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EARLY LIFE HISTORY FACTORS INFLUENCING
LAKE WHITEFISH (<u>COREGONUS</u> <u>CLUPEAFORMIS</u>) YEAR-CLASS
STRENGTH IN GRAND TRAVERSE BAY, LAKE MICHIGAN

presented by

Mark Harlyn Freeberg

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EARLY LIFE HISTORY FACTORS INFLUENCING LAKE WHITEFISH (COREGONUS CLUPEAFORMIS) YEAR-CLASS STRENGTH IN GRAND TRAVERSE BAY, LAKE MICHIGAN

By

Mark Harlyn Freeberg

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ABSTRACT

EARLY LIFE HISTORY FACTORS INFLUENCING LAKE WHITEFISH (C<u>OREGONUS</u> <u>CLUPEAFORMIS</u>) YEAR-CLASS STRENGTH IN GRAND TRAVERSE BAY, LAKE MICHIGAN

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The objectives of this lake whitefish (*Coregonus clupeaformis*) early life history research were to: 1) Determine, in the laboratory, the effect of food ration on larval lake whitefish growth and survival; 2) Measure the magnitude of annual fluctuations in egg and larval survival in Grand Traverse Bay, Lake Michigan; 3) Delineate the factors responsible for these fluctuations and 4) Use this information to estimate relative recruitment strengths of whitefish year classes.

In the laboratory, statistically significant differences were found between larval growth and survival at seven feeding levels. In the field, overwintering egg survival equalled 1.7% through the winter of 1982/1983 when ice did not cover whitefish spawning grounds. Percent survival increased to 5.6% through the colder winter of 1983/84 when ice covered the spawning grounds soon after egg deposition.

Following the warm winter of 1982/83, density of larval whitefish declined slowly through the spring as the number of zooplankton available to each whitefish larvae (z/f) fluctuated little. In1984 densities declined catastrophically when z/f ratios fell to a two year low in week five. Using final larval densities, the 1984 cohort was estimated to be 2.1 times larger than the 1983 cohort, approximating that determined from trawls for juvenile whitefish. Estimates of relative year-class strength of lake whitefish derived from a mathematical model using these early life history data compare favorably (1984 cohort 2.4 times larger than 1983) with predictions made using the aforementioned techniques.

These results indicate that the dynamics of early life history stages of lake whitefish influence whitefish year-class strength. Application of this information to predictive models of Lake Michigan whitefish recruitment should increase the reliability of whitefish yield estimates.

For You, Dad

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name them all, three deserve special mention: Dave Dowling, Martin Smale and Andy Loftus. Thanks, guys.

It is hard to describe what the remaining people mean to the achievement of the goal embodied in this manuscript. I was blessed with a Mother and a Father who understood my goals and contributed in every manner and with every opportunity they could to help me attain them. These words of gratitude are feeble attempts to express to them what their lives have meant to mine.

Can you adequately thank those people who influence your life and your direction through it? Valerie, thank you for listening, for yourself. Con, thank-you for letting me dream and for the thoughts that served as the foundation for many of those dreams. Thank you for your laughter and your smiles; thank you for being there when no one else was and for understanding when no one else could.

My deepest gratitude is extended towards Jesus Christ, His sacrifice for me, the abilities He granted me and the opportunities He provided to me to help me fulfill them. Thank you, Lord.

> "What lies behind us and what lies
> before us are tiny matters compared to
> what lies within us."
>
> Emerson

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INTRODUCTION

Yield prediction in fisheries is an ever changing and ever developing science. Advancement of this science has, however, been slow since the inception of stock-recruitment models in the 1950's (Ricker 1954, 1958; Beverton and Holt 1956, 1957). Although these models have provided limited improvements in the description of fish population dynamics, fisheries scientists have much to learn about the relationship between system functioning and fishery yield. Problems associated with the variability and unreliability of existing yield models will persist until mechanistic solutions to these questions are forthcoming.

Many of the yield models now in use have arisen from mathematical correlations between measurable characteristics of a system (Pella and Tomlinson 1969; Deriso 1980). These characteristics may offer little explanation of the mechanisms responsible for observed conditions. Historically, analytical models have almost exclusively used characteristics of the adult stock (ie. stock size, spawning biomass) to predict year-class strength (Ricker 1958; Beverton and Holt 1957). This practice has produced stock-recruitment relationships with sufficient variability to raise questions as to their usefulness to fisheries management. Inaccurate and unreliable estimates of recruitment and yield will continue to be made until the factors responsible for variations in year-class strength are determined and incorporated into predictive models of recruitment and yield. Admittedly, delineating the mechanisms responsible for fish yield is a much more difficult task than continuing current trends of correlation and curve-fitting. It is, however, a necessary task if advances are to be made in our understanding of the fisheries resource.

These advances would be very applicable to the lake whitefish (Coregonus clupeaformis) fishery in the Great Lakes. In these lakes, the whitefish is the basis of one of the largest commercial fisheries on the North American continent (Baldwin, et. al. 1979). However, due to dramatic variations in whitefish year-class strength and subsequent fluctuations in numbers recruited to the fishable stock, management of this fishery is difficult (Jacobson 1983). These difficulties are accentuated in regions of the lake where an intensive commercial fishery is dependent solely upon the abundance of a single cohort of whitefish (Scheerer 1983). Thus, delineating the factors responsible for year-class size and numbers of recruits would be useful in the management and beneficial to the economic success of the whitefish fishery.

The question as to what factors underlie and are responsible for oscillations in lake whitefish population size has not been answered (Bajkov 1930; Christie 1963; Patriarche 1977). Recent attention, however, to the inherent dynamics of the early life history stages of the lake whitefish (Hoagman 1973, 1974; Frederick 1982) is a step towards an improved understanding of these population fluctuations. The first months of life have proven to be critical to fish survival and future recruitment to several other fisheries (Gulland 1965; Chenoweth 1970). During these stages of development, total mortalities can reach as high as 99.9% (Gulland 1965). As mortality experienced during these stages is severe, strong year to year variations in the future abundance of recruited fish may arise from relatively small fluctuations in the mortality rates. These rates are in turn established via weekly and daily changes in growth or mortality as influenced by interactions with biotic and abiotic mechanisms.

Although previous studies of lake whitefish early life history have provided much needed information regarding the biology of the egg and larval periods, they have failed to describe the interaction between these biotic and abiotic variables and early life history characteristics (Hart 1930; Faber 1970; Reckahn 1970; Hoagman 1973). The importance of factors such as winter severity, prey density, prey size selection and critical periods in larval development largely has been ignored. Furthermore, the influence that these components have on larval growth and survival rates and year-class size has not been considered.

Survival of larval fish is often a function of the amount of food available to these developing individuals (Einsele 1963; O'Connell and Raymond 1970). Significant mortality occurs during a critical period when larval fish move from dependence upon endogenous to exogenous sources of energy (Kurata 1959; Blaxter 1965, 1971). Low densities of crustaceans (Lasker et.al. 1970; Beers and Stewart 1971) or a preponderance of zooplankton sizes or species types unusable by larval fish (Fluchter 1980; Teska and Behmer 1981) may increase mortality. Combined with poor search, capture and feeding abilities of many larvae (Braum 1964), these factors have the potential to substantially reduce larval numbers during the first weeks of exogenous feeding.

In addition to larval mortality, the number of fish in a year-class can be affected by losses during the egg stage of development. If mortality attributed to the egg and larval stages is severe, survival is bottlenecked during the egg and larval periods of development and few fish pass through to later stages. Year-class size is subsequently reduced. If, however, these pressures are moderate, egg or larval survival is increased and the resultant year-class of fish is more abundant. Determining the extent and variation of these pressures is a prerequisite to more accurate estimates of year-class strength and yield.

It is with these thoughts regarding the perceived importance of early life history dynamics to whitefish population characteristics that the question of year-class variability in the Great Lakes lake whitefish is approached. In an effort to understand the source of this variability, an extensive research program investigating the early life history dynamics of lake whitefish in the east arm of Grand Traverse Bay, Lake Michigan (East Traverse) was initiated. This thesis serves as a synthesis of the field research and additional work conducted in the laboratory regarding the same question. In it I evaluate aspects of the species biotic and abiotic environment, including such variables as winter severity, overwintering egg mortality and zooplankton/larval fish interactions. The specific objectives of the research were to:

1. Determine, under laboratory conditions, the influence of zooplankton abundance and availability on larval lake whitefish growth and mortality.
2. Document winter severity and corresponding lake whitefish overwintering egg mortality on the spawning grounds.
3. Describe spring larval lake whitefish dynamics in Grand Traverse Bay, Lake Michigan.
4. Describe spring zooplankton dynamics in Grand Traverse Bay, Lake Michigan.
5. Integrate the information gathered in objectives one, three and four and arrive at conclusions regarding the importance of zooplankton to larval lake whitefish population characteristics.

6. Integrate these findings with data from studies of overwintering egg mortality and model the relationship between lake whitefish early life history characteristics and year-class strength.

The absence of this integrative approach in previous studies of lake whitefish may be responsible for the failure of these studies to successfully explain the population oscillations typifying the whitefish fishery. For decades fisheries research has paid little attention to the importance of fish early life history in observed population dynamics. Nor has it given much attention to the ecosystem or community approach to fisheries problems. As trophic level interactions during early life history development are investigated, the research embodied in this manuscript is a more holistic approach to the analysis of whitefish populations. Data analyzed in regard to each of the above objectives will be considered separately as well as integrated with that obtained from other objectives to shed light on the contention that these factors are responsible for much of the year-class dynamics of whitefish populations in the Great Lakes.

STUDY AREA

Grand Traverse Bay, an inland extension of northern Lake Michigan, consists of a large outer bay and two smaller arms oriented in a general north-south direction. Studies of overwintering egg survival were located on lake whitefish spawning grounds in the east arm (East Traverse)(Figure 1). Particular emphasis was placed on a region at 44°53'7" N, 85°25'5" W identified through historical fishery data and communication with Fisheries Division, Michigan Department of Natural Resources (MDNR) officials as a site where high numbers of spawning whitefish had been recorded.

These spawning grounds cover an area of 69.7 hectares. Water depths average 4.5 m and currents, although variable, move in a general south to north direction over the grounds. Clay overlain by sand, gravel, rock or cobble covers much of the region. Larger particles prevail in the shallower regions ($\leq$ 6 m) while sand and clay are predominantly found in depths of water greater than 6 m.

Spring zoo- and ichthyoplankton sampling were conducted in shallow water regions ($\leq$ 6 m) in East Traverse (Figure 1). For sampling purposes, the eastern shore of East Traverse was divided into twelve, 1000 m wide grids. An additional 1000 m separated each grid. Grids were further subdivided into three subgrids with each subgrid extending from the shoreline to a depth of 10 m. All grid and subgrid boundaries were identified using Loran

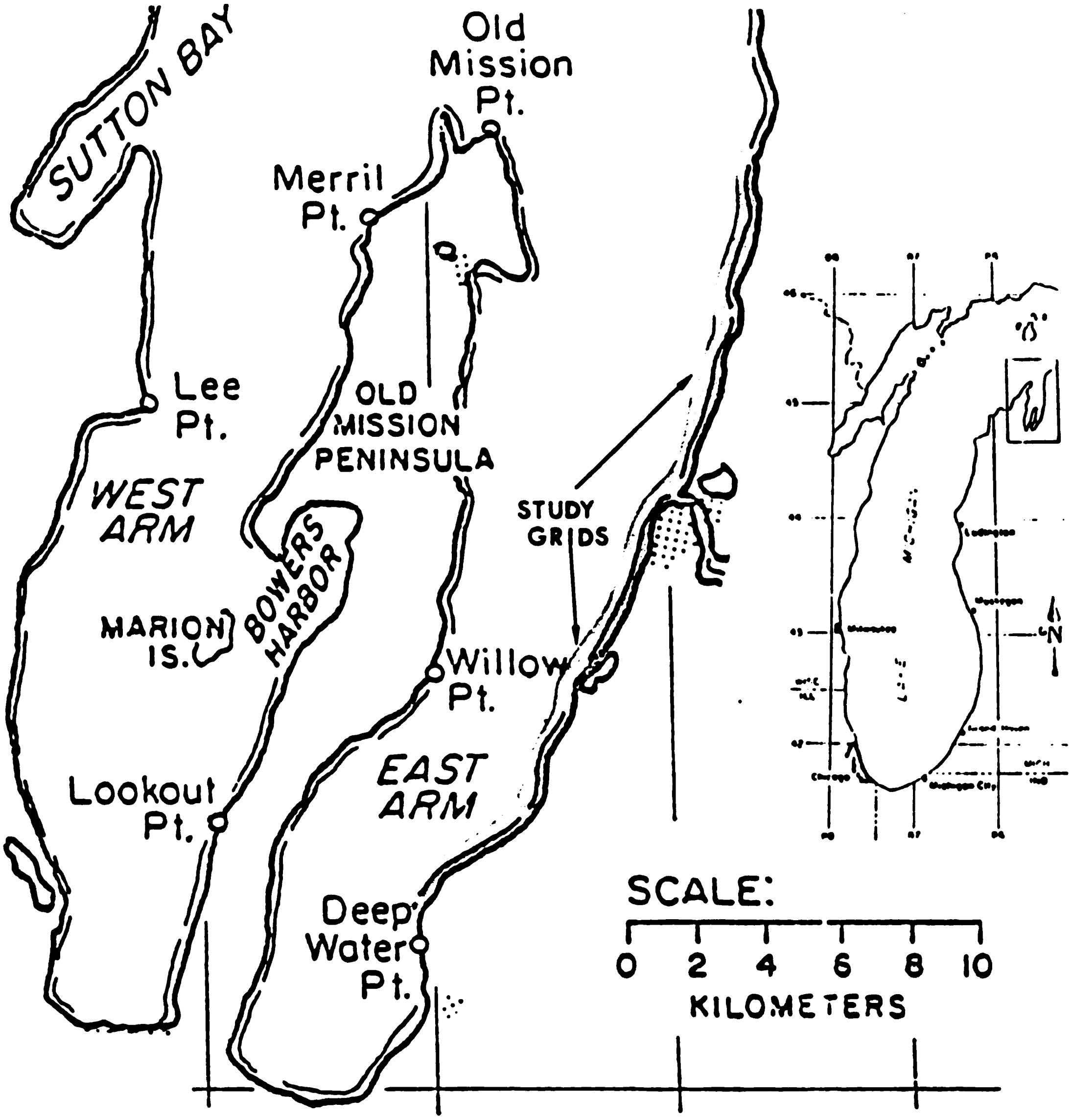

Figure 1. Location map of Grand Traverse Bay, Lake Michigan and lake whitefish early life history study grids in East Traverse.

C latitude/longitude coordinates.

Substrate type characterizing these shallow water areas also consists of clay overlain by sand, gravel, rock or cobble. The lake bottom slopes gradually to depths of roughly 10 m before depths increase sharply to 40 to 60 m and more. Rooted aquatic vegetation is lacking except for small patches of *Chara spp*.

METHODS

Laboratory Feeding Study

Lake whitefish eggs from Lake Simcoe, Ontario that were in late stages of development were obtained from the Ontario Ministry of Natural Resources. These eggs were further incubated and hatched at Michigan State University aquaculture labs from 8 to 15 April, 1983. Immediately prior to egg hatching, eggs in groups of 100 were counted and placed in a series of 20 l aquaria cooled to 12°C by a flow through water bath. Beginning the day after larval hatch, seven densities of 2-day old brine shrimp, *Artemia spp*. were fed twice daily to fish larvae in each of four replicates of each feed density. Any excess brine shrimp remaining from the previous feeding were removed prior to the next feeding by siphoning them off the aquarium bottom. Feeding was conducted on a zooplankton per fish larvae basis to keep the feeding level constant while larval numbers changed over the course of the experiment. Densities fed were 1.8, 3.2, 5.6, 10.0, 18.0, 32.0 and 110 zooplankters/whitefish larvae/12 hour period. The first six densities were chosen for statistical reasons, being equally spaced on the $\log_{10}$ scale, while the latter provided an excess number of zooplankton to each larvae. To prevent or reduce potential mineral buildup or toxicity problems, 1 liter of water was removed, and clean water added, twice weekly in each aquaria. An analysis of conductivity at the close of the experiment showed this practice to be effective in keeping mineral levels low.

Subsamples of five randomly selected larvae were taken twice weekly from all tanks except where larvae were receiving excess food (110 z/f). Lengths (mm) of these larvae were determined by measuring their magnified image (25x) on a microfiche reader. The presence or absence of a yolk sac was determined microscopically. These procedures were repeated on subsamples of three larvae per day taken from the tank where larvae were fed to excess. Dead larvae were removed daily and measured for length and weight.

--Data Analysis--

Since feeding regimes were equally spaced on the $\log_{10}$ scale, statistically significant differences among treatment means could be tested using orthogonal contrasts (Steel and Torrie 1980). Specific growth rate was determined using the equation:

$$u/\text{day} = (\ln L_a - \ln L_b)/T$$

where u/day = specific or instantaneous growth rate per day (mm/day)

L = larval length (mm)

a = length at end of experiment

b = length at beginning of experiment

T = time interval

Overwintering Egg Survival Research

Sampling for lake whitefish eggs began during and continued past the completion of spawning activity in December of 1982 and 1983. A 39 kg iron sled (Stauffer 1981) attached to a diaphragm pump at the surface via a flexible hose 5 cm in diameter was used for egg collections. The egg sled was towed for 5 minutes and moved at an average speed of 0.5 m/s. The sled was towed at depths of 1.5, 3.0, 4.5 and 6.0 m. Replicate trawls were conducted at each depth except at the 3.0 m contour on 9 April, 1984 when wind and wave conditions prohibited further sampling at this depth. The total number of trawls run on each day of sampling varied from 12 to 20 in accordance with weather conditions. All transect locations were identified using Loran C latitude/longitude coordinates.

