GREAT LAKES FISHERY COMMISSION

2005 Project Completion Report[1]

Comparative bioenergetic modelling of lake whitefish populations in Lake Erie and Lake Ontario

by:

Chesley E. Lumb[2], Timothy B. Johnson[3], H. Andy Cook[3], and Jim A. Hoyle[4]

[2]Department of Biological Sciences
University of Windsor
401 Sunset Ave, Windsor, Ontario, N9B 3P4

[3]Ontario Ministry of Natural Resources
Lake Erie Fisheries Station
320 Milo Road, Wheatley, Ontario, N0P 2P0

[4]Ontario Ministry of Natural Resources
Glenora Fisheries Station
RR #4, Picton, Ontario, K0K 2T0

June 2005

SUMMARY

Our analyses demonstrated that lake whitefish in Lake Ontario attain a smaller size-at-age, are in poorer condition, and have a lower energy density than those in Lake Erie. Growth models based on recent (1989-2003) data suggest size-at-age has declined in Lake Ontario. In addition, back-calculated size-at-age for three time periods dating back to the 1950s suggest early growth rate (first 2 years of life) is where most of this decline has occurred. These younger age groups have a much higher reliance on planktonic prey than the older ages examined in our current analyses. However, bioenergetic analyse of these older age groups did suggest that shifts in diet composition and prey availability could account for large changes in lake whitefish growth potential. Temperature played a much more minor role in growth rate potential than did diet and prey availability. We therefore conclude that the decline in lake whitefish growth in Lake Ontario and to a lesser extent in Lake Erie, since the 1960s is a consequence of prey type and prey availability for all life stages of lake whitefish. Loss of *Diporeia,* an historically energy rich prey item, and it's subsequent replacement in the diets by dreissenid mussels is the probable factor regulating lake whitefish growth in Lake Ontario. A more diverse prey field, and a lower historic reliance on *Diporeia*, has buffered lake whitefish in Lake Erie from the same dramatic declines in growth and condition observed in Lake Ontario.

INTRODUCTION

Lake whitefish (*Coregonus clupeaformis*) are a cold-water, benthic-feeding fish native to the Great Lakes basin (Scott and Crossman 1973). This species has supported important commercial fisheries throughout the Great Lakes since the late 1800s (Baldwin *et al*. 2002). In the past, trends in abundance of lake whitefish were similar in Lake Erie and Lake Ontario. Stocks in both lakes declined during the 1950s and 1960s due to eutrophication (Christie 1968; Leach and Nepszy 1976), predation by exotic species, and over-exploitation (Christie 1972; Hartman 1972; Regier and Hartman 1973). Whitefish abundance rebounded during the late-1970s and 1980s due to a combination of factors: the Great Lakes Water Quality Agreement in 1972, which reduced phosphorous loading, commercial harvest management, and declining predator abundance (Casselman *et al*. 1996; Ryan *et al*. 1999; Ludsin *et al*. 2001). During the 1990s, the establishment of the zebra mussel (*Dreissena polymorpha*) and the quagga mussel (*Dreissena bugensis*) resulted in major changes to the ecosystems of the Great Lakes. Increased water clarity (Holland 1993) and reduced algal concentrations were attributed to the filtering activities of *Dreissena* (Johannsson *et al*. 1998). Changes in benthic macroinvertebrate populations were documented in southern Lake Michigan from 1980 to 1993 (Nalepa *et al*. 1998) and Lake Erie from 1979 to 1993 (Dermott and Kerec 1997). The sudden disappearance of the lipid-rich amphipod *Diporeia* from eastern Lake Ontario from 1993 to 1995, after establishment of nearshore dreissenid colonies (Dermott 2001), represented the loss of an important prey item from adult whitefish diets. While the direct cause for the decline of *Diporeia* remains unknown, it has been suggested that dreissenids compete with *Diporeia* by intercepting the supply of fresh algae due to filtering activities (Lozano *et al*. 2001). The amphipod, *Diporeia*, is a surface-feeding detritivore that relies on diatoms and other algae from nearshore waters (Nalepa *et al*. 1998). The populations of lake whitefish in Lake Erie and Lake Ontario have responded differently to changes in the benthic community.

In Lake Erie, the whitefish population is one stock that migrates in the early fall from the eastern basin to the western basin, where spawning occurs from late November until early

December. Whitefish over-winter in the shallow, western basin and move east as temperature increases in the spring. By the first week of July, lake whitefish are found in the eastern basin of Lake Erie, where they remain until the end of September (Hardy 1994). Hypoxic conditions in the central basin during the summer (Hartman 1972) limit habitat for adult whitefish, forcing movement to the deeper, cooler eastern basin in the summer (Cook *et al*. 2004). In Lake Erie, a diverse assortment of benthic prey is consumed by lake whitefish. The burrowing amphipod *Diporeia hoyi* (formally *Pontoporeia*) was historically an abundant benthic invertebrate in the eastern basin but declined in abundance after the colonization of the dreissenid mussels (Dermott and Munawar 1993). During the early 1990s, Hardy (1994) found whitefish diets to consist mainly of *Diporeia*, insect larvae and molluscs (snails and clams). Despite changes in the benthic community, abundance, growth and age-at-maturity of lake whitefish in Lake Erie remained relatively stable through the 1990s (Cook *et al*. 2004). Mean age-at-maturity calculated from index gill netting data for male and female whitefish from 1989 to 2001 was age-4. This was consistent with mean age-at-maturity calculated using commercial data from 1990 to 1993 (Hardy 1994).

In Lake Ontario, there are two spawning stocks of lake whitefish. The bay stock, which spawns in the Bay of Quinte, and the lake stock, which spawns along the south shore of Prince Edward County in the lake proper (Brown and Casselman, 1991). The bay stock spawns in late October to early November, while the lake stock spawns in mid- to late-November. Both stocks mix in the summer in the outlet basin, in the northeastern part of the lake (Christie *et al*. 1987). Historically, the primary diet items of whitefish in Lake Ontario were the burrowing amphipod *Diporeia* and the zooplankter *Mysis relicta*. Molluscs and insect larvae were also consumed (Hart 1931; Ihssen *et al*. 1981). In 1998 and 2001, summer diet analysis revealed dreissenid mussels dominated whitefish diet. Other molluscs were also consumed, such as snails and sphaeriid clams, but *Diporeia* was absent (Hoyle 2004). In 1997, lake whitefish were caught during assessment gill netting in depths of 85m in southeastern Lake Ontario for the first time since monitoring began in 1980 (Owens *et al*. 2003b). It was suggested that whitefish responded to the loss of *Diporeia* from traditional feeding areas in the northeast part of the lake by foraging in deeper water (Owens *et al*. 2003a). Declines in abundance and growth of lake whitefish were first observed in the mid-1990s (Hoyle *et al*. 2003). Mean age-at-maturity began to increase in 1996. Female mean age-at-maturity was age-4 during the mid-1990s and rose to age-7 by 2002 (Hoyle 2004).

