the period 1971-1985 were more accurate than hindcasts for the period 1961-1970 based on mean absolute deviations between the model hindcasts and actual recruitment index values (Median Test, $X^2_1 = 4.44$, $P = 0.035$). Recruitment during this earlier period was highly variable, which may have been caused by extremely low levels of spawning stock during these years. For this area, there

Table 12. Parameter estimates and squared partial correlation coefficients for climate-based recruitment models of lake whitefish in areas MM-1 and MM-3.

<u>Area</u>	<u>Model Parameter</u>	<u>Parameter Estimate</u>	<u>Squared Partial Correlation</u>
MM-1	Beverton-Holt SR	0.768	0.399
	Ice (40%)	1.136	0.216
	Wind (40%, 8 knots)	0.985	0.033
MM-3	Beverton-Holt SR	1.949	0.139
	Ice (70%)	0.702	0.165
	Wind (20%, 8 knots)	0.957	0.031
	Air Temp (May)	1.509	0.252

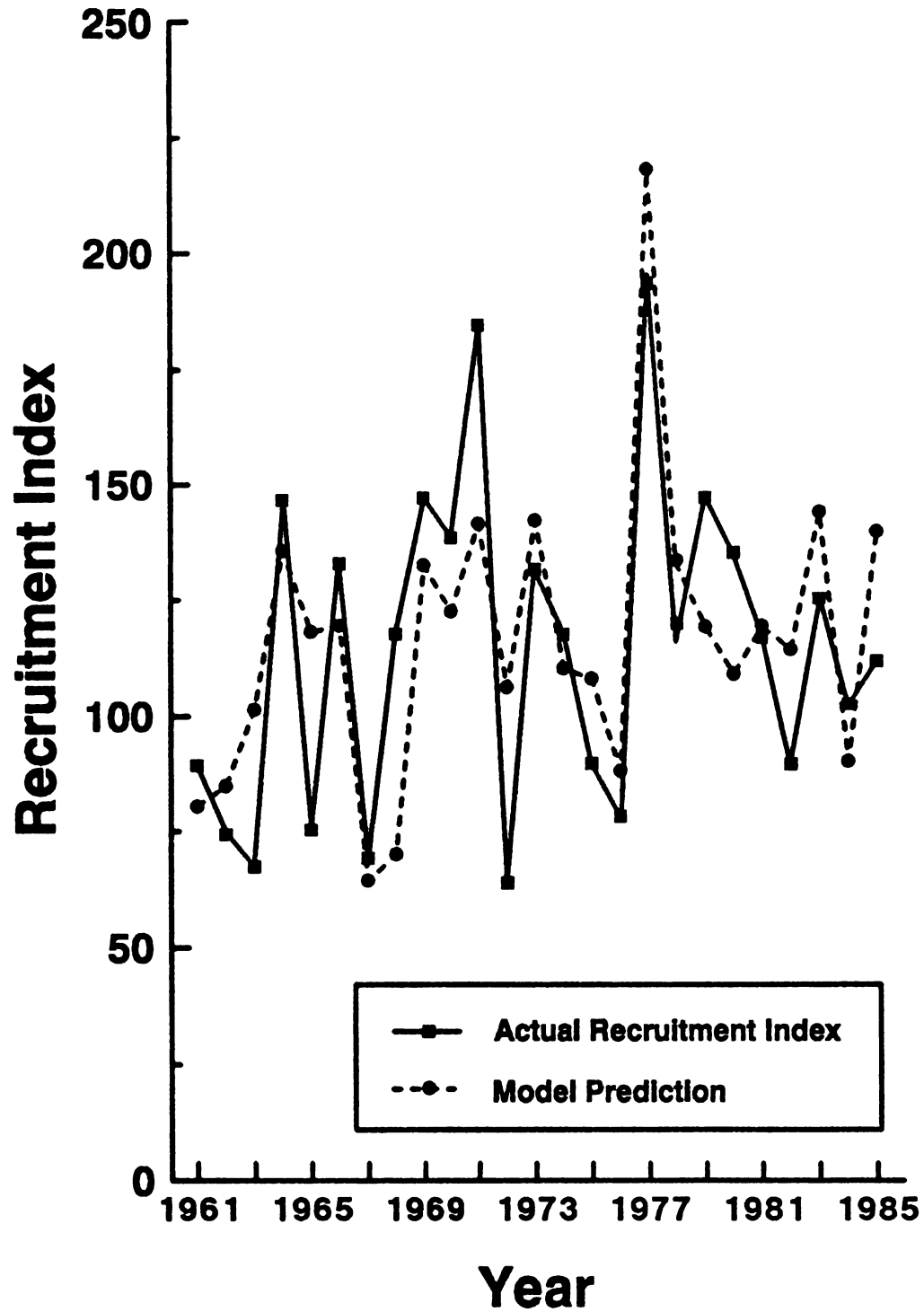


Figure 14. Recruitment model hindcasts and actual cohort abundance index values for the 1961-1985 cohorts of lake whitefish in northern Green Bay, Lake Michigan.

is a trend toward increasing recruitment index and model prediction index values through the time period modelled reflecting the gradual recovery of lake whitefish stocks.

Residual values between the predicted and actual recruitment index values were plotted as a function of time in Figure 15. There was no apparent time related trend in the pattern of the residual values from this regression model.

North Shore Climate-Based Recruitment Models

North Shore recruitment was best modelled as a function of the Beverton-Holt stock-recruitment function, the number of days of ice cover exceeding 70%, the number of days of average wind speeds above 10 knots prior to the onset of ice cover, and the average spring air temperatures in May:

$$R_i = \beta_0 + \beta_1 \frac{1}{\alpha + \frac{\beta}{A_i}} + \beta_2 I_{70\%} + \beta_3 W_{10,0\%} + \beta_4 T_{May}$$

$I_{70\%}$ = number of days of ice cover exceeding 70%;

$W_{10,0\%}$ = number of days of 2-day average wind speed above 10 knots prior to the formation of ice cover;

T_{May} = mean average air temperature in May.

The partial R^2 's for each parameter in this model are listed in Table 12.

