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AN EVALUATION OF THE ROLE OF TOP PISCIVORES IN THE FISH COMMUNITY OF THE MAIN BASIN OF LAKE HURON

By

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ABSTRACT

AN EVALUATION OF THE ROLE OF TOP PISCIVORES
IN THE FISH COMMUNITY OF THE MAIN BASIN OF LAKE HURON

By

Norine E. Dobiesz

Stocking of hatchery-reared fish has been widespread in Lake Huron since the mid-1960's, representing the majority of recruitment for several key predator populations including the introduced chinook salmon and the native lake trout. With recruitment dominated by hatchery plants, natural limitations on recruitment may not be able to prevent predator populations from exceeding the capacity of the forage base. Exceeding forage fish capacity can reduce predator growth, negatively affect predator survival, and delay or impair predator reproductive capabilities. The purpose of my research was to improve our understanding of the forage demand by the key predators in Lake Huron. This was accomplished by analyzing the temporal and spatial characteristics of the caloric content of Lake Huron fish species, using bioenergetics models coupled with age-structured stock assessment models to estimate annual population consumption, projecting future forage demand under different management scenarios; and parameterizing a functional response model for the dominant predator, chinook salmon.

The key predators in the open waters of the main basin of Lake Huron are burbot, lake trout, chinook salmon, and walleye. Estimates of their combined forage demand averaged nearly 36 million kg annually between 1996 and 1998. During this time, lake

trout and chinook salmon were the major consumers, accounting for 74% of the total consumption of prey fish by the key predators. Based on estimates of prey abundance, consumption by the key predators may be approaching prey capacity, supported by recent evidence of declines in predator growth. Projections of forage demand resulting from various management actions suggest that changes to chinook salmon stocking and reductions in sea lamprey-induced mortality have significant effects on predator forage demand.

A functional response model relates the number of prey eaten to prey abundance. We used this model to explore how changes in prey abundance affect consumption and growth. Our functional response model suggested that variations in total consumption and growth have been only weakly tied to measured prey abundance. Age 1-4 chinook salmon were feeding above 60% of their maximum rate of consumption and variations in prey abundance explained little of the variation in observed growth. Model fitting results suggest that the decline in chinook salmon growth between 1974 and 1998 cannot be explained by variations in prey abundance so observed declines in growth must be related to other factors. We noted differences in weight-at-age 1 followed a cohort through its life span such that fish that weighed less at age 1 consistently weighed less throughout their life span than fish whose weight at age 1 was higher. Another possible explanation for our model results is that the assumed relationships and constants we used were substantially in error, and there is actually a stronger relationship between predator consumption and prey availability.

To my Dad, the man who taught me to fish.

Norbert Dobiesz

April 1, 1930 – September 16, 2002

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Chapter 1

Introduction

Among the Great Lakes, Lake Huron is ranked as the second largest in surface area and the third largest in volume (Beeton 1984). Native peoples have inhabited the Lake Huron basin and fished its waters since the Wisconsin ice sheet retreat approximately 12,000 years ago (Spangler and Peters 1995). Settlers in the area fished primarily for food but by the mid 1800s commercial fishing developed causing nearshore fishing to move farther offshore (Spangler and Peters 1995). With technological advances in capture gear, fishing vessels, and preservation techniques, Lake Huron commercial fisheries rapidly grew throughout the early 1900s.

Lake Huron supported one of the world's largest freshwater fisheries before the 1950s, primarily in lake trout, with average annual commercial yields of 2.4 million kg from 1912 to 1940 (Ebener et al. 1995). A downward trend in annual catch during the early 1900s to the mid-1930s was attributed to invasion of exotic species and pollution from industrial development near the littoral zone (Berst and Spangler 1973). Overfishing coupled with the negative effects of sea lamprey *Petromyzon marinus* predation initiated a collapse in Lake Huron piscivore populations during the 1940s (Christie 1974; Mills et al. 1993; Eshenroder et al. 1995). Prior to the collapse of the fishery, Lake Huron's top predators were lake trout *Salvelinus namaycush* and burbot *Lota lota* but by the mid-1960s these piscivores were rare in the upper Great Lakes (DesJardine et al. 1995; Eshenroder and Burnham-Curtis 1999). Today, chinook salmon *Oncorhynchus tshawytscha*, lake trout, walleye *Stizostedion vitreum,* and burbot are considered the major predators in the main basin and their primary forage

fish consist of the exotic prey fish alewife *Alosa pseudoharengus* and rainbow smelt *Osmerus mordax.*

Restoration efforts in Lake Huron have focused on rebuilding piscivore populations, controlling exotic alewife, restoring self-sustaining stocks of lake trout, and promoting the recreational fishery (DesJardine et al. 1995; Great Lakes Fishery Commission 2001). Methods include extensive stocking of salmonines, a sea lamprey reduction program, and control of fishing effort. In the late 1950s, management agencies began chemical treatment of streams to control sea lamprey abundance and reduce mortality on native fish species (Smith and Tibbles 1980). Lake trout stocking began in 1969 with 31,000 fish and increased to 3.3 million in 1992 (Ebener et al. 1995). Other top predators such as chinook salmon and walleye have been stocked since 1968 (Ebener et al. 1995). Today, stocked predators form an important part of the ecosystem and primarily consume exotic prey species (Christie 1974; Kitchell et al. 1994; Eby et al. 1995).

In Lake Huron, stocking of hatchery-reared salmon and trout provides substantial recreational, social, and economic benefits. In 1991 the commercial fisheries in Lake Huron achieved landed harvests of $3.4 million (US) and $6.9 million (CAN) (Dann 1994). Similarly, in 1990 - 1991 the economic value of all Great Lakes' recreational fisheries was estimated to be approximately $1.34 billion (1991, US) and $0.26 billion (1990, CAN) in US and Canadian waters respectively (Bence and Smith 1999). In Lake Huron alone, US recreational fishing effort was estimated at 2,113,000 fishing days while Canadian effort was more than double that at 4,579,000 fishing days (Bence and Smith 1999). Communities bordering the lake

benefit from monies spent by recreational users including expenditures for food, lodging, or other related activities. Indirect economic value can be attributed to a healthy lake ecosystem and its functions (Costanza et al. 1997) such as fresh water storage (Edwards and Abivardi 1998) and nutrient recycling by organisms in the lake (Kraft 1993).

The restoration of naturally reproducing piscivore stocks has met with limited success. Natural reproduction is occurring in some stocks but hatchery-reared fish constitute the majority of recruitment (Ebener et al. 1995). With predator abundance predominantly controlled through stocking, an important natural linkage between predator abundance and prey availability may be disrupted. Therefore, management actions that alter predator abundance could result in predator consumption outreaching the forage fish capacity. However, the effects of fishery management actions on predator-prey dynamics are unknown (Stewart et al. 1981; Kitchell et al. 1994). In Lake Huron, predator forage demand and the effects of changes in prey fish abundance on predator growth are not well understood.

The purpose of my research is to examine how forage demand by the key predators responds to management actions such as changes in stocking or the reduction of sea lamprey-induced mortality. I addressed these questions through four distinct steps: (1) determination of the caloric content of Lake Huron fish species; (2) estimation of prey consumption for an average predator using bioenergetics models; (3) estimation of consumption by extrapolating individual predator consumption to a predator population, and projection of predator consumption under different management scenarios; and (4) parameterization of a functional response model for

the dominant predator, chinook salmon, to explore how changes in prey abundance affect consumption and growth. Estimates of the caloric content, or energy density, of the predators and prey are an important input into bioenergetics models which in turn, estimate consumption of prey by an individual fish given its growth. Stock assessment models then expand this consumption to a population and account for prey consumption by fish that die during the model time step. Results from the first three steps were consolidated into a computer program that allows fisheries managers to project future consumption of prey by the key predators under varying management actions. The following paragraphs address each of these steps.

Energy Density

Several studies have explored the seasonal and annual cycles of energy density of fish species in Lake Michigan (Foltz and Norden 1977; Flath and Diana 1985; Stewart and Binkowski 1986), Lake Ontario (Rand et al. 1994), and Lake Superior (Vondracek et al. 1996; Johnson et al. 1999) but corresponding data are generally lacking for Lake Huron. Further, some studies of forage demand have borrowed energy density from other species (e.g., Hurley 1986; Madon and Culver 1993; Rudstam et al. 1995) or from the same species in other lakes (LaBar 1993). However, energy densities may not be interchangeable since fish condition and thus energy content varies with changes in the fish community, food density, and climatic conditions (Rand et al. 1994). In Chapter 2, I describe the process I used to estimate the energy content of Lake Huron fish species and the statistical analyses (ANOVA and ANCOVA) used to determine how energy content varies regionally and

seasonally. Appendix A contains supplemental material about the samples used to determine energy content.

Bioenergetics

Bioenergetics models relate an individual organism's assimilation and utilization of energy from food, partitioning that energy into growth, metabolism, and waste losses (Adams and Breck 1990; Ney 1993). These models require energy budgets to consist of balanced inputs and outputs (Hewett and Johnson 1995). Here, growth integrates the feeding rate over time so short-term variability in food availability, temperature, etc. is minimized. Fish growth is denoted as an increase in body weight, which is the simplest measure to obtain for an energy budget. In Appendix B I describe the Lake Huron-specific parameters used in the Wisconsin Model, a widely used bioenergetics model (Hewett and Johnson 1995), to estimate year- and age-specific consumption for an average predator. Values of consumption and growth from these models were used to estimate the gross conversion efficiencies (GCE) of the Lake Huron predators. These GCEs become an important input into the estimation of consumption as outlined in the next section.

Estimating Consumption

Balancing predator forage demand and prey fish availability is a major concern for Great Lakes fishery managers. Estimates of recent consumption provide insight into the effects of stocking practices and other management actions on predator forage demand. In Chapter 3, I describe how age-structured population models, using the

production-conversion efficiency approach (Ney 1993), extend consumption by an individual predator to estimates of consumption by a population. Projecting future predator consumption under different management scenarios allows managers to compare the potential effects of management initiatives on predator-prey dynamics. Assumptions regarding mortality rates, weight-at-age, diet composition, and GCE, needed to project predator consumption for the period 1999-2020 are also outlined in Chapter 3.

Consumption Projection Model Computer Program

Prior to this dissertation, preliminary results of predator consumption were contained in the "No Name model", which was used to assess the overall consumption of prey fish by predators in the main basin of Lake Huron using a series of eight linked spreadsheets. While the "No Name model" could be amended with new data and additional calculations, correctly updating the series of spreadsheets was cumbersome, often requiring numerous changes to one or more spreadsheets. Furthermore, to compare multiple management scenarios required a copy of the entire suite of spreadsheets for each scenario. Updating these spreadsheets introduced errors common to spreadsheet manipulation (e.g., copying cells or losing cell formulas).

As part of an ongoing research program to improve our understanding of predator consumption, I created the Consumption Projection Model (CPM). This computer program is a user-friendly replacement for the "No Name model" that greatly simplifies the process of projecting consumption under multiple management scenarios (Dobiesz 2003). The CPM employs a user-friendly Microsoft Windows-based interface

that allows users to quickly and easily obtain and compare consumption projections resulting from various management actions. For projections period, CPM uses assumptions regarding key population attributes (Appendix C). This computer program was distributed to fisheries managers during a training session. Participants were also asked to complete a short survey to determine the usefulness and ease-of-use of the CPM (Appendix D).

Functional Response Model

The amount of prey eaten and the composition of the diet depend upon prey availability in ways that are unknown or only partially understood. The functional response model provides a framework for relating the number of prey eaten per unit time to prey density (Holling 1959; Murdoch 1973). Predation mortality as predicted from functional response models and estimated predator consumption from bioenergetics models provide two ways to view the effects of a consumer on their forage base. Functional response models relate the number of prey eaten to prey abundance. Extending the model to multiple prey species provides insight into how prey consumption changes as the composition of the forage base changes. Similarly, bioenergetics models provide a method of estimating consumption by a single predator that may be extended to an entire population. Consumption estimates from bioenergetics models can be compared to functional response estimates. In Chapter 4, I describe the parameterization of a Type II functional response for chinook salmon, the dominant key predator in Lake Huron, and compare the results from the functional response and bioenergetics models.

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Chapter 2

Energy Density of Key Predators and Their Prey in Lake Huron

Introduction

Lake Huron once supported one of the world's largest freshwater fisheries, primarily in lake trout with average commercial yields of 2.4 million kg from 1912 to 1940 (Ebener et al. 1995). Overfishing coupled with the negative effects of sea lamprey *Petromyzon marinus* predation initiated a collapse in Lake Huron piscivore populations during the 1940's (Christie 1974; Mills et al. 1993; Eshenroder et al. 1995). By the mid-1960's native piscivores were rare in the upper Great Lakes and management agencies began chemical treatment of streams to control sea lamprey abundance and improve the lake ecosystem for salmonines (DesJardine et al. 1995). Since that time, restoration efforts have focused on rebuilding piscivore populations, controlling exotic alewife, and promoting the recreational fishery (DesJardine et al. 1995; Great Lakes Fishery Commission 2001).

Stocked salmon and trout provide substantial recreational, social, and economic benefits (Dann 1994; Bence and Smith 1999) and play an important role as top predators in the lake ecosystem, primarily consuming exotic prey species (Christie 1974; Kitchell et al. 1994; Eby et al. 1995). However, with predator abundance predominantly controlled through stocking, an important natural linkage between predator abundance and prey availability may be disrupted. Such a situation may have occurred in Lake Michigan. As stocked chinook salmon abundance increased in Lake Michigan, their primary prey, alewife, increased in abundance (Madenjian et al. 2002). Bioenergetics models suggested that chinook salmon predation on alewives caused

substantial annual alewife mortality there (Stewart et al. 1981; Stewart and Ibarra 1991). A subsequent trophic-dynamic modeling effort (Jones et al. 1993) suggested that alewife might be driven to very low abundance in Lake Michigan at the salmonine stocking levels of the 1980s and early 1990s. During the late 1980s and early 1990s, chinook salmon in Lake Michigan experienced substantially elevated natural mortality rates (Benjamin and Bence, in press), which may have been the result of a disease.

Bioenergetics models have been used in the Great Lakes for various purposes, including estimation of predator forage demand (Stewart et al. 1981 and 1983; Eby et al. 1995; Negus 1995), projection of changes in predator consumption with changes in predator abundance (LaBar 1993; Negus 1995), prediction of predator-prey dynamics (Jones et al. 1993), and examination of nutrient cycling within aquatic food webs (He et al. 1993; Kraft 1993). Estimates of prey consumption can be calculated from bioenergetics models (e.g., Kitchell et al. 1977; Stewart et al. 1981; Hewett and Johnson 1995), which typically require the energy density of predators and prey as input. For instance, the Wisconsin model (Hewett and Johnson 1995) requires input of predator and prey energy density. While the production-conversion efficiency (Ney 1990) method, a simple method of estimating prey consumption, does not directly use energy density data, id does require an estimate of the gross conversion efficiency (GCE). Typically, this GCE is estimated through application of the more complex bioenergetics models that do require energy density information.

Determining energy density is a time-consuming process that includes collecting, grinding, drying, and bomb calorimetry of individual fish (Brafield 1982). Therefore, measurements of energy density are often not available for a particular

species or from a particular lake. Consequently, energy density values used in bioenergetics models are borrowed from the literature for other species with similar physiology (e.g., Hurley 1986; Madon and Culver 1993; Rudstam et al. 1995) or from the same species occupying other lakes (LaBar 1993). However, energy densities may not be interchangeable because prey fish condition varies with changes in the fish community, food density, and climatic conditions (Rand et al. 1994).

The energy density for various predator and prey species within the Great Lakes has been determined (Cummins and Wuycheck 1971; Rottiers and Tucker 1982; Vondracek et al. 1996; Johnson et al 1999) but data are generally lacking for species from Lake Huron. Additionally, studies of Lakes Michigan, Superior, and Ontario species have identified seasonal, regional, and annual variations in energy density (Foltz and Norden 1977; Flath and Diana 1985; Hurley 1986; Rand et al. 1994; Vondracek et al. 1996; Johnson et al. 1999; Madenjian et al. 2000). Because the Great Lakes are interconnected and share many of the same predator and prey species, we hypothesize that the energy density of Lake Huron species should be very similar to that found in the other Great Lakes. Seasonal patterns in energy density often observed for the introduced prey species, alewife and rainbow smelt, should also be evident in Lake Huron. However, most studies did not find strong trends for the predator species so it seems more likely that these trends will also be missing from Lake Huron species.

Our objectives were to (1) determine the energy density of Lake Huron predators and prey; (2) identify seasonal and regional energy dynamics in these species; and (3) evaluate the relationship between energy density and percent water

content. This study did not span multiple years and could not detect long-term fluctuations in energy density. However, these data represent a fairly comprehensive view of energy density for the primary predators and prey in Lake Huron not previously available as well as provide an important baseline for comparison with future energy density data.

Methods

From June 11, 1996 to September 24, 1997, the Michigan Department of Natural Resources, the Chippewa/Ottawa Treaty Fishery Management Authority, the Ontario Ministry of Natural Resources, and the Biological Research Division (USGS) collected 707 fish representing the major predator and prey species in Lake Huron. The predator species sampled were lake trout *Salvelinus namaycush*, burbot *Lota lota*, chinook salmon *Oncorhynchus tshawytscha*, and walleye *Stizostedion vitreum*. Prey species included alewife *Alosa pseudoharengus*, rainbow smelt *Osmerus mordax*, bloater *Coregonus hoyi*, slimy sculpin *Cottus cognatus*, and ninespine stickleback *Pungitius pungitius*. Each fish was placed intact in a plastic bag and then frozen. Identification tags placed with each fish included information on collector name, site, date, time of day, length, and weight. Prior to grinding and drying the samples, length and weight of each fish were assessed in the lab, and gender and maturity were recorded. Each collection site was identified with a statistical district (Figure 2.1). To analyze regional variation, the statistical districts were consolidated into four lake regions: northern, central, southern, and Saginaw Bay (Figure 2.1).

An alternative collection procedure was sometimes applied to forage fish since their small size did not always allow for accurate measurement of weight. Groups of small forage fish of the same species and from the same collection site were either sorted by size interval into separate bags or grouped together if the collector did not have time to sort by size class. An identification tag was placed in the bag with the same information outlined above. To minimize weight loss, water was added to each bag, which was then frozen or placed on ice until a freezer was available.

Fish collection spanned only one year; therefore we were not able to estimate between-year differences, but we did estimate regional and seasonal variations in energy density. Furthermore, we did not obtain sufficient numbers of stickleback or sculpin to statistically analyze variations in their energy density. These prey species do not contribute significantly to the diets of Lake Huron predators, with the exception of burbot.

Energy density was evaluated for a sub-sample of 203 fishes chosen to provide coverage across the regions, months, and fish lengths. Each fish was ground, and approximately 28 g of slurry was dried at 60-70^{o}C to a constant mass. Approximately 1 g of each dried sample was processed in a bomb calorimeter (Brafield 1982) to determine the caloric content of the sample. The resulting energy density was expressed as cal$\bullet$g^{-1} dry weight and then converted to J$\bullet$g^{-1} wet weight using the water content of each sample. The same grinding and drying process was applied to the remaining 504 fish, but these samples were not processed in the calorimeter due to limited time and manpower.

While energy density was measured directly for only 203 fish, percent water, which is predictive of energy density (Kitchell et al. 1977; Rottiers and Tucker 1982; Hartman and Brandt 1995), was measured for all 707 fish. We used the data from the 203 fish for which energy density was measured directly to develop linear regression models that predicted energy density from percent water. These models were used to predict energy density for all 707 fish. These predicted energy densities were then used in subsequent analyses.

To relate energy density ($J \bullet g^{-1}$ wet weight) to percent water, four different models were examined: (1) a single regression grouping all species; (2) a regression in which predators and prey formed two groups with separate intercepts and slopes; (3) a regression in which prey species were grouped together while predators were identified with separate intercepts and a shared slope (here burbot and lake trout were grouped together). We selected these models for consideration based on an initial examination of scatter plots of energy density versus wet weight, which suggested different linear relationships between predators and prey, more subtle difference in the level (intercept) of the regression lines for predators, and little difference in the relationships between lake trout and burbot or among prey species.

$$\frac{(SSE_r - SSE_f)/(p_r - p_f)}{SSE_f / p_f} \approx F_{(p_r - p_f), p_f} \qquad (1)$$

where SSE_r and SSE_f are the residual sum of squares from the reduced and the full model, respectively, and p_r and p_f are the number of parameters in each model. The models progress from the most reduced form with the fewest parameters to the most

complex form with the most parameters. Therefore, the extra sums of squares test (Neter et al. 1996): was applied to models 1 and 2, and models 2 and 3 to determine whether the added parameters were statistically different from zero ($p < 0.05$).

To explore regional and seasonal variations in energy density, an analysis of variance (ANOVA) was conducted for each species using the energy density values that were predicted from the percent water content. To avoid mixing measured energy densities and estimated energy densities, the energy densities as predicted from the models were used for all fish. Additionally, preliminary analysis showed that most of the uncertainty in energy density for a particular category of fish stems from among fish variation in percent water and not from the uncertainty in estimating the expected energy density given the percent water.

The main effects were region (α) and month (β). A fish's size influences its energy density so wet weight (w) was used as a covariate. The full model was

$$d_{ij} = \mu + \alpha_i + \beta_j + \alpha\beta_{ij} + \gamma(w_{ij} - \overline{w}_{..}) + \varepsilon_{ij} \qquad (2)$$

where d_{ij} was the estimated energy density in $J \bullet g^{-1}$ wet weight for the ith region and jth month; $\alpha\beta_{ij}$ was the interaction between region and month; and γ was the coefficient for the linear regression of d_{ij} on w_{ij}. Differences between levels of the main effects were tested using Tukey's pairwise comparison. Fish samples were not available for all regions or months so subsets of the full model (2) were used as needed (Table 2.1).

Results

Linear relationship between water content and energy density

Simple means for water content and energy density were calculated using all fish of a species for which these were measured. Mean water content ranged from 44.7% to 81.9% (Table 2.2) and mean energy density was inversely related to the mean percent water content among species (Figure 2.2). Forage fish species had higher water content and lower energy density than predator species.

In all cases there were strong negative relationships between energy density and percent water content (Table 2.3). The model that allowed separate intercepts by predator species (with a single slope) and a single linear relationship for a combined prey group (model 3, Figure 2.3) provided a significantly better fit to the data than the model that only recognized one predator and one prey group (model 2), or the model that assumed a single linear relationship for all species (model 1) (Table 2.4). This model (Table 2.5) was then applied to all 707 samples to estimate the energy density in $J \bullet g^{-1}$ wet weight from percent water. Relatively few of these samples fell outside the regression ranges (Table 2.2), and most of these lay close to the modeled ranges.

Analysis of energy density by species

The full ANOVA model could not be applied for all species due to variations among species in data available for particular regions or months (Table 2.1). For the models used in this analysis, the interaction between region and month was either not estimable or not a significant effect. Hence, this interaction was not included in any of the final models. The following results are presented first by predator and then by prey

species. Simple means are reported when the main effects were not significant. Least square means, which are adjusted for the other factors in the model, are reported when the statistical model included other effects (i.e., regions, season, or wet weight as a covariate).

Energy density of burbot did not vary regionally or seasonally and wet weight was not a covariate (Table 2.6). The overall mean energy density of burbot was found to be 5,630.0 $J \bullet g^{-1}$ wet weight. Although the seasonal effect was not significant, there is some suggestion that burbot energy density was higher in March and October, averaging 5,825.2 $J \bullet g^{-1}$ wet weight, and lower from May through August, averaging 5,585.3 $J \bullet g^{-1}$ wet weight.

Chinook salmon samples were obtained in May through October. In this time frame, neither regional (Figure 2.4) nor seasonal (Figure 2.5) differences in energy density were detected but wet weight was a significant covariate (Table 2.6). The mean energy density of a 1.56 kg chinook salmon was 6,451.6 $J \bullet g^{-1}$ wet weight.

Energy density of lake trout was found to vary regionally (Figure 2.4) and seasonally (Figure 2.5); wet weight was also found to be a covariate (Table 2.6). Lake trout exist in regionally distinct stocks with different characteristics such as age composition and size-at-age (Sitar et al. 1999; Eschenroder et al. 1995). Energy density of northern lake trout (6,767.5 $J \bullet g^{-1}$ wet weight) was statistically different from the energy density of central (8,956.5 $J \bullet g^{-1}$ wet weight, $p=0.0222$, $df=143$) and southern (8,378.3 $J \bullet g^{-1}$ wet weight, $p=0.0026$, $df=143$) lake trout. However, there was no difference between the energy densities in the central and southern regions. Lake trout energy density is lowest in April (6,232.82 $J \bullet g^{-1}$ wet weight) and increased during the

summer (9,478.3 $J \bullet g^{-1}$ wet weight), dropping slightly through October (Figure 2.5). July was the only month that was statistically different from all other months sampled.

The majority (44 out of 45) of walleye were taken from Saginaw Bay during the months of August, September, and October. Mean energy density in August was 4,637.6 $J \bullet g^{-1}$ wet weight, but this value was based on a single sample that came from the central region of Lake Huron. Energy density was higher in September (6,564.2 $J \bullet g^{-1}$ wet weight) and lower in October (6,305.9 $J \bullet g^{-1}$ wet weight), but these differences were not statistically significant ($p=0.2570$, $df=41$). Wet weight was found to be a significant covariate (Table 2.6).

Alewife energy density was found to vary by region (Figure 2.4) and by month (Figure 2.6) with wet weight as a covariate (Table 2.6). An interaction between month and region could not be estimated due to lack of samples. Mean energy density of central region alewife was lower (4,400.4 $J \bullet g^{-1}$ wet weight) than that of the southern region alewife (5,138.1 $J \bullet g^{-1}$ wet weight); no samples from the northern region were available. Alewife taken in the months of June through September were analyzed for seasonal trends. Energy density did not differ between June and July, averaging 4,191.1 and 4,368.9 $J \bullet g^{-1}$ wet weight respectively. However, energy density in August was statistically different from June ($p<0.0001$, $df=175$) and July ($p<0.0001$, $df=175$), with a mean of 5,255.9 $J \bullet g^{-1}$ wet weight. The single sample from September was 5,260.9 $J \bullet g^{-1}$ wet weight.