In a recent synthesis describing food web dynamics in Lake Ontario, Mills *et al*. (2003) examined stressors that have led to ecological changes in the ecosystem. Two of the most notable changes were reduction of phosphorous loadings and invasion by dreissenid mussels. Data collected from lakes Erie and Ontario since 1990 allows the status of lake whitefish to be described; however, historic data, needed to conduct temporal comparisons, is incomplete. The objective of this study was to compare changes in biological attributes of lake whitefish from Lake Erie and Lake Ontario from 1990 to 2003 and to describe the ecology of these fish in the lower lakes based on samples collected in 2003.

SUMMARY OF ACCOMPLISHMENTS

Objective 1: Synthesize available physiological parameters for lake whitefish and related species.
Results: The generalised coregonid bioenergetics model (Rudstam et al. 1994) has been updated through laboratory experimentation and field validation by Dr. Charles Madenjian and colleagues (Madenjian et al. in review a and b).

Status: Objective accomplished.

Objective 2: Acquire information on the energy density of lake whitefish and common prey items form the literature. If required, additional samples will be obtained through field sampling.
Results: Energy density (J/g wet mass) of lake whitefish was determined for each lake, using a range of body sizes and sampled throughout the season. Energy density of invertebrate prey was obtained from the literature.
Status: Objective accomplished.

Objective 3: Synthesize available trend through time data on growth, distribution, annual and seasonal thermal history, and diet for populations of lake whitefish from Lake Ontario and Lake Erie.
Results: Historic index data collected by OMNR for both systems was summarised and analysed to evaluate trends in growth and size-at-age, condition, and diet. Thermal history and distribution were inferred from temperature preference data and available water temperature and oxygen data.
Status: Objective accomplished.

Objective 4: Conduct field sampling to better describe dynamics of seasonal growth and diet of lake whitefish.
Results: Lake whitefish were sampled from commercial fisheries and agency programs (OMNR and NYSDEC) for both Lake Erie and Lake Ontario in 2003. Fish were analysed for energy content, diet, and general morphometrics.
Status: Objective accomplished.

Objective 5: Parameterise and calibrate a lake whitefish bioenergetic model for Lake Ontario and Lake Erie.
Results: See objective 1. A meeting as well as electronic and telephone consultation with Dr. Madenjian and Dr. O'Connor (both with USGS-GLSC) provided the opportunity to calibrate their lake whitefish parameter set with Lake Erie and Lake Ontario data. The model performed well in both systems.
Status: Objective accomplished.

Objective 6: Use the models to evaluate the following hypotheses that differences in growth and condition of lake whitefish among the two populations and at various time stanzas are due to: 1) diet, 2) thermal distribution, 3) density-dependence, and 4) interaction of the other mechanisms.
Results: The effects of changing prey regime and thermal regime and their interaction were evaluated using the bioenergetic models calibrated for Lake Erie and Lake Ontario. Density-dependence was not specifically evaluated as insufficient data were available to describe the population demographic in either Lake.
Status: Objective accomplished.

DETAILED RESULTS

Objective 1. Synthesise available physiological parameters for lake whitefish and related species.

Dr Charles Madenjian and colleagues at the USGS – Great Lakes Science Center (Ann Arbor, MI) conducted laboratory experiments and a field validation to revise the generalised coregonid bioenergetic parameter set of Rudstam et al. 1994 (2 manuscripts are currently under review – Madenjian et al. unpubl a, and Madenjian et al. unpubl. b). We regularly communicated with Dr Madenjian and his team, arranged a meeting to share our field summaries from Lake Erie and Lake Ontario, and have been given permission to use their findings (and updated parameters) while their work undergoes peer review.

Objective 2. Acquire information on the energy density of lake whitefish and common prey items from the literature. If required, additional samples will be obtained through field sampling.

Lake whitefish energy density increased with wet mass in both Lake Erie and Lake Ontario (Fig. 1). A single (linear) regression model was fit to the Lake Ontario data (ED = 5002 + 1.4992 W, R^2 = 0.36, N = 41 where ED is lake whitefish energy density (J/g wet mass) and W is body mass (g)). Two regression equations were fitted for lake whitefish from Lake Erie to account for the more gradual increase in energy density for lake whitefish greater than 1000 g. A similar two-phase model has been reported for lake whitefish from Lake Michigan (Madenjian et al. in review a). The regression models for Lake Erie were: ED = 5984 + 3.216 W for fish <1000 g, and ED = 8108 + 1.074 W for fish > 1000 g. Energy density of lake whitefish from Lake Erie was significantly greater than from Lake Ontario ($F_{1,96}$=33.1, P<0.001). In 2003, mean energy density of lake whitefish from Lake Erie was 8907 ± 186 J/g wet mass compared to 6982 ± 200 J/g wet mass for Lake Ontario lake whitefish.
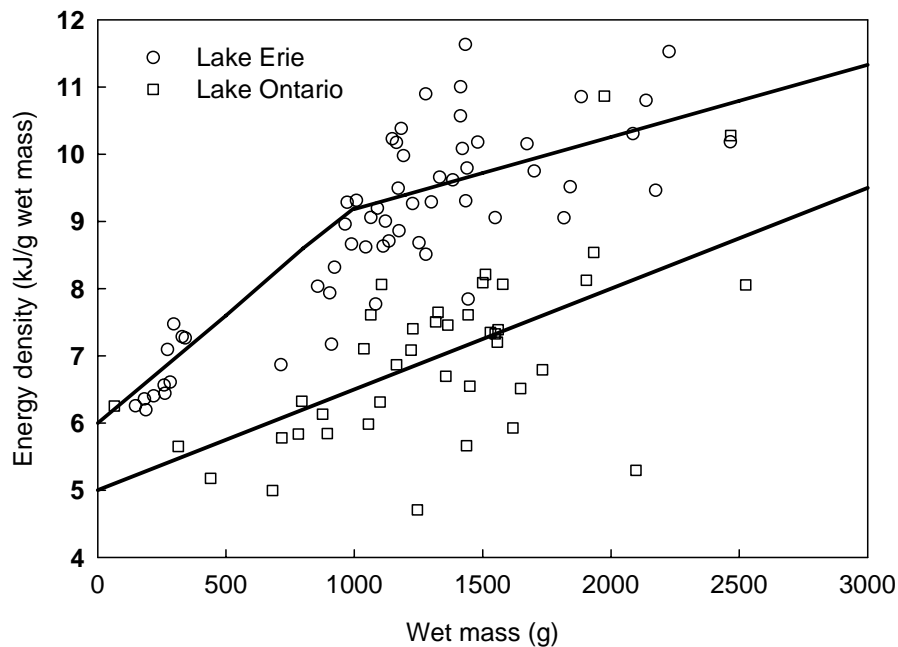
Figure 1.- Energy content (kJ/g wet mass) from whole body homogenates of lake whitefish from Lake Erie and Lake Ontario. Samples were collected May to November 2003.

Estimates of energy density for common prey items of lake whitefish were obtained from the literature (Table 1). Energy density ranged from 1,068 J/g wet mass for dreissenid mussels (when corrected for indigestible shell fraction (Johannsson et al. 2000) to 4,368 J/g for amphipods and 6,247 for fish eggs.

Table 1: Energy density (J/g wet mass) of lake whitefish prey items used in bioenergetics modeling.