After passing through the sled, hose and pump, eggs were deposited on a fine mesh screen at the surface. Live eggs were separated from dead eggs and detritus and preserved in 10% formalin for later identification and enumeration in the laboratory. Eggs that appeared damaged or having an opaque shell were classified as dead. The finding of few dead or damaged eggs indicates, in the very least, that our methods were not destroying the eggs as they passed through the apparatus.

Spring egg sampling commenced during March of both years before the lake whitefish eggs began to hatch. Two methods were used to detect hatching. If empty egg cases or motile larvae were collected by the egg sled, sampling was terminated and the preceding set of egg density data were used to estimate overwintering mortality. Hatching also could be detected by trawls for larval lake whitefish conducted before and after each day of egg collection. Using these procedures, hatching time could be reliably determined.

Temperature data were obtained from the National Weather Service in Traverse City, Michigan. Mean monthly temperatures were determined from average daily temperatures in Traverse City and compared to the 25-year mean for that month in that region. Degrees of departure (°C) from the long term mean were determined for each month from December through March. These values were averaged over these months to arrive at the index of winter severity.

--Data Analysis--

Between year differences in the number of eggs deposited on the grounds in the fall and the number remaining on these grounds in the spring were tested for statistical significance using the Mann-Whitney U nonparametric procedure (Siegel 1956). The mean number of eggs at each depth and date and the standard error of the mean also were calculated.

Spring Zooplankton Research

--Field Procedures--

Zooplankton sampling in Grand Traverse Bay began during March of 1983 and 1984 and continued twice monthly through May of each year. One subgrid on each of three grids was selected at random on each sampling day. Using a 63 u mesh Wisconsin net, three replicate samples were taken at 1, 3 and 5 m (filtering approximately 10.1, 30.3 and 50.5 l, respectively) on each subgrid. Sampling was conducted between 1000 and 1600 hours. To reduce ballooning of crustacean carapaces, all samples were preserved in Koeche's solution (2.3 kg sugar dissolved in 2 l of formaldehyde and 8 l of water) for laboratory analysis.

--Laboratory Procedures--

Plankton in subsamples of two ml were counted and measured using a Sedgewick-Rafter counting cell in conjunction with a calibrated Whipple grid. A minimum of two subsamples were analyzed from each sample. Measurements of total length and maximum width were recorded for all organisms counted in 1983. Total length was measured to the distal end of the caudal rami in all copepods. To improve the reliability of size comparisons between copepods available in the field and those found in larval lake whitefish stomachs, these measurements were augmented by measurements of metasomal length and maximum width observed from dorsal and lateral views in 1984. Sex and number of eggs also were recorded when possible.

During all counts, adult and copepodite copepods were classified to suborder. Nauplii and cladocerans were not subdivided further. In order to obtain some knowledge of the types of zooplankton being analyzed, individuals from March and early April samples were keyed to species. In addition, cladocerans and other organisms which differed noticeably from zooplankton already classified were identified as they became apparent in samples taken later in the spring. Zooplankton were identified using Ward and Whipple (1959) and Pennak (1978).

--Data Analysis--

In addition to within year comparisons, zooplankton densities and relative size distributions on each sampling date were compared between years on the basis of length of time before (Week -1), during (Week 1 and 2) and after (Week 3 to 7) the hatching of larval lake whitefish. Because more than 86% of the total number of larvae captured during the two springs were located in one meter of water, analyses of plankton densities and size distributions were focused on this depth. All statistical tests were made using nonparametric methods. Mean density of zooplankton and standard error of the mean density are presented.

Spring Larval Whitefish Research

--Field Procedures--

Ichthyoplankton trawls began during the third week of March in 1983 and during the first week of April in 1984. Trawls continued through May 21 and May 30 of each respective year. Using the network of grids described earlier, surface trawls lasting five minutes were conducted daily when wind and wave conditions permitted. Special attention was directed towards Grid 5 where high numbers of spawned lake whitefish eggs had been found. Sampling on Grid 5 consisted of three surface trawls at 1 m and two surface trawls at three and five meters. One, ten minute bottom trawl also was conducted at three and five meters. To examine larval dispersal, surface transects at 1 m were made onsuccessive grids to the north and south of Grid 5 after sampling there had been completed. Trawls were conducted between 0600 and 1400 in 1983 but, because the ability of larval fish to escape capture declines at night (Lenarz 1981), were run between 1800 and 0900 in 1984. Night to day capture ratios were determined via catch records from twenty-four hour sampling periods and were used to adjust night to day caught larval fish densities.

A 363 u mesh net with a mouth diameter of one-half meter was used in all trawls in 1983, while one-half meter, 363 and 560 u mesh nets were used in 1984. Nets were three meters in length, cone-shaped and towed at speeds of 0.7 to 1.1 m/s. Larval whitefish remain susceptible to such gear until they attain lengths of 33 mm. Capture efficiency does decline after larvae reach lengths greater than 20 mm (Hoagman 1974). Towing speed, distance travelled and volume of water filtered were calculated from equations incorporating flowmeter readings taken with a General Oceanics flowmeter mounted in the mouth of each net.

Before each trawl, time of day, depth, grid number and Loran C latitude/longitude coordinates were recorded and correlated to trawl number. After each trawl, captured larval fish were removed from the net and placed into chilled 90% alcohol to prevent stomach content egestion. Larvae were separated from algae and detrital matter and transferred to Koeche's solution within 24-48 hours of capture.

The reliability of estimates of relative year-class strength based on the final larval density in 1983 and 1984 was investigated by comparing relative densities of 1 to 3 year-old whitefish sampled in East Traverse. Through cooperation with the Fisheries Division, MDNR, 10 minute transects using a 12.2 m x 2.4 m otter trawl with 1.9 cm cod end mesh were made at depths ranging from 6 to 122 meters. Captured lake whitefish were measured for length and weight and aged using scale analysis. The catch per effort statistic for each age group was determined in order to compare the relative strengths of these classes to the predictions based on the early life history dynamics of this species.

--Laboratory Procedures--

All preserved larval whitefish were measured for length and weight. Weights were recorded to 0.0001 g while lengths (mm) were taken by measuring their magnified image (25x) on a microfiche screen.

Morphological measurements of mouth size (maximum width) and yolk sac volume (length x width x height) were made on all larvae captured in 1983. Owing to the larger sample size in 1984, larvae were pooled by week of capture and these measurements taken on a random subsample of larvae representing 50% of the total number of individuals in each pool.

Stomach content analyses were conducted on those larvae for which morphological measurements were made. Stomach contents were removed via dissection and number and size of all individuals recorded using a compound microscope (10x) in conjunction with a calibrated Whipple grid. Total lengths, as well as metasomal lengths for copepods, were recorded and width measured from both the dorsal and lateral aspects. Linear regression equations of total length on metasomal length and dorsal and lateral widths were constructed. Life stage, number of eggs carried and sex of each individual were determined when possible.

--Data Analysis--

Total numbers of larvae and volume of water sampled were used to estimate larval densities during each spring. Although circumstances prevented sampling during weeks two and three of 1983, densities during these periods were estimated using regression analysis. Mean densities and the standard error of the mean density are presented.

Mean lengths were also determined for larval lake whitefish pooled by week. Larval instantaneous growth rates were determined using the equation:

$$u/\mathrm{day} = (\ln L_a - \ln L_b)/T$$

where u = specific or instantaneous growth rate (mm/day)
L = larval length (mm)
a = mean length in week t
b = mean length in week $t-1$
T = time interval.

Growth rate also was plotted as a function of the number of zooplankton per fish larvae (z/f) using a threshold corrected hyperbolic equation for substrate limited growth:

$$\begin{aligned} u/\mathrm{day} = [u_{max}((z/f)-(z/f)_q)]/[(K_s-(z/f)_q) \\ + ((z/f)-(z/f)_q)] \end{aligned}$$

where u = specific or instantaneous growth rate (mm/day)
u_{max} = maximum growth rate
K_s = one-half saturation value
z/f = substrate level
z/f_q = maintanenence substrate level.

Constants of u_{max} and K_s were calculated using the regression equation:

$$((z/f)-(z/f)_q)/u= K_s/u_{max} + (1/u_{max})((z/f)-(z/f)_q).$$

Instantaneous weekly survival (s) rates were calculated with the equation:

$$s/week = N_t/N_{t-1}$$

where N_i = larval abundance ($\#/m^3$).

Survival and growth rates were plotted in conjunction with zooplankton/fish ratios at 1 m.

Mean yolk volume, gut width and number of eggs and number of prey ingested were determined for larvae pooled by week. The identity (Ward and Whipple 1959; Pennak 1978), life stage and sex of captured prey and the percentage of larval stomachs empty during each week were also recorded. Frequency distributions of total lengths of organisms ingested were compared between weeks. The linear index of prey selection proposed by Strauss (1979) was used to characterize the electivity of prey organisms by larval whitefish. The index:

$$L = r_i - p_i$$

is the difference between the relative abundance of a prey item in a fish gut (r_i) and the relative abundance of that prey item in the field (p_i). Values of the index range from +1 to -1 with positive values indicating selection for a size, 0 no selection and negative values selection against a size class.

RESULTS

Laboratory Feeding Research

Significant differences (Orthogonal contrasts; $p < 0.05$) in length gain (Figure 2; Table 1) were observed among feeding regimes with greater food rations producing greater fish growth. After 21 days, larvae receiving 110 z/f (the number of zooplankton/fish larvae) were 1.37 times as long as those fed 1.8 z/f. For the sake of clarity, only four of the seven feeding levels are depicted in Figure 2 as length gains for feeding levels of 3.2, 5.6 and 10 z/f were intermediate to feeding levels of 1.8 and 18 z/f. No statistically significant length differences were found between tanks within a feeding regime (Orthogonal contrasts; $p > 0.05$).

Instantaneous daily growth rates, as reflected in length gain through the course of the experiment, differed among feeding levels (Friedman two-way analysis of variance; $x^2 = 54.6$; $p < 0.001$) and again were positively correlated to food ration (Figure 3; Table 1). Larvae fed 1.8 z/f grew at a rate 50% of those receiving excess (110 z/f) rations.

The survival of larval lake whitefish depended on the amount of food provided to each fish (Figure 4; Table 1) and was linearly related to growth rate by the equation:

$$\% \text{ Survival} = -108.2 + 8275(\text{Daily Growth Rate}) \quad (r^2 = 0.97)$$

There was no difference in survival between feeding regimes until day 15, when yolk sac resorption was complete and the

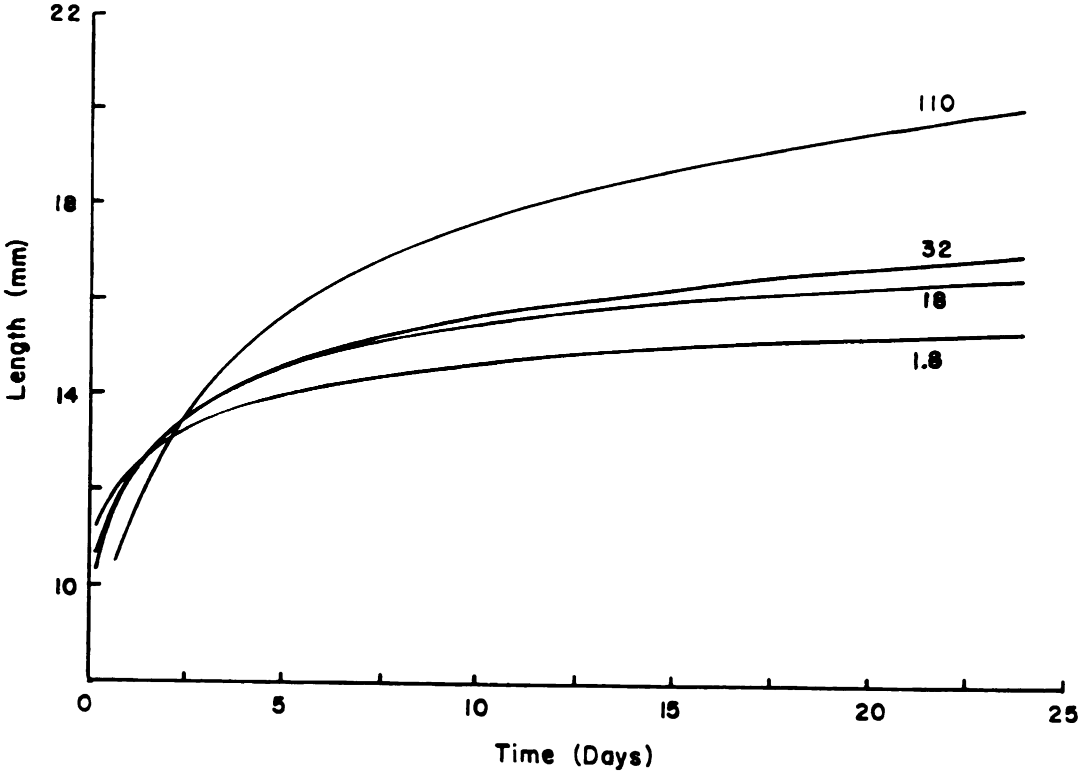

Figure 2. Length of laboratory reared larval lake whitefish fed differing densities of live plankton over a 25 day period. Densities fed were 1.8, 18, 32 and 110 zooplankton per fish per 12 hours.

Table 1: Mean and standard error (+) of the mean length, daily growth rate and cumulative survival of laboratory reared larval lake whitefish fed differing densities of live plankton over a 25 day period. Densities fed were 1.8, 3.2, 5.6, 10, 18, 32 and 110 zooplankton/fish/12 hour period. Lengths are those measured on day 21 of the experiment when all feeding levels were represented.

Feeding Level	Final Length	Standard Error	Growth Rate	Standard Error	Survival Percent	Standard Error
1.8	14.56	0.26	0.0128	0.0112	4.6	1.5
3.2	14.69	0.08	0.0143	0.0125	6.9	2.1
5.6	14.90	0.28	0.0140	0.0096	8.8	1.8
10.0	15.07	0.17	0.0150	0.0107	10.4	2.5
18.0	15.24	0.24	0.0170	0.0099	26.2	4.5
32.0	16.52	0.35	0.0216	0.0096	81.7	4.9
110.0	19.90	0.34	0.0257	0.0100	100.0	-

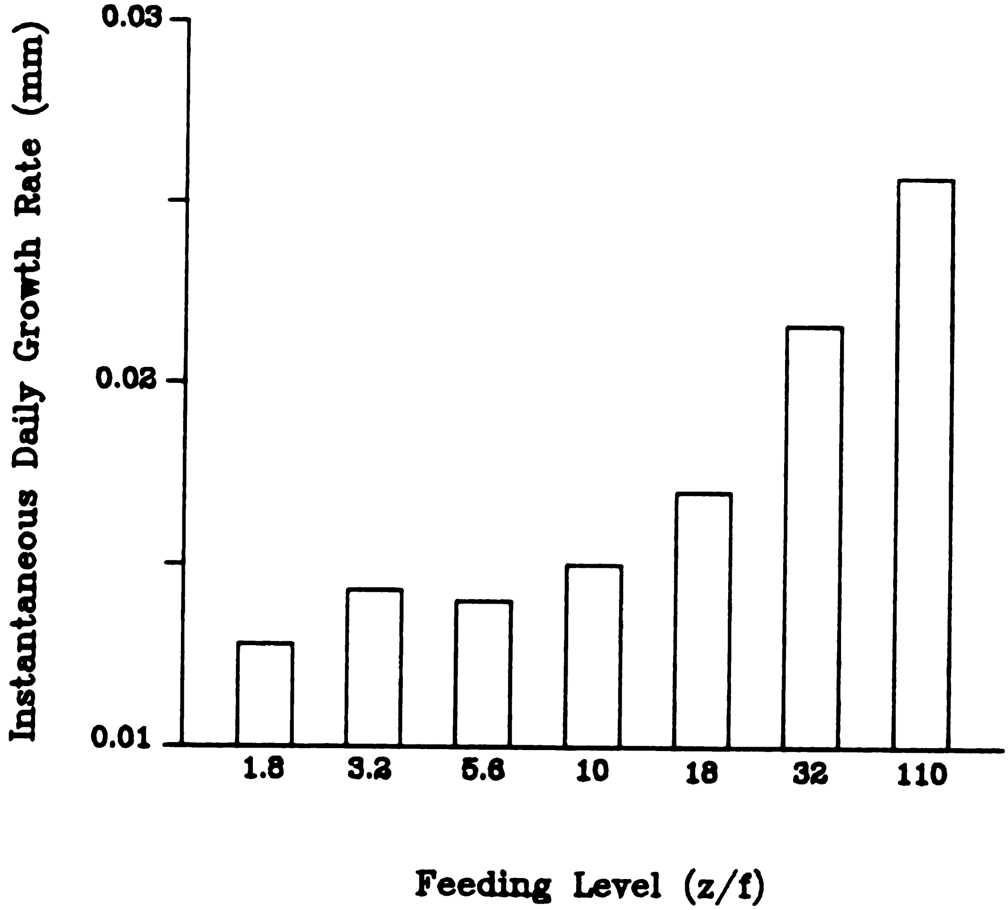

Figure 3. Instantaneous daily growth in length of laboratory reared larval lake whitefish fed differing densities of live plankton over a 25 day period. Densities fed were 1.8, 3.2, 5.6, 10, 18, 32 and 110 zooplankton per fish per 12 hours.