For bloater, only the month (Figure 2.6) and wet weight covariate component of the model were used because all but two samples came from the northern region (Table 2.6). Samples were obtained from January, March, May, and June. In the ANOVA, the

main effect of month was driven by the two June samples. With these two samples eliminated from the ANOVA, month was not a significant effect. While there appears to be a large difference in mean energy density between May (6,020.2 $J \bullet g^{-1}$ wet weight) and June (2,410.3 $J \bullet g^{-1}$ wet weight), the limited number of June samples (N=2) makes this difference very uncertain. A further uncertainty is that both June samples came from the southern region but all other samples (N=34) came from the northern region. Additional data are required to determine if the differences between May and June mean energy densities are related to seasonal trends or regional differences.

Energy density of rainbow smelt varied seasonally (Figure 2.6) but not regionally (Table 2.6). Rainbow smelt mean energy density in July was lower, 4,611.7 $J \bullet g^{-1}$ wet weight, than in May, June, or August. Only energy density during May and August were statistically different from July.

There were only three stickleback samples available for our study. The mean energy density of these samples was 5,194.2 $J \bullet g^{-1}$ wet weight. Similarly, only one sculpin sample was dried, with an estimated energy density of 4,635.5 $J \bullet g^{-1}$ wet weight.

Discussion

Fish communities in the upper Great Lakes share many of the same species and the hydrological connection between Lakes Huron and Michigan have led some to consider them a single waterbody (Beeton and Saylor 1995). We anticipated that energy densities of the Lake Huron species we sampled would be similar to conspecifics from other Great Lakes, and most similar to those observed in Lake Michigan. This was true to some extent. For instance, our estimates of mean

rainbow smelt energy density fell between those observed in Lakes Michigan (Rand et al. 1994) and Superior (Vondracek et al. 1996). Similarly, our estimates of burbot mean energy density were comparable to those found in Lake Superior (Johnson et al. 1999). However, the energy densities for all other Lake Huron species were lower than those reported from the other Great Lakes.

Energy density of salmonid predators from Lake Huron was lower than published energy density from other Great Lakes. The mean reported lake trout energy density was 10,294 $J \bullet g^{-1}$ wet weight (Rottiers and Tucker 1982; Johnson et al. 1999; Madenjian and O'Connor 1999) while the mean energy density for chinook salmon was 6,678 $J \bullet g^{-1}$ wet weight (Cummins and Wuycheck 1971; Rottiers and Tucker 1982). These published energy densities are 20% and 13% higher than those found for Lake Huron lake trout and chinook salmon. One exception to these patterns is the estimated energy density of lean lake trout in Lake Superior (Johnson et al. 1999), which is about 5% lower than lake trout from Lake Huron. However, variations between lake trout phenotypes (Henderson and Anderson 2002) and significantly colder temperatures in Lake Superior could account for these differences.

One possible reason for the low energy density of salmonids is the poor condition of Lake Huron alewife, which had the lowest mean energy content of the major prey species. Alewife is a major constituent in the diets of many top predators including lake trout (43% of ages 1-6 and 66% for ages 7+) and chinook salmon (73% for ages 2+). Lake Huron alewife exhibited much lower energy content than estimates from Lakes Michigan and Ontario for earlier time periods (Rottiers and Tucker 1982; Flath and Diana 1985; Rand et al. 1994). A pattern of declining alewife

energy density can be seen in these results (Figure 2.8). Our results fit the pattern of declining energy density and represent a continuation of that trend. Rand et al. (1994) hypothesized reasons for the declining alewife energy density they observed including density-dependent effects caused by an increasing alewife population or lower lakewide productivity. During our sampling in 1996-1997, alewife abundance in Lake Huron (Figure 2.7) was declining from a peak in 1994 making density-dependent effects a less likely cause for their low energy content. Another possibility is changes in benthic macroinvertebrates abundance that could limit consumption by adult alewife. *Diporeia,* a macrobenthic organism with a high lipid content (Guiguer and Barton 2002), is a primary constituent in alewife diets. Sampling in 1972 found that it was abundant throughout Lake Huron but was virtually absent from the southern portions of the main basin by 2000 (T. Nalepa, Great Lakes Environmental Research Laboratory, Pers. Comm.). While there is some evidence that *Diporeia* were declining in the shallow areas of Lake Huron during 1996 (Nalepa et al. 2003), they were still abundant at a site in the middle of the southern basin (EPA monitoring data).

A preponderance of lower energy density prey may be responsible for lower predator growth in Lake Huron. When prey are energy-dense, fewer prey are required to sustain predator growth. Conversely, predators must increase their daily ration of low energy prey to maintain growth (Brett and Groves 1979). Chinook salmon represent a major demand on forage and their abundance was increasing during our sample collection period of 1996-1997. At the same time, diet information for chinook salmon was difficult to obtain due to the large number of void stomachs (J. Johnson,

Michigan Department of Natural Resources, Pers. Comm.). While the cause of this is not evident or easily explained by low prey abundance, it is possible our results partly reflect low rates of predator feeding.

Regional Patterns in Energy Density

Lake trout are known to exist in spatially separated subpopulations (Eshenroder et al. 1995) and our results indicated that mean energy density of lake trout varied by subpopulation (i.e., lake region). Although the lake regions are contiguous, there is a measurable north-south gradient in water temperature that appears to impact the growing seasons such that lake trout in the northern regions grow slower (Eshenroder et al. 1995). Many physiological functions that affect energy absorption, respiration, and growth depend on temperature (Brett and Groves 1979). Therefore, for lake trout populations that segregate by location but have similar diet composition, we would expect a gradient in energy density with lower values in the northern region, higher in the southern region, and intermediate in the central region. Our analysis found this gradient of decreasing energy density with latitude for lake trout (Figure 2.4). However, this regional relationship was not strongly evident in any other species we sampled.

Lake trout energy density has been shown to be directly related to increasing lipid concentrations (Rottiers and Tucker 1982) and lipids play a key role in determining predator condition (Adams 1999). Madenjian et al. (2000) found variations in lipid concentration between nearshore and offshore lake trout with total length < 600 mm but no variation in lipid concentration for larger lake trout. Similar

to the Lake Huron lake regions we used, their samples included sites in the southeastern, northwestern, and mid-lake regions of Lake Michigan. They did not find a pattern of declining energy density with decreasing latitude. However, their northernmost site was not as far north as the northern region from which our samples came. Further more, the pronounced north-south cline in lake trout growth in Lake Huron is not nearly as evident in Lake Michigan (Bence and Ebener 2002). The mean energy density of lake trout in the northern region of Lake Huron was 8,190 $J \bullet g^{-1}$ wet weight, a value closer to the estimate of lean lake trout energy density in Lake Superior of 7,788 $J \bullet g^{-1}$ wet weight (Johnson et al. 1999). This suggests that the northern part of Lake Huron is more similar to Lake Superior than the lower northern reaches of Lake Michigan.

Seasonal Patterns in Energy Density

Seasonal differences in energy density have been attributed to changes in diet composition, energy density of food consumed, and reproductive status. Studies of temperate fishes have found the highest energy density values in the fall (October and November) and the lowest in early spring (March to May) (Flath and Diana 1985; Hayes and Taylor 1994; Rand et al. 1994; Jonas et al. 1996; Encina and GranadoLorencio 1997; Foy and Paul 1999; Pedersen and Hislop 2001). During the winter or spawning seasons, many fish cease feeding, living off of stored energy reserves, or dramatically reduce feeding due to colder water temperature and its effects on digestion and metabolism (Adams 1999). Consequently, we expected low energy density values at the beginning of the year, increasing through the fall months.

We detected these seasonal patterns for alewife, bloater, lake trout, rainbow smelt, and walleye. However, walleye data were essentially limited to September and October so an actual seasonal pattern cannot be determined.

Rainbow smelt energy density in Lake Huron also varied by month although our samples were limited to the months of May through August (with a limited number of samples from January). In Great Lakes, Foltz and Norden (1977) found that the energy density of smelt in Lake Michigan increased from June to October, and Vondracek et al. (1996) noted an initial decrease in Lake Superior smelt energy density in the spring, leading to an increase through September. In our samples, smelt energy density was highest in May, declining slightly through June and July, then increasing in August (Figure 2.6). If this August increase were to continue through the fall months, this pattern would again place Lake Huron smelt energy densities between those of Lakes Superior and Michigan. However, in Lake Oahe, South Dakota, Bryan et al. (1996) found rainbow smelt energy density was the highest in July, decreasing through the remainder of summer, suggesting that the seasonal patterns in rainbow smelt energy density can vary across lakes.

Our chinook salmon samples were obtained from May through October making it difficult to suggest the pattern of energy density throughout the winter. However, with the exception of the May value, energy density increased from June to October (Figure 2.5) in accordance with other observed seasonal patterns, although the pattern was not statistically significant using our model (Table 2.6). The least square means were roughly constant during the summer months and only increased during September and October. However, there were only four fish sampled during this time period.

While the pattern we observed was not particularly strong, it is similar to the pattern found in Lake Michigan where energy content was higher in the fall and lower in the following spring (A. Peters, unpublished data). Similarly, chinook salmon energy density increased from 4,940 $J \bullet g^{-1}$ wet weight in May to 5,987 $J \bullet g^{-1}$ wet weight in July, and to 6,824 $J \bullet g^{-1}$ wet weight in September in Lake Oahe South Dakota (Bryan et al. 1996). This pattern may have been obscured in our data due to our relatively small sample sizes and large variations among individual fish. Alternatively, it is possible that energy density did not increase over the summer in our study because of poor feeding condition for chinook salmon in Lake Huron during 1997.

Predicting Energy Density from Percent Water Content

There are many reasons for monitoring changes in energy density of both predator and prey species. First, declines in fish growth have been attributed to reductions in the nutritional content of prey (Boisclair & Leggett 1989; Anthony et al. 2000) resulting from lower energy density. Second, population abundance may also be impacted when declines in energy density adversely affect growth, reproduction, and survival of individuals (Henderson and Wong 1998; Holey et al. 1998; Adams 1999). For example, in the late 1980s, chinook salmon abundance in Lake Michigan was reduced by over 50%. This was attributed to nutritional stress caused by low prey availability thought to have been initiated by poor overwinter survival of alewife that entered winter with low lipids levels (Holey et al. 1998). Last, bioenergetics models require estimates of energy density for both predator and prey species. These models

provide important benefits to fishery managers in terms of understanding predator forage demand (e.g., Stewart et al. 1983; Rudstam et al. 1994; Rand and Stewart 1998).

Determining energy density can be costly in terms of manpower and money because samples must be processed using bomb calorimetry with equipment not normally available to fishery managers (Hartman and Brandt 1995), and energy density can vary by season, by location, and over time, requiring frequent and ongoing sampling. One simpler alternative to estimate energy density makes use of the strong negative relationship between percent water content and energy density, which has been observed in many fish species (Kitchell et al. 1977; Rottiers and Tucker 1982; Hartman and Brandt 1995; Jonas et al. 1996; Schreckenbach et al. 2001). This relationship held true in Lake Huron and we further noted that predator species had a lower percentage of water and higher energy density than prey species (Figure 2.2). Since processing a fish sample to determine water content is less expensive than determining its energy content, these measures could be done more often than direct measures of energy content. While our estimates of the energy density – percent water relationship (Table 2.5) were similar to estimates from studies in the other Great Lakes (Rottiers and Tucker 1982; Johnson et al. 1999), the estimated energy density for many species is lower reflecting recent Lake Huron conditions.

The primary focus of this study was to determine energy density for the major predator and prey species in Lake Huron for use in bioenergetics models (Chapter 3). In our analyses, we found temporal and spatial differences in energy density that varied within the lake and across the Great Lakes. This suggests that borrowing energy density values from other studies may not provide the most accurate or

contemporaneous data. Our results point the way towards some pragmatic approaches to more frequent evaluations of energy status. First, water content can be used to predict energy density, although the validity of the relationship for a specific location should periodically be checked. Second, in large lakes energy density may not vary much spatially for widely ranging species (e.g., chinook salmon), or might demonstrate predictable spatial patterns (e.g., lake trout) so that less comprehensive spatial sampling might be sufficient. However, since these observations are based on our limited sampling of energy density in Lake Huron, further sampling and energy density analyses could help determine the validity of these patterns. Last, the observed decline in alewife energy density and the effects this may have on predator condition indicates the need for frequent monitoring of energy density.

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Table 2.1 – Mean and standard deviation of wet weight (kg), and percent water content for predator and prey species collected in Lake Huron during 1996-1997. Samples were collected in Saginaw Bay (B) and the northern (N), central (C), and southern (S) regions of Lake Huron. Months represent the numerical value for each month a sample was collected, with January as month 1.

				Wet Weight (kg)		Percent water	
Species	Location	Months	N	Mean	Std dev	Mean	Std dev
			Predators				
Burbot	N,C,S	3,5,6,8,10	86	1.40	0.86	76.33	3.06
Chinook salmon	N,C,S	5,6,7,8,9,10	96	1.56	2.02	75.14	4.41
Lake Trout	N,C,S	1,3,4,5,6,7,10	153	1.63	1.21	68.94	4.89
Walleye	C,B	8,9,10	45	1.42	0.74	71.74	2.23
			Prey				
Alewife	C,S	6,7,8,9	181	0.02	0.02	80.89	3.91
Bloater	N,S	1,3,5,6	36	0.15	0.07	76.07	5.05
Rainbow smelt	N,C,S	1,5,6,7,8	106	0.03	0.05	77.39	5.15
Sculpin	N	7	1	< 0.003	---	79.26	---
Stickleback	C	7	3	0.00	0.00	69.11	16.85

Table 2.2 – Water content (mean with ±1 sd) for fish samples processed in the bomb calorimeter and those that were only ground and dried.

	Fish processed with bomb calorimetry (N=203)		Fish ground and dried only (N=504)		
Species	N	Percent water content	N	Percent water content	Outside of model range
Burbot	25	75.2 ± 1.4 (65.9 - 81.6)	61	76.8 ± 0.5 (69.8 - 82.9)	3.3%
Chinook salmon	49	73.1 ± 0.9 (64.0 - 79.5)	47	77.2 ± 1.0 (67.1 - 86.9)	14.9%
Lake trout	25	67.8 ± 1.9 (55.3 - 78.1)	128	69.2 ± 0.7 (60.0 - 85.7)	3.1%
Walleye	25	71.3 ± 0.7 (67.2 - 74.8)	20	72.3 ± 0.9 (68.1 - 76.4)	15.0%
Alewife	26	81.9 ± 1.2 (74.8 - 90.6)	155	80.7 ± 0.5 (63.0 - 91.0)	5.2%
Bloater	25	76.1 ± 1.6 (66.9 - 85.9)	11	75.9 ± 3.3 (68.3 - 88.2)	9.1%
Sculpin		--- ---	1	79.3	----
Rainbow smelt	25	78.9 ± 1.7 (68.7 - 92.9)	81	76.9 ± 1.0 (64.3 - 93.5)	7.4%
Stickleback	3	77.2 ± 9.2 (72.3 - 83.1)	1	44.7	----

Table 2.3 – Regression model results for the relationship of energy density to percent water content.

Model	R^2	F	p
(1) Overall	0.9318	$F_{1,201}$= 2745.6	<.0001
(2) Grouped as predators or prey	0.9415	$F_{3,199}$= 1067.28	<.0001
(3) Prey group and separate predator intercepts, with burbot and lake trout combined	0.9573	$F_{5,197}$= 884.11	<.0001

Table 2.4 – Extra sums of squares criterion for models 1, 2, and 3 where SSE_r and SSE_f are the residual sum of squares from the reduced and the full model, respectively, and df_r and df_f are the degrees of freedom in each model.

Model	SSE_r	df_r	SSE_f	df_f	F	p
Overall vs. groups *(model 1 vs model 2)*	4.94E+07	201	4.24E+07	199	16.49	<.0001
Groups vs. prey group with separate predator intercepts, with burbot and lake trout combined *(model 2 vs model 3)*	4.24E+07	199	3.09E+07	197	36.59	<.0001

Table 2.5 – Intercepts and slopes for final model (model 3) used to predict energy density from percent water using the equation: $E = \alpha + \beta W$, where *E* is energy density in $J \bullet g^{-1}$ wet weight and *W* is the percent water content. Model 3 assumed a common slope for all predators but allowed intercepts to vary, and allowed a different linear relationship for prey than predators (different intercept and slope) but assumed the same relationship for all prey species.

Species or group	Intercept (α)	Slope (β)
Prey	26,442.37	-275.13
Burbot and lake trout	32,077.70	-346.49
Chinook salmon	31,609.71	-346.49
Walleye	31,294.05	-346.49

Table 2.6 –ANOVA main effects (month and region) and covariate (predator wet weight) for each sampled Lake Huron species. Least square means are shown with one standard error in parentheses. Missing entries represent effects that could not be tested due to insufficient samples.

Parameter	Alewife	Bloater	Burbot	Chinook salmon	Lake trout	Rainbow Smelt	Walleye
Overall Mean	4,187.3	5,563.2	5,630.0	5,575.0	8,189.7	5,151.0	6,435.3
Region:							
df	1, 175	--	2, 83	2, 87	2, 143	2, 98	--
F	9.35	[a] --	0.69 [b]	0.34	4.92	0.86	[a]--
p-value	0.0026	--	0.5060	0.7095	0.0086	0.4266	--
North	--	--	5693.6	5,736.7	6,767.5	-217.6	--
			(257.7)	(324.8)	(334.8)	(726.1)	
Central	4,400.4	--	5834.5	5,481.7	8,956.5	385.1	--
	(239.1)		(231.9)	(299.1)	(798.5)	(396.3)	
South	5,138.1	--	5517.9	5,820.8	8,378.3	0	--
	(322.6)		(153.4)	(360.3)	(431.3)		
Month:							
df	3, 175	3, 30	4, 79	5, 87	6, 143	4,100	2,41
F	11.11	3.92	1.44	1.24	2.51	3.63 [d]	3.97
p-value	<0.0001	0.0179	0.2301	0.2972	0.0242	0.0083	0.0266
January	--	5,213.9	--	--	8,253.9	4758.7	--
		(440.3)			(776.2)	(402.5)	
March	--	5,244.6	7,402.8	--	8,426.6	--	--
		(720.9)	(796.9)		(1,011.1)		
April	--	--	--	--	6,232.8	--	--
					(1,401.6)		
May	--	6,020.2	5,166.4	6,372.5	7,812.8	6096.3	--
		(266.1)	(394.9)	(432.6)	(371.2)	(407.5)	
June	4,191.1	2,410.3	4,820.5	5,145.4	7,534.8	5048.1	--
	(132.9)	(1111.0)	(393.1)	(334.8)	(543.4)	(296.9)	
July	4,368.9	--	--	5,327.3	9,478.3	4611.7	--
	(159.06)			(434.3)	(492.6)	(258.9)	
August	5,255.9	--	4,597.4	5,483.1	--	5516.5	4637.6
	(180.37)		(712.6)	(280.5)		(232.3)	(709.7)
September	5,260.9	--	--	5,439.9	--	--	6564.2
	(932.9)			(466.9)			(130.9)
October	--	--	7,406.4	6,310.3	8,499.5	--	6305.9
			(841.9)	(667.9)	(380.3)		(182.4)
Covariate							
df	1.175	1,30		1,87	1,143	1,100	1,41
F	12.26	4.75	[c]	28.35	58.53	15.80 [d]	4.66
p-value	0.0006	0.0373		<0.0001	<0.0001	<0.0001	0.0368
Overall mean lab wet wt	0.017	0.151		1.559	1.635	0.030	1.417

[a] Not enough samples for analysis of this main effect
[b] The main effect of month was not significant so the model was refit without it.
[c] Covariate not significant; model refit without it
[d] The main effect of region was not significant so the model was refit without it.

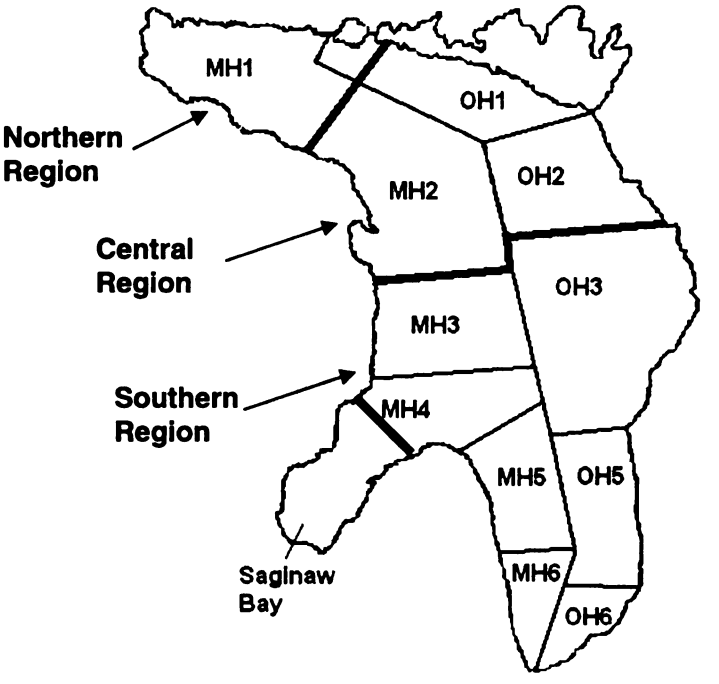

Figure 2.1 – Statistical districts grouped into lake regions (north, central, south, and Saginaw Bay) for the regional analysis of energy density. Statistical districts in the US use MH labels while Canadian waters are labeled with OH (Smith et al. 1961).

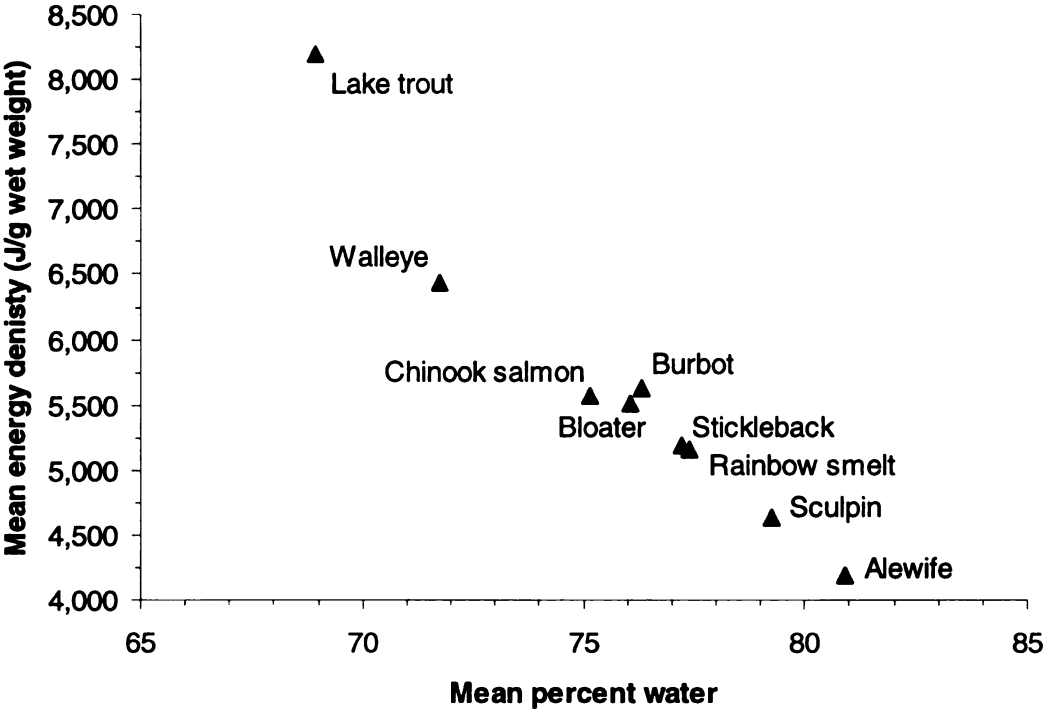

Figure 2.2 -- Relationship between mean percent water content and mean energy density for all sampled Lake Huron species.

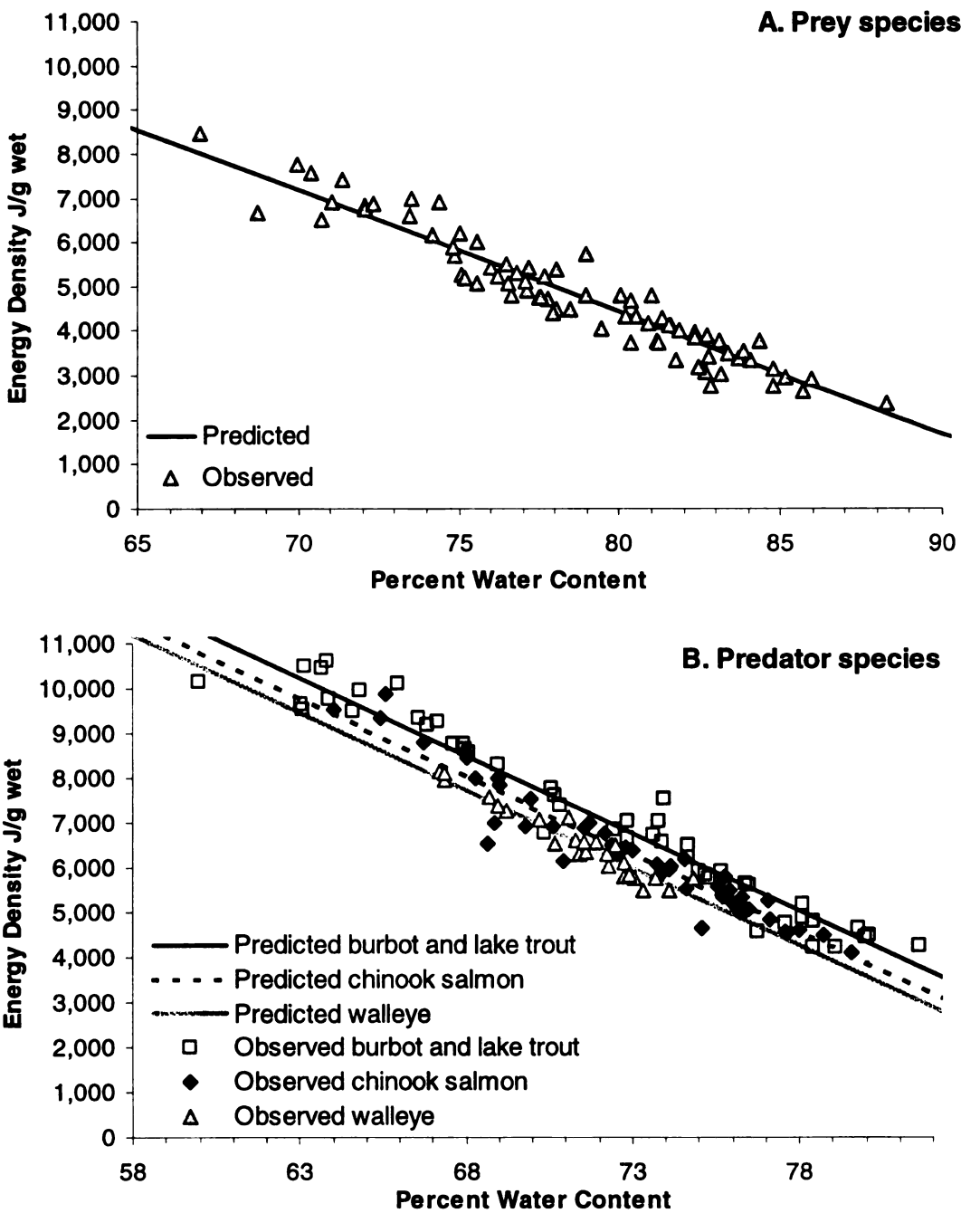

Figure 2.3 – Relationship between energy density and percent water content for predators and prey in Lake Huron. [Note: the x-axis origins are not continuous from zero.]