Taxon	Energy density (J/g)
Zooplankton	2220[a]
Mysis	3924[c]
Dreissenia spp.	2428[b]
*shell corrected	1068*
Pelecypoda	2114[a]
Gastropods	1800[a]
Amphipoda	4368[a]
Chironomidae	3134[a]
Salmonidae eggs	6247[a]
Other prey	2500[a]

Sources: a. Cummins and Wuycheck 1971
b. Schneider 1992 (soft tissue only) *assumes 56% shell mass
c. Madenjian *et al.* (in review B)

Objective 3. Synthesize available trend-through-time data bases on growth, distribution, annual and seasonal thermal history, and diet for populations of lake whitefish in Lake Ontario and Lake Erie.

Length-at-age of lake whitefish from Lake Ontario was significantly smaller in 1997-2003 compared to all other groups (F = 1.85, df = 1258, 1252, *P*<0.001) (Fig. 2). Lake Ontario length-at-age from 1989-1996 was significantly different from Lake Erie (F = 1.15, df = 1256, 1252, *P* = 0.007). There was no significant difference in size between Lake Erie before and after 1997 (F = 1.01, df = 1254, 1252, *P* = 0.431).
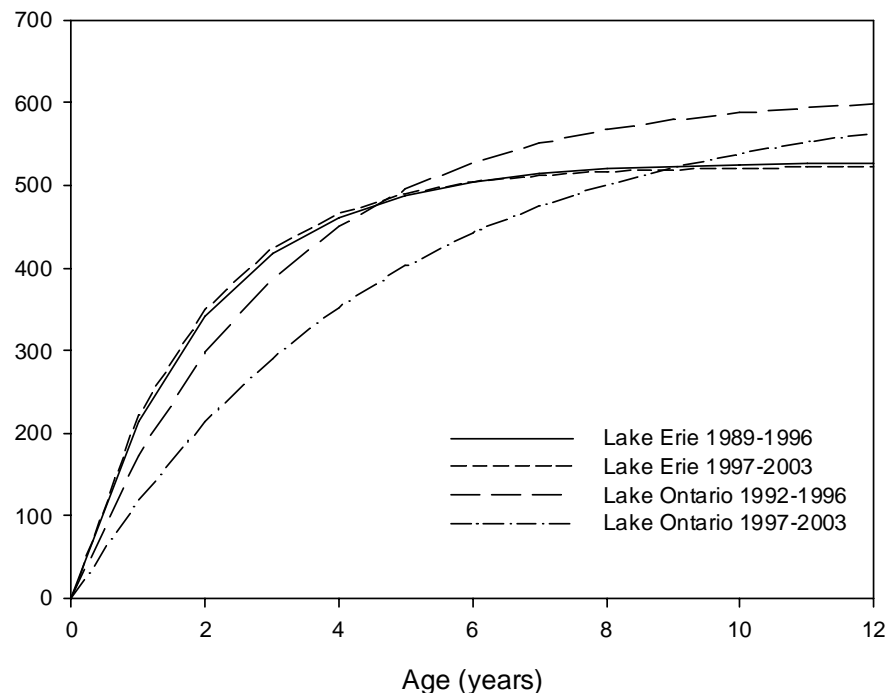

Figure 2.- Predicted length-at-age of female lake whitefish modeled using the von Bertalanffy growth function for Lake Erie and Lake Ontario. Growth was modeled separately for two periods within the time series for each lake: Lake Erie 1989-1996 and Lake Ontario 1992-1996. Growth was modeled individually for both lakes from 1997-2003.

Archived fish scales were used to determine annual growth increment of lake whitefish during three time periods: pre-phosphorous control (1954-58 year-classes), pre-dreissenid invasion (1977-82 year-classes), and post-dreissenid invasion (1991-96 year-classes). In both lakes, mean increment width decreased significantly in the first year of life between time periods 2 and 3 (MANOVA: $F_{2, 69}$=10.90, *P*<0.001, Fig. 3A). Mean increment width also decreased significantly in the second year of life, between time periods 1 and 3 (MANOVA: $F_{2, 69}$=11.97, *P*<0.001, Fig. 3B). In the third year of life, results were interpreted at the level of the interaction of the treatment variables (lake and time period), due to the significant interaction. Mean increment width was significantly different in Lake Ontario between time periods 1 and 2 (Tukey's HSD: *P*=0.02, Fig. 3C), time periods 2 and 3 (Tukey's HSD: *P*<0.001, Fig. 3C), but there was no change in Lake Erie. By the fourth year of life, there was no change in mean increment width in Lake Erie or Lake Ontario (MANOVA: $F_{2, 69}$=0.55, *P*=0.57, Fig.3D).
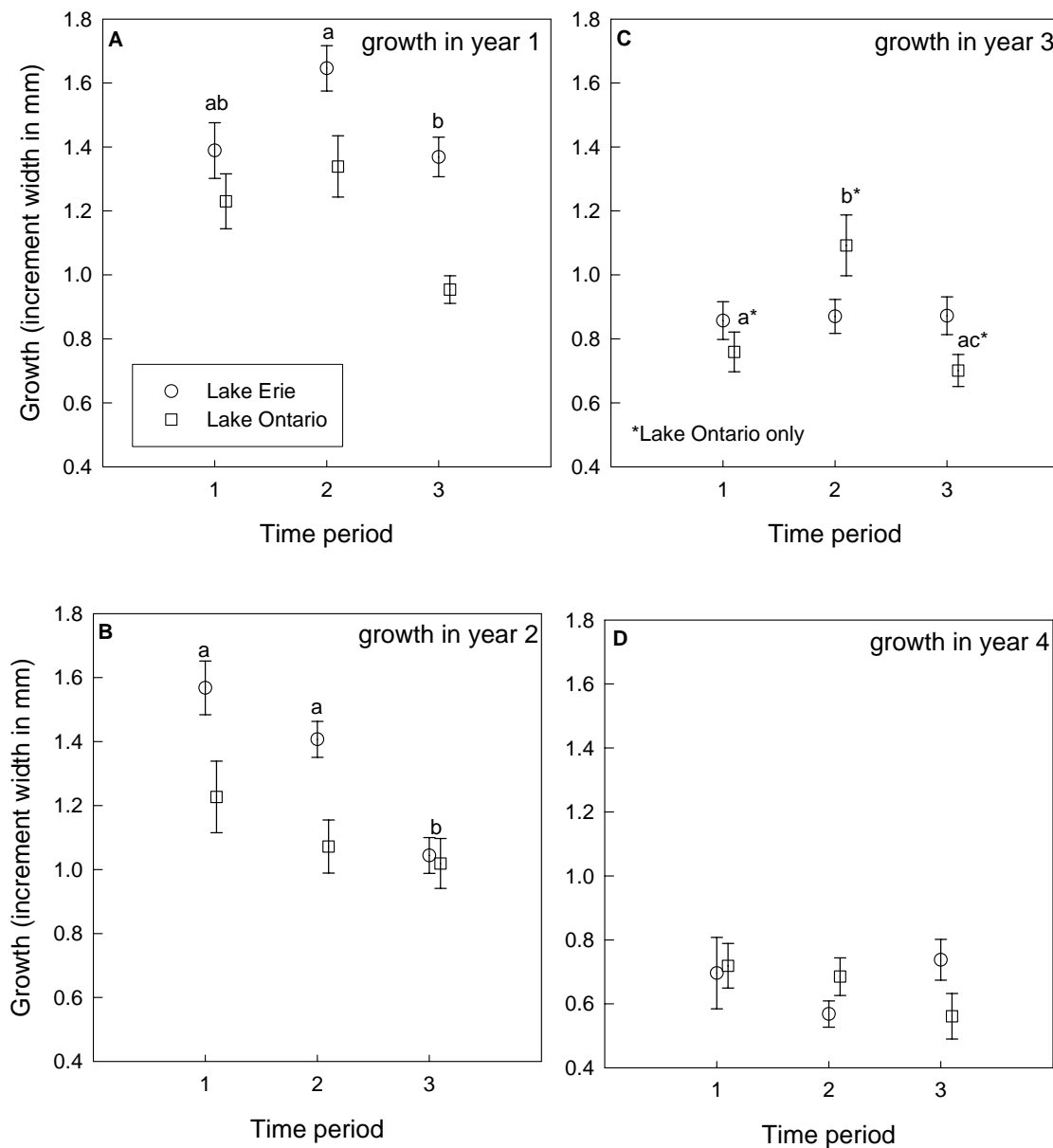
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Figure 3.- Back-calculated weight-at-age for lake whitefish in Lake Ontario (squares) and Lake Erie (circles) for three time periods corresponding to pre-phosphorous control, post-phosphorous control but pre-dreissenid invasion, and post-dreissenid invasion.