This model was used to hindcast recruitment index

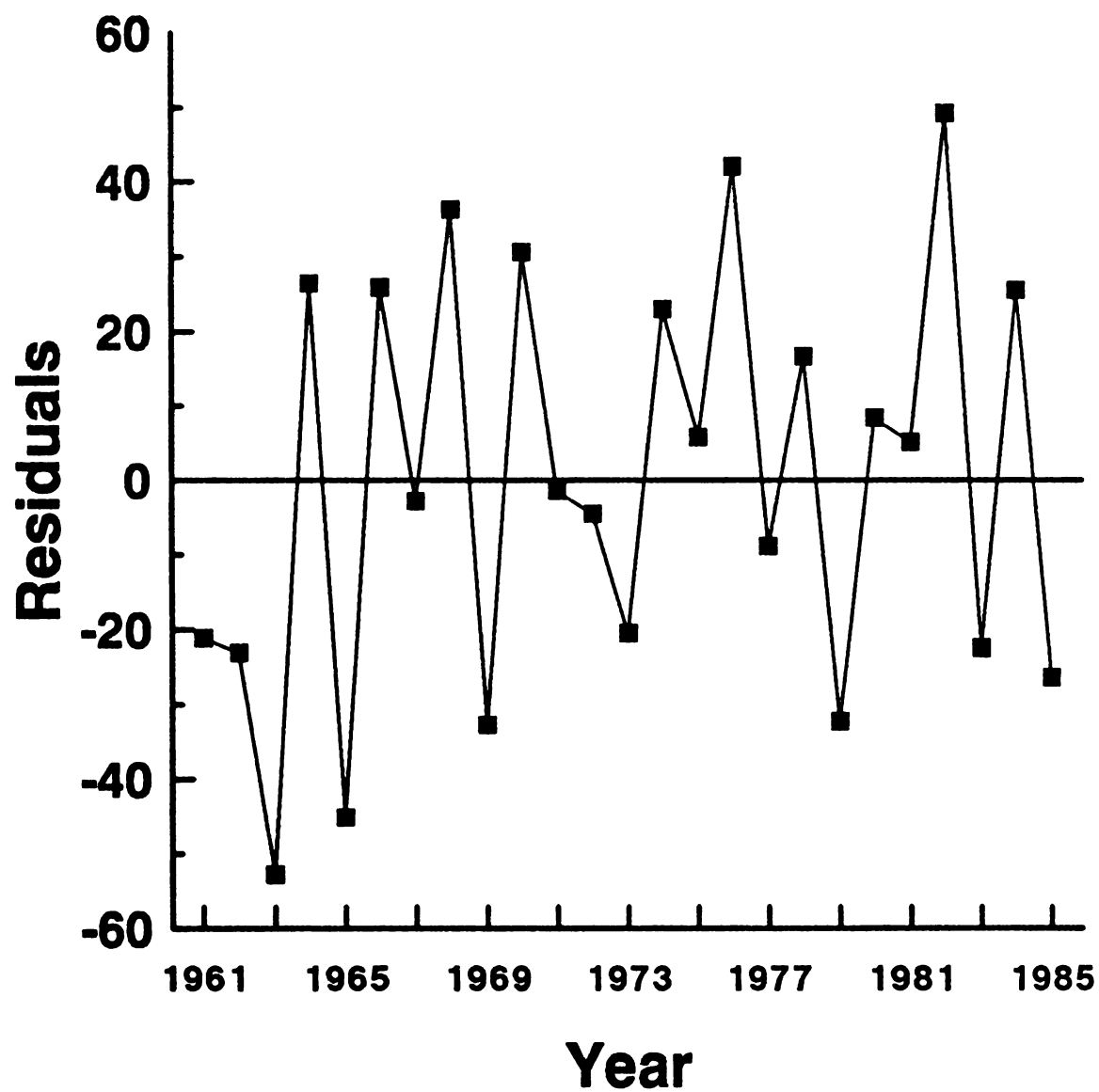


Figure 15. Plot of residual values between recruitment model hindcasts and actual cohort index values for the 1961-1985 cohorts of lake whitefish in northern Green Bay, Lake Michigan.

values for the years 1961-1985, and these values were plotted against actual recruitment index values calculated from catch, effort, and age composition data (Figure 16). Model hindcasts for the period 1973-1985 were no more accurate than hindcasts for the period 1961-1972, based on differences in mean absolute deviations (Median Test, $\chi^2_1 = 0.17$, $P = 0.6820$). The model accurately hindcasted the largest year class during this period (1977), but was less successful in hindcasting the large 1971 year class. Residual values between the predicted and actual recruitment index values showed no apparent time-related trends (Figure 17).

DISCUSSION

Relationship between Spawning Stock and Recruitment

Based on the spawning stock and climate-based recruitment modelling results, it appears that lake whitefish recruitment in northern Green Bay is primarily dependent upon the abundance of spawning stock, and is less dependent upon climatic influences such as ice cover, wind intensity, and spring temperatures over the time period studied. The stock-recruitment relationships for the northern Green Bay area explained a greater proportion of the variation in recruitment when compared to the relationships calculated for the North Shore area. Also,