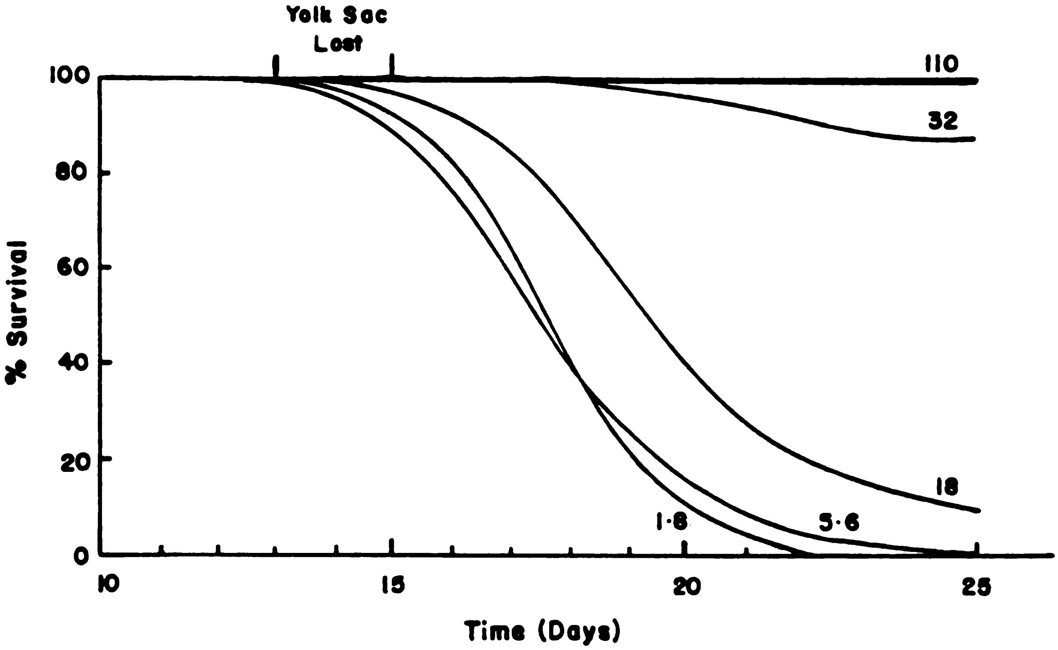

Figure 4. Survival of laboratory reared larval lake whitefish fed differing densities of live plankton over a 25 day period. Densities fed were 1.8, 3.2, 5.6, 10, 18, 32 and 110 zooplankton per fish per 12 hours.

larvae became dependent upon exogenous energy resources. Survival of larvae receiving low rations decreased dramatically after this date. Larvae fed low rations ($\leq$ 10 z/f) exhibited 100% mortality within 7-10 days while those fed excess rations (110 z/f) experienced no mortality. Fish fed medium rations of 18 and 32 z/f exhibited significantly different mortality rates of 90 and 10%, respectively (Kruskal-Wallis one-way analysis of variance; $H = 16.9$; $p < 0.01$). Additionally, time to 50% survival increased with increasing ration.

Overwintering Egg Survival Research

--1982/1983--

In 1982, densities of spawned lake whitefish eggs peaked on 4 December. Although eggs were found to a depth of 6 m, most were at depths of 4.5 m and shallower where large (> 2.5 cm diameter) spawning substrates were most predominant (Figure 5; Table 2).

Unseasonably warm weather during the winter of 1982/1983 prevented ice formation on East Traverse (Figure 6). Consequently, whitefish spawning grounds were exposed to wind and wave action throughout the winter.

Estimates of overwintering egg survival during 1982/83 were calculated from egg densities sampled on 12 March, 1983. Although a total of 15 trawls were conducted from depths of 1.5 to 6.0 m, eggs were found only at the 1.5 m contour in the spring of 1983 (Figure 7; Table 2). Percent survival at this depth equalled 2.4% while egg

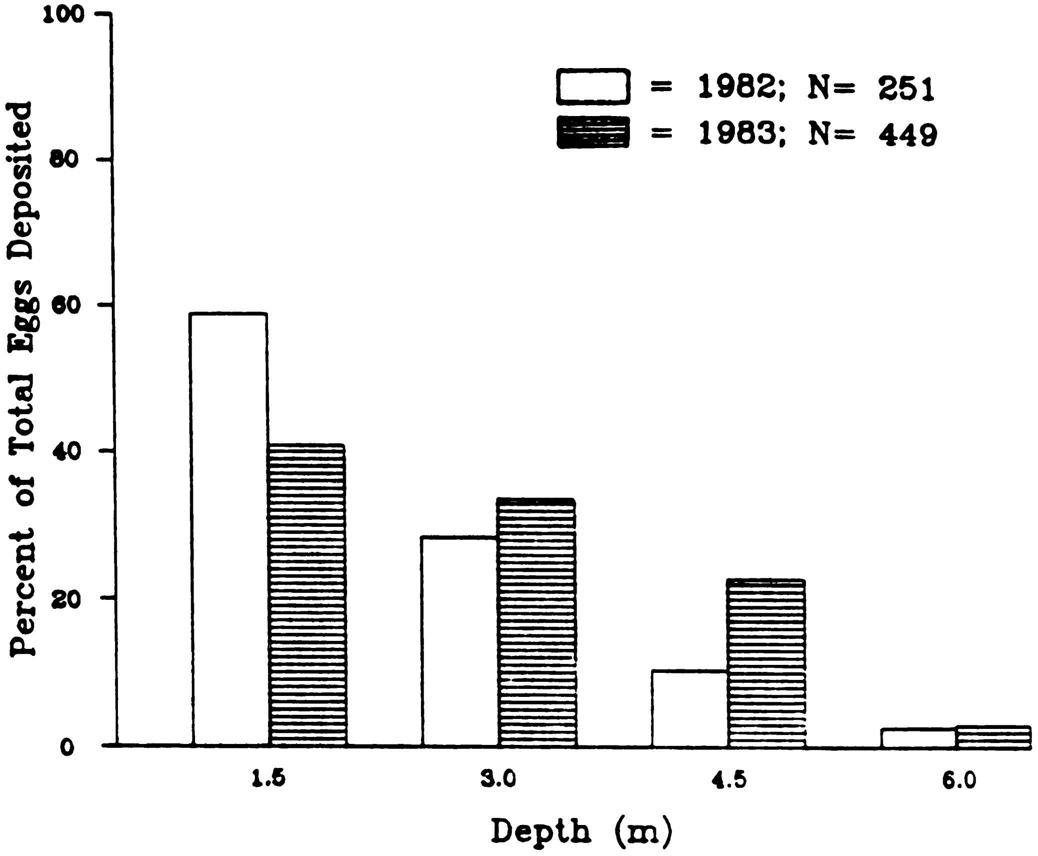

Figure 5. Depth distribution of lake whitefish eggs spawned in Grand Traverse Bay, Lake Michigan in December of 1982 and 1983.

Table 2: Mean and standard error ($\pm$) of the mean number of lake whitefish eggs sampled from 1982 to 1984 in Grand Traverse Bay, Lake Michigan.

DATE	DEPTH	NUMBER OF TRANSECTS	NUMBER OF EGGS	MEAN NUMBER OF EGGS	STANDARD ERROR
12/4/82	1.5	3	171	57.0	13.2
	3.0	2	55	27.5	1.5
	4.5	2	20	10.0	1.0
	6.0	2	5	2.5	2.5
3/12/83	1.5	5	7	1.4	0.2
	3.0	4	0	-	-
	4.5	3	0	-	-
	6.0	3	0	-	-
12/11/83	1.5	3	183	61.0	18.5
	3.0	3	151	50.3	32.7
	4.5	3	102	34.0	19.0
	6.0	3	13	4.3	2.4
4/9/84	1.5	4	15	3.8	0.6
	3.0	1	1	1.0	-
	4.5	4	8	2.0	1.1
	6.0	3	1	0.3	0.3

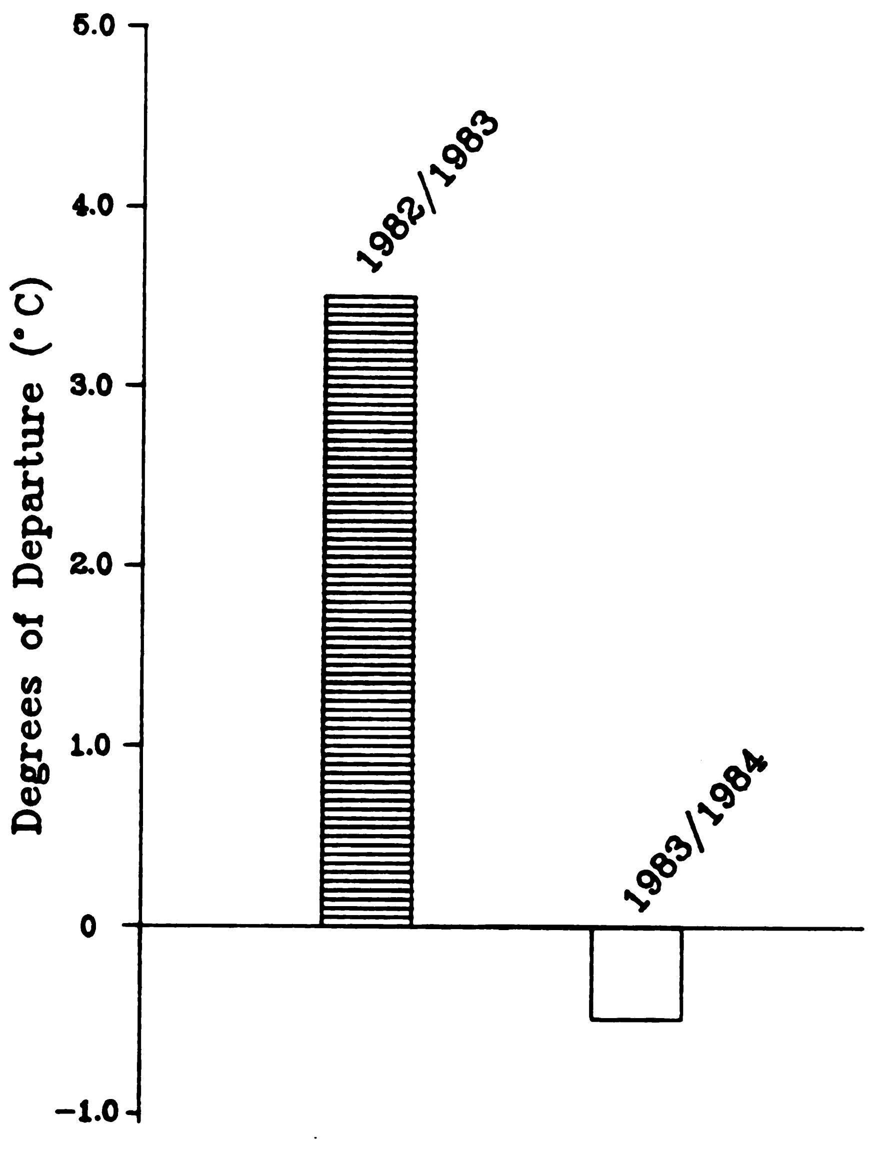

Figure 6. Departure (°C) from the mean winter air temperature during the winter of 1982 and 1983 at Grand Traverse Bay, Lake Michigan.

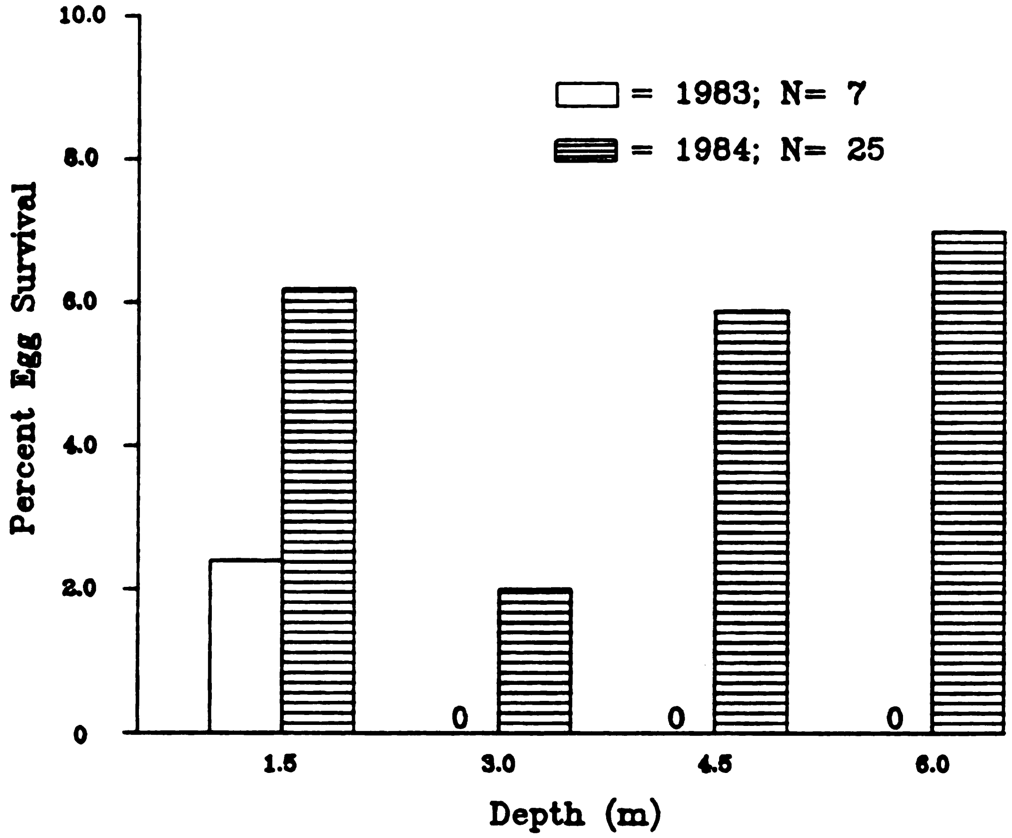

Figure 7. Percent survival of lake whitefish eggs overwintering in Grand Traverse Bay, Lake Michigan in 1983 and 1984.

survival in the entire shallow water region of the spawning grounds ($\leq$ 6.0 m) equalled 1.7% (Figure 7).

--1983/1984--

Densities of spawned lake whitefish eggs were highest on 11 December, 1983. The depth distribution of spawned eggs followed the same pattern as in 1982 with much higher densities occurring in shallower water (Figure 5; Table 2). No significant difference was observed between the two years in terms of the number of whitefish eggs deposited at depths $\leq$ 6.0 m ($U = 47.5$; $p > 0.05$) or at the 1.5 m contour only ($U = 4$; $p > 0.05$).

During the colder winter of 1983/84 (Figure 6), ice covered the spawning grounds soon after egg deposition and persisted until 4 April. The number of live eggs remaining on the spawning ground in 1984 was significantly higher than the number recorded in 1983 (Mann-Whitney U; $U = 36$; $p < 0.01$). Unlike 1983, live eggs were found in depths of water through 6.0 m (Figure 7; Table 2). Percent survival of eggs at depths $\leq$ 6.0 m equalled 5.6%, 3.4 times greater than the percent surviving in 1983. Using the least variable estimates (1.5 m), percent survival equalled 6.2, 2.6 times greater than the value recorded at 1.5 m in 1983.

Spring Zooplankton Research

Calanoid and cyclopoid copepods dominate the spring zooplankton assemblage in Grand Traverse Bay. Of the species present in the bay, *Diaptomus sicilis* and *Cyclops bicuspidatus thomasi* were most frequently observed. *Limnocalanus macrurus* was noted only occasionally. Cladocerans, predominately *Daphnia spp*. and *Bosmina longirostris*, were scarce until the final week of May.

--Densities--

With the exception of densities recorded five weeks after larval lake whitefish had hatched (Week 5), 1984 post-larval hatch zooplankton densities (± SE) at a depth of 1 m exceeded those present in East Traverse in 1983 (Figure 8; Table 3). In 1983, total densities of zooplankton (all species and life stages) increased from 5.1 (± 2.1) individuals/liter (ind/l) in Week -1 to 10.2 (± 2.8) ind/l in Week 1. Densities dropped slightly to 9.8 (± 2.5) ind/l in Week 5 and then increased sharply to 26.5 (± 4.4) ind/l in Week 7. Naupliar densities followed a similar pattern. Adult/copepodite densities exhibited the largest fluctuations. Densities changed little from Week -1 to Week 1. Abundance of these individuals declined from 3.2 (± 1.6) ind/l in Week 1 to 1.3 (± 1.1) ind/l in Week 3. The rate of change in density slowed between Week 3 and Week 5, with Week 5 densities equalling 1.2 (± 0.5) ind/l.