Condition was greater in Lake Erie compared to Lake Ontario throughout the time series (Fig. 4). Declines in condition are evident in both lakes by 1994. During the late 1990s, condition of lake whitefish from Lake Erie fluctuated around the long-term average of 1.12 and began to increase in 2001. Condition remained less than the long-term average (0.85) in Lake Ontario until 2000, when condition began to fluctuate around the long-term average.
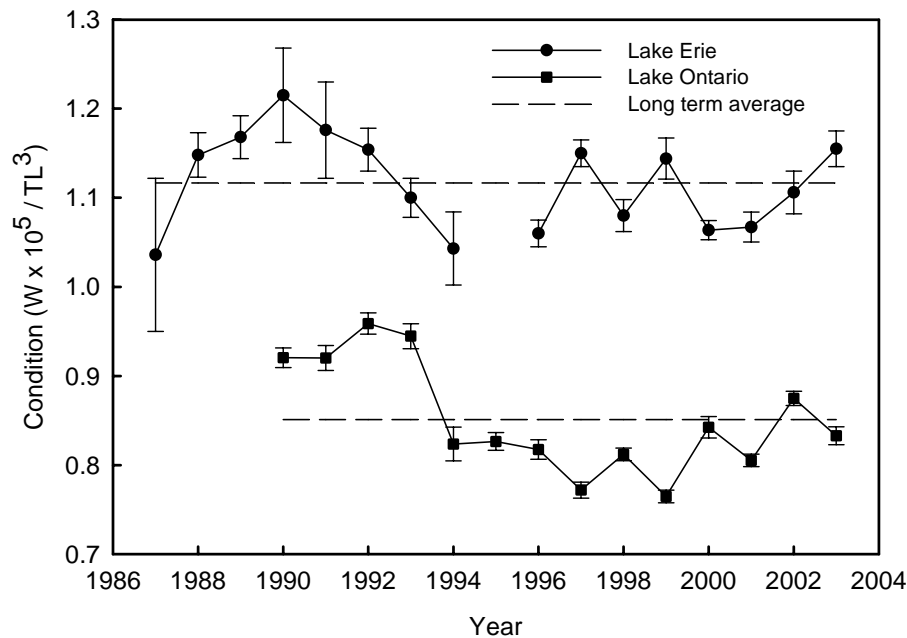
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Figure 4.- Lake whitefish condition factor (weight x 10^5/length^3) for Lake Erie and Lake Ontario, 1987 to 2003. All fish were mature, pre-spawned female lake whitefish collected in the fall from commercial catches or index gill netting. Error bars represent ± one standard error.

To describe thermal history of lake whitefish in Lake Erie and Lake Ontario, we assumed the fish would select the warmest temperature available, up to the physiological optimum (12 C, Christie and Regier 1988). Limited dissolved oxygen data were available from previous years, and results from 2003 suggested no evidence of oxygen limiting the distribution of lake whitefish within their expected summer geographic range. In eastern Lake Ontario, we assumed daily water temperatures recorded at the Kingston municipal water intake (18m depth) reflected the available thermal habitat for lake whitefish. This assumption was supported by regular temperature and oxygen monitoring at a number of locations in the Outlet Basin of eastern Lake Ontario in 2003, as well as more limited data from previous years. There was no evidence of low dissolved oxygen limiting lake whitefish distribution in eastern Lake Ontario. In Lake Erie, we assumed lake whitefish migrated throughout the lake in pursuit of suitable temperature and oxygen conditions. In the spring lake whitefish migrate eastward from the western basin. By July warm temperatures and potential hypoxic conditions in the central basin prompt lake whitefish to move to the eastern basin where they remain until the fall when a westward migration eventually takes the lake whitefish back to the western basin to spawn. Using the 12 C threshold to prompt inter-basin movement, thermal distribution of lake whitefish was reflected by daily water intake temperatures from central (Elgin municipal water works, 9.75m depth) and eastern (Port Dover municipal water works, 4m depth) Lake Erie. Cook et al. (2005) describe the available thermal habitat for lake whitefish in Lake Erie in 2001. These expected thermal distributions are supported by historic and index CPUE data for lake whitefish in both lakes (Hardy 1994 and unpubl. data).
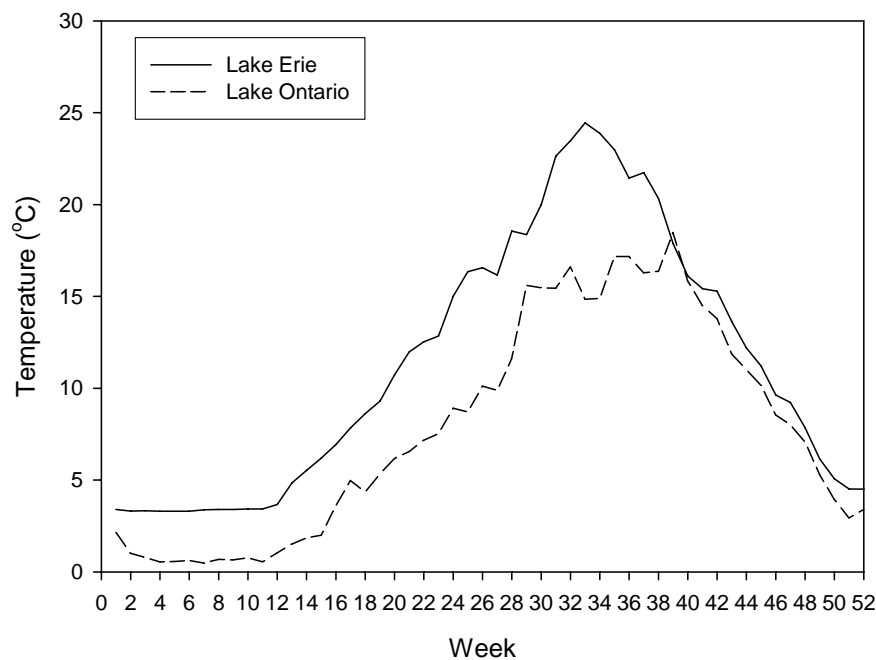
Figure 5.- Estimated weekly water temperature in Lake Erie and Lake Ontario in 2003. Lake whitefish were assumed to occupy the warmest available temperature up to 12 C, their preferred thermal optimum.