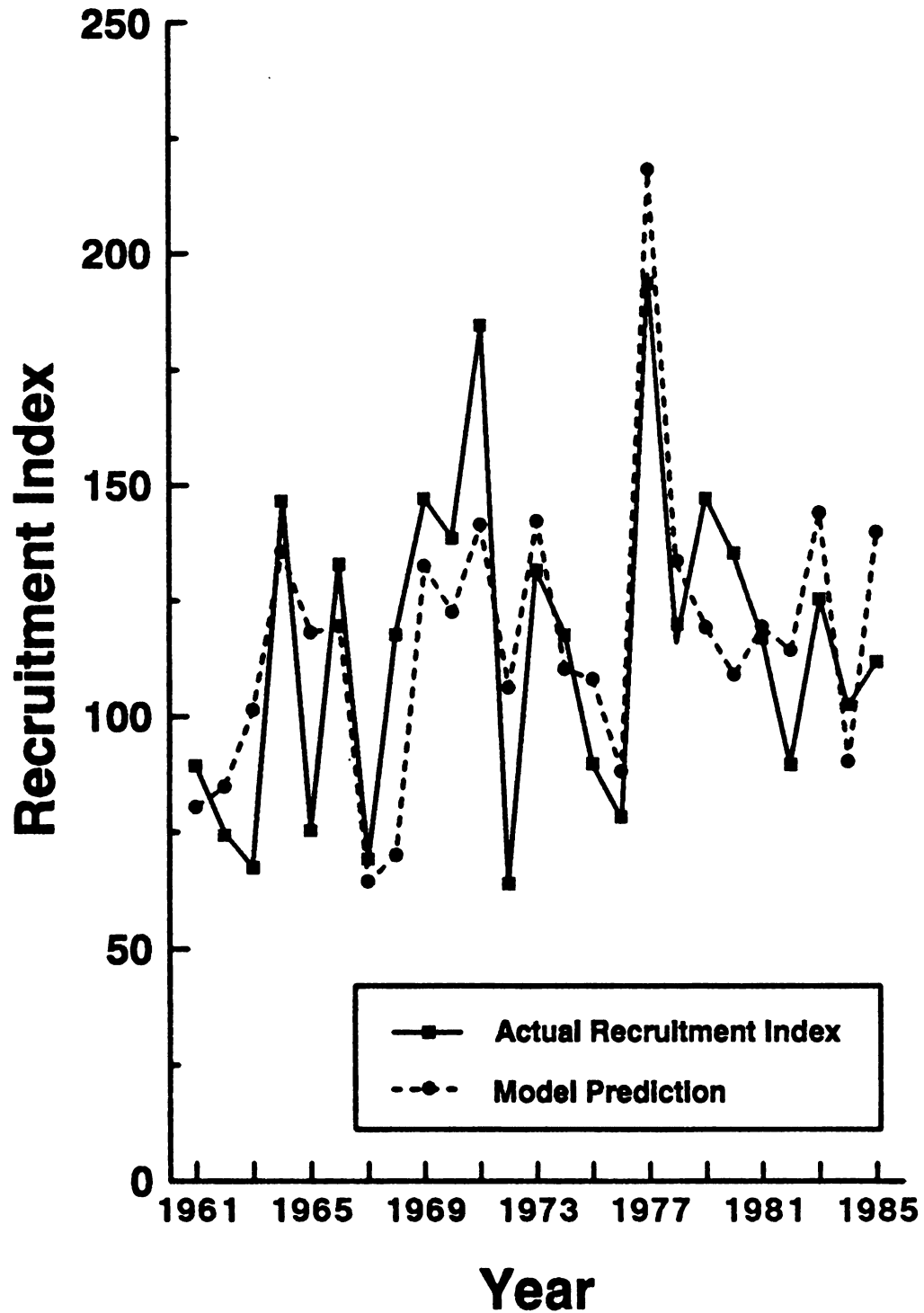


Figure 16.

Recruitment model hindcasts and actual cohort abundance index values for the 1961-1985 cohorts of lake whitefish along the North Shore, Lake Michigan.