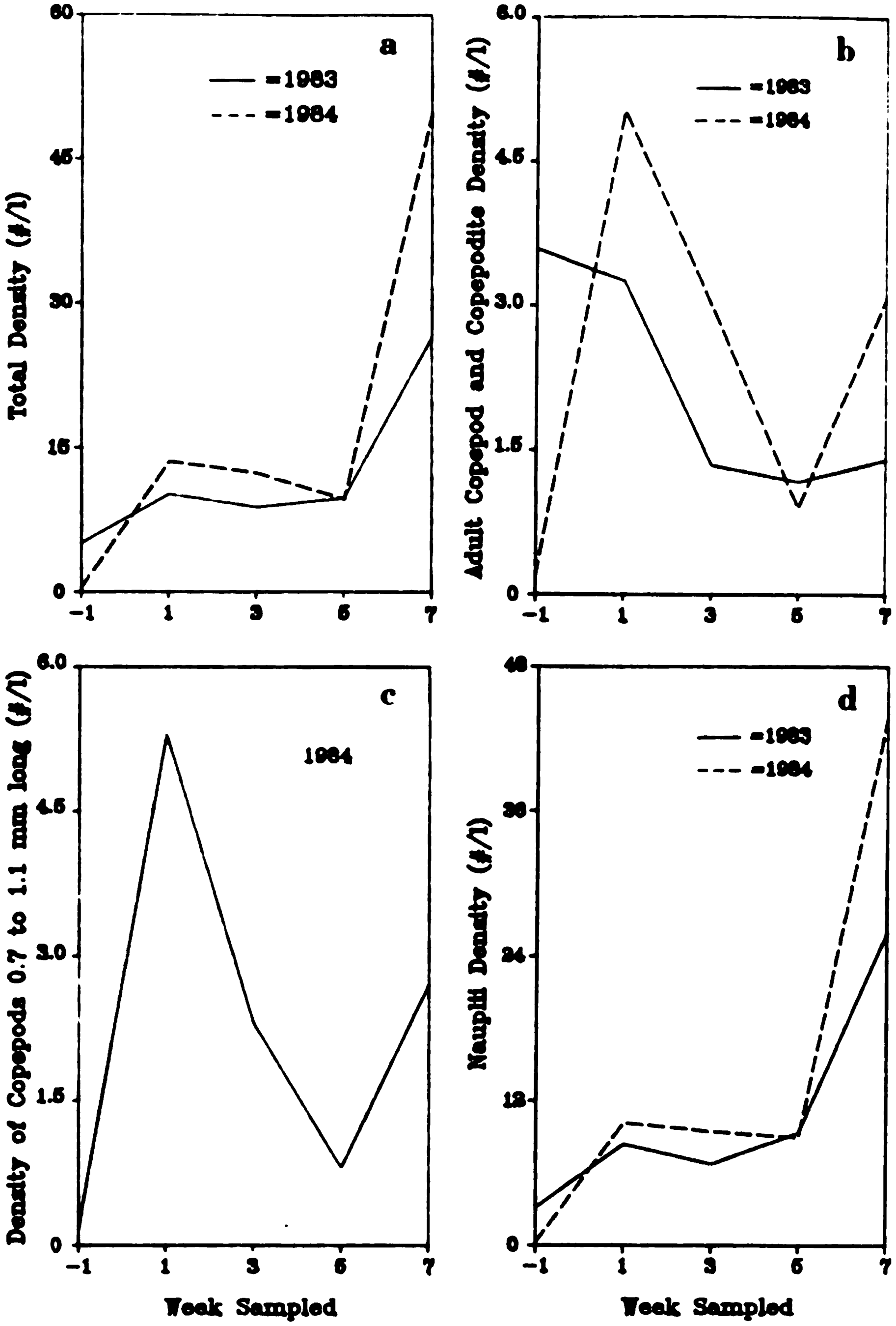

Figure 8. Total zooplankton density (a), combined densities of adults and copepodites (b), densities of copepods 0.70 to 1.10 mm long (c) and nauplii densities (d) in Grand Traverse Bay, Lake Michigan during the spring of 1983 and 1984.

Table 3: Mean and standard error (+) of the mean total zooplankton density, combined density of adults and copepudites, densities of copepods 0.7 to 1.10 mm long and nauplii densities (number/l). Data were collected in Grand Traverse Bay, Lake Michigan during the spring of 1983 and 1984 and tabulated relative to larval lake whitefish hatching and development (Week -1 to Week 7).

1983

Week	Total Density	Standard Error	Adult & Cop't Density	Standard Error	0.7 to 1.1 mm Density	Standard Error	Nauplii Density	Standard Error
-1	5.06	2.11	3.59	0.55	-	-	3.11	1.41
1	10.10	2.75	3.25	1.63	-	-	8.34	2.04
3	8.81	2.55	1.34	1.08	-	-	6.72	3.27
5	9.77	2.48	1.17	0.54	-	-	9.30	2.46
7	26.52	4.36	1.40	0.38	-	-	25.87	3.94

1984

Week	Total Density	Standard Error	Adult & Cop't Density	Standard Error	0.7 to 1.1 mm Density	Standard Error	Nauplii Density	Standard Error
-1	0.43	0.10	0.19	0.07	0.15	0.08	0.17	0.03
1	13.55	2.77	5.03	2.33	5.26	1.36	10.14	1.84
3	12.35	1.91	3.00	0.76	2.32	0.34	9.43	2.30
5	9.64	1.61	0.91	0.39	0.75	0.04	8.93	1.57
7	49.78	7.25	3.07	1.36	2.74	0.54	43.55	8.14

Densities increased to 1.4 (± 0.4) ind/l by the final week sampling in 1983 (Figure 8; Table 3).

Patterns of change in total numbers of plankton and numbers of nauplii in 1984 were similar to patterns described for 1983. Adult/copepodite density fluctuations in 1984 were, however, unlike those observed the previous year. Densities increased sharply from 0.2 (± 0.07) ind/l in Week -1 to 5.0 (± 2.3) ind/l in Week 1 before declining to 3.0 (± 0.8) ind/l by Week 3 (Figure 8; Table 3). Unlike 1983 when the rate of decline in adult/copepodite numbers slowed between Week 3 and Week 5, the high rate of decline persisted through this time span in 1984 and densities decreased to 0.9 (± 0.4) ind/l by Week 5. Adult/copepodite densities increased after Week 5, reaching a value of 3.1 (± 1.4) ind/l in Week 7 (Figure 8; Table 3).

The nonparametric randomization test was used to compare Week 1, 3 and 5 zooplankton densities between the years of 1983 and 1984. Total zooplankton densities differed significantly at a probability of 0.15. Adult densities differed at the 0.20 level of significance while naupliar densities differed significantly at the 0.10 level.

Fluctuations in the density of adult and copepodite zooplankton 0.70 to 1.10 mm long were further scrutinized in 1984. Densities, which reached a peak of 5.3 (± 1.4) ind/l during Week 1, fell to a density of 0.7 (± 0.04) ind/l by the fifth week of larval growth (Friedman two-way analysis of variance; $x^2 = 5.7$; $p < 0.10$). Abundance increased by the final week of the study, attaining a density of 2.7 (± 0.5) ind/l at this time (Figure 8; Table 3).

--Size Distribution--

The 1983 and 1984 frequency distributions of numbers of zooplankton in size categories ranging from 0.1 to 1.2 mm in total length were similar. In both years, a large peak at 0.10 mm in length and a much smaller one at 0.90 mm was apparent (Figure 9). Analyzing the 0.70 to 1.10 mm lengths in 1984 reveals significant (Friedman two-way analysis of variance; $p < 0.01$) changes in the frequency distribution of these sizes within a year (Figure 9). Except for the 0.70 mm length group, for which the abundance increased between Week 1 and 3, the relative abundance of these sizes decreased between Week 1 and 5. Between Week 3 and 5 this decline was also apparent for sizes in the 0.70 mm group. Relative abundance of all sizes increased in Week 7.

Spring Larval Whitefish Research

--Density Changes--

A total of 848 larval lake whitefish were captured during the two years of the study, 119 in 1983 when trawls were conducted during the day and 729 in 1984 when sampling occurred throughout the 24 hour period. Densities in 1984 remained significantly higher than those recorded in 1983

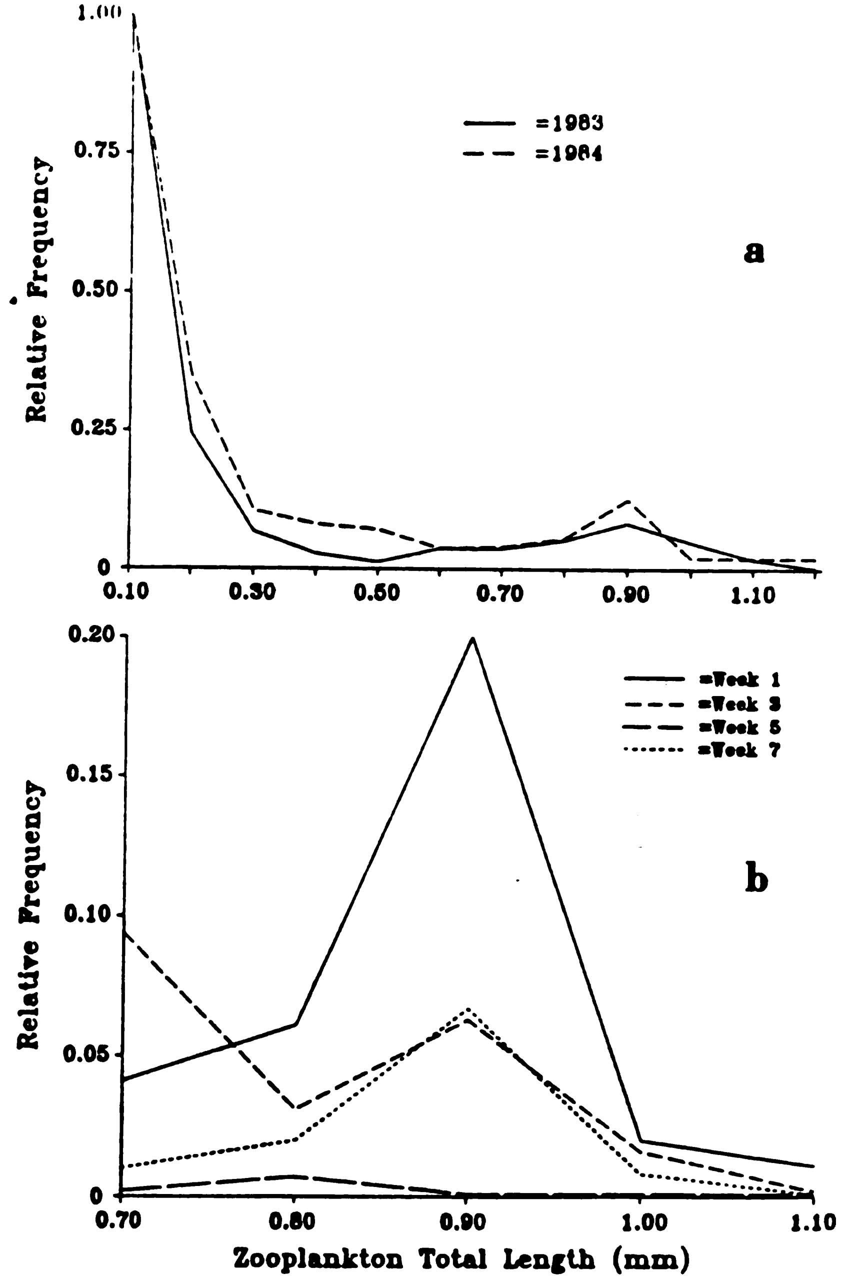

Figure 9. Relative length frequency of zooplankton in Grand Traverse Bay, Lake Michigan during Spring, 1983 and 1984 (a) and changes in the relative length frequency of zooplankton 0.70 to 1.10 mm long during Spring, 1984.

even after the 1983 data were adjusted using night to day capture ratios based on 1984 trawl records (Randomization test; $p < 0.01$). Densities of larval lake whitefish equalled 0.004 (± 0.002) and 0.014 (± 0.003) ind/m^3 during the first week of life in 1983 and 1984, respectively (Figure 10; Table 4). Hatching continued into Week 2 in 1984 with densities reaching a spring maximum of 0.071 (± 0.0073) ind/m^3 at this time. The Week 2 density was estimated to be 0.019 ind/m^3 in 1983.

Densities declined slowly from Week 2 to 6 during 1983. A similar pattern was observed in 1984 until three to four weeks after feeding was initiated, at which time densities dropped sharply from 0.065 (± 0.005) to 0.039 (± 0.021) ind/m^3. This loss rate slowed between Week 5 and 6 of 1984 but remained greater than recorded between Week 5 and 6 of 1983. Densities declined sharply during Week 7 of each year when larval whitefish moved into deeper water (Figure 10; Table 4).

--Growth and Survival Rates--

Weekly estimates of larval lake whitefish instantaneous growth rates are presented in Figure 11 and Table 4. In 1984, daily growth rates were high during the first two weeks of growth. Growth rates declined to a value of -0.0033 during Week 5, then increased to 0.0091 in Week 7 (Figure 11; Table 4).

Survival rates remained high throughout the spring of 1983 and cumulative survival equalled 0.724 (Figure 11;

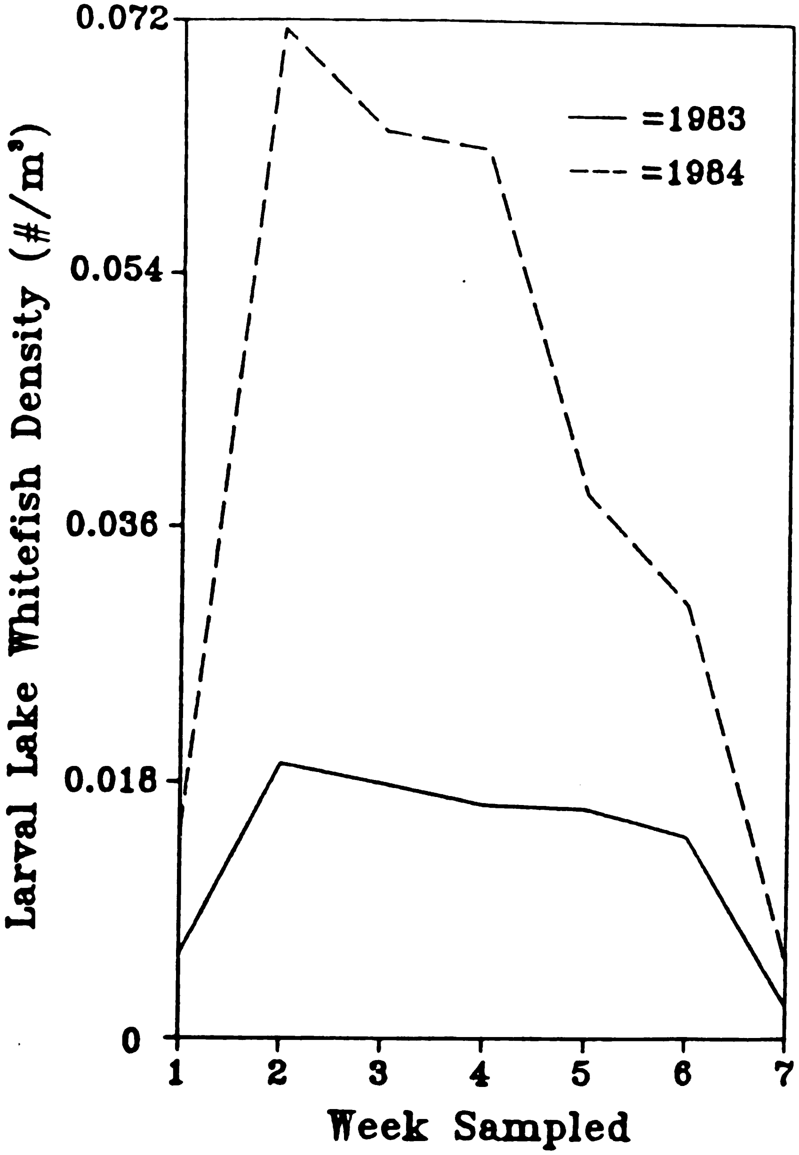

Figure 10. Density of larval lake whitefish caught in Grand Traverse Bay, Lake Michigan during Spring, 1983 and 1984. Catches pooled by week of capture.

Table 4: Mean and standard error (±) of the mean larval lake whitefish density (number/m^3) and the growth (daily) and survival (weekly) rates of these larvae. Data were collected in Grand Traverse Bay, Lake Michigan during the spring of 1983 and 1984 and tabulated relative to larval lake whitefish hatching and development (Week -1 to Week 7).