Historic diet data is extremely limiting in both lakes. We therefore used stable isotopic signatures derived from lake whitefish scales to infer large scale changes in feeding behaviour. The stable isotope result is described more fully under objective 6.

Objective 4. Conduct field sampling to better describe dynamics of seasonal growth and diet of lake whitefish. Samples will be obtained from multi-mesh index gillnet set at strategic locations, as well as from routine commercial catch sampling.

In total, 327 and 167 lake whitefish were sampled from Lake Erie and Lake Ontario, respectively, in 2003. These fish were sampled for basic morphometrics (length, weight, age), with a subset being processed for energy density, diet, and reproductive output (GSI and fecundity).

Chironomids, dreissenid mussels and sphaeriids made up the bulk of lake whitefish diet in Lake Erie during 2003 (Table 1). Zooplankton and gastropods were also consumed. Compared to diet in Lake Erie, lake whitefish diet in Lake Ontario demonstrated more seasonal variability. Amphipods and fish eggs were a large proportion of spring and fall diets, but were absent from the summer diet. Dreissenid mussels were consumed in all seasons, and constituted the majority of summer diet. Zooplankton and gastropods were also consumed in both lakes.

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Table 2.- Seasonal diets of lake whitefish from Lake Erie and Lake Ontario calculated as percent wet weight (weighted means). Spring = Apr-Jun; Summer = Jul-Sep; Fall = Oct-Dec. Sample sizes represent the number of stomachs examined with contents. Other category consisted mostly of unidentifiable digested material also cladoceran eggs, fish scales, isopods and nematodes.

Prey item	Lake Erie			Lake Ontario		
	spring	summer	fall	spring	summer	fall
	n=18	n=29	n=23	n=8	n=48	n=16
amphipods	0.0	0.9	4.3	50.0	0.0	27.8
chironomid larvae	6.5	7.8	0.1	0.0	4.8	0.0
chironomid pupae	30.4	14.6	0.0	0.0	2.1	0.0
dreissenid mussels	18.7	18.7	22.4	15.6	70.8	12.4
eggs	2.7	0.9	0.0	12.5	2.1	19.9
gastropods	3.3	0.0	11.8	9.4	10.4	39.9
other	5.5	3.5	1.1	0.0	3.9	0.0
sphaeriids	30.0	34.4	52.6	0.0	1.8	0.0
zooplankton	2.9	18.5	7.7	12.5	4.1	0.0

Objective 5. Parameterize and calibrate a whitefish bioenergetic model for Lake Ontario and Lake Erie. Inherent in this objective is the development of lake whitefish population models for each system. This work will build on previous efforts (CAGEAN) while utilizing the more robust programming environment available in AD Model Builder.

The generalized coregonid bioenergetics model (Rudstam et al. 1994) was refined and validated for lake whitefish by Madenjian *et al*. (in review a and b) using laboratory and field data. The Madenjian *et al*. model was calibrated using field data collected during 2003 to create lake-specific models: one for Lake Erie lake whitefish and one for Lake Ontario lake whitefish. Historic data from three time periods were used to investigate changes in growth rate between ages of 4 and 5. Time periods were defined as follows: time period 1 = 1954-1962 (pre-phosphorous abatement), time period 2 = 1977-1986 (post-phosphorous abatement but pre-dreissenid invasion), and time period 3 = 1991-2003 (post-dreissenid invasion).

For the 2003 calibration data set, the model performed well using normal diagnostics (annual growth trajectory / shape, estimated gross conversion efficiency). The magnitude of the bioenergetic p-value was lower than expected, but was very similar to that observed by Madenjian and colleagues when applying the model to Lake Michigan and Lake Huron lake whitefish stocks.

Objective 6 – Use the models to evaluate the following hypotheses that the differences in growth and condition of lake whitefish among the two populations and at various time stanza are due to:
   a. **differences in diet composition;**
   b. **differences in thermal distribution related to seasonal movement modified by changing environmental conditions (i.e. hypoxic conditions, changes in prey distribution and abundance);**

    c. density-dependent effects of lake whitefish and declining populations of Diporeia, and;

    d. interaction among the above factors (diet, temperature, and density-dependence).

       A sensitivity analysis was performed on the model to evaluate the potential importance of changes in diet and thermal habitat. Given our assumptions about thermal distribution (upper limit of 12 C), large differences in annual thermal pattern yielded relatively small differences in growth rate potential. The coldest year (1977) (Fig. 6) simulation yielded a 6% reduction in weight-at-age for age 5 lake whitefish in Lake Erie, while the warmest year (1990) resulted in an 8% increase in weight-at-age relative to the 2003 baseline. Interannual variation in temperature was therefore considered unlikely to explain large changes in growth rate.
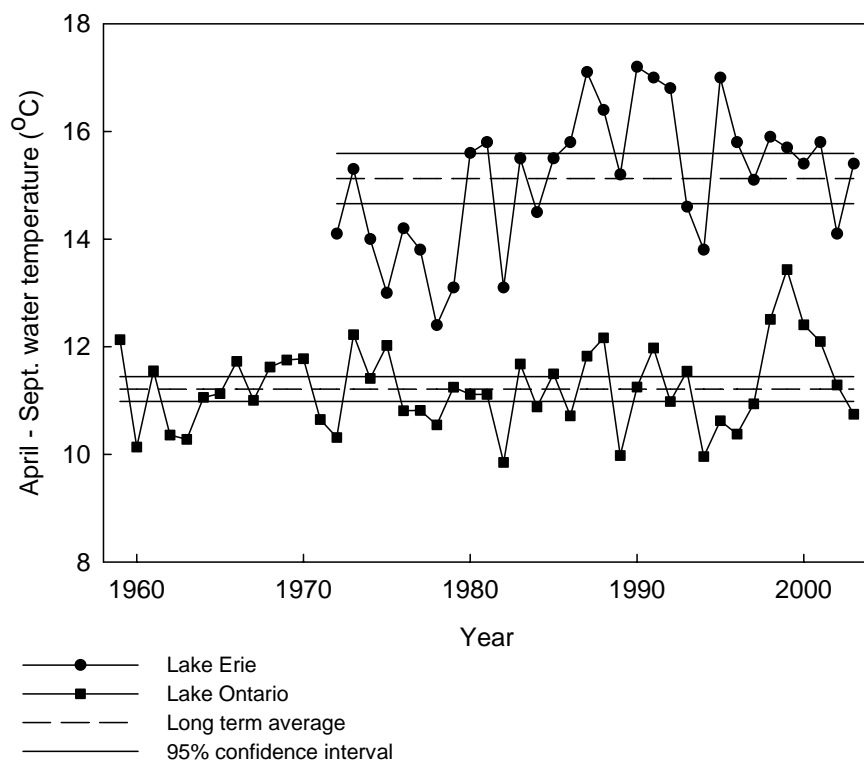

Figure 6.- Annual mean temperature for Lake Erie and Lake Ontario for the growing season, April to September revealed Lake Erie is warmer than Lake Ontario. The coldest and warmest years from Lake Erie were used in bioenergetics run simulations to determine how much temperature influences weight-at-age 5. Observed weight-at-age 5 was compared to weight predicted by the bioenergetics models for Lake Erie lake whitefish. Growth chronologies were constructed using lake whitefish scales to calculate observed weight at age.