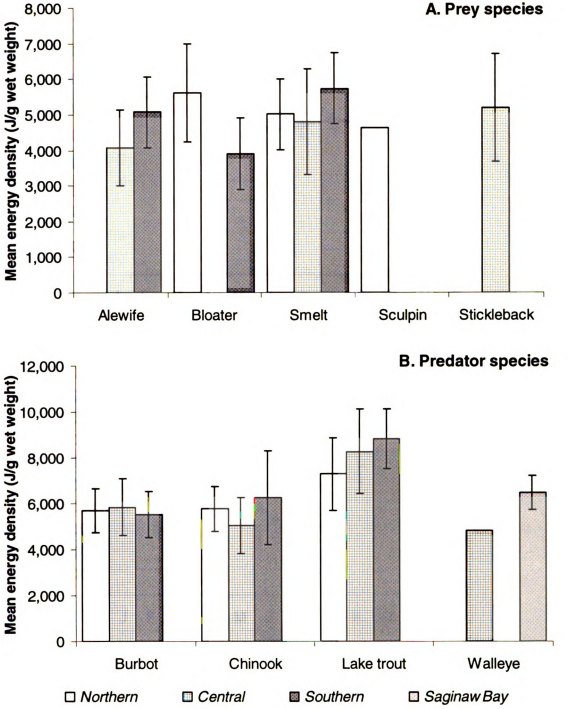

Figure 2.4 – Mean regional energy density of the key predators and their prey in Lake Huron during 1997. Least squares means are shown with one standard error.

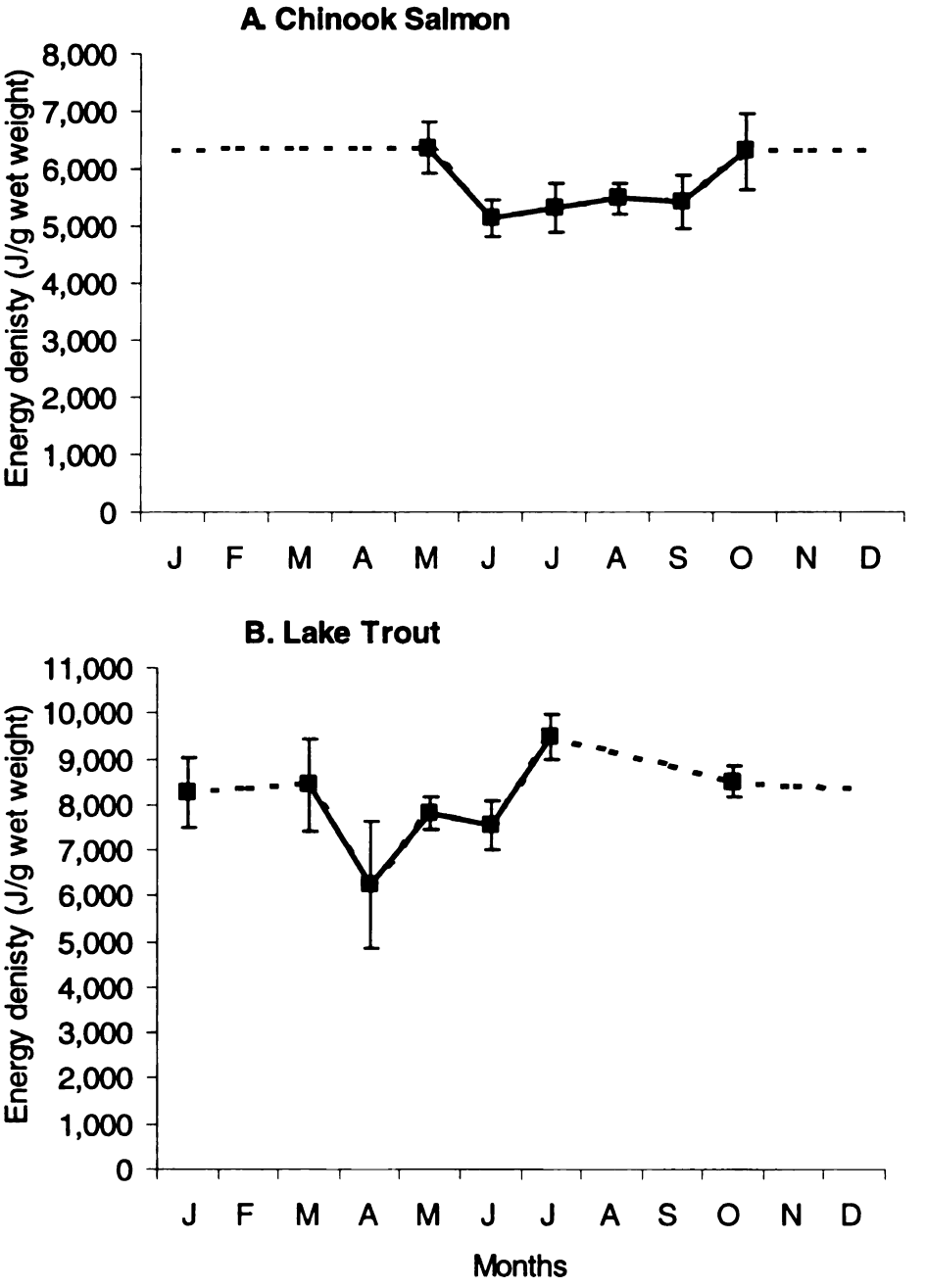

Figure 2.5 – Mean seasonal energy density of the chinook salmon and lake trout in Lake Huron, 1996-1997. Least squares means are shown with one standard error.

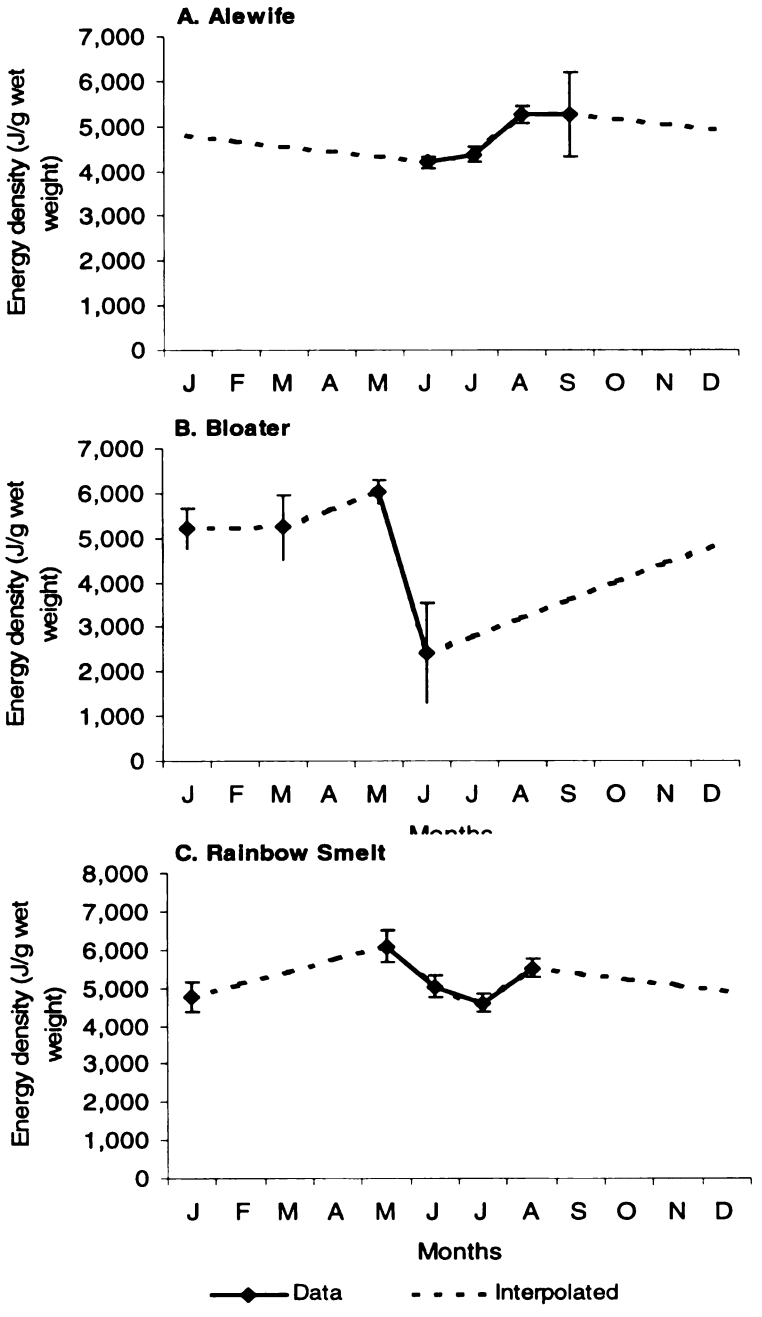

Figure 2.6 – Mean seasonal energy density of the primary prey species in Lake Huron during 1996-1997. Least squares means are shown with one standard error.

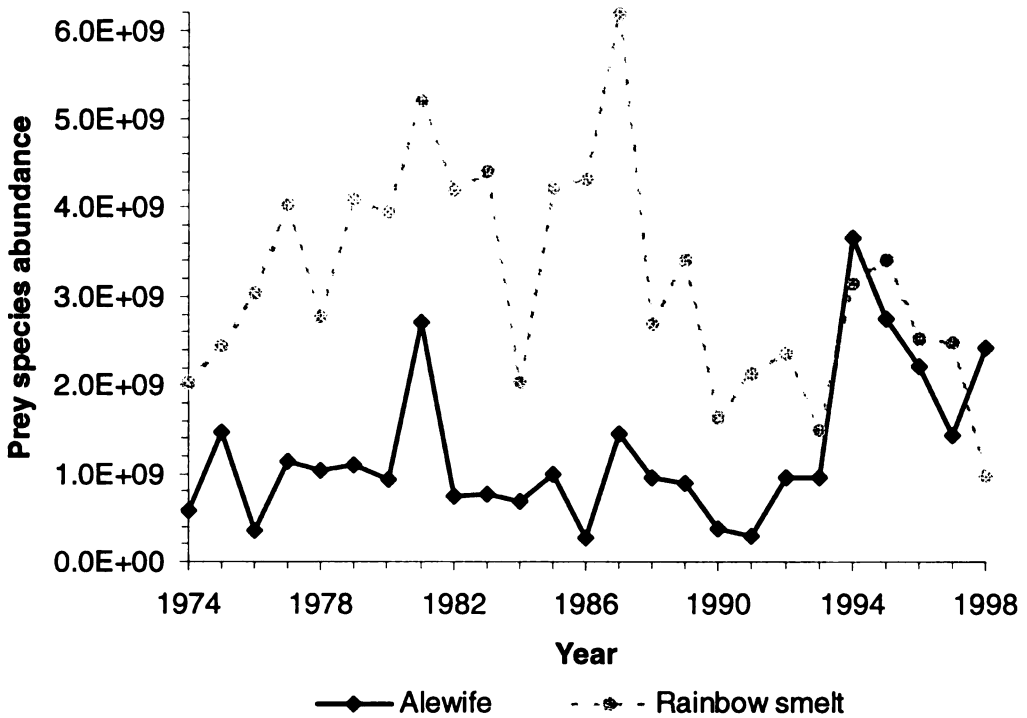

Figure 2.7 – Annual alewife and rainbow smelt abundance in the main basin of Lake Huron during 1974-1998.

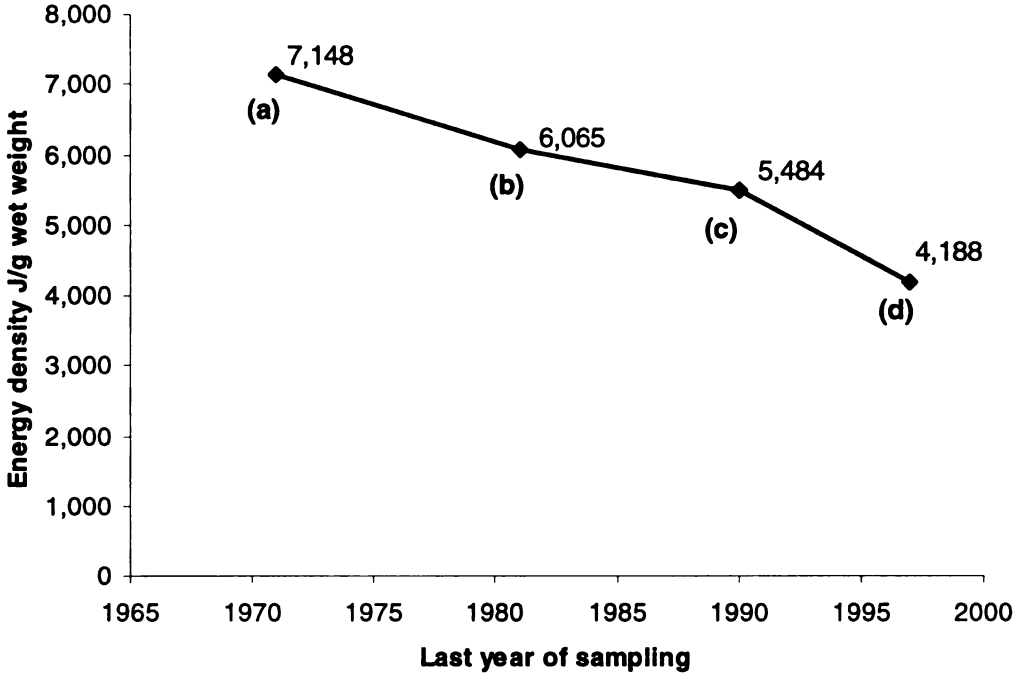

Figure 2.8 – Pattern of declining alewife energy density within the Laurentian Great Lakes. Mean energy density from each study is plotted against the last year of the study where (a) Rottiers and Tucker 1982; (b) Flath and Diana 1985; (c) Rand et al. 1994; (d) this study.

Chapter 3

Recent and projected estimates of forage fish consumption by key predators in the main basin of Lake Huron

Introduction

In non-managed systems, interactions between predator and prey populations can potentially regulate the abundance of predator populations. However, in a hatchery-dependent system, balancing predator forage demand and prey fish availability becomes a major concern for fishery managers. In Lake Huron, for example, overfishing and parasitism by introduced sea lamprey *Petromyzon marinus* were the principal causes for the collapse of the fishery during the 1940s (Smith 1972; Eshenroder and Burnham-Curtis 1999). Management reacted with efforts to control sea lamprey and by stocking hatchery-reared chinook salmon *Oncorhynchus tshawytscha* and lake trout *Salvelinus namaycus* (Ebener et al. 1995). Although some salmonines reproduce naturally (Ebener et al. 1995), stocked fish make up a majority of the recruitment for all species and nearly all recruitment of native lake trout (Eshenroder et al. 1995). This hatchery-dependent system may have disrupted the natural feedbacks between predator abundance and the dynamics of their prey, raising the possibility of overreaching the productive capacity of the prey fish base (Kitchell and Crowder 1986; Eby et al. 1995). An inadequate forage base may lead to declines in predator growth, delays in reproduction, and reduced survival (e.g. Oglesby 1977; Boisclair and Leggett 1989; Rand et al. 1994; Holey et al. 1998).

Understanding predator forage demand requires knowledge of individual consumption rates and population dynamics. The consumption rate of an individual fish can be estimated from gastric evacuation rates (e.g., Swenson and Smith 1973), laboratory feeding experiments (e.g., Boisclair and Sirois 1993; Elliott and Hurley 2000), or by applying bioenergetics models (e.g., Stewart and Ibarra 1991; Rand et al. 1994). While there are drawbacks to each of these methods (Ney 1990), bioenergetics models have been widely used to promote understanding of predator consumption (e.g., Stewart et al. 1983; Hurley 1986; Negus 1995) and have often been found to be representative of actual consumption given appropriate input variables (Rice and Cochran 1984; Petersen and Ward 1999; Schaeffer et al. 1999; Madenjian et al. 2000)

A bioenergetics model provides a method for estimating food consumption utilizing a conceptual model that relates water temperature to consumption and growth. An individual organism's assimilation and utilization of energy from food is partitioned into energy for growth (B), metabolism, and waste losses (Adams and Breck 1990; Ney 1993; Hewett and Johnson 1995)

$$\frac{dB}{Bdt} = C - (R + F + U) \qquad (1)$$

where consumption and respiration (C, R) are temperature and size dependent while egestion and excretion (F, U) are functions of consumption. Using this methodology, growth integrates the feeding rate over time so short-term variability in food availability, temperature, etc. are minimized. Fish growth is denoted as an increase in body weight, which is the simplest measure to obtain for an energy budget. For a

given temperature and fish size, the energy budget can be solved to determine the amount of food eaten to produce the observed growth.

Bioenergetics models have been applied to Lake Michigan salmonine predators to establish the importance of these predators and their impact on prey communities (e.g., Kitchell et al. 1977; Stewart et al. 1981; Stewart and Ibarra 1991; Hansen et al. 1993; Kitchell at al. 1994). The application of bioenergetics models also aided the parameterization of the SIMPLE model (Jones et al. 1993), which played a role in the decision to reduce stocking in Lake Ontario (Lange et al. 1995). There have also been many other applications of bioenergetics models including estimating walleye consumption (Hurley 1986), evaluating trends in forage fish predation (Eby et al. 1995), and investigation of PCB, DDE, and mercury dynamics in Lakes Ontario (Borgmann and Whittle 1992) and Michigan (Madenjian et al. 2000) lake trout.

Data from bioenergetics models must be coupled with predator mortality and growth data to extend consumptive demand from an individual to a population. One such approach is the production-conversion efficiency method (Ney 1990, 1993) that incorporates estimates of predator production and gross conversion efficiency (GCE). Using gross production instead of abundance at the start of the year, allows consumption to be estimated for fish that live only a portion of the year. The GCE provides a measure of how well an animal converts ingested food into new tissue (Brett and Groves 1979) and typically declines as fish body size increases (Adams et al. 1982). While it can be determined experimentally (e.g., Kelso 1972; Edsall et al. 1999), it is often estimated from bioenergetics models.

Fishery managers have identified chinook salmon, lake trout, walleye *Stizostedion vitreum*, and burbot *Lota lota* as the key open water predators in the main basin of Lake Huron. While these predators are prominent in the lake (Ebener et al. 1995), information about their consumption levels is lacking. The objectives of this paper are to (1) estimate annual consumption of forage fish by the major predators in the open waters of the main basin of Lake Huron; (2) compare this forage demand to recent prey availability and historical consumption; and (3) project future consumption levels resulting from various possible management actions. Estimates of recent consumption are useful for understanding patterns of consumption and forage demand (e.g. Kitchell and Crowder 1986; Eby et al. 1995; Negus 1995) and provide an important basis for evaluation of future management actions. Projecting predator consumption under different management scenarios provides valuable insights into the effects of management initiatives (LaBar 1993). Several alternative management scenarios are projected to explore how various management actions affect predator forage demand.

Methods

We estimated consumption by the key predator populations using the production-conversion efficiency approach (Ney 1990, 1993). Estimates of age-specific population abundance and mortality rates from age-structured population models, together with information on weight-at-age, were used to estimate production. Production estimates were then divided by gross conversion efficiency (GCE) estimates to compute year- and age-specific consumption. We estimated age-specific GCEs from

bioenergetics models (Hewett and Johnson 1995 version 3.0b) using Lake Huron specific data on fish growth, diet, energy density, and water temperature.

Stock Assessment Models

Age-structured population models have been developed for each of the key predator populations in the main basin of Lake Huron between 1974 and 1998. These models included one for burbot in the main basin, one for chinook salmon in the main basin, three for lake trout corresponding to a northern, central, and southern region of the main basin, and two for walleye, one for Saginaw Bay and one for the main basin south of Saginaw Bay (Figure 3.1). Modeling lake trout across three lake regions and walleye between the main basin and Saginaw Bay was necessary because these populations exhibit differences in survival, growth, and/or diet composition that required separate stock assessment models. The critical information needed for each predator population was year- and age-specific abundance and mortality rates. These were obtained from the parameters of existing age-structured population models (Bence and Dobiesz 2000). The parameters of these models were estimated by fitting them to available fishery and survey data. Parameters included abundance-at-age in the initial year of the time period being modeled, recruitment each year and additional parameters determining mortality rates needed to project population dynamics over time (Bence and Dobiesz 2000; Bence and Ebener 2002; McLeish et al. In preparation).

Lake trout, walleye, and burbot

Lake trout, walleye, and burbot population models operate with annual steps. Starting with initial numbers for the first year modeled, numbers-at-age (N), except for the youngest age, were updated by:

$$N_{a+1,y+1} = N_{a,y} e^{-Z_{ay}} \tag{2}$$

using species-specific year (y) and age (a) ranges. For lake trout and burbot, total mortality (Z) is broken into components for background natural mortality (M), sea lamprey-induced mortality (L), and fishing (F):

$$Z_{a,y} = M_a + L_{a,y} + F_{a,y} \tag{3}$$

For walleye, only background natural mortality and fishing components are included:

$$Z_{a,y} = M + F_{a,y} \tag{4}$$

Abundance estimates from the population models along with mortality and growth rates were used to calculate gross production over time for each species. Gross production each year is estimated as the sum of yield, biomass of fish that die from other causes, and change in standing stock biomass. For burbot, walleye, and lake trout, biomass ($B_{a,y}$) is the product of number- and weight-at-age for each age and year. Gross production ($P_{a,y}$) is calculated on an age- and year-specific basis accounting for population abundance, mortality rates, and estimates of individual growth rate (Bence and Dobiesz 2000). It represents predator biomass produced through the year including losses due to natural mortality and harvest.

$$P_{a,y} = (B_{a+1,y+1} - B_{a,y}) + B_{a,y}\, Z_{a,y} \left(\frac{1}{G_{a,y}} - Z_{a,y} \right) \left(\exp(G_{a,y} - Z_{a,y}) - 1 \right) \quad (5)$$

where $Z_{a,y}$ is the instantaneous mortality rate for a given age and year and $G_{a,y}$ is the instantaneous growth rate estimated by

$$G_{a,y} = \ln(W_{a+1,y+1} / W_{a,y}) \quad (6)$$

where $W_{a,y}$ is weight-at-age for year y. $G_{a,y}$ was assumed to be constant over years for burbot, northern lake trout, southern lake trout, and walleye. Age- and year-specific values were used for central lake trout where weight-at-age was found to vary with time. The instantaneous growth rate cannot be estimated for the last age from the weight-at-age data; therefore, $G_{a,y}$ was assumed to be zero for the last age group.

Weight-at-age estimates for burbot were obtained by fitting a von Bertalanffy curve to mean weights for ages 3 –17 (Jim Johnson, Michigan Department of Natural Resources, Pers. Comm.) (Appendix B). For the lake trout models, weight-at-age was estimated from data collected during spring gill net surveys conducted by the Michigan DNR (Appendix B). Walleye weight-at-age was estimated from 1985-1995 Lake Huron creel data (Appendix B).

Chinook Salmon

The population model for chinook salmon uses two time periods within a year consisting of the first seven months (prior to a "pulse" of harvest and maturation) and then the remainder of the year (Bence and Dobiesz 2000). The annual update equation is:

$$N_{a+1,y+1} = N_{a,y} e^{-M} \; (1 - P_{F,a,y}) \, (1 - P_{m,a,y}) \tag{7}$$

where $P_{F,a,y}$ and $P_{m,a,y}$ are the proportions of fish that die due to fishing or maturation respectively. The numbers at the end of the first time period (prior to the pulse) and at the beginning of the second time period (immediately following the pulse) are given by:

$$N_{a,y,i}^{*} = N_{a,y,i} \; e^{-\frac{7}{12}M} \tag{8}$$

$$N_{a,y,i+1} = N_{a,y,i}^{*} \; e^{-\frac{5}{12}M} \, (1 - P_{Fa,y}) \, (1 - P_{m,a,y}) \tag{9}$$

Here $N_{a,y,i}$ indicates the numbers for period i, and the "*" indicates if the numbers are for the end rather than the beginning of the period. In calculations of harvest numbers and return of mature fish it is assumed that fishing mortality occurs prior to maturation.