Week	Larval Density	Standard Error	Growth Rate	Survival Rate
		1983		
1	0.0045	0.0019		
			-	-
2	0.0193	-		
			-	0.93
3	0.0179	-		
			-	0.92
4	0.0164	0.0042		
			-	0.98
5	0.0161	0.0149		
			-	0.87
6	0.0140	0.0144		
			-	-
7	0.0022	0.0013		
		1984		
1	0.0136	0.0031		
			0.0143	-
2	0.0714	0.0073		
			0.0083	0.96
3	0.0683	0.1120		
			0.0066	0.96
4	0.0653	0.0054		
			-0.0033	0.60
5	0.0393	0.0214		
			0.0091	0.74
6	0.0290	0.0017		
			0.0191	-
7	0.0069	0.0034		

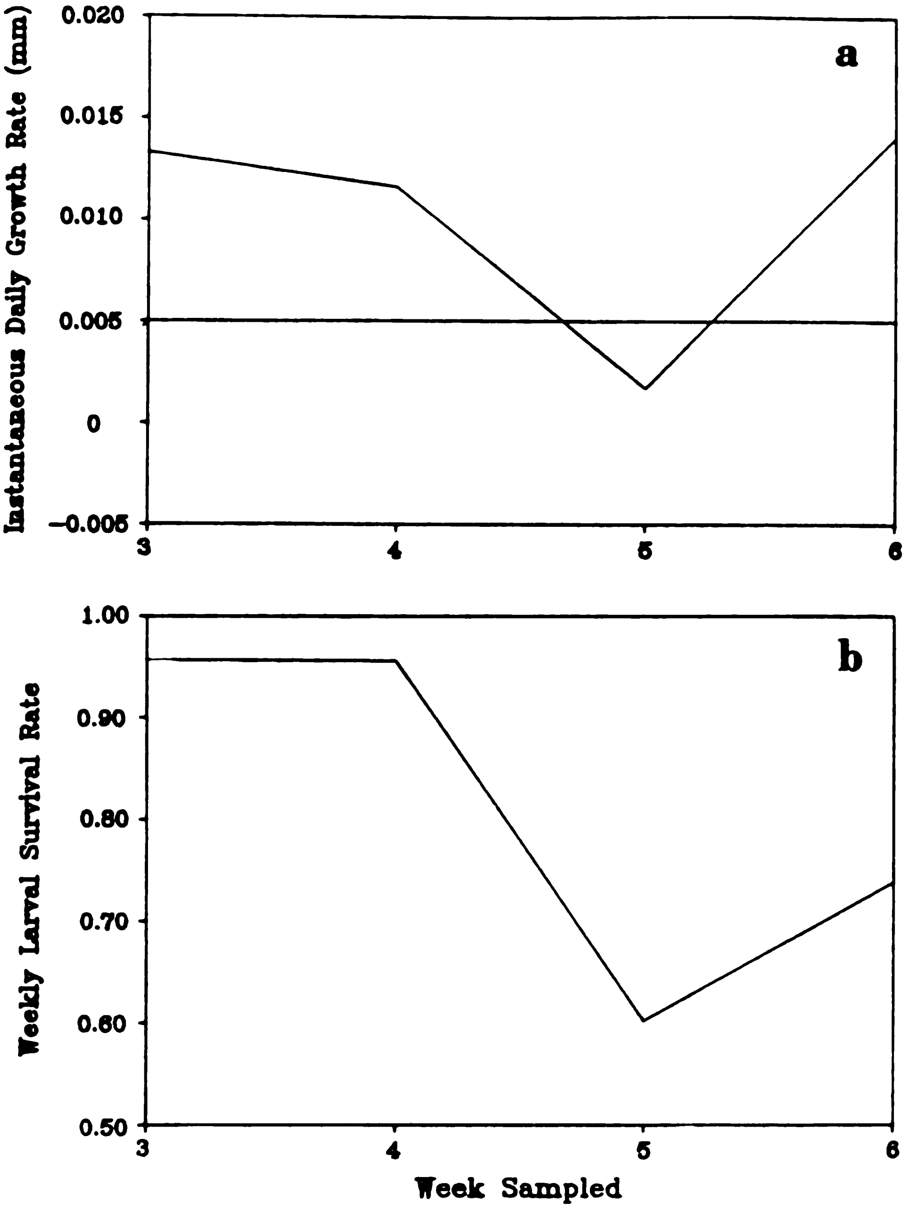

Figure 11. Changes in larval lake whitefish instantaneous daily growth (mm)(a) and weekly survival (b) rates in Grand Traverse Bay, Lake Michigan during Spring, 1984. Larval whitefish pooled by week of capture.

Table 4). In 1984, survival was initially high but declined dramatically in Week 5 and increased only slightly by Week 6. Cumulative survival through the spring of 1984 is 0.0406, 56% of the 1983 value.

--Stomach Content Analyses--

Larval yolk volume declined from 4.7 to 0.5 mm^3 during the first two weeks of life (Figure 12). By Week 7, all of the yolk had been resorbed. Although 83% of all larval stomachs were empty during Week 1, this percentage declined throughout the spring until all stomachs contained food of some type in Week 7 (Figure 12). The mean number of prey in larval stomachs increased dramatically between Week 1 and Week 4, changed little in Week 5 and more than doubled by Week 7 when it reached a maximum of 13.3 individuals/stomach (Figure 12). The mean number of copepod eggs in larval guts fluctuated even more severely. Copepod egg numbers increased dramatically through Week 4 before dropping sharply in Week 5 to less than one-half the number recorded the previous week. Egg number again increased in Week 6 and 7 (Figure 12).

The distribution of total length of organisms in larval whitefish gut contents pooled over all weeks demonstrates the importance of copepod adult and late copepodite stages to the larvae (Figure 13). In 1983, two modes were observed in the data, one centered at 0.60 mm and another at 0.90 mm. Only one mode centered at 0.80 mm characterizes the 1984 frequency distribution.

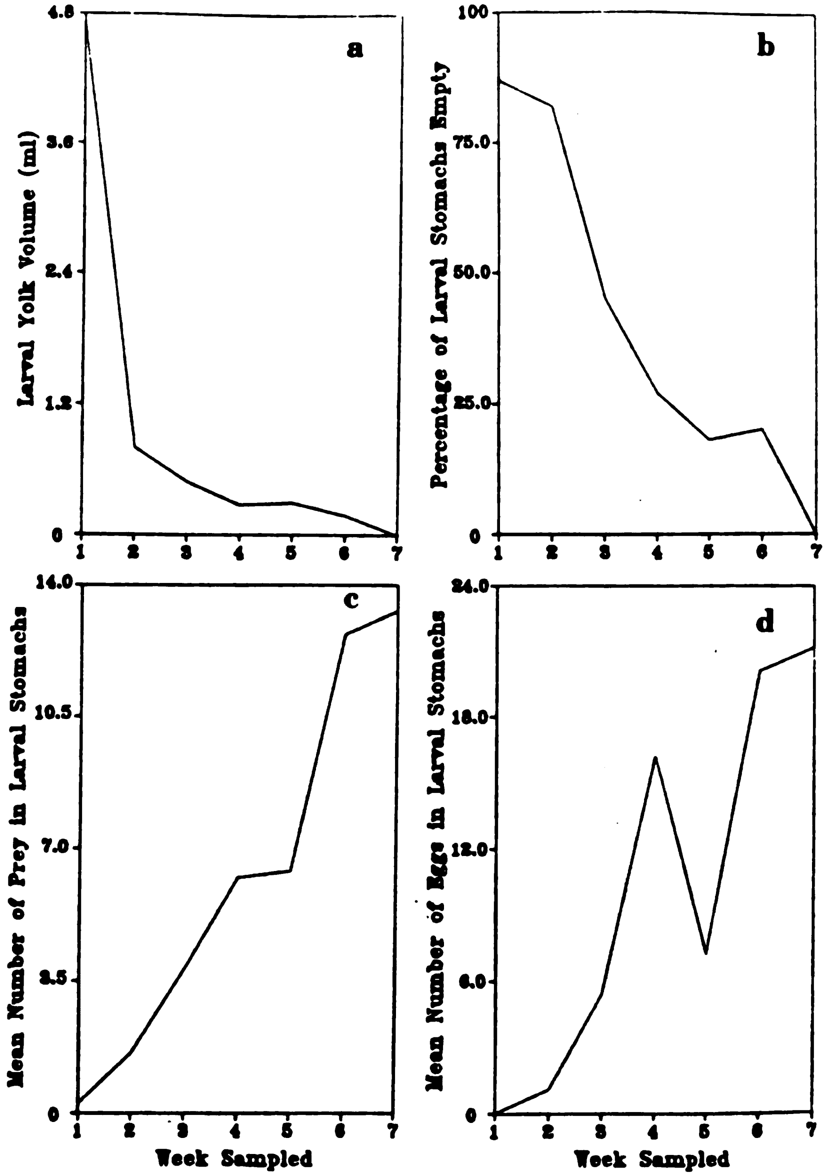

Figure 12. Larval yolk volume (a) and the percentage of larval stomachs empty (b), as well as the mean number of prey (c) and mean number of copepod eggs (d) ingested by larval lake whitefish in Grand Traverse Bay, Lake Michigan during Spring, 1984. Catches pooled by week of capture.

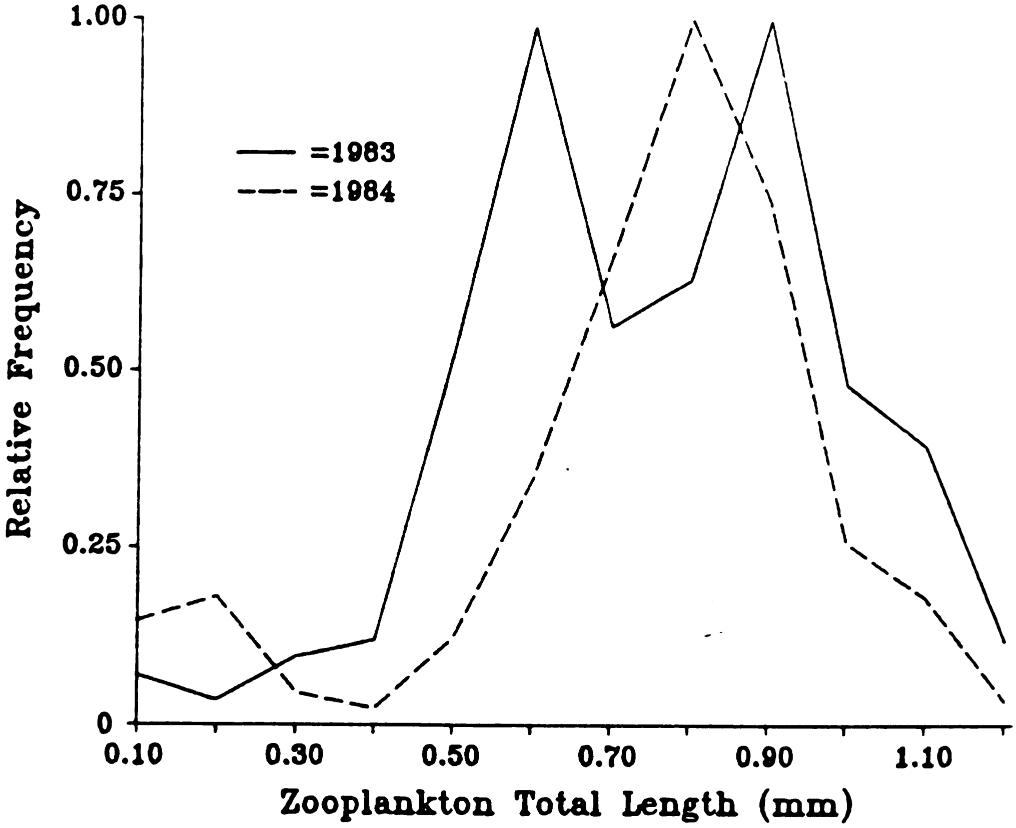

Figure 13. Relative length frequency of prey organisms ingested by larval lake whitefish in Grand Traverse Bay, Lake Michigan during Spring, 1983 and 1984.

Strauss' electivity indices calculated using these data increase from a low of -0.85 for prey 0.10 mm long to a maximum of 0.99 for prey 0.80 mm long (Figure 14). Indices are slightly negative for prey 0.20 to 0.40 mm in length, near zero for lengths of 0.50 and 1.20 mm and slightly positive for zooplankton 0.60, 1.00 and 1.10 mm long. Zooplankton 0.70 to 0.90 mm in length occurred in larval whitefish diets at much higher rates than their abundance in the environment would predict (Figure 14).

Integrating this prey selection information with prey abundance and larval fish densities provides a more accurate estimate of the amount of food available to the larvae each year. This estimate, labelled the z/f ratio, is the amount of adult and copepodite zooplankton available to an individual larval whitefish in East Traverse. Dramatic differences in the value of this ratio exist between the spring of 1983 and 1984 (Mann-Whitney U; $U = 0$; $p < 0.05$)(Figure 15). Ratios were high and fairly constant through the spring of 1983 when larval densities were low. With higher numbers of larvae in 1984, values of the z/f ratio were markedly lower and decrease through much of the spring. These characteristics may help to explain the changes in growth and survival documented in 1984.

Zooplankton/fish ratios are plotted in conjunction with 1984 daily growth and weekly survival rates in Figure 16. As the ratios declined from Week 3 to 5, growth and survival rates decreased. These rates increased when the

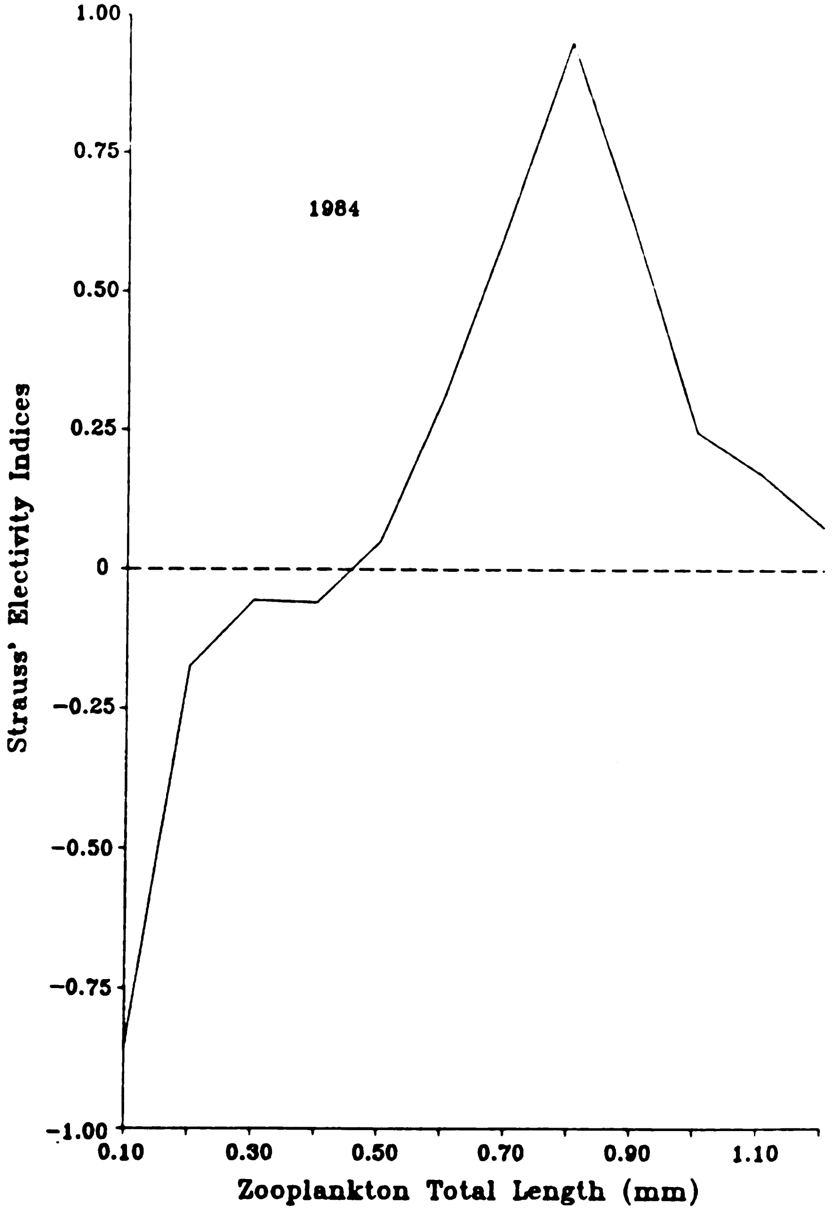

Figure 14. Strauss'electivity indices for prey organisms ingested by larval lake whitefish in Grand Traverse Bay, Lake Michigan in 1984.

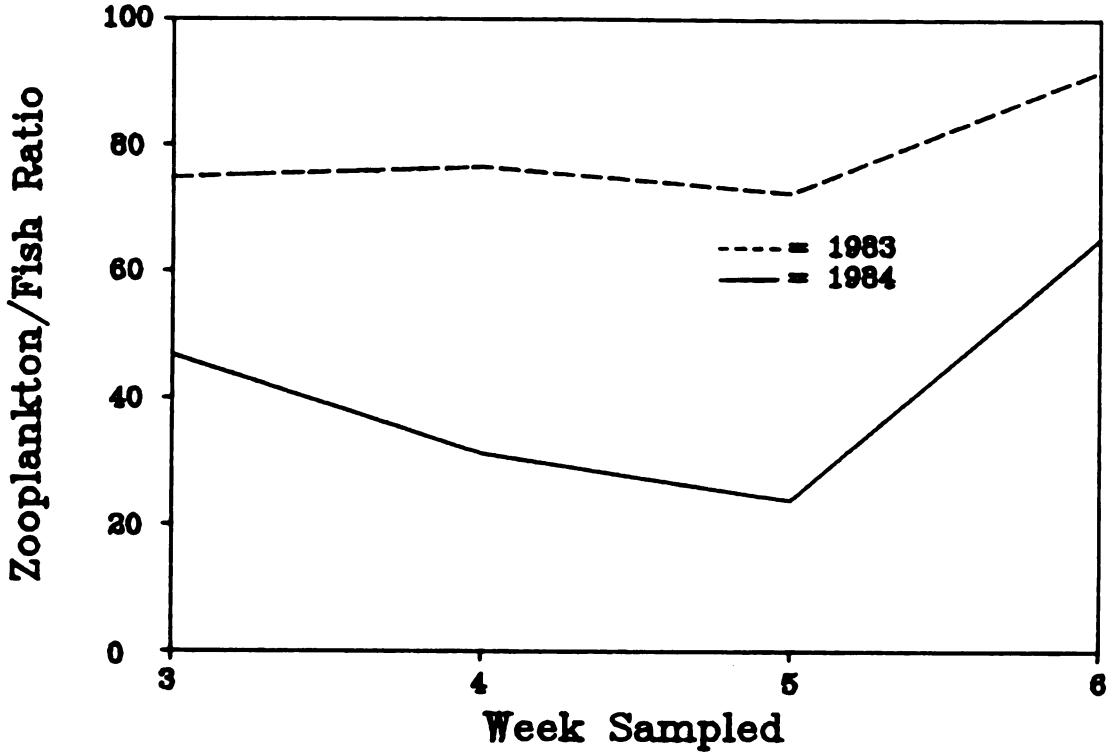

Figure 15. Changes in the number of zooplankton per fish larvae during Weeks 3 through 6 in Spring, 1983 and 1984.