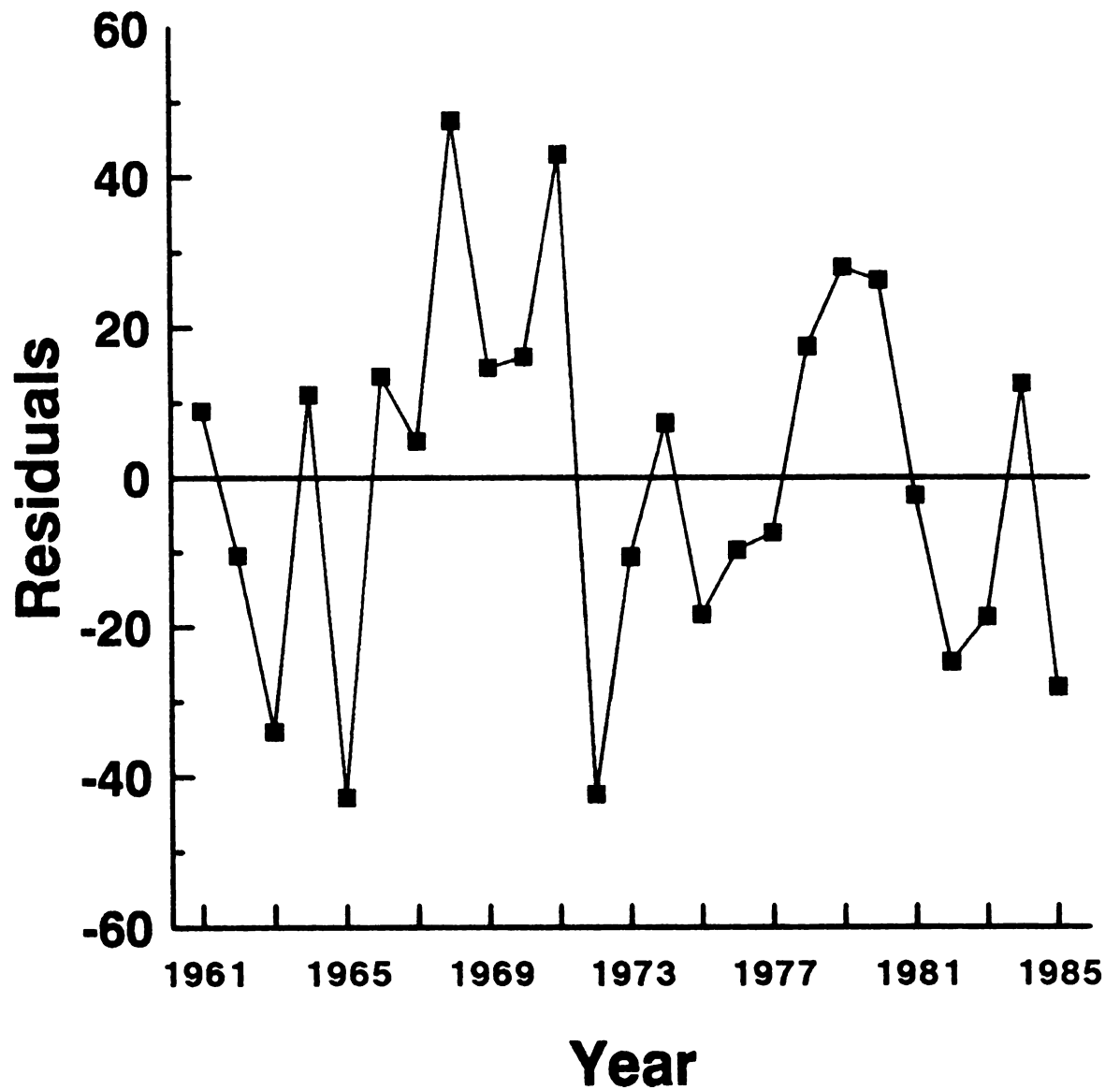


Figure 17.

Plot of residual values between recruitment model hindcasts and actual cohort index values for the 1961-1985 cohorts of lake whitefish along the North Shore, Lake Michigan.

the partial R^2 's from climate-based recruitment modelling indicate that the stock-recruitment term made a greater contribution to the northern Green Bay model than it made to the North Shore model.

One possible cause for differences in the importance of climatic factors between the two areas is related to variation in ice cover. Because northern Green Bay is relatively protected from wind and lake currents, there is less variation in the timing and extent of ice cover formation. During the years in which ice cover was modelled, ice cover normally formed during or just after lake whitefish spawning. Because there was little variation in the timing of ice cover formation, there was also less variation in the wind events affecting egg survival prior to ice cover formation. In contrast, ice cover and wind events were more variable in the North Shore area, and this climatic variability appears to be more important in determining egg survival, cohort strength, and eventual recruitment of lake whitefish in this area.

A second possible reason for the stronger relationship between stock size and recruitment is related to the range of stock abundances present during the modelling time period. While abundance and cohort strength indices are site-specific and not directly comparable between sites, the range of stock abundances appears to be larger for the northern Green Bay area as reflected by catch data (Figure

13). Low levels of abundance prior to 1970 may have amplified the apparent relationship between stock abundance and recruitment.