Gross production by chinook salmon was calculated for two intervals – pre-harvest and post-maturation. Annual production is the sum of production over these two intervals for a given year. Biomass of age-a fish at the start of interval i in year y is

$$B_{a,y,i} = N_{a,y,i} \times W_{a,y,i} \tag{10}$$

$N_{a,y,i}$ and $W_{a,y,i}$ are the number- and weight-at-age at the start of the interval. Production lost to natural mortality during each period is

$$D_{a,y,i} = B_{a,y,i} \; M \; [1/G_{a,y,i} - M)][\exp(G_{a,y,i} - M) \; t_i - 1] \tag{11}$$

where M is the natural mortality rate, $G_{a,y,i}$ is the instantaneous growth rate applying to interval i, and t_i is the proportion of a year represented by the interval. For chinook

salmon, t is 7/12 and 5/12 for the pre-harvest and post-maturation intervals respectively. The instantaneous growth rate is estimated by

$$G_{a,y,i} = \frac{\ln(W_{a,y,i+1}/W_{a,y,i})}{t_i} \tag{12}$$

When the ith interval is the last interval in the year, $W_{a,y,i+1}=W_{a+1,y+1,1}$.

Instantaneous growth rate for the last age of the post-maturation interval (age 5+) was assumed to be zero. Chinook salmon weight-at-age was determined by fitting a von Bertalanffy model to weight-at-age while allowing the parameter representing the asymptotic maximum length (L_∞) to vary over time (McLeish et al., In preparation). The growth and population models were fit simultaneously to produce age- and year-specific weight-at-age information (Appendix B).

Total production over the entire year is given by:

$$P_{a,y} = \sum_i \Delta_{a,y,i} + \sum_i D_{a,y,i} \tag{13}$$

where $\Delta_{a,y,i}$ represents the change in age-specific standing stock biomass during period i. This can be reexpressed as:

$$P_{a,y} = \Delta_{a,y} - R_{a,y} + \sum_i D_{a,y,i} \tag{14}$$

where $R_{a,y}$ are the pulse removals of fish (in biomass) due to fishing and maturation between the two periods of natural mortality.

Bioenergetics Models

The Wisconsin bioenergetics model (Hewett and Johnson 1995, updated to V3.0b) was used to estimate consumption for an average individual fish by employing the option to fit consumption as a function of change in weight. Separate models were used to represent each predator population in parallel with the stock assessment models. Lake Huron-specific values were used for diet composition, energy density of predators and prey, and water temperature (Appendix B). Age-specific gross conversion efficiency (GCE) for each predator population was obtained by dividing annual growth estimates from weight-at-age information (Appendix B) by estimates of consumption from the bioenergetics models.

Estimating Recent Consumption

The production-conversion efficiency method (Ney 1990, 1993) was used to compute estimates of prey consumption by each predator population. Age- and year-specific gross production was divided by age-specific GCE and summed over all ages to obtain total consumption. Consumption on a prey species basis was computed by multiplying total consumption by estimates of the proportion (by weight) that each prey species contributes to the diet. This approach, along with several key assumptions regarding future changes (Appendix C), was also used to project consumption under several typical management scenarios.

Sensitivity Analysis for Estimates of Recent Consumption

To approximate Lake Huron conditions, our bioenergetics models used Lake Huron-specific values for water temperature, diet composition, and energy density of the predators and prey (Appendix B). Since energy density is a time-consuming and difficult quantity to measure, values are often borrowed from other lakes or other time periods within the same lake. We tested the sensitivity of the annual consumption estimates to two types of variation in energy density. First, we explored the effects of using regionally-varying energy density versus a basin-wide mean. Our previous research found a unique pattern of regionally-varying energy density for lake trout, with lake trout from the northern region having significantly lower energy density than lake trout in the central or southern regions (Chapter 2). We tested the importance of using regional lake trout energy density against the basin-wide mean by running each lake trout bioenergetics model with the basin-wide mean energy density and all other data held constant. From these runs we obtained the GCEs and then estimated population level consumption.

Second, we examined the impact of using published energy density of predator and prey species from other Great Lakes instead of data obtained from Lake Huron. Energy density has been found to vary between ecosystems related to variations in the fish community, food density, and climatic conditions (Rand et al. 1994; Foy and Paul 1999; Pazzia et al. 2002). We noted that energy density of predators and prey in Lake Huron was lower than that found in other Great Lakes (Chapter 2). We tested the importance of using Lake Huron-specific values of energy by rerunning each bioenergetics model using published mean energy density for both predator and prey species from other Great Lakes (Table 3.1).

Estimating Historic Lake Trout Consumption

As a benchmark for comparison of current consumption levels, we estimated the consumption by lake trout during 1912 to 1940. Our basic approach was to estimate a level of recruitment and associated population abundance that could have produced an equilibrium yield equal to the average observed yield during the period (Bence and Dobiesz 2000). In these calculations we assumed that the fishery was stable. We proposed an overall mortality rate that would not cause a collapse, and subtracted an estimate of natural mortality to obtain the corresponding fishing mortality rate. We then used numerical algorithms built into Microsoft® Excel Solver to adjust the recruitment level until the equilibrium yield equaled the observed average. This produced estimates of equilibrium abundance, biomass, and related quantities. With estimates of historical diet composition and GCEs (Appendix B), the production-conversion efficiency method (Ney 1990, 1993) was used to estimate annual consumption by lake trout. While burbot likely played an important predatory role historically, we lacked information to estimate their abundance and consumption levels.

Projecting Future Consumption

Projecting consumption under various management scenarios can improve our understanding of how these actions may affect prey consumption by the key predators. We project annual consumption for three possible scenarios. The "baseline" scenario includes changes to lake trout stocking and harvest regulations resulting from the 2000 consent decree for waters ceded by the 1836 Treaty of Washington (United States v. Michigan 2000), and the 20% reduction in chinook salmon stocking that began in 1999.

All other factors affecting abundance and consumption are held constant, at 1998 levels. The "sea lamprey reduction" scenario includes all "baseline" factors but reduces sea lamprey-induced mortality on lake trout and burbot assumed to result from enhanced efforts to control sea lamprey in the St Marys River. With chinook salmon dominating prey consumption, especially in recent years, it is informative to explore a scenario resulting in decreased chinook salmon abundance. The last scenario, "chinook stocking reduction", adds a 50% reduction in chinook salmon stocking beginning in the year 2002 to the "sea lamprey reduction" scenario.

To estimate future consumption, several assumptions were made regarding mortality rates, weight-at-age, diet composition, and GCE, during the projection period, 1999 through 2020. Natural mortality rates (excluding sea lamprey-induced mortality) for the projection period were constant and set to the value used in the last year of the assessment models. Several different assumptions were used for estimating fishing mortality during the projection period. For southern walleye and burbot a single source of fishing mortality was set to the value of the last year of data; for Saginaw Bay walleye the average of the last three years was used. All three lake trout models and the chinook salmon model contained commercial and recreational fishing mortality calculated as the product of selectivity and fishing intensity. The chinook salmon and southern lake trout models used constant selectivity from the last year of data and time varying fishing intensity as the average of the last three years. For northern and central lake trout, selectivity and fishing intensity were allowed to vary over time in the stock assessment models, while the average of the last three years was used for projections. For chinook salmon, the maturation proportion was set to the estimates for the last year in the

assessment model. Sea lamprey-induced mortality was applied to the burbot model and all three lake trout models. For the projection period, this mortality source was adjusted by a scaling factor (Schleen et al. 2002) intended to reflect the reduction of sea lamprey abundance resulting from treatment of the St Marys River. The scaling factor did not apply to the "baseline" scenario.

For the projection period, weight-at-age was assumed fixed for the assessment models that did not use time-varying weight-at-age (northern and southern lake trout, burbot, and Saginaw Bay and southern region walleye), while the mean of the last three years was used for those models using time-varying weight-at-age (chinook salmon and central lake trout). Diet composition and GCE were assumed constant for estimates of recent and projected consumption.

Results

Gross conversion efficiency and gross production

Patterns in production for the main basin (Figure 3.2) are roughly similar to those of consumption (Figure 3.3). Gross conversion efficiency (GCE) decreased with age and varied among species and predator populations (Table 3.2). Burbot made up a larger portion of consumption than of production because of relatively low GCEs (Table 3.2). Consumption by chinook salmon increased faster than production because of a shift toward lower GCEs (resulting from slower growth) over time.

Predator Biomass and Mean Consumption for 1984-1998

For the period in which all predators were modeled (1984-1998), estimated annual mean total consumption in the main basin was 32 million kg. Consumption has varied about this mean with a minimum of 26 million kg in 1984 and a maximum of 41 million kg in 1998 (Figure 3.3). In the main basin, the major consumers are lake trout and chinook salmon. On average their forage demand represents 71% of the total demand by the major predators. From 1984 to 1998, chinook salmon increasingly dominated the total consumption of prey in the main basin (Figure 3.3). Consumption data shown here include consumption of "other prey" by Saginaw Bay walleye that are not typically part of the main basin forage mix.

Trends in consumption, production, and biomass for chinook salmon from 1968 through the mid-1980s show their biomass and consumption of prey increasing (Figure 3.4). Consumption by chinook salmon increased by an average of 13% per year between 1968 and 1987, reaching 15.4 million kg from a low in 1968 of 514,000 kg (Figure 3.4). Chinook salmon biomass also increased from nearly zero (933 kg) in 1968 to 4.3 million kg in 1998 (Figure 3.4). Consumption, production, and biomass leveled off and then declined in the late 1980s and early 1990s, then began increasing during the mid-1990s.

Lake trout biomass in the main basin declined from 4.1 million kg to 2.1 million kg from 1984 to 1998 (Figure 3.5). Most of this decline occurred in the southern region of the main basin (Figure 3.1). In 1984 biomass estimates for the northern region and the central region were 505,000 kg and 604,000 kg respectively. Modest gains occurred in the central region through 1998 with biomass estimated at 734,000 kg while the northern region experienced modest losses with biomass estimated at 469,000 kg.

Annual consumption by lake trout (Figure 3.3) followed biomass (Figure 3.5) declines and was exacerbated because the decline occurred in the area where lake trout growth is highest. However, consumption was offset because the remaining biomass was concentrated in younger, faster growing fish. Total consumption by lake trout declined from a high of 11.0 million kg in 1984 to 6.5 million kg in 1998 (Figure 3.3). Consumption increased from 1991-1994 by an average of 7% per year caused by relatively strong year classes in 1992-1993 in the southern basin (Figure 3.6). Consumption declined after 1994 by an average of 9% per year.

Mean prey consumption by burbot (1984-1998) was estimated at 4.8 million kg annually (Figure 3.3). The temporal pattern was a product of our assumption that recruitment was constant. However, with limited information on burbot, assumptions needed to determine their population dynamics are open to question (Bence and Dobiesz 2000); therefore, we can only evaluate burbot consumption for general trends as data is lacking to determine specific consumption rates. Their overall forage demand seemed to lie between that of lake trout and walleye (Figure 3.3).

During 1984-1998, Saginaw Bay walleye biomass increased from 1.2 million kg to 2.0 million kg while the biomass of southern walleye declined from 1.2 million kg to 514,000 kg. Mean walleye biomass (1984-1998) for the main basin was 2.6 million kg. Total consumption by both the Saginaw Bay and southern region walleye was at its maximum in 1986 with 5.3 million kg consumed (Figure 3.6). Consumption declined since that time by approximately 4% per year, with total consumption of 3.6 million kg in 1998.

Sensitivity Analysis Using Basin-Wide Energy Density

Using basin-wide energy density, total annual lake trout consumption increased 1% in the northern region and decreased 2.5% in the central, and 1.5% in the southern lake regions. This was accompanied by a mean reduction in the age-specific GCEs of 1.5% in the northern region and a increase in GCEs of 7% and < 1% in the central and southern regions. The effect of using basin-wide energy density across the lake trout regions was to increase the energy density of northern and central lake trout by 10% on average but decrease the energy density of southern lake trout by 2%.

Sensitivity Analysis Using Published Energy Density

For burbot and walleye, literature mean energy densities produced lower age-specific annual consumption estimates by 5% and 17% respectively. The estimated energy density for Lake Huron burbot was higher than the value used in Rudstam et al. (1995), which was estimated from Atlantic cod (Table 3.1). Since we used the same bioenergetics parameters as used in Rudstam et al. (1995), the lower estimated consumption is primarily related to the energy density differences. The reduction in walleye consumption using literature mean energy denisty was larger and likely attributed to a higher mean energy density for Lake Huron walleye compared to that used by Kelso (1972) (Table 3.1). However, the Lake Huron estimate of walleye energy density was based on a limited number of samples over a brief two month period and may not be representative of their energy density over the entire year. Given the results using literature energy density, this may have caused our walleye consumption estimates to be higher than expected.

Both chinook salmon and lake trout consumption estimates were higher using the literature values for energy density of predators and prey as compared to Lake Huron-specific values. Our estimated energy density for salmonines in Lake Huron (Chapter 2) was substantially lower than most of the reported literature values (Table 3.1). The higher energy density value from the literature accounted for a 4% and 9% increase in consumption by lake trout and chinook salmon respectively. However, these differences are relatively small compared to other uncertainties in the bioenergetics and age-structured models.

Comparison To Historic Consumption by Lake Trout

The historical (1912-1940) average yield was 1.8 million kg in the main basin (Baldwin et al. 1979). The model matched this yield when recruitment slightly exceeded 5 million yearling recruits per year. Historical lake trout consumption during this period was estimated at 38.2 million kg (Bence and Dobiesz 2000). While total consumption by the major predators has approached this level, it was exceeded only in 1998 (Figure 3.7).

Consumption of Forage Species

Recent mean consumption (1996-1998) of alewife and rainbow smelt by all of the major predators was 29.0 million kg (Table 3.3). Over 90% of consumption by lake trout and chinook salmon was composed of alewife and rainbow smelt (Figure 3.8). In contrast, the burbot diet included substantial amounts of invertebrates and sculpin resulting in a lower reliance on alewife and rainbow smelt, which accounted for only 40% of their diet (Table 3.3). The walleye diet consisted of a high proportion of "other"

food items representing feeding inside Saginaw Bay on a mix of prey species not normally found in the main basin of Lake Huron (Table 3.3). However, 63% of prey consumption by walleye included alewife and rainbow smelt, with nearly 80% of this amount attributed to alewife.

We compared estimated consumption by the key predators (1984-1998) with the combined alewife and rainbow smelt swept area biomass obtained from the US Geological Survey fall bottom surveys (Figure 3.9). This survey method expands the numbers of fish in each trawl from the actual area trawled to the numbers of fish in all US waters. This expansion is based on the area swept by the trawls in different regions of the lake at a series of depth strata, accounting for the total bottom area in each region and depth station. Consumption of alewife and rainbow smelt by the key predators was substantially lower than the swept area prey biomass estimates until the early 1990s. From this period on, prey consumption by the key predators more closely approached the swept area estimates.

Projected Consumption Under Several Management Scenarios

Projections approximated a steady-state for the period 2010-2020 (Figure 3.10). Each projected value below represents the mean annual consumption by all of the key predators during 2010-2020. In the "baseline" scenario, the mean consumption for this period was 43 million kg. Mean consumption for the "sea lamprey reduction" scenario was 52 million kg, representing an increase in consumption of 21% over the "baseline" scenario consumption levels. This increase is exclusively related to reducing sea lamprey-induced mortality on lake trout and burbot. Mean consumption for the "chinook

stocking reduction" scenario was 38 million kg. In this scenario, mean consumption decreases from the "sea lamprey reduction" scenario by approximately 26% and decreases from the "baseline" scenario by 10%.

Discussion

Intensive stocking of Pacific salmon began in Lake Michigan in the 1960s, because these fast growing species were expected to consume substantial numbers of exotic prey fish and to be attractive to anglers (Tody and Tanner 1966). These expectations have been borne out across the Great Lakes as the number of stocked chinook salmon has increased substantially from the 1960s through the 1980s (e.g. Lange et al. 1995). In recent years chinook salmon have become the dominant predator in Lakes Michigan (Stewart et al 1981; Stewart and Ibarra 1991), Ontario (Rand and Stewart 1998), and Minnesota waters of Lake Superior (Negus 1995) as well as Lake Huron. This domination is partly due to the substantial numbers that have been stocked (e.g., Bence and Smith 1996), but it also results from their rapid growth rates, especially relative to native predators (e.g., Stewart and Ibarra 1991). We found that chinook salmon accounted for 54% of the prey biomass consumed in the main basin in Lake Huron (1996-1998), although their biomass was roughly equal to that of each of the other species (Figure 3.3). Chinook salmon have also been found to consume a disproportionate amount relative to their biomass in other lake ecosystems (Hill 1997).

Lake trout are the dominant native predator accounting for 20% of consumption of prey biomass in Lake Huron (1996-1998); however, total consumption by lake trout declined from a high in 1984 to its lowest level in 1998. Lake trout consumption

followed biomass declines and was exacerbated because the decline occurred in the area where lake trout growth is highest (southern region), but offset because the remaining biomass was concentrated in younger, faster growing fish..

Walleye are also important predators, especially in Saginaw Bay and southern Lake Huron, with estimated total walleye abundance exceeding that of lake trout in 1998. However, known movement of walleye between Saginaw Bay and the southern main basin was not included in the population models so walleye abundance may be overstated. Lack of spawning habitat (Colby et al. 1994), lower water temperatures (Christie and Regier 1988), and predation on larval walleye by alewife (Fielder 2002) are possible reasons for the lack of walleye in the main basin. Similarly, burbot may be a more important predator in the main basin but we lacked the data to estimate burbot abundance with high confidence.

Consumption and GCE Estimates Across Lakes

Consumption by and GCE of lake trout have been estimated for Lakes Michigan (Stewart et al. 1983; Stewart and Ibarra 1991), Ontario (Rand and Stewart 1998), and Superior (Negus 1995). Estimated GCEs for Lake Ontario lake trout ages 1-3 averaged 12.7% (Rand and Stewart 1998), substantially lower than Lake Huron estimates (approximately 18%). However, GCEs from both lakes were nearly identical for older ages. Rand and Stewart (1998) used slower growth rates in young lake trout and higher energy density for all lake trout, which likely explains these differences. In contrast, GCEs estimated for Lake Michigan lake trout were 24.4 – 7.4% for ages 1-9 (Stewart et al. 1983), nearly identical to our GCE estimates (Table 1). Similarly, the GCE of 9.2%

for a 3 kg Lake Superior lake trout (Negus 1995) was within the range of GCEs for 3 kg lake trout in all Lake Huron regions (7.3 - 9.3%). Information on lake trout GCEs appears to be restricted to the Great Lakes, but the estimated GCE for hatchery brown trout averaging 300 g was 16% (Elliott and Hurley 2001), comparable to Lake Huron lake trout of the same size with mean (across lake regions) GCE of 18.3%.

Chinook salmon GCE and consumption have also been studied across the Great Lakes (Stewart and Ibarra 1991; Negus 1995; Rand and Stewart 1998). For chinook salmon ages 1-4, the Lake Huron mean GCEs across the two growth periods (Table 1) were lower by 16 % (ages 1-2) and 40 % (ages 3-4) than Lake Ontario GCEs that ranged from 29 – 12% (Rand and Stewart 1998). However, the Lake Huron GCE for age 0 chinook salmon was 15 % higher than the Lake Ontario estimate (Rand and Stewart 1998). In Lake Superior, a 3 kg chinook salmon (Negus 1995) also had a higher GCE (23.4%) than a similar sized fish in Lake Huron (GCE = 17.8%). With similar growth rates between Lake Ontario and Lake Huron (except for age 2), lower GCEs imply that higher consumption is needed to obtain the same growth. Additionally, chinook salmon energy densities used in the Lake Michigan and Lake Ontario models (Stewart and Ibarra 1991; Rand and Stewart 1998) were higher than our Lake Huron value and influenced our GCE estimates. Since our energy density is based on a one-year sample (Chapter 2), the estimated GCEs may reflect a time of higher feeding due to poor prey fish condition during the sampling period. Using these GCE estimates, we may be overstating chinook salmon forage demand over the entire time frame we modeled. Generally, GCE estimates from other Great Lakes were at least 15% higher while GCE estimates from Lake Oahe, South Dakota were

approximately 14% lower (Hill 1997) than Lake Huron. A sensitivity analysis using GCEs that were ± 15% of the Lake Huron values produced mean annual consumption estimates for the period 1996 – 1998 that were 13% lower and 15% higher. This analysis indicates that our chinook salmon consumption estimates may be off by ± 20% but not by orders of magnitude.

Both Lake Huron walleye populations had GCEs that were comparable to the annual mean GCEs in the Bay of Quinte, Lake Ontario (Hurley 1986) and experimental feeding studies on walleye in Lake of the Woods, Minnesota (Swenson and Smith Jr. 1973). Hartman and Margraf (1992) used bioenergetics models to estimate annual consumption of Lake Erie walleye during 1986-1988. Their estimates of individual consumption ranged from 1,642 g for age 2 fish to 3,486 g for age 6. Estimates from Lake Huron walleye populations were similar to Lake Erie for ages 2-3 but higher for ages 4-6. Individual walleye from the Saginaw Bay population consumed an average of 1,643 g for age 2 fish to 4,329 g for age 6 fish while individual walleyes in the southern population consumed slightly less at 1,499 g to 3,837 g (ages 2-6). In Lake Erie, walleye diets were dominated by clupeids (Hartman and Margraf 1992) whereas diets of the Lake Huron open water walleye populations were dominated by alewife. Since the growth rate for age 2-6 walleye was similar between Lake Erie and Lake Huron, the differences in water temperature, diet, and energy density used in the bioenergetics models account for the differences in consumption.

Effects of energy density on consumption estimates

Using region-specific energy density had only a minimal effect on lake trout consumption estimates. Considering the numerous areas of uncertainty associated with bioenergetics models, the mean 1.4% change over all lake regions represents a modest increase in consumption and indicates that a fair approximation of consumption by lake trout could be obtained using basin-wide mean energy density. We caution, however, that this conclusion might reflect the specifics of the situation. For example, during most of our time series, fish from the southern region dominated lake trout abundance. A major change such that lake trout became much more abundant in the northern region, could invalidate the use of the basin-wide mean as an appropriate approximation.

Our evaluation of the effect of using lake-wide means for energy density or values borrowed from the literature suggests that doing so would not be unreasonable. For instance, although the mean published lake trout energy density was 20% higher than the Lake Huron mean, estimated consumption by lake trout using the literature mean was only 4% higher than our estimates. We suspect that in many cases using published energy density data would cause moderate percentage changes, and would be very unlikely to alter estimates of consumption by a factor of two. However, some caution is needed when using published energy density data because this measure is affected by many factors including changes in the fish community, food density, and climatic conditions (Rand et al. 1994). When possible, local evaluations of energy density are preferable. Further, since bioenergetics models provide estimates of

individual consumption that are expanded to an entire population, better estimates of predator abundance are also critical when estimating predator forage demand.

Comparison to Benchmarks

The observed patterns showing recent levels of consumption approaching standing stock estimates of prey (Figure 3.8) and estimates of consumption by historical lake trout populations (Figure 3.6) are of concern. Evidence of a corresponding decline in lake trout and chinook salmon growth (McLeish et al., in preparation) suggest a possible imbalance between predator and prey abundances. Therefore, caution should be exercised with regard to either increasing stocking further or maintaining the current level of stocking. If piscivores are exceeding forage fish capacity, stocking plans would need to be changed to assure continued growth and survival of all piscivores.

In 1998, consumption apparently exceeded the prey biomass (Figure 3.8) because consumption is estimated on an annual basis while prey biomass is measured at a point in time. Annual production to standing stock biomass ratios can exceed unity, especially for small fish, which means prey availability exceeds standing stock. Second, swept area biomass estimates tend to underestimate the biomass. Estimating the proportion of fish present in the area swept by the trawl gear that are actually retained by the gear is difficult and can effect biomass estimates by a factor of two or more . Finally, it is important to recognize that the stock assessments and other calculations on which our consumption estimates were based have substantial uncertainty, although we have no reason in particular to suspect they overestimate the biomass consumed.

Rand and Stewart (1998) estimated prey fish exploitation rates by dividing predator consumption by prey fish production. While they found only modest exploitation rates (approximately 13%) during 1990-1991, they noted that most of the forage demand was directed at adult alewife where the exploitation rate exceeded 100%. In Lake Huron, exploitation rates have varied over time (Table 3.4) and were generally much higher than the 13% observed in Lake Ontario, but much closer to the estimated 50% (Brandt et al. 1991) observed in Lake Michigan in 1987.

Although forage fish abundance declined (Figure 3.8) while predator abundance (Figure 3.3) increased over time, we cannot say with certainty that the predators were the major cause of the decline. Forage demand per gram of predator in Lake Huron has varied only slightly over time and only apparently exceeded the grams of prey available per predator in 1998 (Table 3.4). Forage fish population abundance estimates were highly variable over time and do not reflect a simple connection to predator numbers. However, given the change in the predator-prey ratio, especially in recent years (Figure 3.9), predators will likely exert a larger role in future years.

To put current consumption levels in perspective, we compared contemporary predator abundance and prey consumption against estimates of these quantities for lake trout (the dominant predator historically) in the main basin of Lake Huron during the period of a stable fishery, 1912 to 1940. Current consumption levels approached our estimates of historic prey consumption (Figure 3.6). Our estimates of historic lake trout abundance and consumption required many assumptions (Bence and Dobiesz 2000) and the analysis did not include burbot, a second potentially important native predator. Nevertheless, our analysis suggests that current and historical prey consumption was

reasonably similar, despite the dependence of the current predator community on stocking.

Projections of Consumption

Projecting consumption under various management scenarios can improve our understanding of how these actions may affect prey consumption by the key predators in Lake Huron. We explored three alternative management scenarios: a baseline, a reduction in sea lamprey-induced mortality, and a 50% reduction in chinook salmon stocking (Figure 3.9). The Baseline is informative as a reference point of consumption estimates if the status quo management plan is followed. Reduction in sea lamprey-induced mortality on lake trout and burbot related to the treatment of the St Marys River improves survival of these predators with a corresponding increase in consumption. Similarly, reducing chinook salmon stocking lowers their abundance and future consumption. While these management actions have an effect on predator forage demand, neither result represents more than a 40% change in consumption levels.