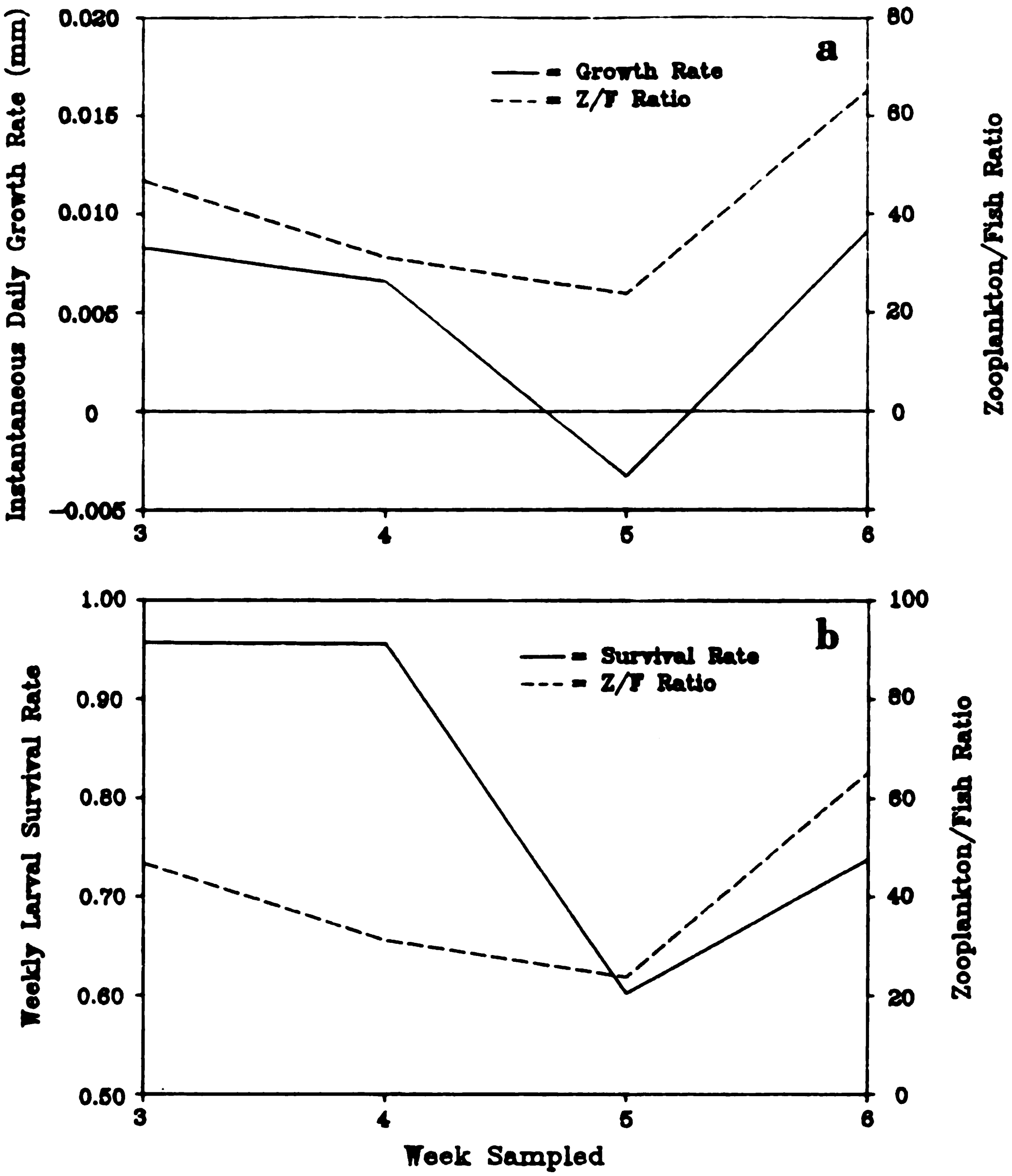

Figure 16. Changes in larval lake whitefish instantaneous daily growth (a) and weekly survival (b) rates in relation to changes in the number of zooplankton available to individual fish larvae in Grand Traverse Bay, Lake Michigan during Spring, 1984. Larval whitefish pooled by week of capture.

z/f indices increased after Week 5.

A plot of growth rate as a function of the number of zooplankton per fish larvae revealed a hyperbolic relationship with increasing z/f ratios increasing the instantaneous daily growth rate of larval lake whitefish (Figure 17). The threshold corrected hyperbolic equation for substrate limited growth rate fitted to this data was:

$$u/\text{day} = [0.0199((z/f)-25.0)]/[24.3 + ((z/f)-25.0)]$$

with the appropriate constants being calculated from the slope and y-intercept values of the regression of $((z/f)-(z/f)_q)/u$ on $(z/f)-(z/f)_q$:

$$((z/f)-(z/f)_q)/u = 1221.0 + 50.3\ ((z/f)-(z/f)_q).\quad (r^2 = 0.99)$$

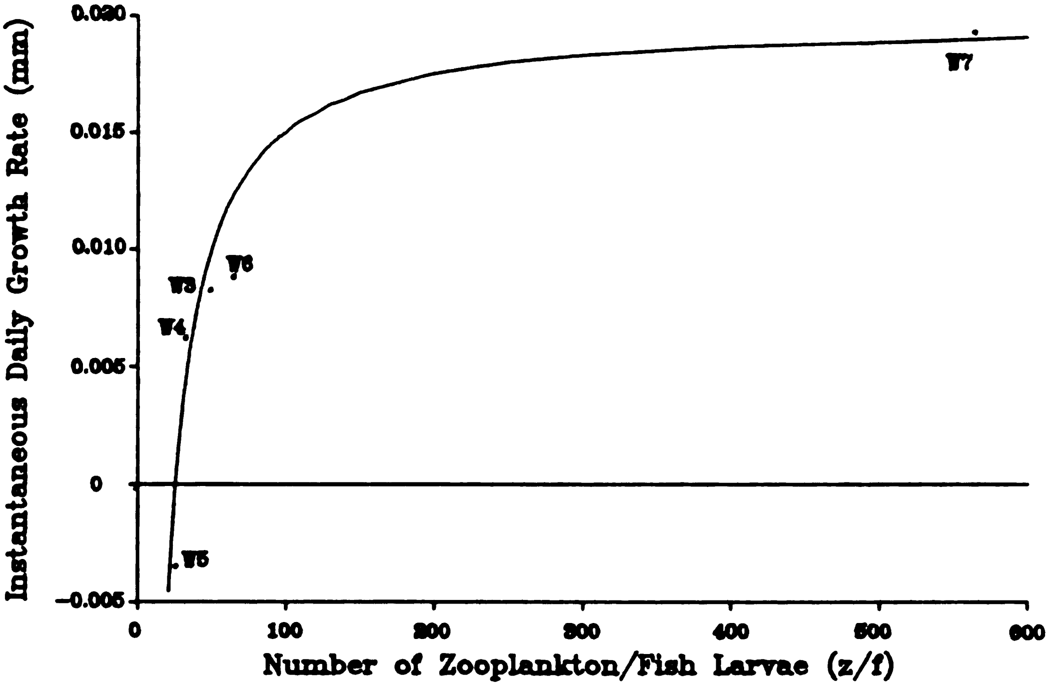

Figure 17. Instantaneous daily growth rate of larval lake whitefish sampled in Grand Traverse Bay, Lake Michigan in 1984. Growth rate plotted as a function of the number of zooplankton per fish larvae. Larval whitefish pooled by week of capture.

DISCUSSION

--Variability--

Quantitative analyses of ecological systems are made more difficult by the complexity of these systems. This complexity can be accompanied by variability within and between component parts of the ecosystem. Representative samples removed from the system should reflect, and their analysis consider, this variability. This was accomplished with egg, zooplankton and larval fish samples collected in East Traverse throughout the course of this study.

Although lake whitefish prefer a gravel or cobble-sized substrate for spawning, these broadcast spawners will deposit eggs over a wide range of bottom types. Eggs deposited on fine substrates are moved by wind or wave action to other poor substrates where damage or death may occur or to coarse substrates where they may collect. Eggs spawned on coarse substrates will be disturbed to a lesser degree. The non-random distribution of these eggs can be documented by sampling a lake bottom of mixed substrates such as those in East Traverse.

This non-random pattern will be accentuated in egg samples taken after a winter of heavy egg mortality, when, relative to egg densities in the fall, very few eggs will remain on the spawning grounds by the time hatching begins in the spring. Surviving eggs will be those deposited on substrates which provided the best incubation sites.

Estimates of variability in numbers of eggs alive and sampled reflect this clumped distribution pattern.

This clumped, non-random distribution is also observed in zooplankton and larval fish samples collected in East Traverse. Patterns of zooplankton and larval fish patchiness are phenomena frequently recorded in the marine literature (Cassie 1963; Smith 1973; Steele 1978; Hewitt 1981; Omori and Hamner 1982). Individuals aggregate or swarm in response to behavioral or environmental conditions that are not completely understood (Laurence 1974; Omori and Hamner 1982). The occurrence of these aggregations in East Traverse is reflected in plankton samples collected there. As this pattern appears to be a characteristic inherent in plankton and larval fish populations, intensified sampling efforts may reduce but likely will not eliminate such variability. Considering the non-random, patchy distribution of individuals in the population, commonly used statistical significance levels of 0.05 or 0.01 are often difficult to attain. Given the amount of time and effort expended on sampling such patchy distributions, significance levels as low as 0.10 or 0.20, obtained in this study, appear to represent good precision. Had time allowed acquisition of a much greater number of samples, higher significance levels would have been expected.

--Field and Laboratory Research--

Lake whitefish egg survival appears to be dependent upon the severity of the winter through which the eggs incubate. The exact mechanism responsible for this difference in survival is unknown. However, physical factors, primarily wind and wave action whose impact is regulated by ice cover, are likely candidates (Miller 1952; Clady and Hutchinson 1975). When ice forms over whitefish spawning grounds soon after the eggs are deposited, spawned eggs are protected from damage and mortality caused by wave and wind action. Eggs are less likely to be moved to substrates where damage or death may occur due to burial or abrasion. Higher rates of egg survival result.

Eggs are exposed to these mortality factors throughout a warm, iceless winter or for extended periods of time during mild winters when ice does not form until late January or February. Eggs deposited on or moved to sand, silt or clay bottoms would suffer the highest rates of mortality as these substrates provide little protection from wind and wave action (Johnson 1961; Rupp 1965). Egg mortality on large substrates prevalent in shallow water regions in northern Lake Michigan also would be high during mild winters. However, eggs settling into the deepest crevices in these substrates would not be destroyed and a small percentage of eggs would survive through the winter. Overlying anchor ice which extends short distances out from the shoreline would also improve shallow water egg survival during mild winters.

In protective embayments or on lee shores away from prevailing winds, mild winters may influence egg survival in a manner different than observed in this study. With little fetch, wind driven waves that destroy deposited eggs cannot develop. In addition, some ice may develop in these calm, protected areas during mild winters even though temperatures are warm enough to prevent its formation in regions of the lake where wind and waves are omnipresent. If suitable spawning substrates are available and dissolved oxygen is not limiting, spawning grounds located in these areas should be ideal incubation sites and consequent egg survival should be high.

In more exposed regions like East Traverse, annual fluctuations in overwintering egg survival likely would be more severe, and their influence on lake whitefish year-class strength, more extensive. Because of the large number of eggs deposited by whitefish, small amounts of variation in egg mortality from year to year have the potential to produce substantial differences in the number of fish recruited to the fishery. With an average fecundity in East Traverse of 30,000 eggs/female, approximately 1100 more eggs/female reached the larval stage in 1984, when egg survival equalled 5.6%, than in 1983 when it equalled 1.7%. Over 500,000 more larvae were present in 1984 than in 1983 if this change in egg survival is extrapolated to a hypothetical spawning population of

500 females in East Traverse. Application of these survival percentages to later stages of development, the juvenile period for example, will remove far fewer individuals from the latter cohort and influence year-class size to a lesser degree. Thus, the importance of winter severity to year-class strength lies as much in its existence as in the timing of its occurrence during the life history of the whitefish. Moving its severity from the egg stage where the potential for massive changes in numbers is great to a later period would reduce its impact on whitefish dynamics. In its present position, however, it may serve as one of the driving forces behind these changes.

The effect of winter severity and overwintering egg mortality on year-class strength goes beyond the impact of the direct mortality imposed by it on developing embryos. It also may play a controlling role in the growth and survival dynamics of the larval stage of development. Fundamental to growth and development is the availability of energy to the individual organism. This energy becomes inadequate for further growth and survival when the demand for it exceeds the rate of its supply. By influencing the density of food organisms serving as sources of energy for larval whitefish, as well as determining the number of fish entering the larval period, winter severity influences both the supply and demand sides of the energy equation.

Energy is supplied to developing larvae in the early spring in the form of copepod zooplankton that have overwintered in East Traverse. These copepods begin producing eggs soon after breeding in March and early April (Selgeby 1975). The largest peak in the overall size distribution of zooplankton in the bay is comprised of early instar nauplii that have hatched from these eggs. A second and much smaller peak in this size distribution consists of the late copepodite as well as the early adult stages and arises from an increase in the length of time spent by copepods as adults relative to the time spent in other development stages (Gehrs and Robertson 1984).

Changes in zooplankton densities and length frequency distributions through the spring result from factors inherent in the mature population of overwintered adults typifying early spring zooplankton assemblages (Selgeby 1975; Makerewicz and Likens 1982). Densities decline through April and much of May when recruitment from younger copepodite stages fails to balance the losses due to mortality in the adult size classes (Selgeby 1975). In addition, high loss rates of reproductive individuals precludes large increases in nauplii and early copepodite densities at this time.

Initial densities of these zooplankton may, however, be influenced by the severity of the winter through which individual plankton live. Periphyton present on the lake bottom during dives through the ice in 1984 was not present during dives in the warm, iceless winter of 1983. Energy is expended by zooplankton searching for the phytoplankton food resource kept dispersed throughout the water column by wave action in 1982/83. Zooplankton overwintering during 1983/1984 utilized an energy resource that, relative to 1982/83, may have been more readily available and abundant. Energy expended on search costs the previous winter may have been available to meet growth and maintenance costs in 1983/84 when the resource appeared to be aggregated at the lake bottom. If there was more energy to meet maintanence and other requirements in 1984 than in 1983, higher densities of zooplankton should have survived through the winter of 1983/84.

The upward trend in standing crops of zooplankton following the loss of ice cover in 1984 is driven by additional amounts of sunlight penetrating into the water and warming water temperatures at this time. Coupled with these factors is the increased agitation of the water column due to wave action after ice out. Thus, zooplankton samples collected in Week 1 accurately depict between year differences in densities. Samples collected at earlier dates may not have reliably estimated plankton densities. Distributional differences of these plankton at these earlier dates may have made them inaccessible to the sampling gear.

Improvements in the density of the zooplankton resource are not the only consequence of the cold, ice-covered winter of 1983/1984. High egg survival during this winter produced high numbers of larvae hatching in early April. Although zooplankton were more abundant in 1984, fewer plankton were actually available to individual whitefish larvae because densities of these larvae in 1984 were 3.7 times higher than in 1983. These larvae may have found it difficult to obtain enough energy for growth and maintenance.

Laboratory studies illustrated the impact of inadequate food rations or energy supplies on larval dynamics. In the laboratory, larval lake whitefish growth and survival rate were affected by altering available energy. A reduction in growth rate at low z/f values could influence larval lake whitefish dynamics. The larval stage of fish is potentially very susceptible to predation (Lindstrom 1962). Larval fish can minimize this predation pressure by growing rapidly into a less vulnerable size class where fewer predators can ingest them. If larvae encounter low z/f ratios in the spring, larvae would experience a reduced rate of growth into a stage less vulnerable to predation. Consequent increases in predation mortality might prove costly to year-class strength.