Climate-Based Recruitment Modelling

Incorporation of climate variables increased the recruitment hindcasting ability of recruitment models in both areas. Ice cover was an important variable in both models, although the concentration of ice cover that was most significant in predicting recruitment was different in each area. Several levels of ice concentration were used as inputs in recruitment modelling because of uncertainty regarding the critical level of ice cover concentration necessary to protect lake whitefish eggs. In the northern Green Bay area, 40% ice concentration was identified as being most significant, while in the North Shore area, 70% was most significant. These differences in critical ice cover concentrations may be due to differences in the lake basin morphology and prevailing storm patterns in each area.

The importance of abiotic variables such as ice cover and wind speed to the recruitment process of lake whitefish in different areas of the Great Lakes is dependent upon a number of factors including the quantity and quality of spawning substrate and lake basin morphology. Ice cover may play a more critical role in protecting lake whitefish eggs in areas with marginal spawning substrate quality by protecting eggs from wind and wave action. In these areas,

lake whitefish eggs are more vulnerable to displacement and destruction by abrasion than in areas with quality spawning substrate. Freeberg et al. (1990) found that ice cover was critical for protecting lake whitefish eggs in the marginal spawning areas of Grand Traverse Bay, Lake Michigan.

The two areas modelled in this study, northern Green Bay and the North Shore occur along a geological band of limestone, which produces substrate that is optimal for incubation of lake whitefish eggs (J. Reckhan, Ontario Ministry of Natural Resources, personal communication). The relatively large availability of quality spawning areas may be one reason why these two areas have consistently had the highest production of lake whitefish in Lake Michigan (Baldwin et al. 1979).

Other Factors Affecting Recruitment

Several factors not included as inputs in recruitment modelling may have a significant influence on the recruitment of lake whitefish in these two areas. Variation in the production of spring zooplankton resources has been identified as a mechanism which influences the larval survival of lake whitefish (Reckhan 1970; Freeberg 1985; Freeberg et al. 1990). Only one set of surrogate variables, spring water and air temperatures, is directly related to the production of zooplankton prey resources. Site-specific studies of fine-scale nature are needed to identify factors important in controlling the production of these prey

resources.

Other biotic factors such as competition and predation may be important factors influencing recruitment mechanisms. Competition between larvae of several species including lake herring, alewife, and rainbow smelt may be a locally significant factor influencing lake whitefish recruitment. Likewise, predation by adults of several species on lake whitefish including rainbow smelt (Loftus and Hulsman 1987) and alewife (Hoagman 1974) also may be significant in some areas.

Results of this study provide a basis for identifying and incorporating climatic variables into recruitment modelling. These recruitment models provide a basic model which predicts the potential recruitment of lake whitefish based on the egg and larval survival of lake whitefish. While variation in climatic variables appears to be important in determining recruitment of lake whitefish, recruitment models incorporating climatic variables and only one biotic variable (stock abundance) can not be expected to explain all of the variability in lake whitefish recruitment. Other biotic factors influencing prey productivity and availability, intra- and interspecific competition, and predation need to be incorporated into further efforts to model lake whitefish recruitment in order to produce finer-scale models for specific areas of Lake Michigan.

Conclusions

Lake whitefish recruitment in northern Green Bay was modelled as a function of the Beverton-Holt stock-recruitment function, the number of days of ice cover exceeding 40%, and the number of days of average wind speeds above 10 knots prior to the onset of 40% ice cover. The climate-based recruitment model ($R^2 = 0.65$) for northern Green Bay demonstrated improved hindcasting ability when compared to the Beverton-Holt stock-recruitment model ($R^2 = 0.37$) for the 1961-1985 cohorts. North shore recruitment was modelled as a function of the average spring air temperatures in May, the number of days of ice cover exceeding 70%, the Beverton-Holt stock-recruitment function, and the number of days of average wind speeds above 10 knots prior to the onset of ice cover. The climate-based recruitment model ($R^2 = 0.57$) for the North Shore demonstrated improved hindcasting ability when compared with Ricker stock-recruitment model ($R^2 = 0.13$). Based on the stock-recruitment and climate-based recruitment modelling results, the abundance of spawning stock is more important in determining lake whitefish recruitment in northern Green Bay than in the North Shore area. Climatic factors such as ice cover, wind intensity, and spring temperatures appear to be more important in determining lake whitefish recruitment in the North Shore area than in northern Green Bay.