Fishery managers need estimates of predator forage demand in order to define a quantitative measure of how much consumption can be supported without high risk of forage fish stock collapses. Our estimates of consumption by the key predators were based on static diet information and energy density collected during one year. These and other data are known to vary by season and lake region. Estimates of consumption could be enhanced by the continued collection of data such as diet, predator weight-at-age, and energy density, collected seasonally and spatially where unique predator populations exist. Improved understanding of predator-prey interactions in Lake Huron should also

include stock assessment models to estimate key predator consumption in Georgian Bay and the North Channel, and investigation of functional response models to improve our understanding of the connection between forage fish dynamics and piscivore consumption.

These projections could be improved by addressing areas of uncertainty in our estimates of predator abundance, biomass, production, and consumption. We have the highest confidence in the estimates for lake trout, which were based on age-structured stock assessment models fit to fishery and survey data. In contrast, we have the lowest confidence in the estimates for burbot, which were based on estimates of the relative abundance of burbot using lake trout abundance (Bence and Dobiesz 2000). Some uncertainty in these estimates could be minimized by the following actions: (1) a fishery independent assessment of trends in chinook salmon abundance; (2) improved understanding of wild recruitment of chinook salmon; (3) assessments of burbot abundance; and (4) a study of the mixed population of walleye in Saginaw Bay and the main basin of Lake Huron including the sources of fish in different regions of the lake and the seasonal patterns of movement.

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Table 3.1 – Mean energy density used for sensitivity analyses. Lake Huron energy density was determined in Chapter 2. These represent the mean basin-wide values. '*' represent species that used seasonally or regionally varying energy density in the bioenergetics models. Published energy density values represent the mean value for all noted references for the species.

Species	Lake Huron energy density $J \cdot g^{-1}$ wet weight	Mean published energy density $J \cdot g^{-1}$ wet weight	References
Alewife*	4,187	6,232	Rottiers and Tucker (1982); Flath and Diana (1985); Rand et al. (1994)
Burbot	5,630	4,661	Rudstam et al. (1995); Johnson et al. (1999)
Bloater	5,514	8,665	Rottiers and Tucker (1982); Vondracek et al. (1996)
Chinook salmon	5,575	6,678	Cummins and Wuycheck (1971); Rottiers and Tucker (1982)
Lake trout*	8,190	10,294	Rottiers and Tucker (1982); Johnson et al. (1999); Madenjian and O'Connor (1999)
Rainbow smelt*	5,151	5,269	Cummins and Wuycheck (1971); Rottiers and Tucker (1982); Lantry and Stewart (1983); Rand et al. (1994); Rudstam et al. (1995); Vondracek et al. (1996)
Walleye	6,435	4,605	Kelso (1972)

Table 3.2 -- Gross conversion efficiency estimated from bioenergetics models

	Burbot	Chinook salmon		Lake trout			Walleye	
Age		1973-84	1985-99	North	Central	South	Sag Bay	South
0		0.321	0.316					
1	0.078	0.247	0.254	0.215	0.171	0.218		
2	0.066	0.185	0.171	0.195	0.192	0.175	0.168	0.185
3	0.083	0.083	0.079	0.148	0.156	0.139	0.174	0.189
4	0.082	0.059	0.066	0.118	0.130	0.116	0.154	0.173
5	0.077			0.105	0.114	0.105	0.151	0.170
6	0.072			0.108	0.111	0.110	0.142	0.160
7	0.068			0.092	0.095	0.094	0.129	0.147
8	0.069			0.081	0.084	0.085	0.118	0.135
9	0.066			0.072	0.076	0.077	0.107	0.123
10	0.064			0.066	0.069	0.070	0.092	0.106
11	0.062			0.060	0.064	0.065	0.079	0.091
12	0.060			0.056	0.060	0.061	0.079	0.092
13	0.058			0.053	0.056	0.057		
14	0.057			0.051	0.053	0.072		
15+	0.054			0.042	0.055	0.063		

Table 3.3 – Estimates of mean consumption in millions of kg for 1996-1998

	Burbot	Chinook	Lake Trout	Walleye	Total
Alewife	1.1	10.7	3.4	1.9	17.1
Rainbow smelt	1.0	6.9	3.4	0.5	11.9
Other	3.3	1.9	0.3	1.4	6.9
Total	5.4	19.6	7.1	3.8	35.9
Alewife+Smelt	2.1	17.7	6.8	2.4	29.0

Table 3.4 – Summary of predator consumption and forage demand in the main basin of Lake Huron, 1984-1998.

Year	Consumption by all predators (millions kg)	Alewife and rainbow smelt abundance (millions kg)	Total predator biomass (millions kg)	Prey available per predator biomass (kg/kg)	Consumption per predator biomass (kg/kg)
1984	26.47	59.78	9.18	6.51	2.88
1985	28.54	123.59	8.91	13.87	3.20
1986	33.30	68.99	9.93	6.95	3.35
1987	33.29	160.91	10.38	15.50	3.21
1988	32.15	79.65	11.02	7.23	2.92
1989	32.32	96.21	10.54	9.13	3.07
1990	32.47	44.70	10.02	4.46	3.24
1991	29.95	46.67	10.02	4.66	2.99
1992	28.89	47.58	10.08	4.72	2.87
1993	29.10	45.99	9.91	4.64	2.94
1994	31.27	104.50	9.89	10.56	3.16
1995	32.86	67.58	10.47	6.46	3.14
1996	32.64	52.80	10.86	4.86	3.01
1997	33.92	42.61	11.38	3.75	2.98
1998	41.04	34.90	11.61	3.01	3.53

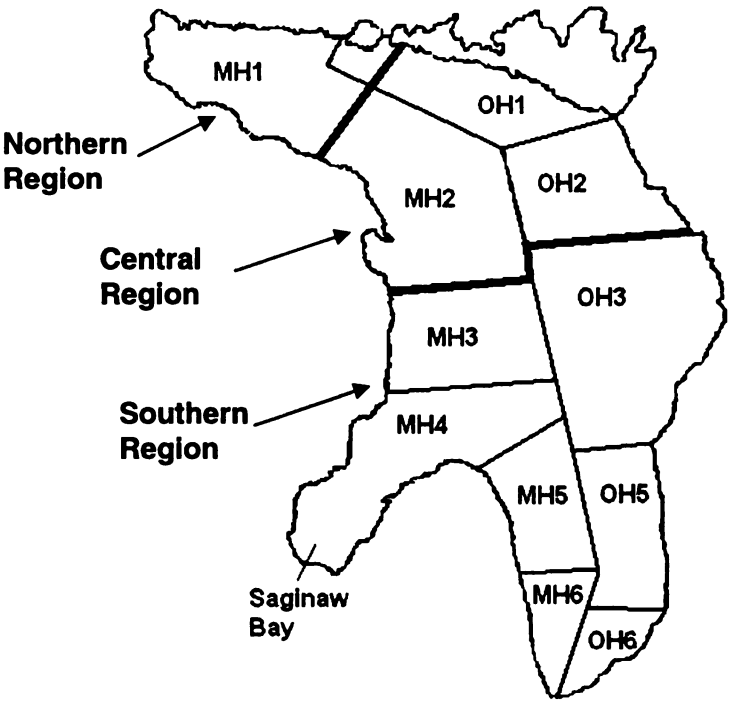

Figure 3.1 – Statistical districts in the US and Canadian waters of Lake Huron (Smith et al. 1961) grouped into lake regions. Statistical districts, used in sampling to denote location, are shown as MH- (Michigan waters) or OH- (Ontario waters)

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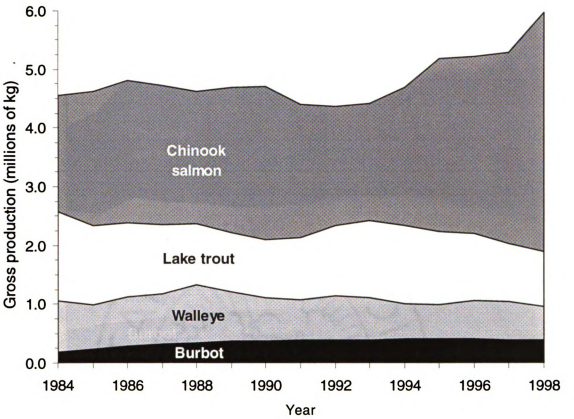

Figure 3.2 – Estimated gross production of key predators in the main basin of Lake Huron from 1984-1998.

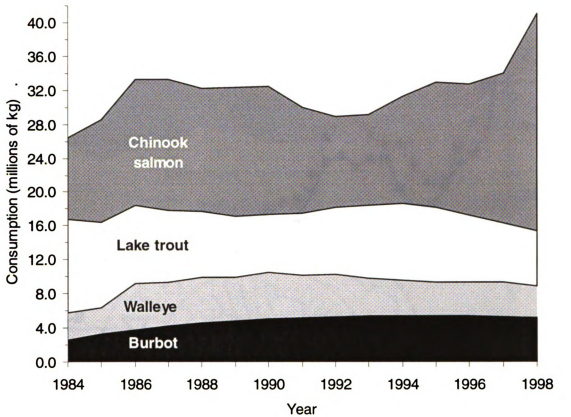

Figure 3.3 – Estimated total consumption by key predators in the main basin of Lake Huron from 1984-1998

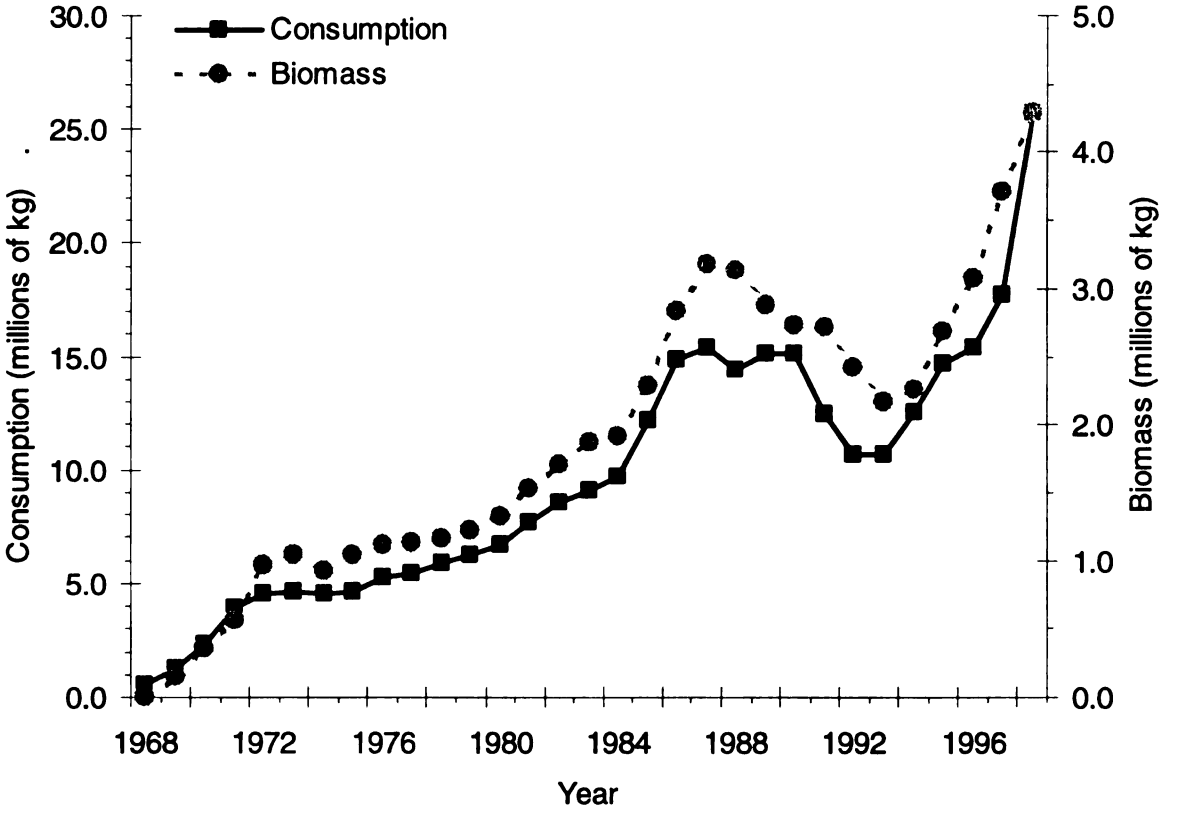

Figure 3.4 – Estimated chinook salmon consumption and population biomass in the main basin of Lake Huron from 1968-1998.

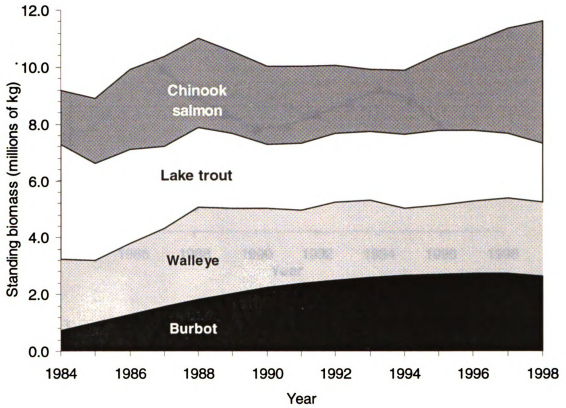

Figure 3.5 – Estimated biomass of key predators in the main basin of Lake Huron from 1984-1998.

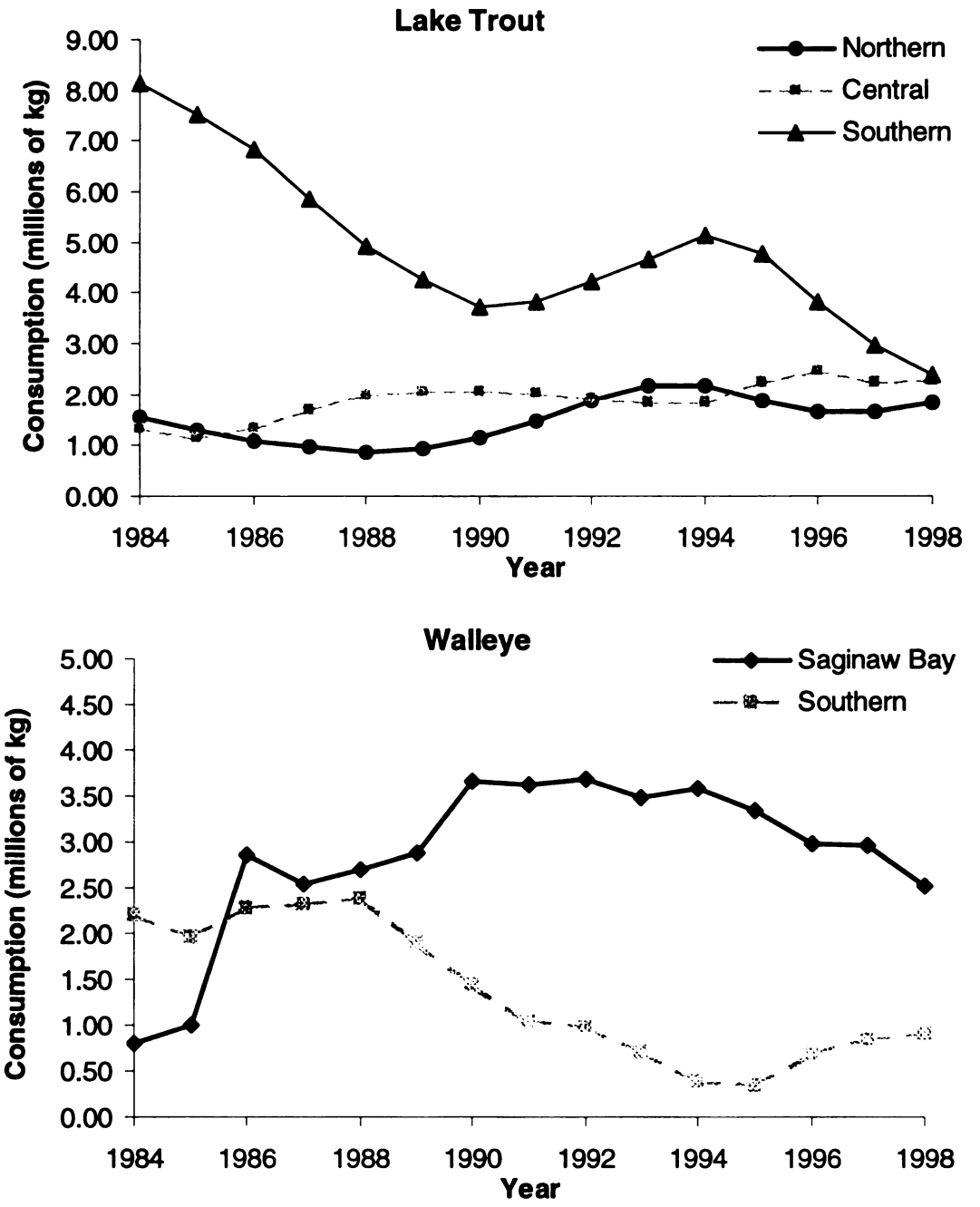

Figure 3.6 – Estimated annual consumption by lake trout and walleye by lake region, 1984-1998

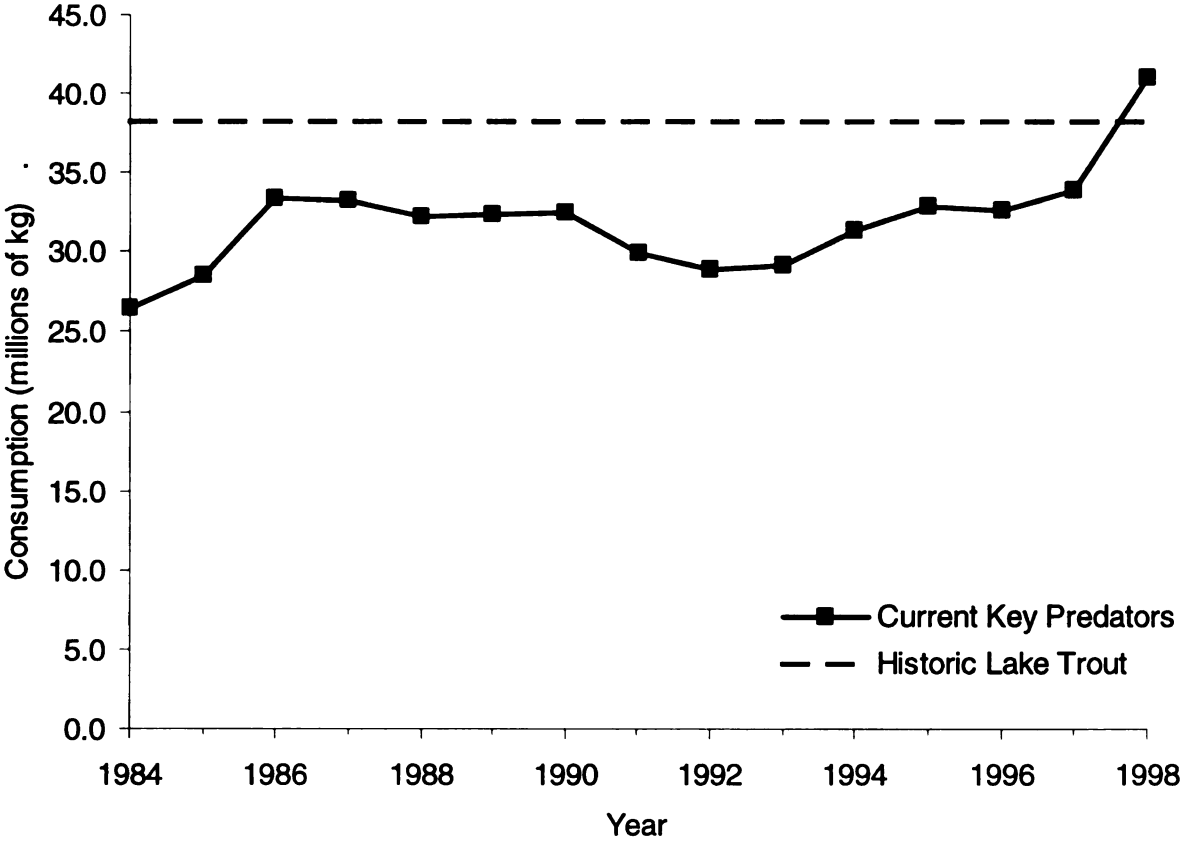

Figure 3.7 – Comparison of estimated current key predator consumption in the main basin of Lake Huron to estimated consumption by pre-collapse lake trout.

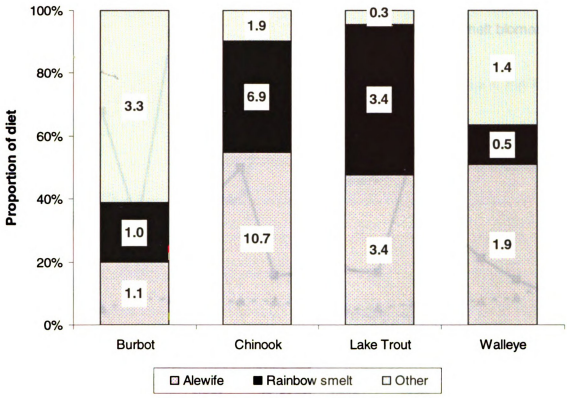

Figure 3.8 – Diet composition of the key predators in the main basin of Lake Huron. Proportion of each prey type in the diet represents the mean by weight for 1989 – 1999.

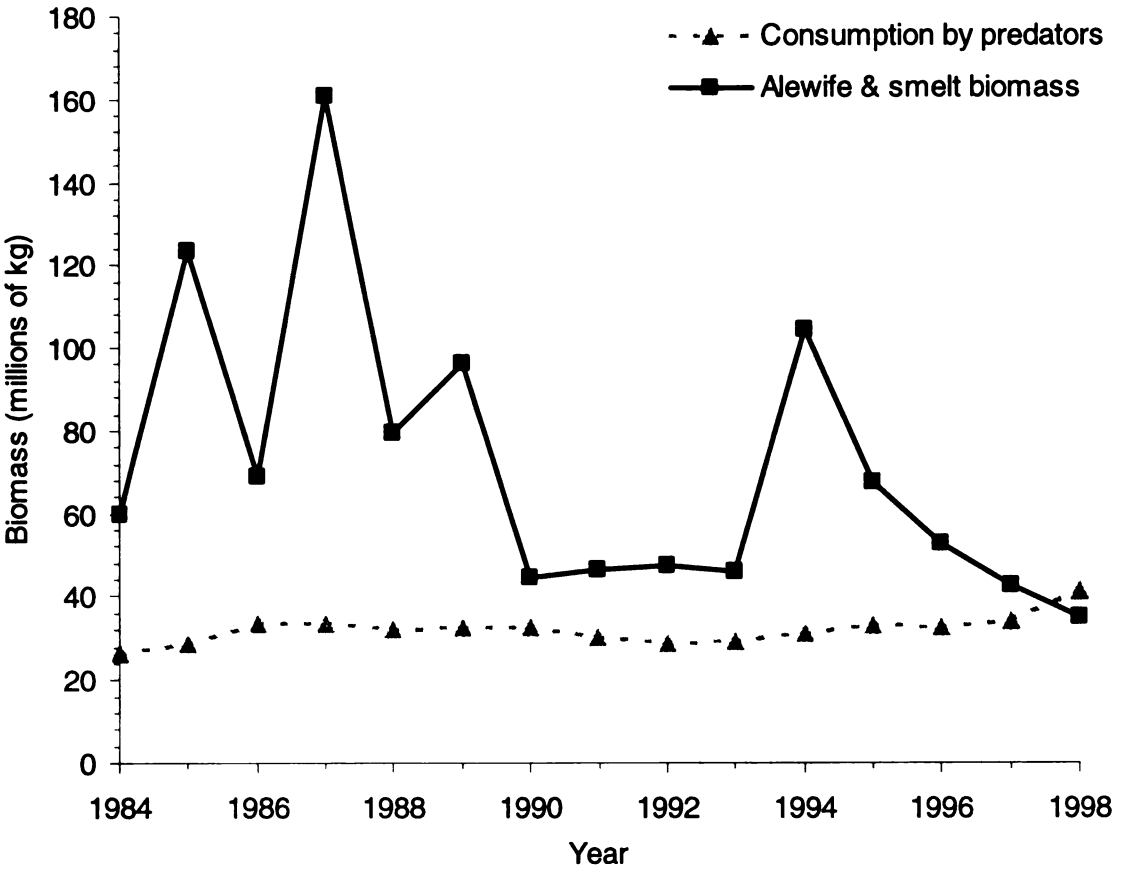

Figure 3.9 – Comparison of estimated key predator consumption to estimated combined alewife and rainbow smelt biomass in the main basin of Lake Huron from 1984-1998.