Physical or chemical stresses such as temperature changes and wave or current action also may influence larval survival and year-class strength. Even if such factors were relatively constant from year to year, their influence on larval dynamics could depend to a large extent on the zooplankton/fish ratio. If the ratio is low, not only will larvae be unable to acquire enough food to adequately deal with the stresses, but growth and survival also may be hindered. Larval survival would be lower than during years when the z/f ratio is high and growth is more rapid. Laboratory observations of larval behavior revealed that larvae receiving higher rations were robust and active while those being starved or fed reduced rations spent much of their time lying quietly at the bottom of the tank. It appears these larvae could ill afford to expend energy on stresses additional to maintanence and growth.

Predation and the influence of physical or chemical stresses are indirect means by which larval lake whitefish might be affected by low zooplankton/fish ratios. Laboratory experiments further demonstrated survival to be directly influenced by food rations. Three findings in particular merit discussion: the presence of a critical period, the ability of even poorly fed larval lake whitefish to survive at 12°C for 2 to 3 weeks and the eventual mortality these larvae experience relative to larvae held under conditions of high plankton densities.

The presence or absence of a critical period in fish has long been debated (Marr 1956). My laboratory study delineates its presence in larval lake whitefish. Regardless of feeding level, mortality was essentially zero until day 15 of the experiment. After this date, which coincided with yolk sac absorption and the switch by the larvae to complete reliance on exogenous food sources for energy, mortality increased in tanks receiving rations of 18 z/f and less. Prey densities in these tanks did not provide enough energy to compensate for the loss of energy resources previously available in larval yolk reserves. In contrast, no large increase in mortality was experienced in tanks where higher prey densities were available (32 and 110 z/f). Critical period expression thus appears to be a function of available food densities rather than something intrinsic to larval fish development.

The ability of larval lake whitefish to live on poor rations for roughly two weeks while experiencing very little mortality could be considered adaptive for these larvae. These fish hatch in late winter to early spring when zooplankton densities are customarily low. Being able to survive for an extended period of time with low zooplankton densities may allow larvae to survive until the spring zooplankton bloom occurs. They could then take advantage of these higher densities and grow more rapidly, thereby circumventing high mortality which would otherwise occur if they required zooplankton soon after hatching.

It is important to note that if no improvement in zooplankton abundance occurs in 2-3 weeks, post-hatch larval mortality would be severe. Larvae experiencing low zooplankton rations went from 100 to 0% survival within a week to 10 days of yolk sac resorption. As major changes in survival are noted with minor changes in food density, a slight change in food abundance may thus have a significant effect on the number of fish in a cohort.

Several characteristics of larval lake whitefish growth and survival dynamics apparent in or hypothesized from laboratory results also were expressed by field populations of larvae in East Traverse. Changes in the number of zooplankton available to individual fish larvae were followed by corresponding fluctuations in the rate of daily growth in length of these larvae. Rates decline from 1.43%/day when larvae were drawing upon yolk reserves and available zooplankton for energy to -0.33%/day when yolk reserves were exhausted and zooplankton populations depleted. At this later date, growth declines as energy is diverted from growth and allocated to meet maintenence requirements. Survival declines when available energy and energy intake are not sufficient to meet maintenence costs. Thus, variation in growth appears to be a precursor to other changes in cohort characteristics that occur during the larval stage of development.

Their exist a plethora of equations or models that attempt to reliably predict individual growth in size (von Bertanlaffy 1938; Silliman 1967; Knight 1969). In these equations, size is modelled as some function of past size and growth rate, with little,if any, attention given to factors responsible for these values. The Monod or, more correctly, threshold corrected hyperbolic equation for substrate limited growth addresses these factors by incorporating into its formulation values characterizing individual growth kinetics and values representing energy units from which these indices are derived. When applied to field data from East Traverse and calculated growth rates plotted as a function of available energy (z/f), the resulting threshold corrected equation describes a curve that falls from high to zero growth with little change in the z/f ratio. Over this range, larval growth rates are severely altered by relatively small changes in zooplankton density or the abundance of larval whitefish. As such, larval growth may be a sensitive indicator of the amount of energy available to larval fish in their environment.

Because growth is sensitive to environmental conditions and because changes in it often precede fluctuations in other characteristics of the cohort, accurate estimates of growth would be useful in the analysis of larval dynamics. Accurate growth estimates also would be a prerequisite to the successful use of these rates as predictive tools. Thus, it would be wise to investigate the reliability of the predictive threshold corrected growth equation discussed previously and from which these rates are calculated. Internal reliability of this equation was checked by using it to calculate growth rate based upon densities of zooplankton and larval fish measured in the field. Larval length predicted from these growth rates could then be compared to means determined for field caught larvae from East Traverse. Actual and predicted length values differ very little through the course of the spring (Mann-Whitney U; $U = 11$; $p = 0.42$). Actual final larval lengths are only 0.15 mm less than predicted (Table 5). This result lends credence to the usefulness of this equation as a tool in further modelling of larval dynamics.

It is apparent that larval survival parallels larval growth quite closely. Reductions in survival are coincidental to decreases in growth which are a consequence of lower amounts of energy available to individual larvae. This becomes particularly apparent in 1984 when higher larval densities reduced the amount of zooplankton available to individual fish larvae.

Available energy is further limited by larval whitefish prey size selection. These larvae do not ingest the small nauplii and early instar copepodites which are very abundant in the water column. Instead, they utilize pools of energy available in the large copepodite and adult stages of copepods, particularly those individuals 0.70 to 1.10 mm long. The resorption of the yolk sac, coupled with the near exhaustion of densities of these sizes of organisms in Week 5 of 1984, reduced larval growth and survival rate. Zooplankton/fish ratios fell below levels necessary to meet maintenence costs and larval survival declined sharply. The decline in density over this time span accounted for 59.9% of the total reduction in spring

Table 5: Actual mean weekly lengths of field caught larval lake whitefish in 1984 (Weeks 3 through 7) and lengths calculated from the predictive growth equation derived using field growth rates and zooplankton/fish ratios.

Week	Actual Length	Predicted Length
3	13.83	13.91
4	14.48	14.30
5	14.15	14.20
6	15.08	15.43
7	17.91	18.06

larval density. This period appears to be critical to larval survival and year-class strength in 1984. Thus, critical period expression does not appear to be a phenomena confined to laboratory observations.

Much of the debate over the existence of a critical period in field populations of developing larvae might be explained if its expression is in large part dependent upon prey abundance factors. The presence of a critical period would not be recorded in the field if high zooplankton densities are available when endogenous sources of energy are exhausted. In this case, low mortality would occur during the transition to exogenous feeding. Such reasoning may explain why higher mortality rates did not coincide with severe reductions in yolk volumes between hatching and Week 3 of 1984. However, as in Week 5 of 1984, a critical period would be apparent if extant zooplankton densities do not provide enough energy to maintain larval growth and survival rates when the larvae are forced to rely upon these exogenous food sources for much of their energy. Slowed growth rates result and are followed by high rates of mortality and low larval fish densities.

Larval density declined by 60% through the spring of 1984 when initial larval abundance was high and z/f ratios reduced. Larval abundance declined by only 27.5% in 1983 when z/f ratios were higher. Thus, 1984 density initially 3.7times greater than recorded in 1983 falls to level 2.1 times higher than the 1983 value by the end of the spring of 1984. If, as hypothesized, the egg and larval stages of lake whitefish are critical to establishing lake whitefish year-class strength, the 1984 cohort should be slightly more than double the size of the 1983 year-class. Trawls for juvenile lake whitefish in East Traverse demonstrated that the 1984 year-class was 2.5 to 3.0 times larger than the 1983 cohort (Figure 18).

It is possible to develop a model predicting year-class strength in East Traverse by integrating zooplankton abundance and larval fish growth and survival data with records of overwintering egg survival in the bay. Again, it is assumed that year-class size and recruitment are a function of these periods of development. Reliability of the model could be checked by comparing its year-class size predictions to those documented during the larval and juvenile stages of development.

Cumulative larval survival from Weeks 2 through 6 of 1983 equalled 0.724 and corresponded to a calculated daily growth rate of 0.0164 over this time span. Growth rate dropped to 0.0081 in 1984 and survival declined to 0.0406. Assuming linear increases in survival with growth rate, the following equation is produced when cumulative survival rate is regressed on growth rate:

$$\text{Survival/Spring} = 0.0957 + 38.3\ (\text{u/day})$$

It has already been demonstrated that larval growth is reliabily predicted by the threshold corrected hyperbolic

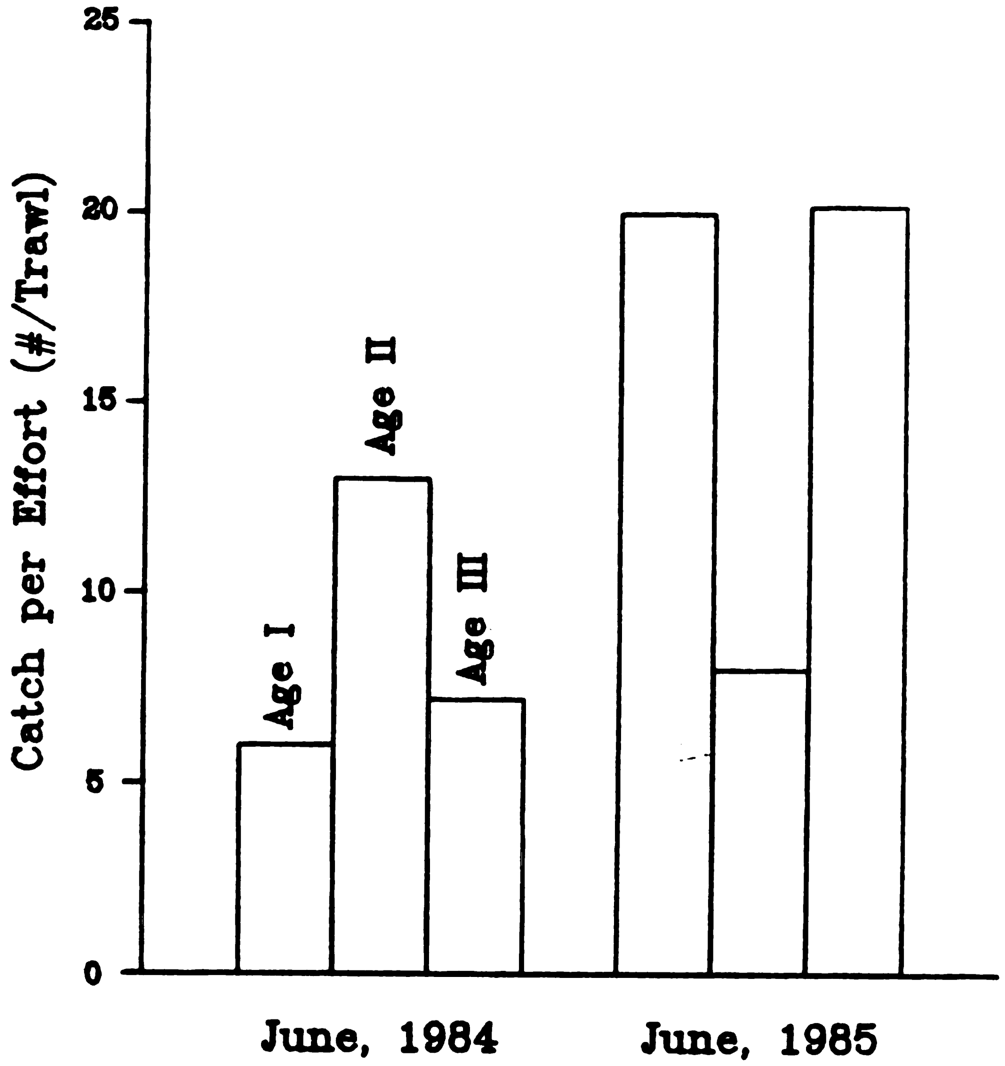

Figure 18. Catch per effort of 1, 2 and 3 year old lake whitefish in Grand Traverse Bay, Lake Michigan during June of 1984 and 1985.

equation for substrate limited growth and the zooplankton/larval fish ratio embodied in it. Thus, substituting this equation for u produces:

$$\text{Survival/Spring} = 0.957 + 38.3[(0.0199\ (z/f - 25))/(z/f + 49.3 - 50)]$$

Using this equation, changes in survival/spring as a function of changes in the z/f ratio are depicted in Figure 19. This equation describes the survival of larval lake whitefish from the time of larval hatch to deepwater movement of the individuals. To estimate larval survival over this time span, the weekly estimate of zooplankton density in the numerator of the z/f ratio in the equation is replaced by the mean density of adult and copepodite zooplankton recorded in the spring during weeks preceding the deepwater movement of the whitefish. This mean value provides an index of spring zooplankton abundance each year. The fish denominator of the ratio is replaced by the density of eggs surviving through the preceding winter, hatching in the spring and encountering the extant zooplankton densities.

Assuming zooplankton density does not increase in parallel with the number of eggs surviving through the winter, any increase in egg survival will lower survival through the larval stage as the amount of energy available to each individual is reduced. Energy available to individual larvae is lowest following winters of high egg

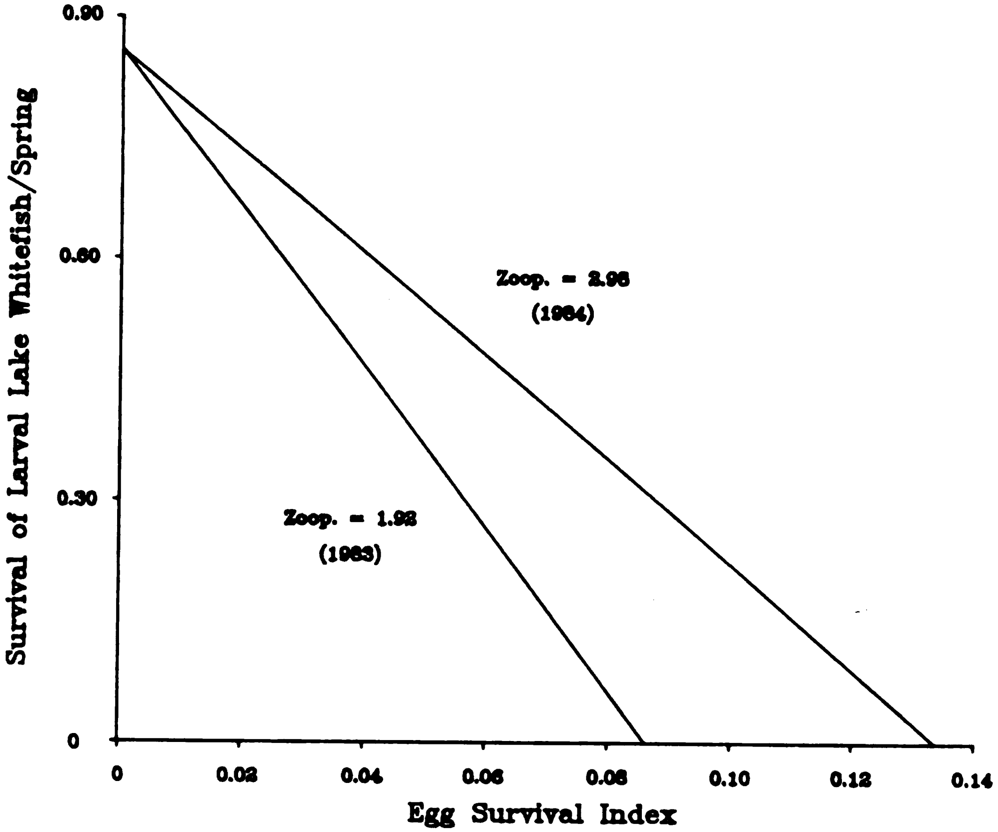

Figure 19. Spring survival of lake whitefish larvae as a function of changes in the number of whitefish eggs hatching in the spring and the amount of zooplankton available to the developing larvae. Zooplankton densities are held constant at 1.92/1 (Spring, 1983)and 2.98/1 (Spring, 1984) while egg numbers are varied from 0.001/m^2 to 0.13/m^2.

survival and low zooplankton production. Thus, larval survival dynamics will influence cohort size and whitefish year-class strength to the greatest extent following cold, ice-covered winters. The rate of supply of food is adequate to meet the requirements of the low number of larvae hatching after open winters. In these years, survival during the egg, not the larval, stage of development is critical to year-class strength.