Recruitment models incorporating both abiotic and biotic variables have the potential to produce forecasts of lake whitefish cohort strength several years in advance to recruitment into the fishery.

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Appendix 1.

Appendix 1. Length, weight, and age data of female lake whitefish sampled from Bayport and Naubinway and data for those fish whose eggs were used in laboratory experiments.

Bayport				Field				Naubinway			
ID#	Length	Weight	Age	ID#	Length	Weight	Age	ID#	Length	Weight	Age
1	605	2000	7	1	572	1000	6				
3	522	1300	5	4	499	550	5				
5	587	1900	6	7	507	650	4				
7	557	1750	5	10	567	1250	6				
9	582	1800	6	13	607	1475	7				
11	551	1550	5	16	542	960	5				
13	587	1850	6	19	509	900	4				
15	529	1250	5	22	613	1810	7				
17	506	1150	4	25	546	1150	5				
19	595	1750	7	28	585	1490	6				
21	632	2350	8	31	468	550	4				
23	598	2000	7	34	508	800	5				
25	541	1525	5	37	537	950	6				
27	560	1350	6	40	455	375	4				
29	641	2550	8								
31	535	1550	5								
33	543	1500	5								
Mean	569	1713	5.9	Mean	537	994	5.3				
SE	9.1	89.3		SE	12.5	105					

Bayport				Laboratory				Naubinway			
ID#	Length	Weight	Age	ID#	Length	Weight	Age	ID#	Length	Weight	Age
3	522	1300	5	1	572	1000	6				
7	557	1750	6	7	507	650	4				
15	529	1250	5	13	607	1475	7				
17	506	1150	4	22	613	1810	7				
19	595	1750	7	34	508	800	5				
21	632	2350	8	37	537	950	6				
Mean	557	1591	5.8	Mean	557	1114	5.8				
SE	18	168		SE	18	164					

Appendix 2.

Appendix 2. Egg composition data for female lake whitefish sampled from Bayport and Naubinway.

Fish #	Wet Weight(mg)/egg		Bayport Dry Wet(mg)/egg		Percent Water	
	Mean	SE	Mean	SE	Mean	SE
1	10.16	0.247	2.92	0.000	71.21	0.710
3	8.01	0.134	2.41	0.014	69.83	0.585
5	10.24	0.129	2.98	0.019	70.93	0.367
7	9.46	0.199	2.55	0.005	73.05	0.571
9	9.91	0.233	2.87	0.011	70.97	0.637
11	8.37	0.564	2.41	0.022	70.90	1.653
13	8.88	0.176	2.65	0.003	70.16	0.575
15	7.49	0.064	2.19	0.031	70.69	0.535
17	10.16	0.272	2.96	0.081	70.84	0.127
19	8.65	0.326	2.57	0.048	70.24	0.894
21	11.00	0.200	2.94	0.085	73.32	0.346
23	9.94	0.064	2.66	0.005	73.26	0.213
25	8.15	0.133	2.48	0.018	69.50	0.340
27	8.98	0.078	2.44	0.003	72.79	0.223
29	10.89	0.490	2.69	0.054	75.20	0.852
31	9.51	0.039	2.68	0.007	71.78	0.099
33	8.66	0.072	2.86	0.010	66.92	0.289
Total	9.32	0.242	2.66	0.055	71.27	0.443

Fish #	Wet Weight(mg)/egg		Naubinway Dry Wet(mg)/egg		Percent Water	
	Mean	SE	Mean	SE	Mean	SE
1	8.34	0.091	2.96	0.010	64.46	0.413
4	7.88	0.052	2.52	0.017	68.01	0.379
7	6.98	0.215	2.30	0.010	66.93	0.948
10	10.83	0.308	3.05	0.011	71.72	0.884
13	8.78	0.068	3.19	0.016	63.67	0.454
16	7.37	0.050	2.52	0.024	65.76	0.179
19	9.47	0.078	2.29	0.015	75.85	0.230
22	8.71	0.134	2.79	0.012	67.90	0.406
25	8.94	0.178	2.84	0.017	68.16	0.452
28	7.60	0.071	2.57	0.022	66.18	0.280
31	8.42	0.166	2.42	0.017	71.22	0.681
34	8.97	0.199	2.68	0.022	70.07	0.502
37	8.01	0.089	2.64	0.003	67.08	0.358
40	5.11	0.052	1.68	0.022	67.07	0.436
Total	8.24	0.339	2.60	0.097	68.15	0.822

Appendix 2 (Cont.)