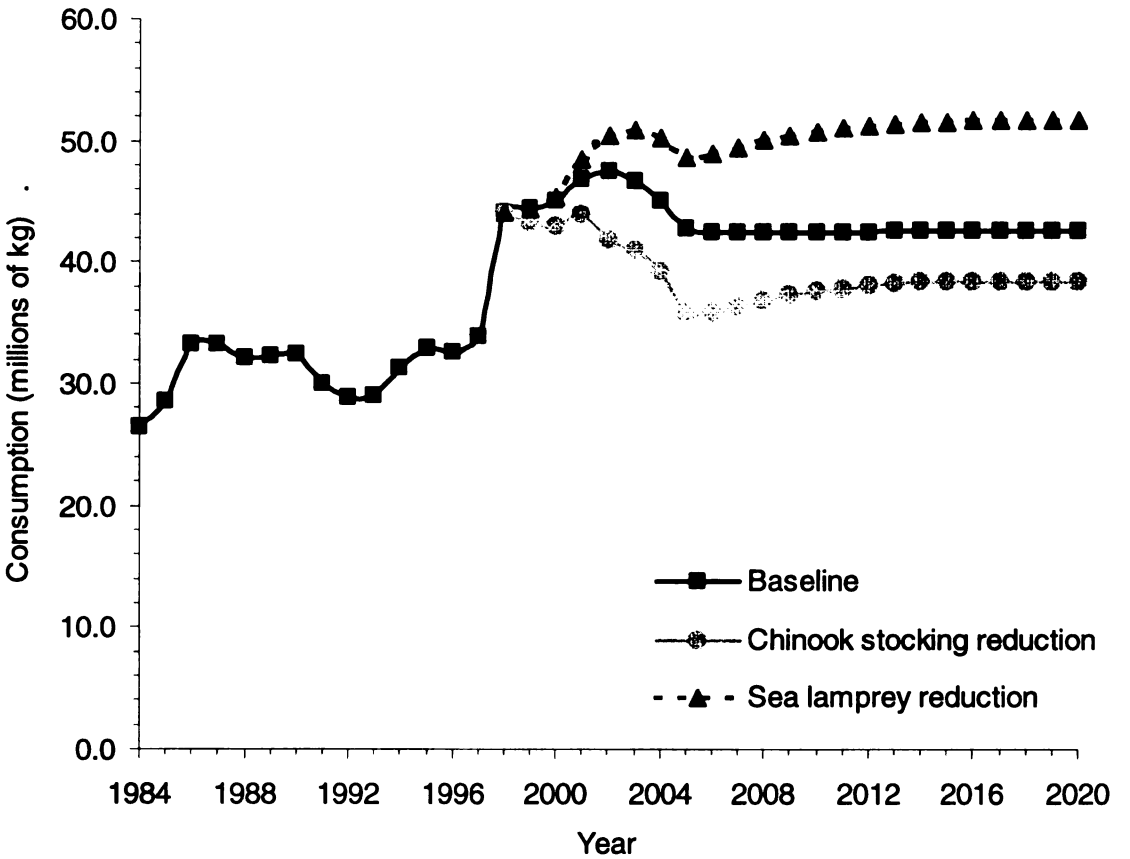

Figure 3.10 – Projected consumption by key predators in the main basin of Lake Huron through 2020 under three management scenarios.

Chapter 4

Parameterization of a Functional Response Model For Chinook Salmon In The Main Basin of Lake Huron.

Introduction

Stocking of chinook salmon *Oncorhynchus tshawytscha* in Lake Huron tributaries began in 1968 and has increased from 265,000 to approximately 4 million fish annually (Ebener et al. 1995). Natural reproduction was not detected before 1988 (Ebener et al. 1995) but current levels of wild recruitment are believed to be approximately 15% of total recruitment, although the actual amount is uncertain and may be much greater. Increases in the number of chinook salmon stocked along with improvements in survival of stocked fish and possible increases in wild recruitment account for approximately 60% increase in abundance and consumption from the mid 1980s to peak values in the late 1990s (Chapter 3).

Stocking also influences the abundance of other piscivores in Lake Huron, especially lake trout *Salvelinus namaycush*, with hatchery-reared fish constituting the majority of recruitment (Ebener et al. 1995). Additionally, recent attempts have been made to reduce the abundance of sea lamprey *Petromyzon marinus* (Bergstedt et al. 1998), a parasite that causes significant mortality to lake trout. Improving the survival of lake trout should increase their abundance and consumptive demand on the forage base. While all of the piscivores share the same forage base, the fast growing chinook salmon and long-lived lake trout take the largest proportion of the available prey fish, primarily consuming the exotic species alewife *Alosa pseudoharengus* and rainbow smelt *Osmerus mordax*. (Chapter 3).

Increases in salmonine stocking, unknown quantity of chinook salmon wild recruitment, and various management actions that may increase lake trout abundance have led to concerns that piscivore abundance could exceed the forage fish availability. In Lake Michigan, declines in alewife abundance during the early 1980s precipitated numerous changes throughout the Lake Michigan food web (Kitchell and Crowder 1986) and may have caused the collapse of chinook salmon in Lake Michigan (Holey et al. 1998; Benajmin and Bence In press (a); Benajmin and Bence In press (b)). Total abundance of alewife and rainbow smelt, the main constituents in the diet of Lake Huron chinook salmon, have also varied nearly fourfold between 1974 and 1998 (Figure 4.1). Between 1974 and 1984 chinook salmon growth declined in Lake Huron and although there have been subsequent years with improved growth, it has not recovered to the pre-1984 levels (Figure 4.2). While changes in prey abundance are often associated with changes in growth, this relationship is not clearly evident for chinook salmon in Lake Huron (Figure 4.3). Lacking critical data on the relationship between growth and prey density, and concerned that Lake Huron predators may be exceeding forage fish capacity, management agencies decreased chinook salmon stocking by 20% in 1999 in an attempt to avoid a possible collapse of the predator populations.

In Lake Huron, predator forage demand and the effects of changes in prey fish abundance on predator growth are not well understood. The amount of prey eaten and the composition of the diet depend upon prey availability in unknown or only partially understood manners. Researchers studying Lakes Michigan (Stewart et al. 1981; Stewart and Ibarra 1991; Eby at al. 1995), Ontario (Jones et al. 1993), and Superior (Mason et al. 1998) have used various approaches including bioenergetics models, foraging theory, and

functional response models to help clarify predator-prey dynamics in those lakes. We developed bioenergetics models and coupled them with age-structured population models of the key predators in Lake Huron (Chapter 3). Estimates from this effort showed that chinook salmon predation accounts for 54% of the total annual consumption of open-water prey fishes between 1996 and 1998. However, this approach does not predict how consumption changes with variations in prey densities or how changes in the forage base impact predator growth. Linking changes in growth to changes in prey density may provide an indicator of disruptions in the balance between predator numbers and prey abundance, and where predator abundance is primarily supported through stocking, allow fishery managers to reduce stocking and avoid a possible collapse of the predator population.

A functional response model (Holling 1959) is needed to link predator consumption with prey density. We developed a functional response model that estimates the number of prey fish consumed by chinook salmon in the main basin of Lake Huron based on prey abundance. Growth was linked to consumption through the conversion of food ingested to changes in body mass.

The final model fitting was done by varying the numbers of search rate parameters to test four hypotheses. In Model 1, our hypothesis was that the search rate was independent of predator age or prey type being consumed. Since differences in prey behavior or other species-specific factors can affect a predator's reaction to prey, in Model 2 we tested the hypothesis that prey type affects consumption by associating a separate search rate parameter with each prey species. In Model 3, we evaluated the effect of predator age on the model. Age 1 chinook salmon possess several unique

attributes not found in older fish. For instance, age 1 fish grow at a much faster rate than other age classes (Figure 4.2) and they selectively consume smelt while other age classes select for alewife (Appendix B Table B.3). Therefore, in Model 3 search rate parameters are dependent on predator age but not prey type, with age 1 fish and ages 2-4 forming two age groups. To evaluate the combined effects of predator age and prey species, Model 4 allows search rates to vary by prey type and predator age.

Methods

Our goal was to develop a model that predicts annual consumption of prey by an individual chinook salmon based on the abundance of prey of each type (species and size category) and the size of chinook salmon. Symbols used in equations throughout this document are given in Table 4.1. Equations not given in the text are in Table 4.2. We used a multi-species Type II functional response (Holling 1959 and Murdoch 1973)

$$P_{j,y,a,b} = \frac{S_{j,y,a,b}\, N_{j,y,b}\, t_a}{1 + \sum_j (h_{j,y,a,b}\, S_{j,y,a,b}\, N_{j,y,b})} \qquad (1)$$

which predicts consumption of prey (P) in year y by a chinook salmon of age a based on prey abundance (N) of each type (j) and size category (b). The search rate (S) and handling time (h) are related to chinook salmon size and its influence on a predator's ability to locate, catch, and digest its prey. The amount of time spent foraging in the lake (t) adjusts for age 4 chinook salmon that spawn and die before the end of the year. While chinook salmon consume other prey items, the vast majority of prey eaten consists of

alewife and rainbow smelt (Appendix B Table B.3); therefore, the functional response model includes only these two prey species.

We assumed the search rate depended on predator length, the ratio of prey to predator length, and dietary preference (Table 4.2) in a known fashion with these effects operating in a multiplicative way, following Jones et al. (1993). First, search rate was assumed to be directly proportional to predator length because swimming speed is proportional to predator length. Second, the relative search rate was adjusted using a dome-shaped "preference" function (Figure 4.4) determined by the ratio of prey to predator length, which peaked at an optimal ratio of 0.25 (Jones et al. 1993). Finally, based on recent dietary studies, age-1 chinook salmon were assumed to prefer rainbow smelt over alewife, whereas older ages were assumed to prefer alewife to rainbow smelt. These effects only set the relative search rates for different prey types. When the model was fit to observed data (see below), an unknown scalar ($\alpha_{j,a}$, Table 4.1) that determined absolute search rates was estimated. Additionally, when search rates for alewife and rainbow smelt were allowed to differ (Models 2 and 4), predator diet composition is not held constant by the dietary preference assumption but allowed to vary with prey abundance.

Handling times depended upon predator and prey sizes following relationships assumed to be known (Table 4.2, Figure 4.5). Based on results from bioenergetics modeling (Chapter 4 Appendix), handling times decreased with predator size because the maximum mass of prey that could be consumed in a year (*Cmax*) increased with chinook salmon size (Figure 4.5). Conversely, handling times increased with prey size because larger prey weigh more. For age 4 chinook salmon, *Cmax* was lower (Figure 4.5)

because we only predicted consumption for this age through the time of spawning (day 214).

Data available for parameterizing the model included chinook salmon annual weight-at-age, and annual prey abundance by type and size category for a time-series extending from 1974 through 1998. Chinook salmon weight-at-age was used in two different ways in the model. First, weight-at-age was used to determine chinook salmon length, an important component in the handling time and search rate. Second, annual changes in weight-at-age provided estimates of chinook salmon growth. We needed estimates of observed growth because we lacked direct estimates of consumption to compare with model predictions. Instead, we used equation 1 to estimate consumption of prey given prey abundances and then converted these estimates of individual consumption into predictions of individual chinook salmon growth. We then compared the predicted growth to observed growth, which was calculated from the annual change in weight-at-age.

Chinook salmon weight-at-age information was based on a combination of data from creel surveys and sampling spawning runs (Bence and Dobiesz 2000). Direct observations of weight were not available for some year and age combinations or were represented by very small sample sizes. A catch-at-age model for chinook salmon in Lake Huron included a dynamic von Bertalanffy growth model (e.g., Szalai et al. 2003) and produced a smoothed estimate of weight-at-age over time to account for large measurement errors (Bence and Dobiesz 2000).

Prey abundance was obtained from annual fall bottom trawl surveys of US waters in Lake Huron conducted by the USGS Great Lakes Science Center. When using this

survey method, numbers of fish in each trawl are expanded from the actual area trawled to all US waters based on the area swept by the trawls in different regions of the lake at a series of depth strata, accounting for the total bottom area in each region and depth station. Mid-year values of abundance for each prey species and size category were used in the functional response (Chapter 4 Appendix).

Equation 1 predicts the numbers of each prey type and size category consumed by a predator of a given age. Total biomass consumed by a predator was determined by multiplying the predicted numbers of each prey type and size category by the associated prey weight and summing over all prey sizes and prey types (Table 4.2). We converted predicted biomass consumed into chinook salmon growth (increment in weight) using an estimate of gross conversion efficiency (GCE) obtained from bioenergetics models (Chapter 4 Appendix).

The overall model fit was measured by the concentrated negative log-likelihood:

$$-\ln(\Gamma) = \frac{100}{2} \log \left[\sum_{y} \sum_{a} (G_{observed} - G_{predicted})^2 \right] \qquad (2)$$

which was minimized using a quasi-Newton numerical approach to adjust the unknown parameters using ADModel Builder (Otter Research 2000). Inferences based on this objective function depend upon the assumption that deviations from expected growth were normally distributed. Estimates obtained from this concentrated likelihood are equivalent to those obtained from the full negative log-likelihood equation, but the numerical search is simplified because the residual variance is obtained analytically rather than as an additional parameter adjusted during the search. We note that the

resulting point estimates are simply least squares estimates and the use of the concentrated likelihood only plays a role when making inferences.

The final model fitting was done by varying the numbers of parameters to evaluate the following hypotheses that the search rate: (1) was the same for all chinook salmon ages and both prey types; (2) varied by prey type; (3) varied between age 1 and age 2-4 chinook salmon but was the same for each prey type; (4) was dependent upon prey type and predator age. We computed the Akaike's Information Criterion (AIC) (Hilborn and Mangel 1997) for each configuration to compare the models.

Sensitivity Analysis

In the process of estimating the unknown search rate parameter(s), several quantities were treated as known including chinook salmon maximum consumption, the average day of consumption, and the size preference function shape variables. The effects of these values on the model estimates were evaluated by refitting the model using alternative values for each quantity in turn (Table 4.3). In addition to computing AICs, the estimated minimum and maximum values of the proportion of maximum ration (*Pmax*) will be used to compare the effects of these assumed quantities.

Age-specific maximum consumption (*Cmax*) by chinook salmon plays a key role in determining the handling time. A scalar, k_a, was used to proportionally increase or decrease (Table 4.3) the value of *Cmax* obtained from the length-dependent function (Chapter 4 Appendix) by ±20%. In a third alternative case, *Cmax* was held constant for each age at the 1974 level, a time of high predator growth (Table 4.3). This represents an

extreme case but should evaluate our assumption that *Cmax* changed over time as chinook salmon growth declined.

The average day of consumption (Chapter 4 Appendix) was used to adjust prey abundance and predator length to a mid-year value. Changes in consumption by each age caused the mid-year value to be different for each age, although ages 2 and 3 were almost identical (Chapter 4 Appendix). To evaluate the effect of this age-specific mid-year adjustment, we reran the model using the calendar mid-year, day 182, for all ages.

The parameters of the size preference function (Tables 4.1 and 4.2) were borrowed from a functional response model for Lake Michigan (Jones et al. 1993, E. Szalai, Pers. Comm.). It is based on the optimum prey to predator length ratio of 0.25, with "preference" declining above and below that ratio. In the standard model, we treated both prey types the same. We made two changes to the size preference function, and evaluated how sensitive the model was to the joint effect of these changes. First, because of differences in body dimensions, alewife of a given length tend to weigh more than rainbow smelt of the same length. Using the length-weight relationship for each prey species (Chapter 4 Appendix), we determined that at equal mass, an alewife would be 84% of the length of a rainbow smelt. We applied this percentage to the optimal prey to predator length ratio, setting it to 0.21 for alewife while keeping the 0.25 ratio for rainbow smelt (Figure 4.4). Second, we noted a significant lack of consumption of small prey sizes during model fitting. To increase the preference for the smallest prey sizes, we adjusted the left-hand limb of the size preference curve (Figure 4.4) by changing v in the size preference function (Table 4.2) from 0 (Table 4.3). A different value of w (Tables

4.2 and 4.3) was chosen for the two species to avoid unintended effects to the right-hand side of the preference function (e.g., negative values).

Results

We compared the fit of four functional response models (denoted as Models 1-4), with different search rate parameterizations, to observed growth of chinook salmon. We used likelihood ratio tests (Berry and Lindgren 1996) to compare models with different numbers of parameters and the AIC (Hilborn and Mangel 1997) to determine the final model (Tables 4.4 and 4.5). Model 1, with a single estimated parameter, fit observed growth poorly for all predator ages (Table 4.4). Although Model 2 was an improvement over Model 1, its predictions for all predator ages substantially exceeded observed growth during the 1990s (Figure 4.6). Model 3 had a lower AIC than Models 1 and 2 (Table 4.5) and its predictions matched observed growth better during the second half of the time series (Figure 4.7). Model 4 matched observed growth somewhat better than either Models 2 or 3, and had a lower (better) AIC than Models 1 through 3. Increasing the number of estimated search rate parameters from one to two, either to distinguish predator groups or prey species, significantly improved the fit of the model (Table 4.4). Increasing the number of parameters to four, to allow a unique search rate parameter for each combination of prey species and predator group, provided a closer match to observed growth as compared with models 2 and 3 (Table 4.4).

Although Model 4 outperformed the other models, there were three specific areas where the model predictions did not match observed values. First, growth for age

2 was overestimated in all but three years. The substantially better match to observed data for other ages obscured this outcome in the AIC. Since age 2 chinook salmon share many of the same attributes with age 3 fish (i.e., diet and growth rate), the reasons for the differences in how the model fits growth for these ages are not obvious. Second, Model 4, like each of the other models, missed a sudden increase in growth between 1989 and 1991 occurring in each age (Figure 4.7). Third, Model 4 failed to match the decline in growth of age 1 fish during 1987 and 1988. It appears that no functional response model of the type we considered would predict the increase in growth during 1989-1990, because prey abundance of both rainbow smelt and alewife were decreasing at this time.

Consumption

Over the modeled time series, prey abundance has varied dramatically from year to year (Figure 4.1). We expected to see a response in consumption to these varying levels of prey abundance, especially since growth varied over time (Figure 4.2). However, the functional response predictions of consumption of prey biomass change much less than proportionately with total prey biomass (Figure 4.8). There are substantial variations in predicted consumption, unrelated to total prey abundance, which stem from the composition of prey types and changes in predator size-at-age. However, the pattern in Figure 4.8 suggests conditions where predators may be feeding near their maximum capacity.

To better illustrate how predictions of consumption respond to prey abundance, the composition (percent of each type) was fixed at the average proportions seen between

1985 and 1996, and prey abundance was set to fixed values ranging between 3.3E+08 and 8.26E+09, which spanned the observed total prey abundance. Predator weight-at-age was fixed at either a high level (1974) or a low level (1984). The four estimated search rate parameters from Model 4 (Table 4.5) were used to generate predictions of per capita consumption (Figure 4.9). At the lowest observed prey abundance, the functional response model is predicting that consumption is increasing much less than proportionately to increases in prey abundance. Ages 2 and 3 being the fastest growing fish in the model have the lowest handling time and therefore are not as close to their saturation value.

Growth

Since our previous analyses suggested that variations in growth were only weakly tied to prey abundance, the root cause for the substantial changes in size-at-age over time remains unclear. To explore this we examined the relationship between the consumption by a cohort and its initial size at age-1 (Figure 4.10). When age 1 fish were smaller for any given cohort, subsequent ages within that cohort grew less and consumed less prey biomass than cohorts that began age 1 at a larger size. The regression model predicted a 28% decrease in estimated consumption between the cohorts with the smallest age 1 fish (1984) and the largest (1974).

Comparison to bioenergetics models

Using bioenergetics models with Lake Huron specific data (Appendix B) we generated estimates of age-specific annual consumption for an average chinook salmon

(Chapter 3). The functional response model produced estimates of numbers of prey consumed, which we converted into estimates of biomass. Comparing the estimates from these two models shows that they are similar and track the downward trend in consumption over time (Figure 4.11). The models tended to estimate very similar consumption for ages 1 and 3. However, the functional response model tended to estimate higher consumption for ages 2 and 4 than the bioenergetics model.

Sensitivity analysis

With *Cmax* values reduced by 20%, estimated search rate parameters were larger than Model 4 parameters (Figure 4.12) and the AIC was the lowest of all alternatives analyzed (Table 4.6). Lowering *Cmax* also lowers the minimum and maximum values of *Pmax* obtained in the model (Figure 4.13). The effects of higher *Cmax* values, produced by increasing the base by 20% or by using *Cmax* values fixed at 1974 levels, was to lower the values of the estimated search rate parameters from those in Model 4 (Figure 4.12) and increase the AICs (Table 4.6). The range of *Pmax* values is more highly affected by fixing the *Cmax* value than by increasing it by a fixed amount (Figure 4.13).

Changing the prey size preference function did not have a large impact on the model parameter estimates (Table 4.6) or minimum and maximum estimated for *Pmax* (Figure 4.12). There is only a slight increase in the maximum *Pmax* values for ages 2-4, whose diet preference favors alewife.

Setting the adjustment day to the actual middle of the year produced estimates of the search rate parameters that were higher than those estimated by Model 4 (Figure

4.13). Changing the mid-year adjustment day to day 182 slightly lowered the AIC (Table 4.6) and had its biggest effect on the estimates of search rate parameters for age 1 (Figure 4.13).

Overall, our assumptions regarding the prey size preference and the mid-year adjustment day had a much smaller effect on the model than changes to *Cmax*. Handling time sets the upper limit on consumption and is inversely related to *Cmax*. Additionally, each sensitivity analysis produced some changes in *Pmax* when compared to Model 4 but direction of these changes were essentially the same across predator ages (Figure 4.13), although fixing *Cmax* at 1974 levels substantially reduced both the minimum and maximum values of *Pmax*.

Discussion

Studies of Lakes Michigan and Ontario (Stewart et al. 1981; Jones et al. 1993) have shown the potential for stocked salmonids to outreach the forage fish capacity. In Lake Huron, chinook salmon growth declined between 1974 and 1998 (Figure 4.2) leading to concerns that predator growth was being limited by forage fish availability. Since chinook salmon are the dominant predator in Lake Huron (Chapter 3), we parameterized a functional response model to evaluate how chinook salmon consumption was affected by prey abundance. We converted these estimates of consumption to estimates of chinook salmon growth using GCEs estimated from bioenergetics models. While our analysis did not include all factors that influence chinook salmon growth, we expected that if variations in prey abundance were a primary determinant of chinook

salmon growth, and prey availability were limiting during the time period evaluated, this would be uncovered by fitting a functional response model.

Growth is closely tied to consumption but varies with food availability, food quality, water temperature, time of hatching, gonad production, age, and activity costs, making it difficult to find a simple relationship between growth and consumption (Boisclair and Leggett 1989a, b; Hewett et al. 1991; Hewett and Kraft 1993). Studies have attempted to correlate changes in growth with changes in prey abundance with varying success (e.g., Stewart and Ibarra 1991; Breck 1993; Eby et al. 1995). Our functional response model attempted to uncover a more subtle relationship by taking into account variations in prey species and size composition. However, our analysis suggests that variations in total consumption (and hence growth) have been only weakly tied to measured prey abundance (Figures 4.3 and 4.8). Density-dependent effects related to chinook salmon abundance were not evident (Figure 4.14) suggesting that chinook salmon could always find enough prey to feed close to *Cmax*.

Our functional response model suggests that over a large range of prey abundance age 1-4 chinook salmon were feeding above 60% of their maximum rate of consumption (*Pmax*) and variations in prey abundance explained little of the variation in observed growth (Figure 4.14). This was also true when assumed known constants were varied in the sensitivity analyses, with the exception being when *Cmax* values were constant over time and set at values based on size-at-age observed in 1974. One explanation for why the model predicted that predators were feeding near saturation (i.e., high Pmax values) could be that observed growth was not related to measured prey abundance in a straightforward way. The functional response model can only make growth weakly

related to large variations in prey abundance if the predicted feeding level is near the asymptotic feeding rate at the lowest observed prey abundance.

Between 1974 and 1998, chinook salmon size-at-age varied substantially, with an overall downward trend. The model fitting results suggest that this decline cannot be explained by variations in prey abundance. Nevertheless, the model was able to predict some of the observed declines in growth (Figure 4.7). Accepting the model fit at face value, observed declines in growth must be related to other factors. We noted that significant differences in the weight-at-age 1 followed the cohort through its life span. Weight-at-age 1 has varied from 1.21 kg in 1974 to 0.712 kg in 1987. Fish that weighed less at age 1 consistently weighed less throughout their life span than fish whose weight at age 1 was higher. The functional response model predicts lower growth of cohorts that begin age 1 at a smaller size because they have a lower *Cmax* and less capacity for growth (Figure 4.10). The nearly constant instantaneous growth rate (Figure 4.2) we observed suggests that fish that start out smaller cannot "catch up" to fish that start out larger. With the majority of recruitment coming from stocking, age 0 fish should be approximately the same size, therefore, factors that effect early growth have an important impact on subsequent consumption, and these factors were not represented in our model of growth from age 1 to age 4.

These results have implications for the current mix of stocked and naturally reproducing chinook salmon in Lake Huron. Studies in other ecosystems have shown that hatchery-reared chinook salmon are smaller than wild recruits (Roni and Quinn 1995; Unwin and Glova 1997). If this were also true in Lake Huron, wild fish might have a significant advantage over stocked fish. If they begin life in Lake Huron at a

larger size, they could eat larger prey, and salmonids have been shown to grow larger when they eat larger prey (Kerr 1971; Mittelbach and Persson 1998; Pazzia et al. 2002). The cause of annual differences in weight-at-age 1 are unclear but growth has been shown to be heritable in chinook salmon (Withler et al. 1987) and slower growth in some cohorts could be driven by prey abundance, but in ways we were unable to uncover.

Another possible explanation for our model results is that the assumed relationships and constants we used were substantially in error, and there is actually a stronger relationship between predator consumption and prey availability. Of particular concern were the assumptions that age-specific GCEs were constant over time and estimates of these GCEs were based on maximum chinook salmon growth during 1974 but energy density of predators and prey observed during 1996-1997. Values of *Cmax* for a given size chinook salmon were based on this same relationship between maximum growth and consumption. Our values for energy density (Chapter 2) tended to be lower than those published in the literature for other lakes and earlier time periods. Lower energy densities would tend to lower the GCEs. If GCEs declined over time, the amount of consumption required to achieve the maximum amount of growth, which may be a physiological limit, might have increased. Thus, *Cmax* might have increased over time if energy density of prey fish declined. If this occurred as we speculated in Chapter 2, chinook salmon growth may have been limited by available prey even when prey abundance was not declining. Additionally, since chinook salmon size-at-age changed over time, *Cmax*, and therefore handling time, may have shifted in a way that was not captured by our model.

There were also substantial uncertainties associated with our measurements of predator growth and prey abundance. We lacked annual weight-at-age for chinook salmon and instead used a dynamic von Bertlanfy growth model to estimate a smoothed weight-at-age over time, reducing large measurement errors. The type of assessment gear used to estimate relative prey abundance changed in 1992 with some concern about proper adjustments to estimates. Also, prey fish abundance as measured in the fall may not accurately reflect availability of prey to chinook salmon (Eby et al. 1995), or spatial and temporal changes in prey availability may effect predator consumption (Kerr 1971; Goyke and Brandt 1993). However, these uncertainties do not seem large enough that they would obscure a strong relationship between predator growth and prey abundance.