       Like the temperature analysis, extreme diets were used to determine how much diet composition could affect growth rate potential (weight-at-age 5). Two hypothetical diets were created, one with 100% dreissenid mussels (an energy-poor diet item) and one with 100% amphipods (an energy rich diet item). Predicted weights were compared to the observed weight-at-age 5. In Lake Erie, the exclusive dreissenid mussels diet decreased weight-at-age 5 by 53%, while the 100% amphipod diet increased weight at age by 61%. Similarly, in Lake Ontario, the

exclusive dreissenid mussels diet decreased weight-at-age 5 by 42%, while the 100% amphipod diet increased weight at age by 81%.

   The bioenergetics models were used to test the effect of diet composition on growth rates. Keeping all other conditions constant, diets were switched between Lake Erie and Lake Ontario for all three time periods (Fig. 7). For the most recent time period, Lake Erie fish would be expected to grow poorly if provided a Lake Ontario diet, while Lake Ontario fish would grow well eating a Lake Erie diet. In other words, the current state of the prey resource, as reflected by lake whitefish diets, does explain the recent observation of poor lake whitefish growth in eastern Lake Ontario while Lake Erie lake whitefish continue to grow well.
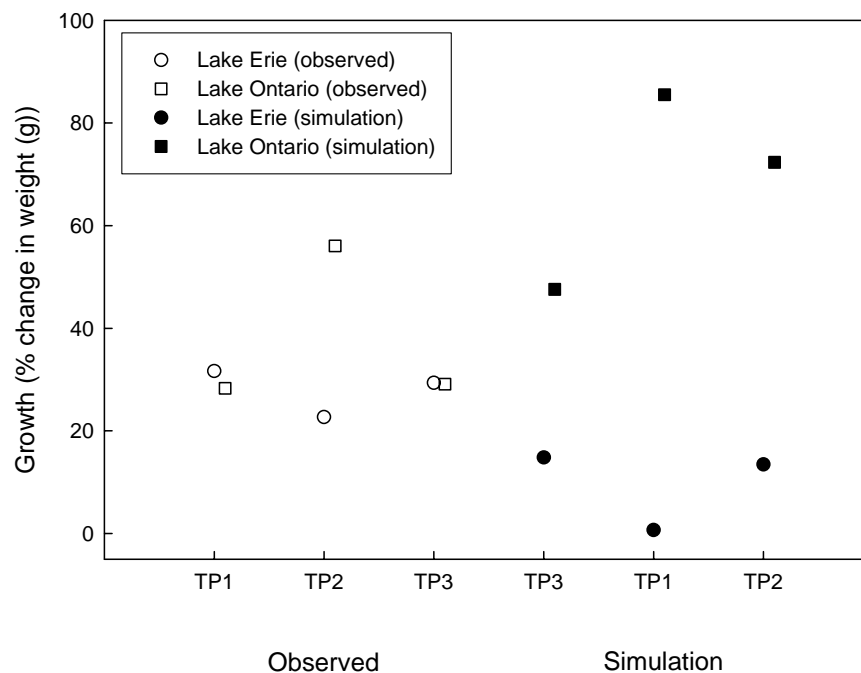

Figure 7.- The effect of reciprocal diet crosses on lake whitefish growth between Lake Erie and Lake Ontario during three periods (TP1~1954-1962, TP2~1977-1986, TP3~1991-2003). Result is expressed as the percent change in weight for a lake whitefish growing from age-4 to age-5 (i.e. $(weight_5 - weight_4) / weight_4$). Observed weight-at-age was estimated from back-calculated length-at-age using length-weight relationships for each lake in each of the 3 time periods. Simulated weight-at-age was generated using a lake whitefish bioenergetics model modified for Lake Erie and Lake Ontario, based on three reciprocal crosses where diets were switched between the two lakes, within time periods 1, 2, and 3.

   To evaluate the simultaneous effects of diet and environmental quality, simulations were run where lake whitefish were exposed to diets from the first time period (1954-62) while experiencing all other conditions (temperature, initial weight, spawning losses, resource quality (p-value)) characteristic of that lake in the current time period. Similar "experiments" were done for both lakes and reversing time periods) (Fig. 8). In both lakes, present day lake whitefish would attain a larger body size if historic prey were available at comparable densities to present day prey. In other words, the higher p-value observed in the most recent time period reflects a greater availability of prey, but the quality (energy density) of historic prey was greater.
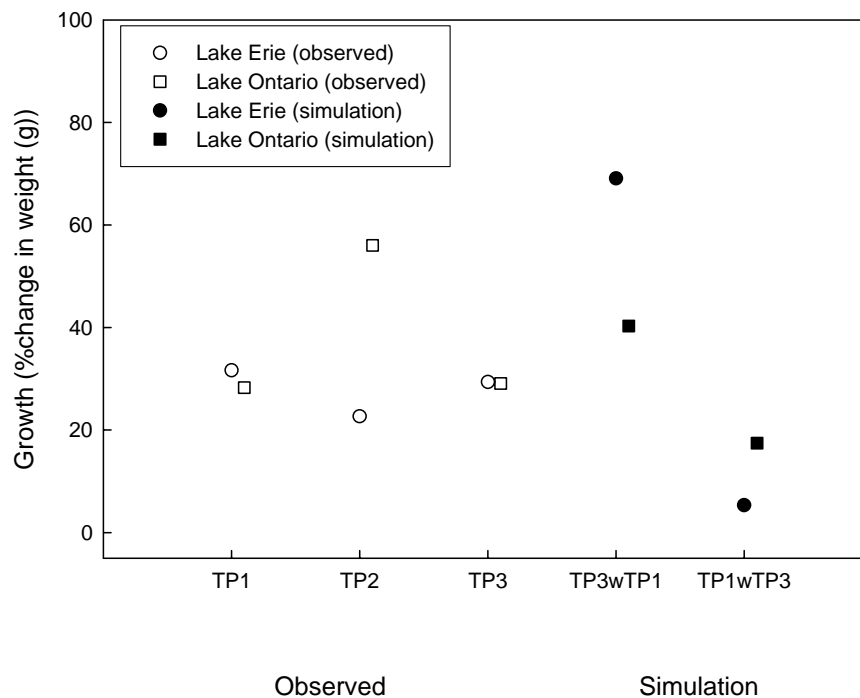
Figure 8.- The effect of diet reciprocal crosses between time periods 1 and 3 on growth of lake whitefish within Lake Erie and Lake Ontario, calculated as % change in weight between the ages of 4 and 5. Observed weight-at-age was estimated from back-calculated length-at-age using length-weight relationships for each lake, in 3 time periods: TP1~1954-1962, TP2~1977-1986, TP3~1991-2003. Simulated weight-at-age was generated using a lake whitefish bioenergetics model modified for Lake Erie and Lake Ontario, based on two reciprocal crosses where diets were switched within each lake, across time period 1 and 3 (time period 3 with time period 1 diet [TP3wTP1] and time period 1 with time period 3 diet [TP1wTP3]).