Appendix 2. Egg composition data for female lake whitefish sampled from Bayport and Naubinway.

Fish Number	Bayport			
	Cal/Egg		Cal/g	
	Mean	SE	Mean	SE
1	19.7	0.027	6.74	0.0091
3	15.2	0.091	6.30	0.0050
5	19.0	0.124	6.38	0.0089
7	16.8	0.037	6.61	0.0038
9	19.0	0.078	6.63	0.0104
11	15.4	0.145	6.41	0.0104
13	17.0	0.030	6.43	0.0094
15	14.0	0.201	6.39	0.0039
17	18.8	0.514	6.34	0.0191
19	16.8	0.317	6.55	0.0117
21	19.1	0.552	6.50	0.0030
23	16.8	0.039	6.34	0.0070
25	15.9	0.116	6.41	0.0077
27	16.0	0.029	6.55	0.0092
29	16.7	0.340	6.21	0.0150
31	17.7	0.060	6.60	0.0139
33	18.9	0.066	6.59	0.0050
	17.2	0.386	6.47	0.0033

Fish Number	Naubinway			
	Cal/Egg		Cal/g	
	Mean	SE	Mean	SE
1	19.7	0.069	6.66	0.0079
4	16.4	0.116	6.49	0.0139
7	15.0	0.068	6.52	0.0104
10	20.6	0.079	6.73	0.0093
13	21.3	0.116	6.67	0.0125
16	16.4	0.160	6.52	0.0107
19	15.0	0.101	6.58	0.0058
22	18.1	0.079	6.47	0.0066
25	18.9	0.119	6.63	0.0160
28	17.0	0.144	6.63	0.0067
31	15.5	0.112	6.40	0.0113
34	17.7	0.151	6.59	0.0136
37	17.4	0.046	6.61	0.0161
40	10.8	0.143	6.41	0.0049
	17.1	0.688	6.56	0.0256

Appendix 2 (Cont.)

Appendix 2. Egg composition data for female lake whitefish sampled from Bayport and Naubinway.

Bayport				
Fish Number	Percent Lipid Content		Lipid Content (mg/egg)	
	Mean	SE	Mean	SE
1	22.81	0.475	0.666	0.011
3	15.45	0.440	0.373	0.025
5	23.43	0.466	0.697	0.010
7	18.85	0.244	0.480	0.014
9	19.39	0.482	0.557	0.008
11	17.65	0.520	0.425	0.007
13	21.52	0.440	0.570	0.010
15	17.60	0.188	0.386	0.020
17	15.44	0.466	0.458	0.007
19	16.18	0.195	0.415	0.010
21	22.22	0.134	0.652	0.022
23	20.55	0.538	0.546	0.011
25	19.64	0.091	0.488	0.007
27	21.69	0.132	0.530	0.011
29	16.73	0.372	0.450	0.010
31	22.08	0.357	0.593	0.006
33	21.72	0.454	0.622	0.011
Total	19.6	0.629	0.524	0.024

Naubinway				
Fish Num	Percent Lipid Content		Lipid Content (mg/egg)	
	Mean	SE	Mean	SE
1	23.23	0.423	0.688	0.024
4	20.09	0.581	0.506	0.014
7	17.71	0.462	0.408	0.007
10	23.98	0.382	0.732	0.012
13	20.67	0.399	0.660	0.020
16	16.62	0.584	0.419	0.021
19	18.26	0.128	0.417	0.006
22	18.96	0.544	0.530	0.010
25	16.78	0.356	0.477	0.014
28	21.16	0.393	0.544	0.012
31	13.80	0.186	0.334	0.009
34	20.24	0.428	0.543	0.006
37	18.75	0.442	0.494	0.024
40	16.95	0.556	0.285	0.019
Total	19.09	0.703	0.502	0.033