Our intention was to improve our understanding of the linkage between chinook growth and prey abundance. While we used the best available data, these efforts would benefit from improved prey assessments that measured changes in seasonal and temporal patterns of prey fish availability. Similarly, annual measurements of predator and prey energy density as well as seasonal diet information could improve model estimates. Additionally, we examined only predator dynamics but studies that link both predator and prey dynamics (e.g., Jones et al. 1993) could further enhance our understanding of the relationship between predator growth and prey abundance.

Appendix

This appendix contains details and equations used in the chinook salmon functional response model.

Day of average consumption

The day of the year when the average consumption occurred was determined using bioenergetics models that estimate daily consumption. This day was used to adjust prey abundance and chinook salmon length to a mid-year value. The day of the year when the average consumption occurs is given by

$$D_a = \left(\sum_{d=1}^{T} d\ C_d \right) \div \left(\sum_{d=1}^{T} C_d \right)$$

where d is the day of the year with January 1st being day 1;

T is the number of days the predator is resident in the lake with ages 1-3 resident for 365 days and age 4 resident for 214 days; and

C_d is the consumption on day d.

The average consumption occurs on day 234 for age 1, day 208 for ages 2-3 and day 150 for age 4.

Prey abundance and size categories

Estimates of prey abundance in US waters were extended to estimates for the entire main basin using a constant multiplier of 1.767 (G. Curtis, USGS Great Lakes

Science Center, Pers. Comm.). Prey abundance was divided into 5 mm size categories. The smallest and largest size categories contained many missing values over the time series. These were combined into two plus groups representing 10-40 mm and 215-250 mm. Each was treated as a single bin with prey sizes fixed at 40 and 250mm, representing the most common size *[Note: all fish larger than 250mm were classified as 250mm]*. Each prey size category was adjusted to the average day of consumption by assuming prey abundance changed exponentially with a constant per capita instantaneous rate between two prey assessments:

$$\varpi = \ln(M_{j,y,b} / M_{j,y-1,b}) / 365$$

$$N_{j,y,b} = M_{j,y,b} \exp(\varpi (D_a + 77))$$

where ϖ is the instantaneous rate of change between the previous and current prey assessments, assumed to occur on October 15th,

$M_{j,y,b}$ is the estimate of prey abundance for prey j in year y and bin b

$N_{j,y,b}$ is estimated prey abundance on day D_a for prey j in year y and bin b,

D_a is the day of the year when the average consumption by chinook salmon occurs for age a, with a constant (77) to adjust for the start date of October 15th rather than January 1st.

Prey Weight

The functional response model produces numbers of each prey type eaten from each length bin. The numbers eaten were converted to biomass eaten using a weight-

length relationship (J. Schaeffer, USGS Great Lakes Science Center, Pers. Comm) for each prey species:

$$W_{j,b} = \begin{cases} (4.223\times10^{-05}\times b^{2.662})/1000 & j = alewife \\ (6.935\times10^{-06}\times b^{2.945})/1000 & j = smelt \end{cases}$$

where $W_{j,b}$ is the mean weight (kg) of prey type j in bin b, and

b is the mid-point of the prey length bin (mm).

Predator Weight and Length

A weight-length relationship was determined from data collected from weir sampling on the AuSable River, Michigan during 1974-1981 and 1996-1999 (J. Johnson, Michigan Department of Natural Resources, Pers. Comm.). The length-at-age is given by

$$L_{y,a} = \exp(6.122)\times\left(W_{y,a}\right)^{0.325} + 0.0014$$

where $L_{y,a}$ is the length-at-age a in year y adjusted to day D_a, and

$W_{y,a}$ is the weight-at-age a in year y adjusted to day D_a.

Predator length was adjusted to the age-specific average day of consumption (D_a) by first adjusting the weight-at-age to D_a then applying a weight-length relationship. Chinook salmon weight-at-annulus was assumed to change exponentially between the start and end of the year:

$$\varpi = \ln(V_{y+1,a+1} / V_{y,a})/365$$

$$W_{y,a} = V_{y,a}\exp(\varpi D)$$

where ϖ is the exponential rate of growth between the start and end of the year,

$V_{y,a}$ is the weight-at-age a in year y at annulus, and

$W_{y,a}$ is the weight-at-age a in year y adjusted to day D_a.

We assumed that age 4 fish (the last age group) mature and die on day 214 so we used the weight-at-annulus in the beginning of the year and the fall weight in the same year to estimate the weight on day D_a. The input data also contained an extra year (1999) of weight-at-age data to allow the weight in the last year to be adjusted to day D_a.

Cmax

Handling times were based on estimates of the annual maximum amount of consumption possible (*Cmax*) by a chinook salmon of a given size and the mean weight of a prey fish in each size category

$$C\max_a = k_a\,(q_a\,L_{y,a}{}^{r_a})$$

where k_a age-specific scalar for *Cmax* used in sensitivity analysis, otherwise set to 1;

q_a age-specific intercept of power function (Table 4.3) relating length of predator to *Cmax*;

$L_{y,a}$ is the length-at-age a in year y adjusted to day D_a; and

r_a Slope of power function (Table 4.3) relating length of predator age a to *Cmax*

Cmax was estimated directly from age-specific bioenergetics models (Chapter 3) that predicted consumption from observed growth during 1974, the assumed period of maximum growth. An exponential function relating predator length to *Cmax* was developed from these data. A separate relationship was needed for ages 1-3 and age 4 since the annual maximum consumption of age 4 fish is limited by their maturation in the time step (Figure 4.5). However, the difference between ages 1-3 and age 4 was not proportional to the number of days spent in the lake, especially for larger fish. The weight of a prey fish in each size category, the other key element in estimating handling time, was determined from a weight-length relationship (see above).

Gross Conversion Efficiency

Using a bioenergetics model (Appendix B), age-specific GCEs were estimated from observed growth during 1974, and were representative of the mean over the time series 1974-1998 (Figure 4-15). GCEs were 0.226 for age 1, 0.140 for age 2, 0.130 for age 3, and 0.066 for age 4 chinook salmon.

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Table 4.1 – Symbols used in the chinook salmon functional response model.

Symbol	Variable description	Units
Cmax	Maximum consumption by a predator of given length	kg
G	Annual growth in year *y* for predator age *a*	kg
GCE	Gross conversion efficiency for predator age *a*	
h	Handling time for prey type *j* by predator age *a* in year *y*	yr
L	Predator length	mm
N	Prey abundance adjusted to mid-year value	
P	Per capita consumption by chinook salmon	yr^{-1}
R	Ratio of prey length to predator length	
S	Search rate of chinook salmon	yr^{-1}
W	Mean weight of prey type *j* in each size category *b*	kg
Z	Size preference of an age *a* chinook salmon for prey type *j* with length *b*	
Γ	Log-likelihood	
	Constants assumed as known	
d	Dietary preference for prey type *j* for an age *a* predator	
k	Age-specific scalar for *Cmax*	
q	Intercept of power function relating length of predator age *a* to *Cmax*	
r	Slope of power function relating length of predator age *a* to *Cmax*	
t	Proportion of a year the predator age *a* is resident in the lake	
u	Optimum prey:predator length ratio for prey type *j*	
v	Preference for smaller sizes of prey type *j* in size preference dome curve	
w	Width of the size preference curve for prey type *j*	
	Estimated parameters	
α	Estimated search rate parameter for predator age a and prey type *j*	
	Subscripts	
a	Chinook salmon ages 1 - 4	
b	Prey size category in 5mm increments	
j	Prey type (alewife or smelt)	
y	Year (1974-1998)	

Table 4.2 – Equations used in chinook functional response model. Descriptions of variables are shown in Table 4.1.

Handling time

$$h_{y,a,b} = \frac{W_{j,b}}{C\max}$$

Maximum consumption (*Cmax*)

$$C\max_a = k_a\,(q_a\,L_{y,a}{}^{r_a})$$

Search rate

$$S_{j,y,a,b} = \alpha_{j,a}\,L_{y,a}\,Z_{j,y,a,b}\,d_{j,a}$$

Size Preference

$$Z_{j,y,a,b} = \frac{\exp(-1.0\,R_{y,a,b} - u_j)}{w_j} + v_j(u_j - R_{y,a,b})$$

Estimated growth

$$G_{y,a} = \left[\sum_j \sum_b P_{j,y,a,b}\,W_{j,b}\right] GCE_a$$

Table 4.3 – Values of assumed constants used in the functional response model and the sensitivity analyses. "Base model" denotes the functional response model with four estimated search rate parameters (Model 4, by prey type and predator age). Other scenarios represent the configurations for sensitivity analyses. All assumed constants used in the "Base model" are listed with subscript indicators and values. Sensitivity analyses scenarios list only those constants that were changed in the scenario.

Scenario name	Symbol	Subscript Value(s)	Value
Base model	*d*	alewife, predator age 1	0.3194
		rainbow smelt, predator age 1	0.6806
		alewife, predator age 2+	0.7585
		rainbow smelt, predator age 2+	0.2415
	k	predator ages 1-4	1.00
	t	predator ages 1-3	365
		predator age 4	214
	q	predator ages 1-3	4.93E-06
		predator age 4	4.90E-06
	r	predator ages 1-3	2.340
		predator age 4	2.244
	u	alewife and rainbow smelt	0.25
	v	alewife and rainbow smelt	0.0
	w	alewife and rainbow smelt	0.0183
Cmax at 120%	*k*	predator ages 1-4	1.20
Cmax at 80%	*k*	predator ages 1-4	0.80
Cmax fixed	*Cmax*	predator age 1	15.755
		predator age 2	30.961
		predator age 3	44.574
		predator age 4	27.686
Adjust to day 182		See Chapter 4 Appendix for details	
Alternative species-specific size preference	*u*	alewife	0.21
		rainbow smelt	0.25
	v	alewife	0.25
		rainbow smelt	0.6
	w	alewife	0.03
		rainbow smelt	0.03

Table 4.4 – Likelihood ratio tests for all combinations of model configurations.

Model Comparisons	df	Chi-2	p-value
1 vs. 2	1	13.594	0.0001
1 vs. 3	1	43.924	<0.00001
2 vs. 4	2	62.332	<0.00001
3 vs. 4	2	32.002	<0.00001

Table 4.5 – Model hypotheses and estimated search rate parameter(s) on the log scale with asymptotic standard errors for parameter estimates shown in parentheses. The search rate parameters ($\alpha_{j,a}$) control the overall search rates for the predator on a prey species after adjusting for predator and prey sizes. The first subscript is the prey type-specific scalar for alewife (j=1) and rainbow smelt (j=2). The second subscript is the predator age grouped by age 1 (a=1) and ages 2-4 (a=2). Some models ignored one or more of these subscripts and these are represented by dashes in place of a value for the subscript.

Model / Hypothesis	AIC	Parameters	
Model 1 One search rate parameter for all chinook salmon ages and for both prey species	297.09	$\alpha_{-,-}$= -19.04 (0.072)	
Model 2 Search rate scalar by prey type	285.49	$\alpha_{1,-}$= -18.61 (0.101)	$\alpha_{2,-}$= -20.375 (0.421)
Model 3 Search rate scalar by predator age	255.16	$\alpha_{-,1}$= -19.925 (0.108)	$\alpha_{-,2}$= -18.880 (0.063)
Model 4 Search rate scalar by predator age and prey type	227.16	$\alpha_{1,1}$= -20.46 (0.844) $\alpha_{1,2}$= -20.293 (0.352)	$\alpha_{2,1}$= -19.798 (0.175) $\alpha_{2,2}$= -17.884 (0.101)

Table 4.6 – Results of the sensitivity analysis using alternate values for assumed quantities (Table 3). Estimated parameter values are shown with asymptotic standard error in parentheses. For the search rate parameters ($\alpha_{j,a}$), the first subscript is the prey type-specific scalar for alewife (j=1) and rainbow smelt (j=2) and the second subscript is the predator age grouped by age 1 (a=1) and ages 2-4 (a=2).

Model	AIC	$\alpha_{1,1}$	$\alpha_{1,2}$	$\alpha_{2,1}$	$\alpha_{2,2}$
Cmax at 80%	153.84	-19.900 (0.990)	-19.159 (0.201)	-19.319 (0.401)	-17.142 (0.139)
Cmax at 120%	268.95	-20.759 (0.853)	-20.083 (0.171)	-20.723 (0.360)	-18.203 (0.094)
Cmax fixed	308.95	-21.186 (1.330)	-20.058 (0.189)	-21.172 (0.487)	-18.276 (0.096)
Adjust to day 182	214.03	-20.171 (1.238)	-19.409 (0.216)	-20.245 (0.370)	-17.805 (0.101)
Size preference by weight of prey	218.17	-20.382 (0.788)	-19.848 (0.167)	-20.418 (0.320)	-18.114 (0.098)

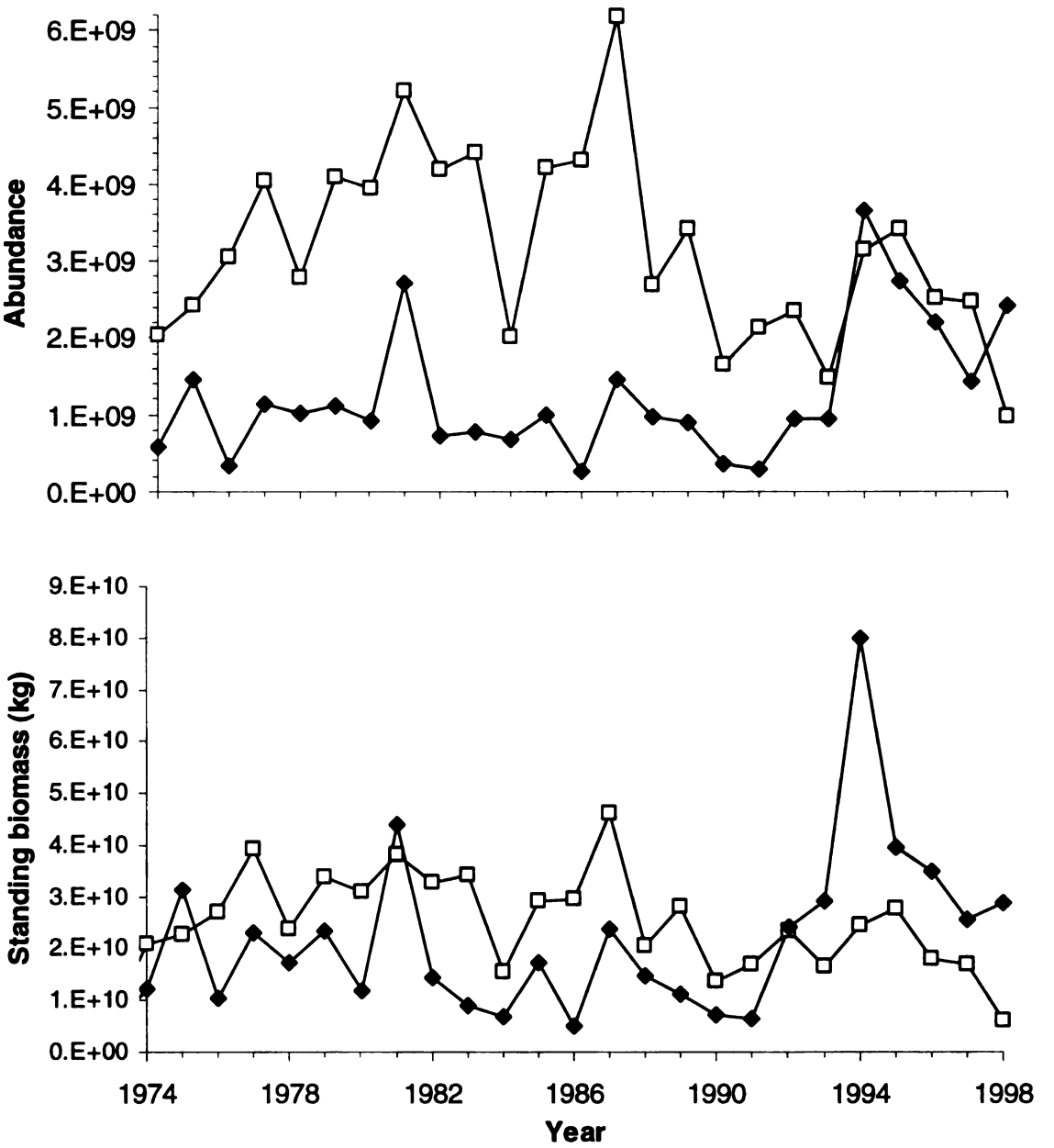


Figure 4.1 –Combined alewife and rainbow smelt abundance and standing stock biomass for the main basin of Lake Huron from 1974-1998.

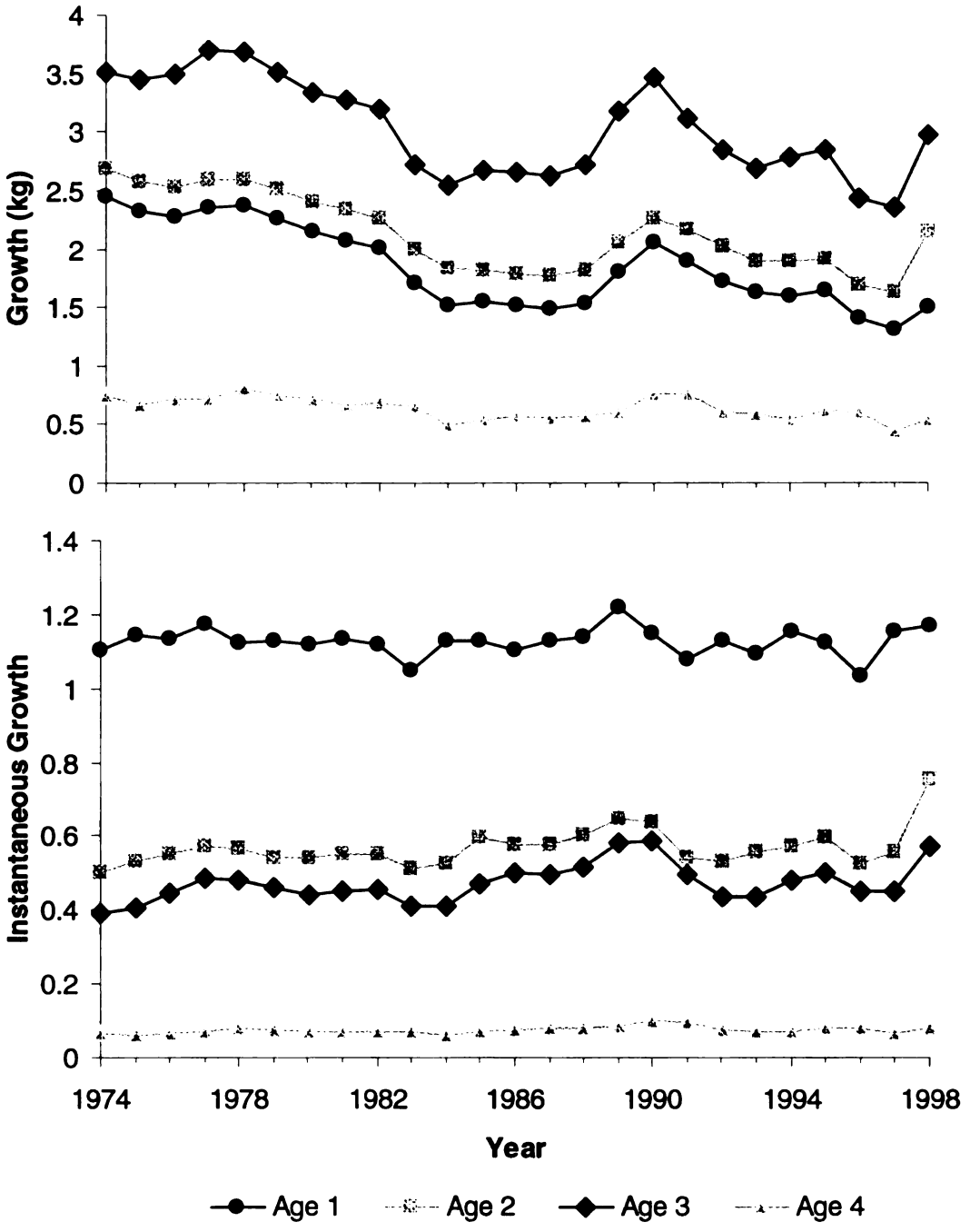


Figure 4.2 – Annual age-specific chinook salmon growth (top panel) and instantaneous growth (bottom panel) from weight-at-age data.

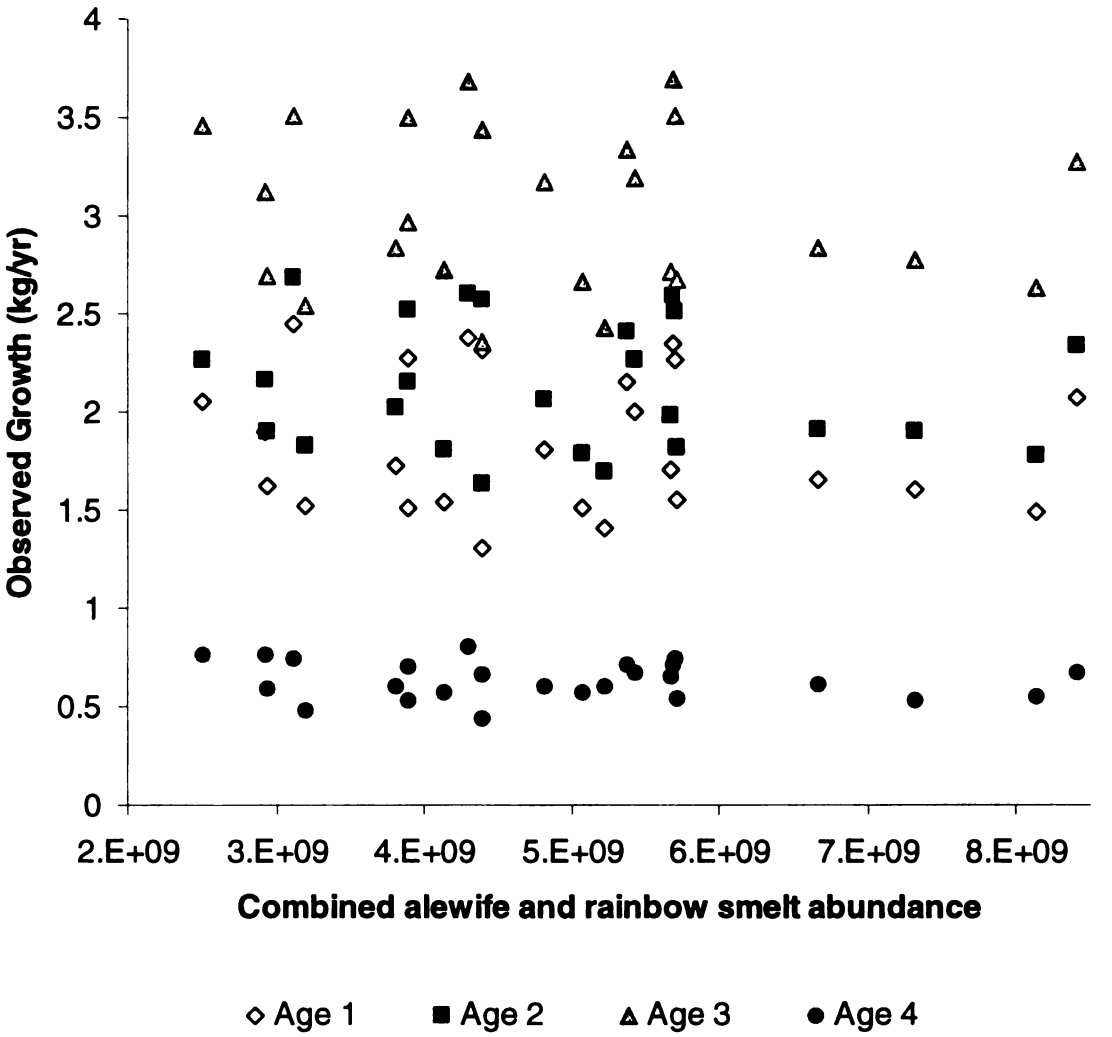


Figure 4.3 – Relationship between observed chinook salmon growth determined from weight-at-age data and the combined alewife and rainbow smelt abundance between 1974 and 1998.