To further explore the relationship between quantity and quality of prey, we simulated the effect of changing the proportion of dreissenid mussels in the diet on the growth rate potential of lake whitefish (Fig. 9). Continued increases in the density (and therefore the assumed dietary proportion) of dreissenid mussels by 10-20% would lead to a net increase in lake whitefish growth, producing a final weight at age similar to that seen in the second time period (1977-1986). However, increases in dreissenid density of 50% of more will result in substantial declines in lake whitefish growth rate potential.

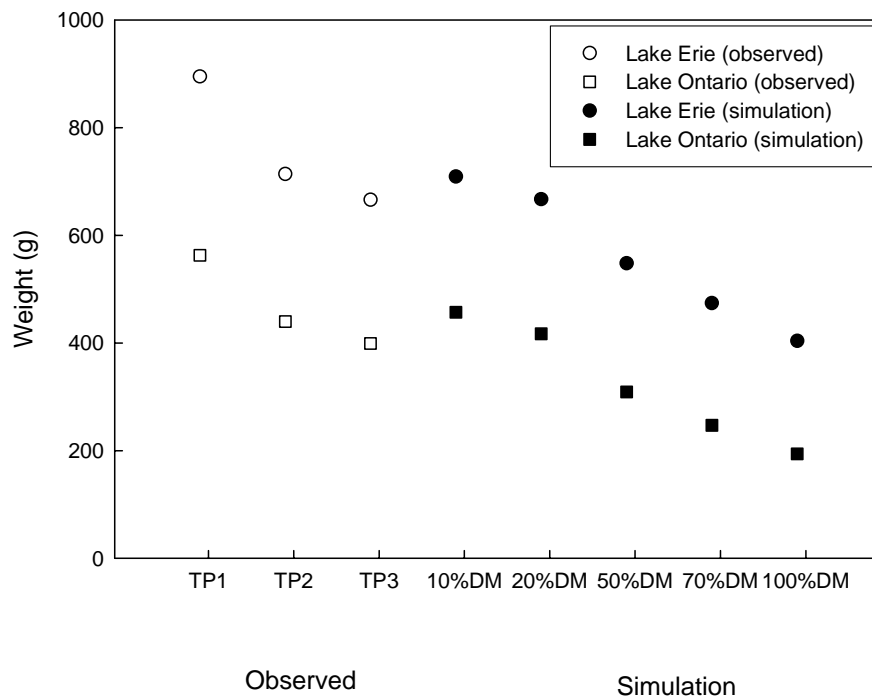Observed   Simulation

Figure 9.- The effect on weight-at-age 5 of increased dreissenid mussels in diets of lake whitefish from Lake Erie
and Lake Ontario. Observed weight-at-age was estimated from back-calculated length-at-age using length-
weight relationships for each lake, in 3 time periods: TP1~1954-1962, TP2~1977-1986, TP3~1991-2003.
Simulated weight-at-age was generated using a lake whitefish bioenergetics model modified for Lake Erie
and Lake Ontario. Increasing proportion of dreissenid mussels were the same for Lake Erie and Lake
Ontario: 10% [10DM], 20% [20DM], 50% [50DM], 70% [70DM] and 100% [100DM].

To supplement historic diet data, stable isotope analyses were used to characterise broad
changes in lake whitefish diet. Stable carbon and nitrogen isotopic ratios were used to compare
lake whitefish feeding ecology during the three time periods (Fig. 10). The relationship between
$\delta^{13}C$ and $\delta^{15}N$ in fish scales and dorsal muscle of lake whitefish collected from Lake Erie and
Lake Ontario during 2003, was used to predict $\delta^{13}C$ and $\delta^{15}N$ in muscle based on archived scale
samples. There was a significant relationship between $\delta^{13}C$ in scale and muscle in both lakes
($P<0.001$) and a significant relationship between $\delta^{15}N$ in scale and muscle in Lake Erie
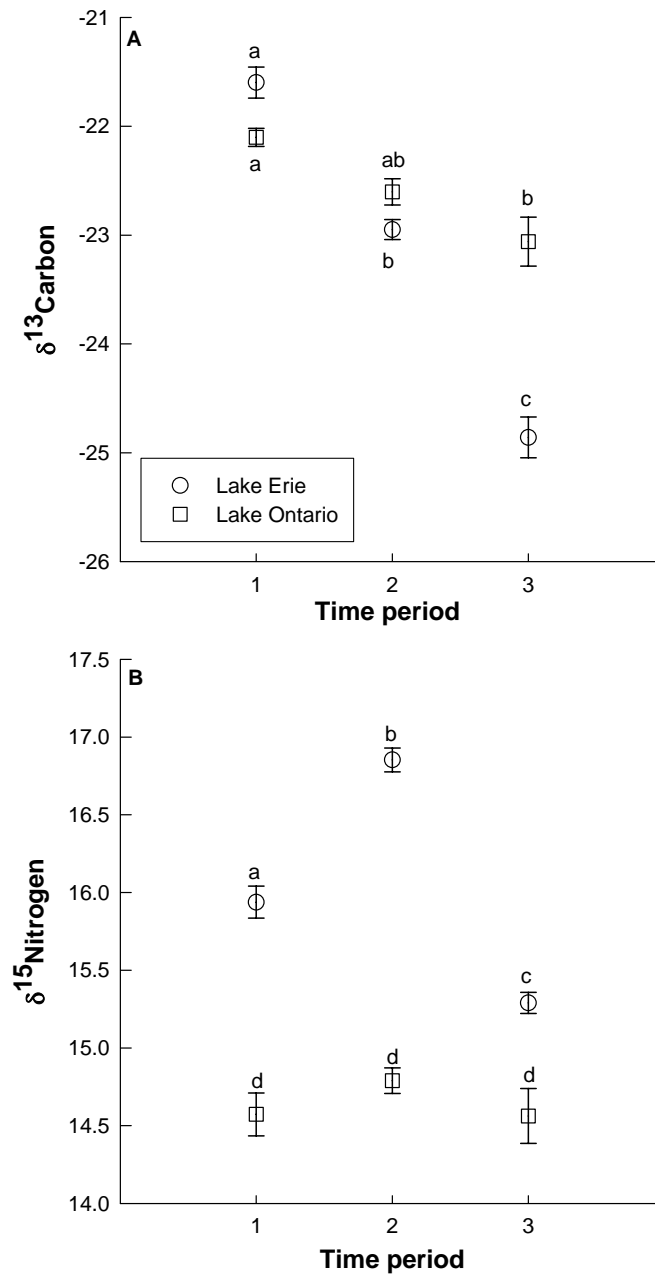($P=0.002$) but not in Lake Ontario ($P=0.07$).

Figure 10.- Mean $\delta^{13}C$ (A) and $\delta^{15}N$ (B) (±1 SE) of lake whitefish from Lake Erie and Lake Ontario during 3 time periods: 1~1954-1962, 2~1977-1986, 3~1991-2003. Statistically different groups ($P<0.05$) are represented by letters (a-d).