Regardless as to what stage of whitefish early life history is most responsible for determining year-class size, the model demonstrates that interrelated changes in the number of eggs spawned, the survival of these eggs through the winter and the density of zooplankton available in the spring are the driving forces behind these dynamics. Stock size and winter severity determine the number of larvae hatching each spring. Varying these two factors while holding zooplankton density constant will produce a wide range of year-class sizes. For my purpose, zooplankton density was held constant at the mean for the spring of 1983 and 1984 and the number of eggs, and consequently larvae, entering this period varied from 0.001 to $0.13/m^2$. This procedure produced two hyperbolic curves reminiscent of the Ricker stock-recruitment function under resource limited conditions (Figure 20). As egg number, which incorporates into it the number of eggs spawned and overwintering survival of these eggs, increases, larval survival declines and year-class strength increases to a

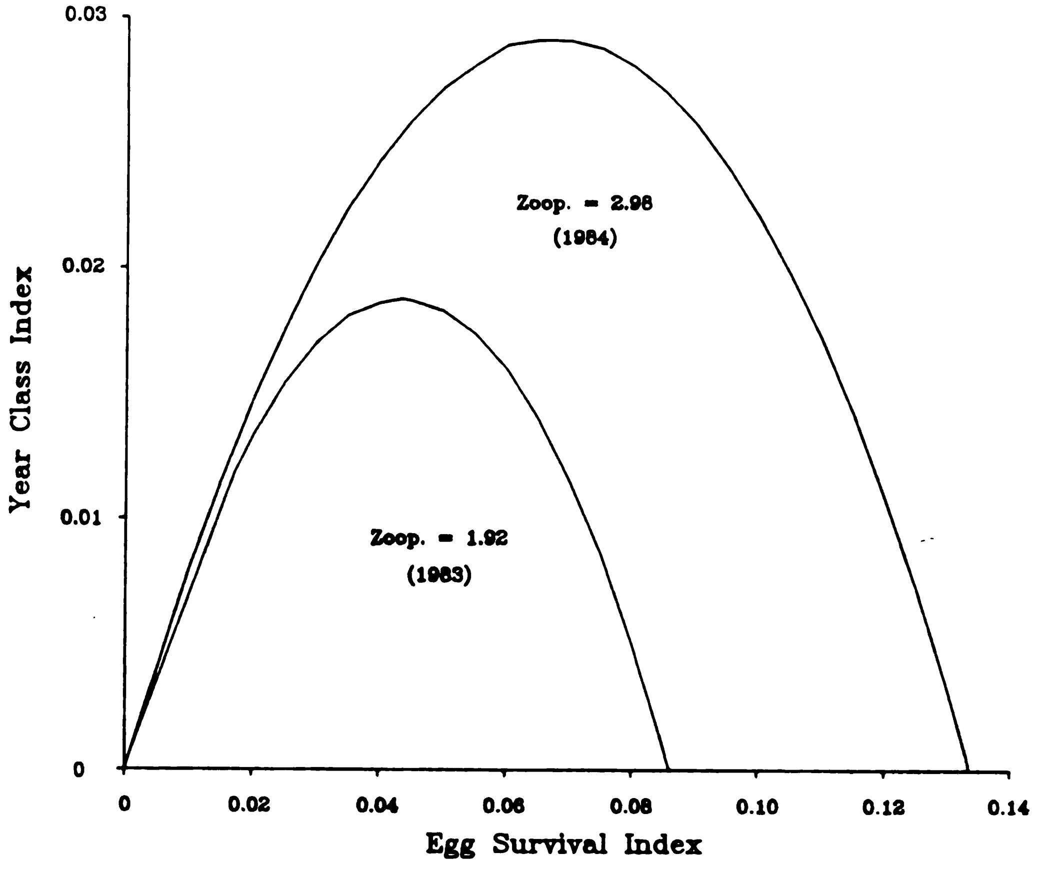

Figure 20. Range of year-class indices possible during Spring, 1983 and 1984. Indices determined by integrating overwintering egg survival with spring larval survival. Zooplankton density held constant at 1.92/l and 2.98/l during 1983 and 1984, respectively.

maximum of 0.187 in 1983 and 0.291 in 1984. Further increases in egg number reduce year-class strength. Over the descending portion of the curve, low z/f ratios eliminate gains made in density due to high egg survival. This result once again points to the degree of interaction between overwintering egg survival and the extent of mortality during the larval stage of development.

Using this equation in collaboration with data pertaining to overwinter egg survival in East Traverse will provide estimates of spring larval survival and relative year-class strength to which values actually recorded in the bay can be compared. Predicted values of larval survival of 0.693 and 0.505 in 1983 and 1984 approximate values recorded in the field during each respective year. The prediction of relative year-class strength made by the model (1984 cohort 2.4 times the size of the 1983 cohort; Figure 21) compares favorably to other estimates of relative size. As mentioned previously, cohort abundance was 2.1 times higher at the close of the larval period in 1984 than it was in 1983. Trawls for juvenile whitefish in East Traverse demonstrated that the 1984 cohort was 2.5 to 3.0 times greater than the 1983 year-class (Figure 18). It appears relative year-class size of whitefish in East Traverse can be fairly accurately predicted with data pertaining to overwintering egg and spring larval survival. Incorporation of these data into a mathematical description of the system produces a reliable estimator of the relative

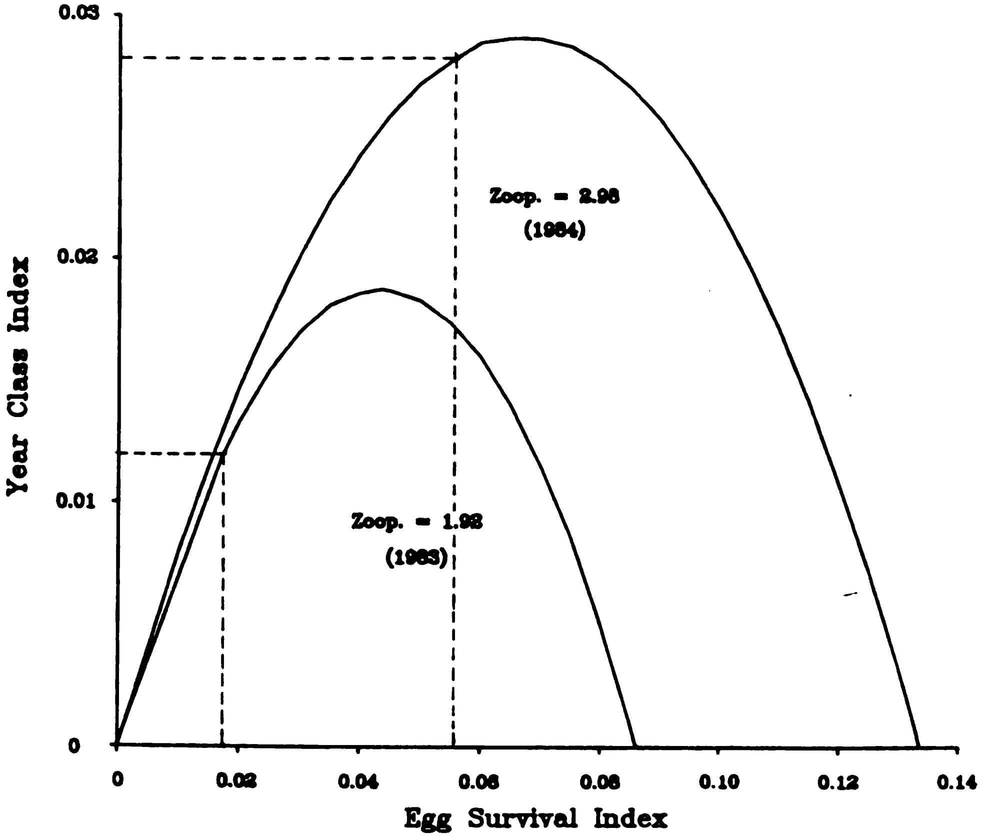

Figure 21. Year-class indices predicted by the early life history recruitment model for Spring, 1983 and 1984. Zooplankton density held constant at 1.92/l and 2.98/l during 1983 and 1984, respectively. Egg survival equals 0.017/m^2 and 0.056/m^2 in 1983 and 1984, respectively.

size of year classes of whitefish in the bay.

Analysis of model behavior also can provide clues as to the stage of development controlling these annual fluctuations in cohort abundance. Given the zooplankton conditions in 1983, a year-class curve is produced that peaks at a cohort size index of 0.0187 (Figure 21). If the egg survival (ie. fish number) recorded during that year is plotted on this curve, the index corresponding to the point of intersection of the egg survival value and the year-class parabola is well below the maximum value possible given available spring zooplankton densities (Figure 21). Severe overwintering egg mortality during the iceless winter of 1983, not the ensuing spring larval dynamics, was responsible for the reduced size of the 1983 year-class. Increases in cohort abundance to a value as much as 1.6 times higher than observed would have been possible if egg survival had been higher. Higher densities of spring zooplankton only would have made this discrepancy between realized and potential year-class size more severe.

The scenario is different in 1984. Egg survival during the preceding winter corresponds to a year-class near the peak of the curve of cohort indices (Figure 21). Given existing zooplankton densities, further increases in the number of eggs surviving through the winter would do little to increase and may actually decrease eventual year-class strength. Thus, plankton densities limit the size of the 1984 cohort. Higher densities of zooplankton would have produced a curve of greater magnitude and severe mortalities would have been avoided as more zooplankton would have been available to individual fish larvae. Cumulative larval survival would have been increased and more fish would have passed through the critical early life history stages of development. Under prevailing conditions, however, the amount of zooplankton produced in the bay was not adequate to meet the energy requirements of the developing larvae. Although zooplankton abundance was greater following the ice-covered winter of 1983/84, this increase could not keep pace with changes in the number of surviving eggs or larvae. Excess fish unsupportable by the system were eliminated and densities at the close of the larval stage were near the maximum sustainable by spring zooplankton conditions.

It is evident that the dynamics of the larval stage of whitefish development are tied intimately to the severity of the previous winter and its corresponding egg mortality. The larval stage of whitefish development appears to act as a bottleneck retarding the movement of these fish to older stages and larger sizes. This bottleneck operates most severely when winter conditions have been favorable for egg survival. Because of its position before other stages of development, winter severity and egg mortality can function as a driving force behind early life history dynamics. The larval period responds to the annual fluctuations in density in a manner analogous to an engine governor.

Control over the rate of flow through the system is tightened when too many particles, ie. larvae, enter it and loosened when their rate of entry is low. Thus, larval dynamics are dependent upon and operate within limits described by overwintering egg mortality to further delineate year-class size.

In considering these changes, it is critical to realize that larval dynamics cannot be interpreted without regard to the importance of fluctuations in the ratio of zooplankton numbers to fish numbers. Without considering larval densities, cumulative larval whitefish survival in 1984 would be expected to increase over 1983 values with higher zooplankton densities in 1984. Owing to improved overwintering survival of lake whitefish eggs, however, high densities of larval whitefish in the spring of 1984 lower the ratio relative to what was recorded in 1983. Thus, fewer zooplankton are available to individual larvae in 1984, energy became limiting and survival declined.

Hoagman (1974) states, "It is exceedingly doubtful that wild (whitefish) larvae would be unable to find and capture sufficient food for growth and maintanence. Thus, natural starvation seems remote...". In focusing only on characteristics of the larvae, however, Hoagman failed to consider trophic level interactions, interactions critical in controlling fish population dynamics. Interpreting the dynamics of larval lake whitefish in East Traverse, in light of their integration with zooplankton dynamics and overwintering egg mortality, reveals that larval lake whitefish are at times unable to find and capture sufficient food for growth and survival at critical stages of development. The integration of these dynamics into a comprehensive model describing whitefish year-class characteristics provides a critical prerequisite to an accurate management perspective of mechanisms controlling changes in the whitefish resource.

MANAGEMENT IMPLICATIONS

The stock-recruitment model has generally failed as a predictive tool in fisheries management. Due to the scope of the variability inherent in the stock-recruitment relationships, yield estimates can be inadequate and are often incorrect. The source of much of this variability and, consequently the low reliability of these realtionships, lies in the failure of these models to consider factors other than the fish stocks themselves as agents responsible for changes in year-class size. Attention is not directed to mechanisms operating in other life stages or originating from dependencies upon other trophic levels and abiotic factors. As these factors alter numbers throughout the pre-recruitment period, it is not surprising to find actual recruitment is often times much different than what is predicted by stock values.

By delineating some of the mechanisms which interact to control lake whitefish dynamics, this study may provide insights into improved forecasts of whitefish recruitment and yield. Within Grand Traverse Bay these estimates should be particularly reliable. Variations in winter severity influence both the number of eggs surviving to the larval stage and the initial abundance of zooplankton in the spring. During mild winters, control originating at the egg stage is responsible for eventual recruitment strength. The larval stage exerts its influence when numbers of larvae overwhelm the production capacity of food in the bay. During these years, survival through the larval stage is very important in determining year-class strength. The integration of these factors into a deterministic model provides a relationship between egg survival, a surrogate for stock size, and year-class strength similar to that described by Ricker for resource limited conditions. Basic differences, however, separate the two models. Instead of being highly correlative in nature, the equation described herein is mechanistic in scope. Recruitment is a function of factors clearly demonstrated as influencing year-class size rather than being related simply to the given stock size from which it is spawned. The early life history equation is also dynamic rather than fixed in nature. The magnitude of the curve produced by the equation responds to variations in the amount of energy available to individual organisms. As such, the year-class strength predicted from a given egg survival varies in accordance with prevailing zooplankton conditions each spring. Thus, a given egg survival may result in an array of recruitment levels as zooplankton density varies from year to year. Traditional models fail to incorporate these changes and predict one level of recruitment for each stock size.

Variations in spawning location and lake productivity may alter between variable relationships delineated in East Traverse. With different relations to prevailing wind conditions, ice movements and upwellings at other spawning locations in the lake, the interaction between these controlling mechanisms is likely site specific. This is most clearly demonstrated when latitudinal differences are considered. In higher latitude lakes, the role winter severity plays in year-class variability is reduced. Lakes are covered with ice each year and the catastrophic effects of open winters are eliminated. The larval stage is left as the period when year-class size is established. Differences in lake productivity between lakes within a year, or between years within a lake, largely determine recruitment. Increases in available energy with higher levels of productivity will allow a greater percentage of emergent larvae to live through the spring. Year classes will be higher than in lakes where or years when productivity, available energy and survival is poor. As the whitefish is well within its range in these northern lakes, biotic factors appear to be controlling its dynamics (Lack 1954).

In regions farther south, the importance of winter severity and overwintering egg mortality increases. Some years will be ice covered and others will not. Recruitment will be a function of egg survival during years without ice as losses during this stage cannot be compensated for with higher survival at later stages. During years of ice cover the year-class control sequence becomes much like that already described for more northern latitudes.

Unlike these northern regions, ice may seldom, if ever, cover spawning grounds at still more southern latitudes. As the whitefish is now on the edge or boundary of its range, abiotic factors replace biotic mechanisms as those controlling lake whitefish dynamics (Andrewartha and Birch 1954). Year-class strength becomes highly dependent upon the severity of the winter through which eggs incubate. Lake productivity, although generally higher at lower latitudes, (Brylinsky and Mann 1973) will influence year-class strength little as numbers of individuals have very likely been severely reduced previously. A few strong year classes will be apparent and resulting from years with cold, ice-covered winters. Survival of these cohorts at other stages of development is high owing to the higher level of productivity and available energy at these southern latitudes.

Consideration of these early life history factors and their inter-relationships may prove enlightening in the analysis of the dynamics of this cosmopolitan species of fish. Further studies investigating the question of interactions between environmental factors, the dynamics of fish life history and their relationship to recruitment are indeed necessary. Without them, improvements in our understanding of a species dynamics, and the biotic or abiotic mechanisms responsible for much of this variation, will be slowed. With them, advances in the ability of fisheries biologists to accurately predict yield will be forthcoming.

SUMMARY

1. Using data collected from laboratory experiments as well as field research in Grand Traverse Bay, Lake Michigan, overwintering lake whitefish egg survival was integrated with larval lake whitefish growth and survival rates and concurrent levels of prey abundance.

2. Annual variations in overwintering egg survival appear to influence lake whitefish year-class strength. Abundance of individuals in cohorts incubated in mild winters on spawning grounds lacking ice cover is significantly reduced relative to numbers hatching after severe winters when lakes are covered by ice. The number of eggs remaining on the spawning grounds following the cold winter of 1983/84 was 3.4 times greater than the number remaining after the warm winter of 1982/83 when ice did not form over the spawning ground.

3. A linear increase in larval survival with increasing specific growth rate was recorded in the laboratory. Larval growth rate and survival increased as the amount of zooplankton per fish larvae per 12 hour period became greater. Dramatic changes in survival occur between prey levels of 18 and 32 zooplankton per fish larvae per 12 hour period (z/f). Total mortality of larvae receiving low food rations ($\leq$ 10 z/f) rises sharply after larval yolk reserves are exhausted. Larvae being fed 32 and 110 z/f, however, exhibit little fluctuation in mortality subsequent to yolk sac resorption. Thus, prey density factors appear to be largely responsible for the expression of critical periods in larval whitefish development.

4. Trends similar to those recorded in laboratory research are apparent in field studies of larval growth and survival rates in 1984. Growth and survival rates again vary in proportion to the number of zooplankton available to each fish larvae (z/f). As z/f ratios decline to 23.5, growth rates fall below zero, survival rates decrease sharply, larval densities decline and a critical period in larval whitefish development is realized. Larval densities do not decline and a critical period in development is not apparent in 1983 when z/f ratios are high and constant.

5. Characteristics of larval whitefish prey selection are in large part responsible for the critical nature of Week 5 in 1984. Higher densities of smaller particles are ignored through much of the spring. Diets instead consist almost exclusively of adult/copepodite stages of copepods, with larvae ingesting zooplankton 0.70 to 1.10 mm long at higher rates than the abundance of these lengths in the environment would predict. Thus, near exhaustion of pools of energy available in larger prey organisms in Week 5 of 1984 contributes to the low survival and reduction in density observed at this time.

6. Incorporating prey selection data with information regarding overwintering egg survival, spring larval survival and spring zooplankton density results in a predictive model of whitefish year-class size in East Traverse. Using this model, the 1984 year-class of whitefish appears to be 2.4 times as large as the 1983 cohort. This prediction corresponds well with year-class estimates derived from spring larval whitefish samples (1984 2.1 times larger than 1983) and trawls for juvenile whitefish in East Traverse (1984 2.5 to 3.0 times larger than 1983). It is apparent that lake whitefish year-class strength can be reliably predicted given an accurate description of the early life history factors influencing the recruitment process.

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