When $\delta^{13}C$ values and $\delta^{15}N$ values were plotted together for lake whitefish from Lake Erie and Lake Ontario over time, in combination with benthic invertebrates collected from both lakes in 2003, it appeared that dreissenid mussels had more depleted $\delta^{13}C$ values relative to other benthic invertebrates (Fig. 11). The depleted delta carbon-13 values that were observed in lake whitefish in time period three reflects the inclusion of dreissenid mussels in the diet.
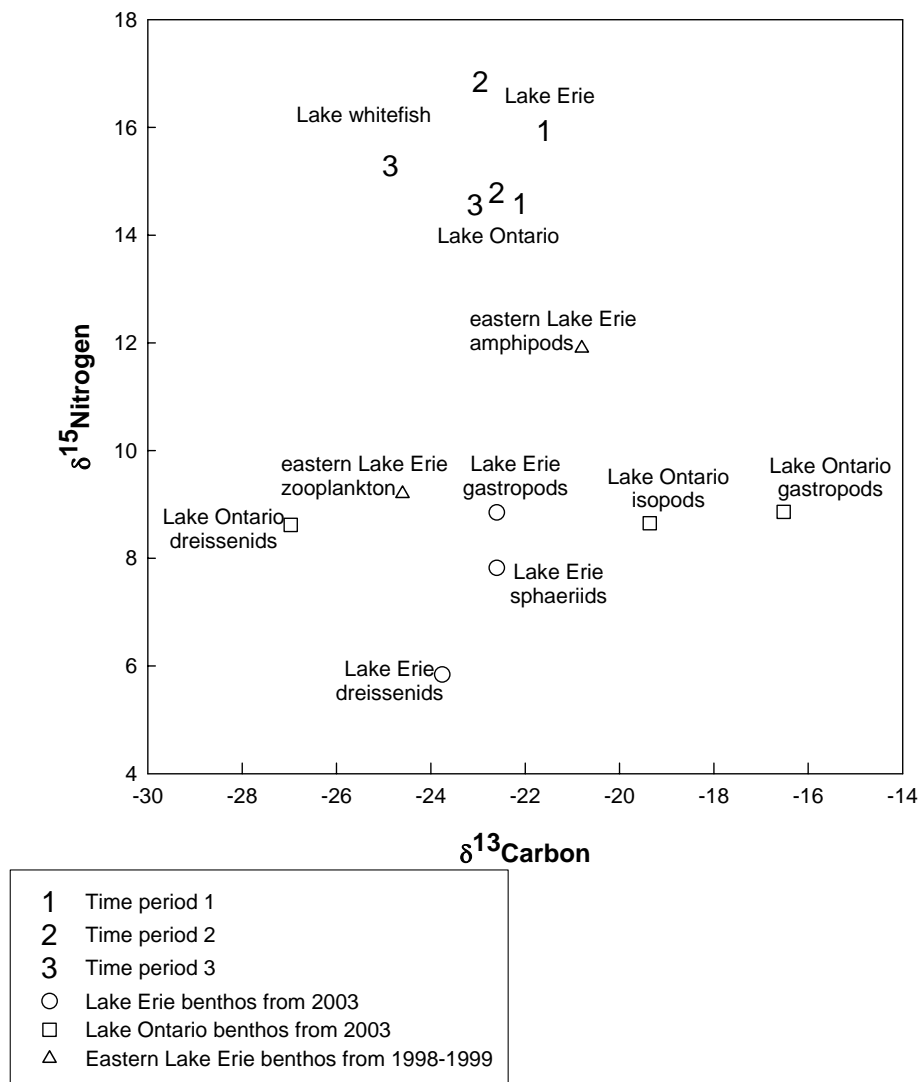
Figure 11.- Delta carbon-13 (δ^{13}C) and delta nitrogen-15 (δ^{15}N) isotopic composition of lake whitefish from Lake Erie and Lake Ontario during 3 time periods: **1**~1954-1962, **2**~1977-1986, **3**~1991-2003 and benthic invertebrates collected from Lake Erie and Lake Ontario in 2003. Also plotted are isotopic composition of zooplankton and amphipods collected from eastern Lake Erie by Vega (2000) in 1998-1999.

CONCLUSIONS

Our analyses demonstrated that lake whitefish in Lake Ontario attain a smaller size-at-age, are in poorer condition, and have a lower energy density than those in Lake Erie. Growth models based on recent (1989-2003) data suggest size-at-age has declined in Lake Ontario. In addition, back-calculated size-at-age for three time periods dating back to the 1950s suggest early growth rate (first 2 years of life) is where most of this decline has occurred. These younger age groups have a much higher reliance on planktonic prey than the older ages examined in our current analyses. However, bioenergetic analyse of these older age groups did suggest that shifts

in diet composition and prey availability could account for large changes in lake whitefish growth potential. Temperature played a much more minor role in growth rate potential than did diet and prey availability. We therefore conclude that the decline in lake whitefish growth in Lake Ontario and to a lesser extent in Lake Erie since the 1960s is a consequence of prey type and prey availability for all life stages of lake whitefish. Loss of *Diporeia,* an historically energy rich prey item, and it's subsequent replacement in the diets by dreissenid mussels is the probable factor governing lake whitefish growth in Lake Ontario. A more diverse prey field, and a lower historic reliance on *Diporeia*, has buffered lake whitefish in Lake Erie from the same dramatic declines in growth and condition observed in Lake Ontario.

ACKNOWELDGEMENTS

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Appendix 1.- Products generated from this research project.

Presentations

1. Lumb, C.E., T.B. Johnson, H.A. Cook, and J.A. Hoyle. Comparative bioenergetics of lake whitefish (*Coregonus clupeaformis*) in lakes Erie and Ontario. 48th Ann. Conf. Int. Assoc. Great Lakes Res., Ann Arbor, Michigan, May 24-27, 2005.
2. Lumb, C.E., T.B. Johnson, H.A. Cook, and J.A. Hoyle. Comparison of growth of lwf c c in lakes Erie and Ontario. Canadian Conference for Fisheries Research, Windsor, Ontario, Jan 6-9, 2005.
3. Lumb, C.E., T.B. Johnson, J.A. Hoyle, and H.A. Cook. Constraints to growth of lake whitefish (*Coregonus clupeaformis*) in lakes Erie and Ontario. 47th Ann. Conf. Int. Assoc. Great Lakes Res., Waterloo, Ontario, May 25-28, 2004.

Thesis

1. Lumb, C.E. Comparison of growth of lake whitefish (*Coregonus clupeaformis*) in Lake Erie and Lake Ontario. M.Sc. thesis, Department of Biological Sciences, University of Windsor, Windsor, Ontario (June 2005).

Publications

1. Lumb, C.E., **T.B. Johnson**, H.A. Cook, and J.A. Hoyle. Ecology of lake whitefish (*Coregonus clupeaformis*) in Lakes Erie and Ontario, 1990-2003. J. Great Lakes Res. (in prep).
2. Lumb, C.E., **T.B. Johnson**, Retrospective growth analysis of lake whitefish (*Coregonus clupeaformis*) in Lakes Erie and Ontario, 1954-2003. Can. J. Fish. Aquat. Sci. (in prep.).