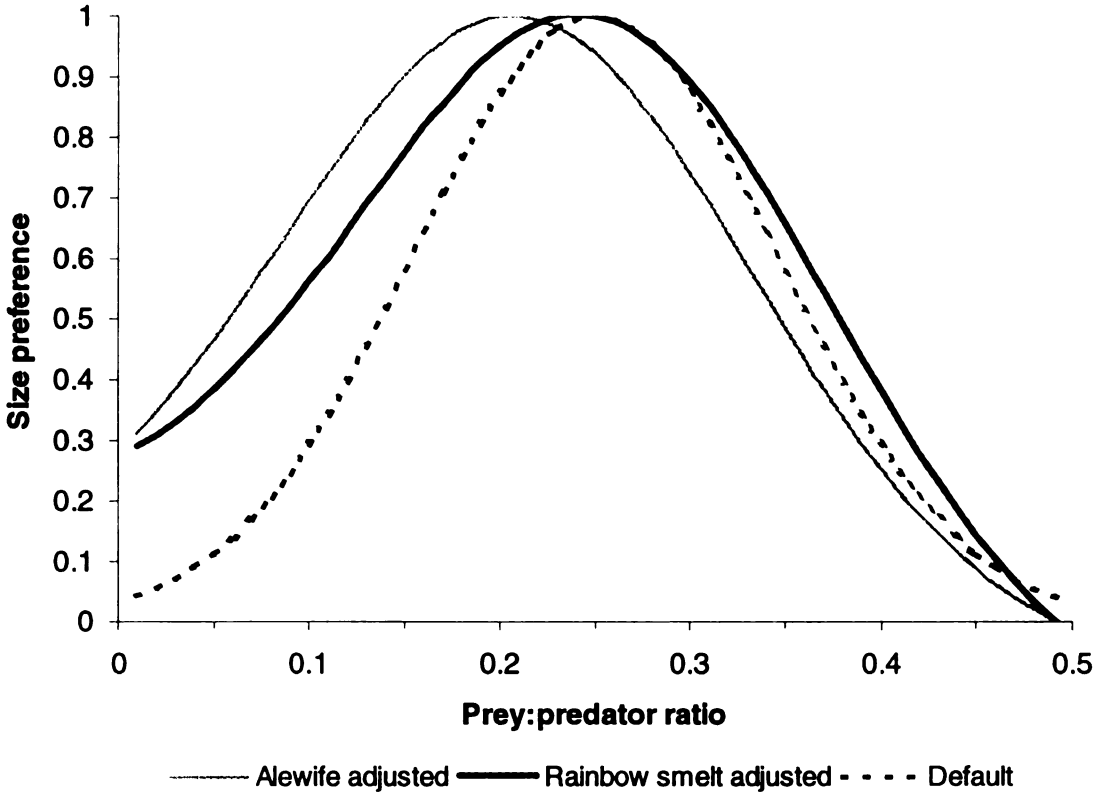
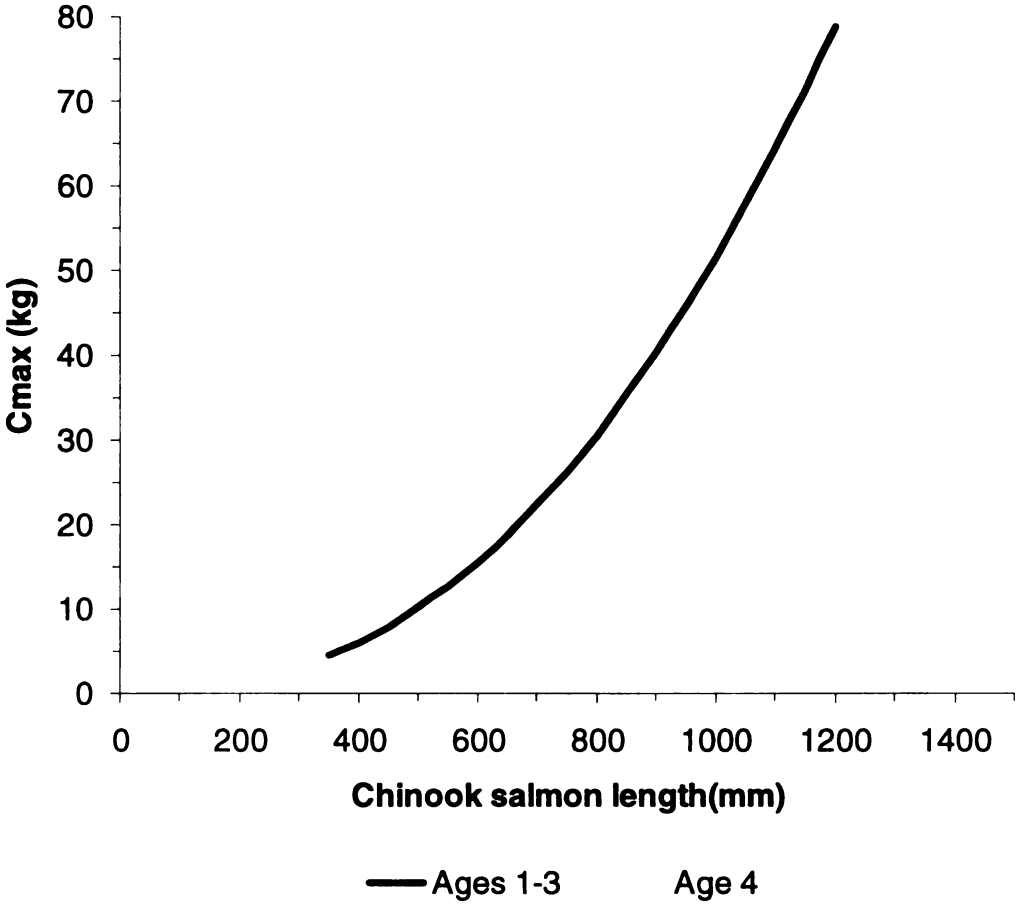


Figure 4.4 – Predator size preference for the prey species. The values of the function shape variables are given in Table 4.3. The Default curve was used for both prey species in the model fitting process. The adjusted curves were used to test the sensitivity of the size preference function to differences in prey weight for a given size category.



$$C\max_a = k_a\,(q_a\,L_{y,a}{}^{r_a})$$

Figure 4.5 – Relationship between age-specific maximum consumption (Cmax) and chinook salmon length (mm) used to determine handling time in the functional response model.

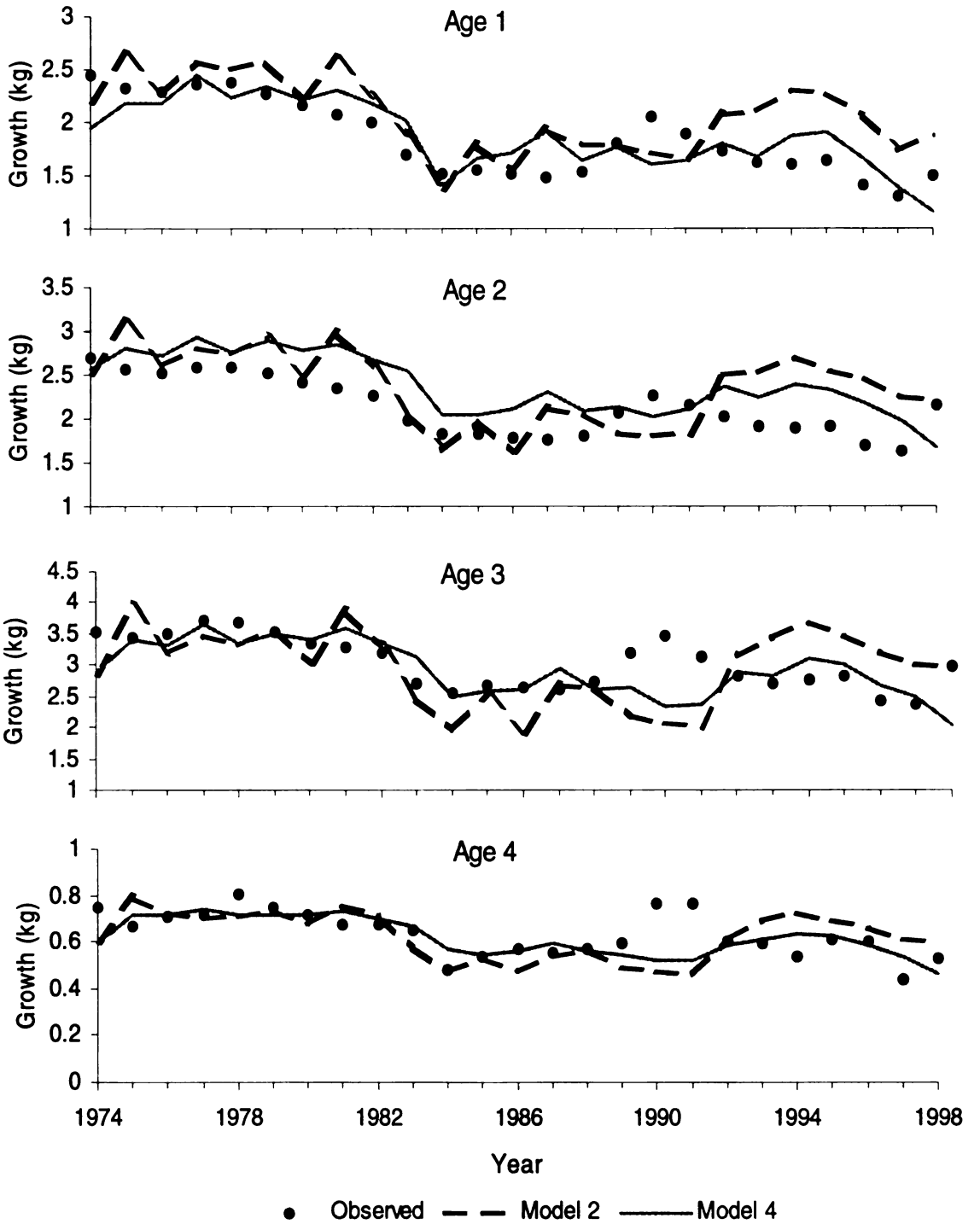


Figure 4.6 – Observed and predicted growth with search rate parameter related only to prey type (Model 2) or related to both prey type and predator age (Model 4)

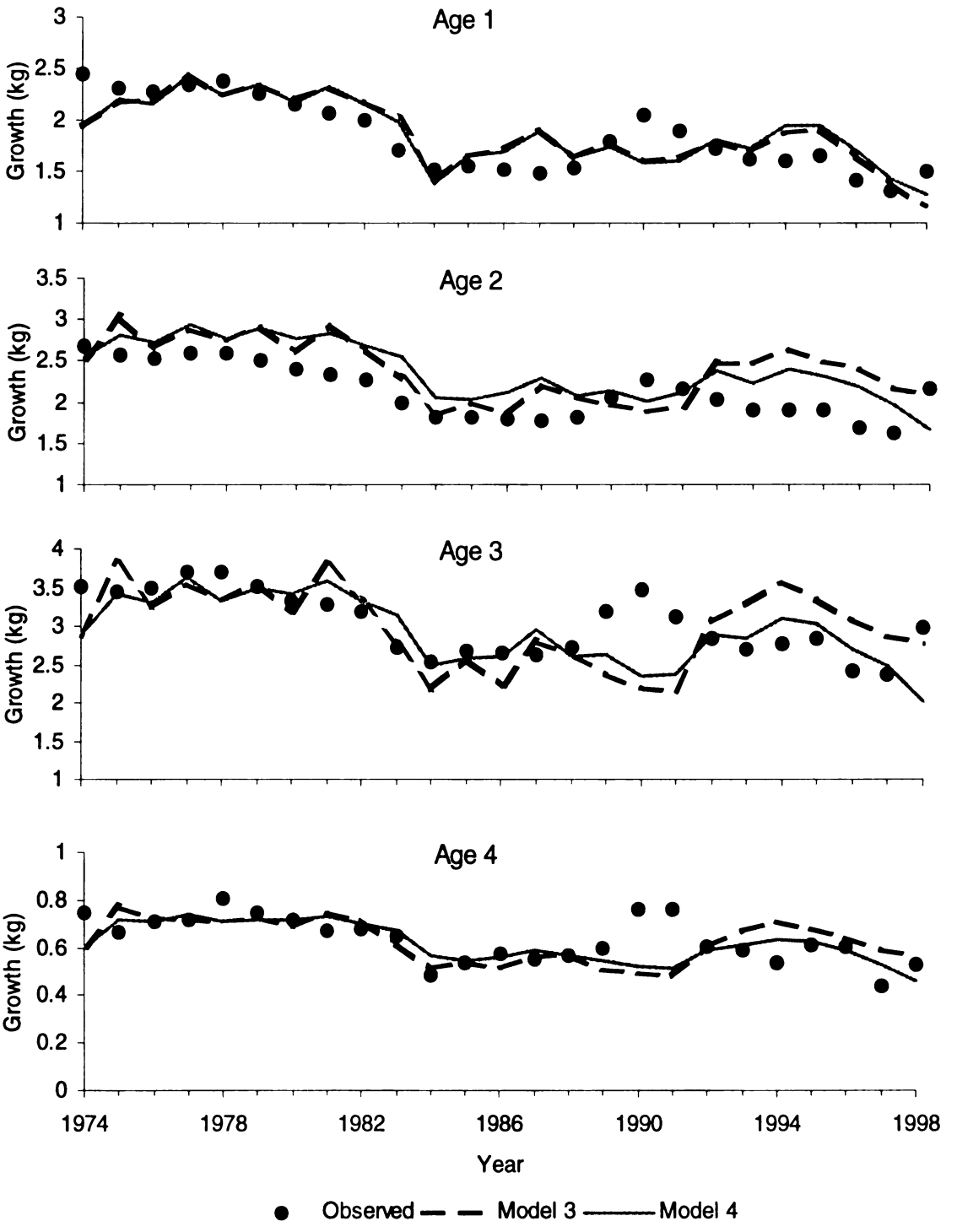


Figure 4.7 -- Observed and predicted growth with search rate parameter related only to predator age (Model 3) or related to both prey type and predator age (Model 4).

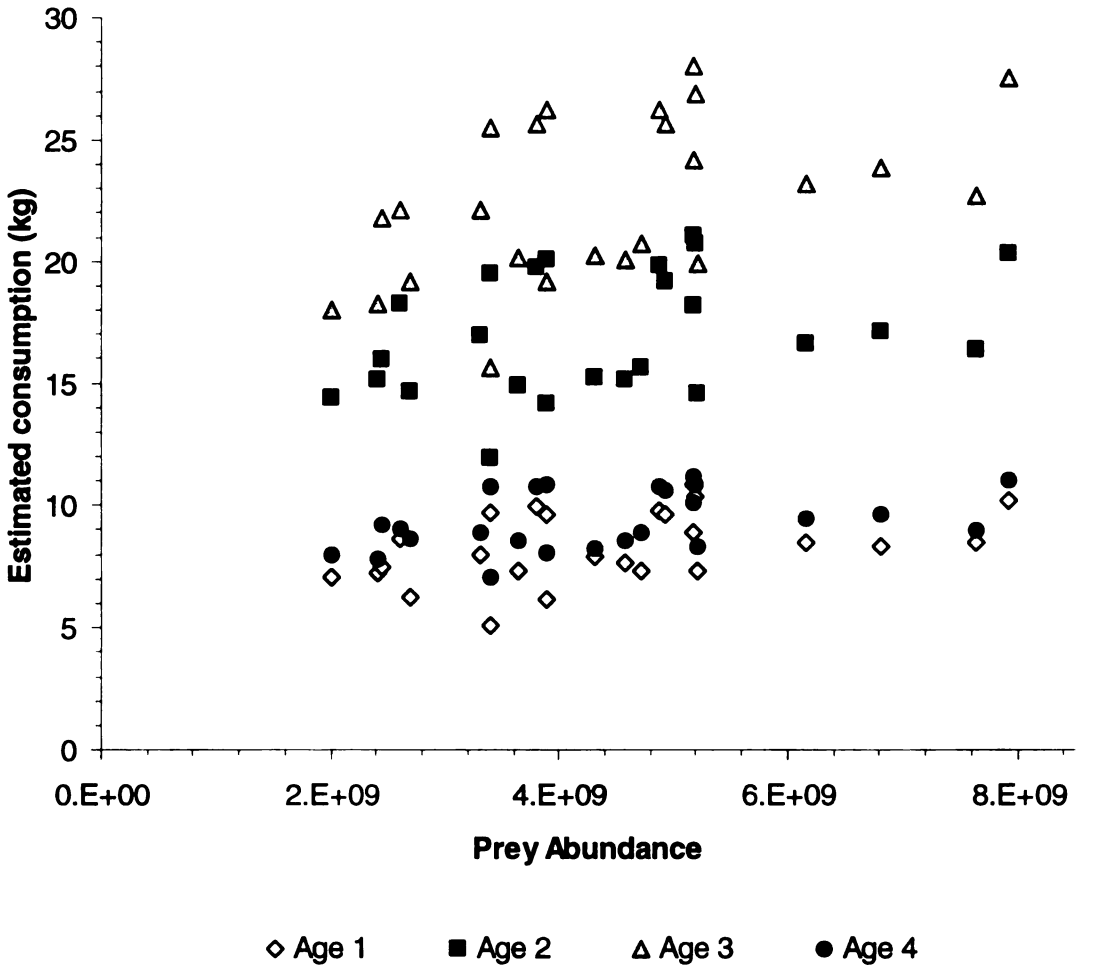


Figure 4.8 – Relationship between the estimated age-specific consumption of prey biomass (kg) and combined alewife and rainbow smelt abundance.

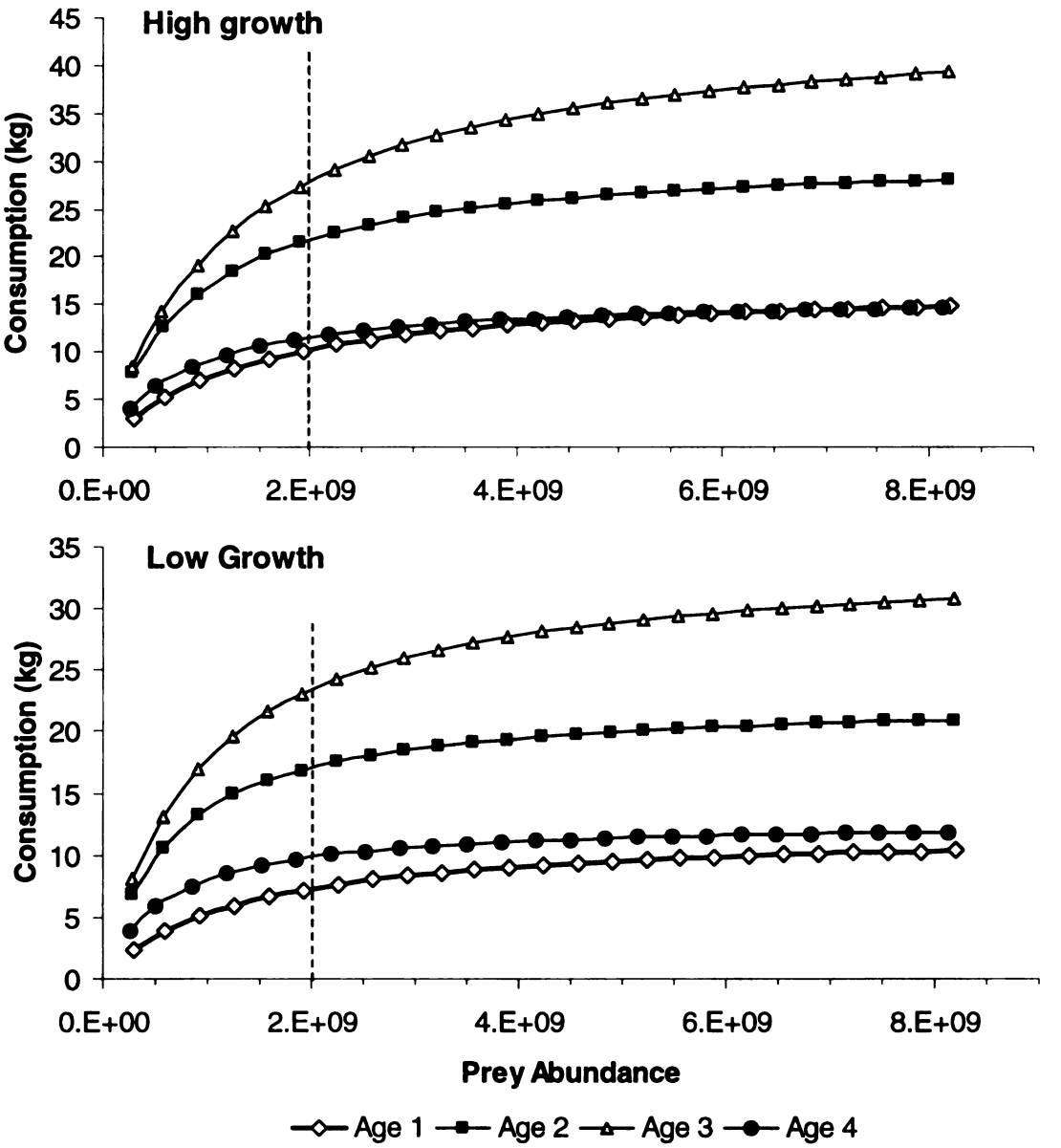


Figure 4.9 – Estimates of consumption from Model 4 using incremental prey abundance and two levels of fixed predator size representing high (1974) and low (1984) growth periods. The vertical dashed line represents the lowest observed prey abundance between 1974-1998.

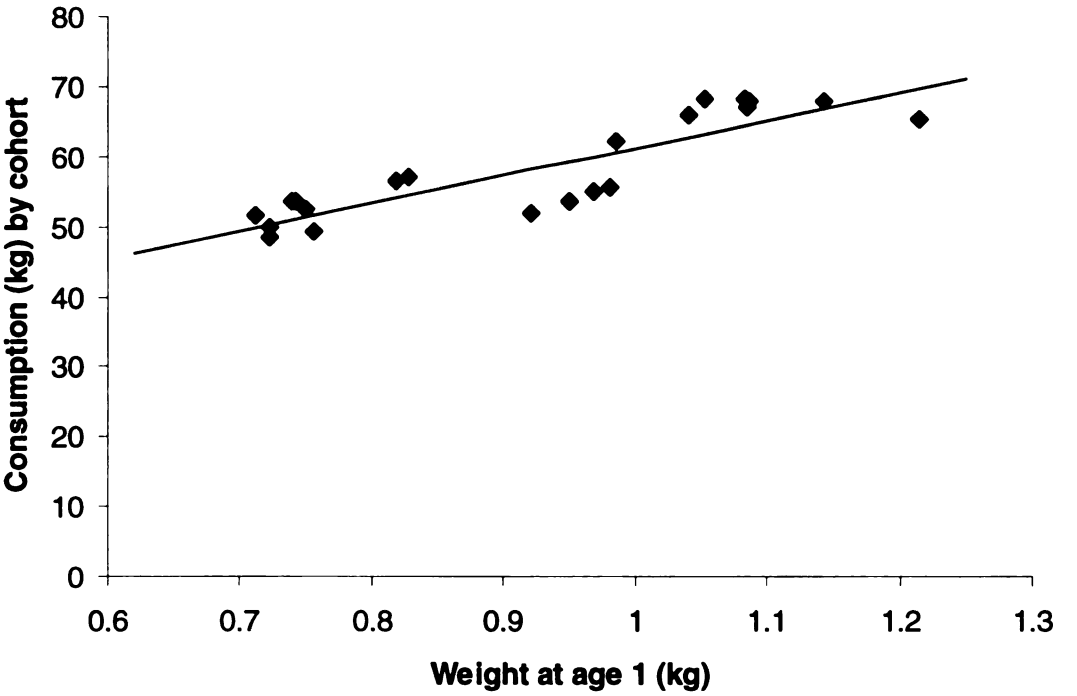


Figure 4.10 – Consumption by a cohort and weight at age 1. Consumption = 39.76 W + 21.49 with $R^2 = 0.7696$, where W is weight-at-age 1 (kg). Consumption is shown for 21 full cohorts over 1974—1998 (1995 was last cohort).

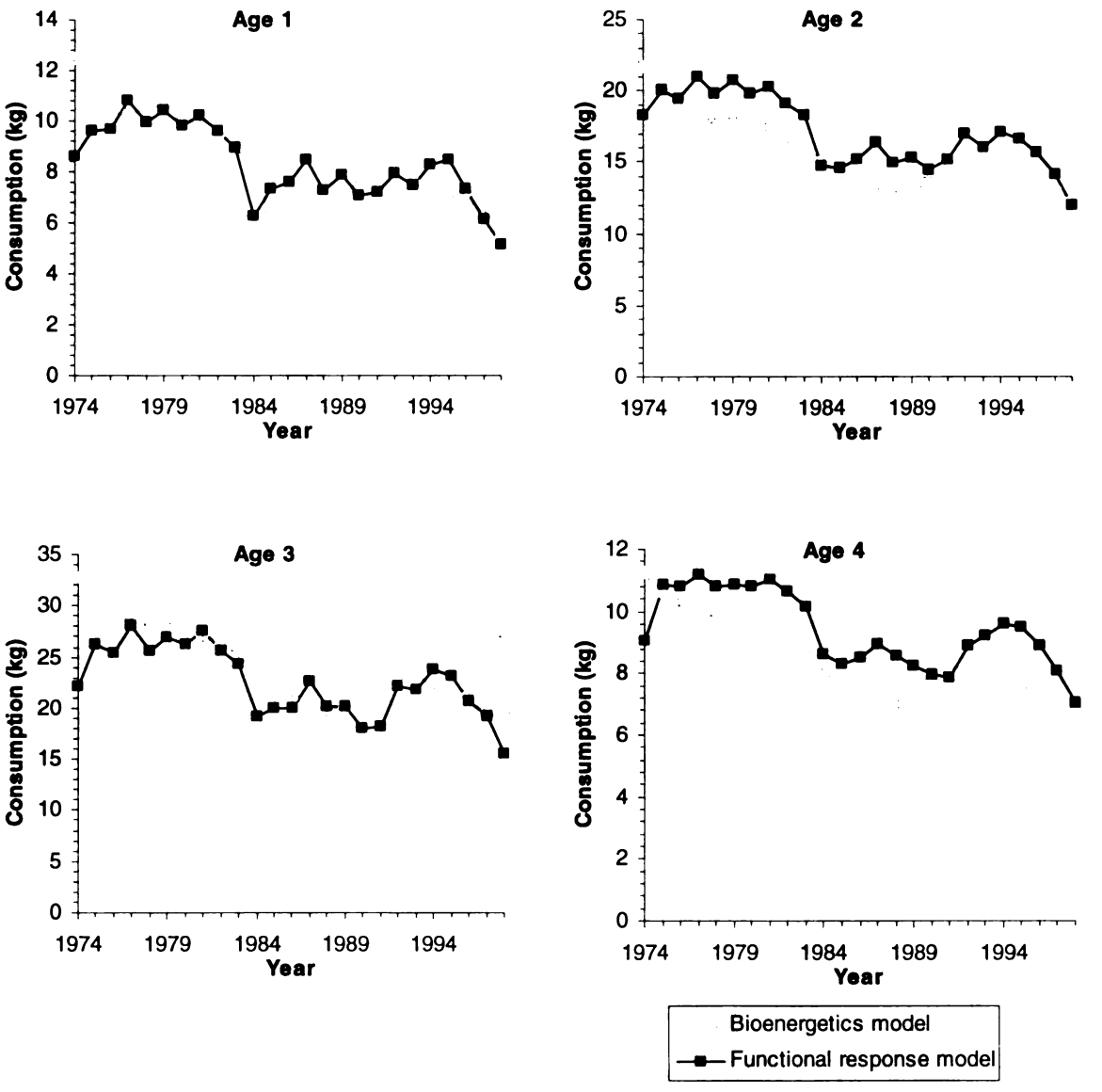


Figure 4.11– Comparison of age-specific consumption from the bioenergetics models (Chapter 3) and the functional response model.

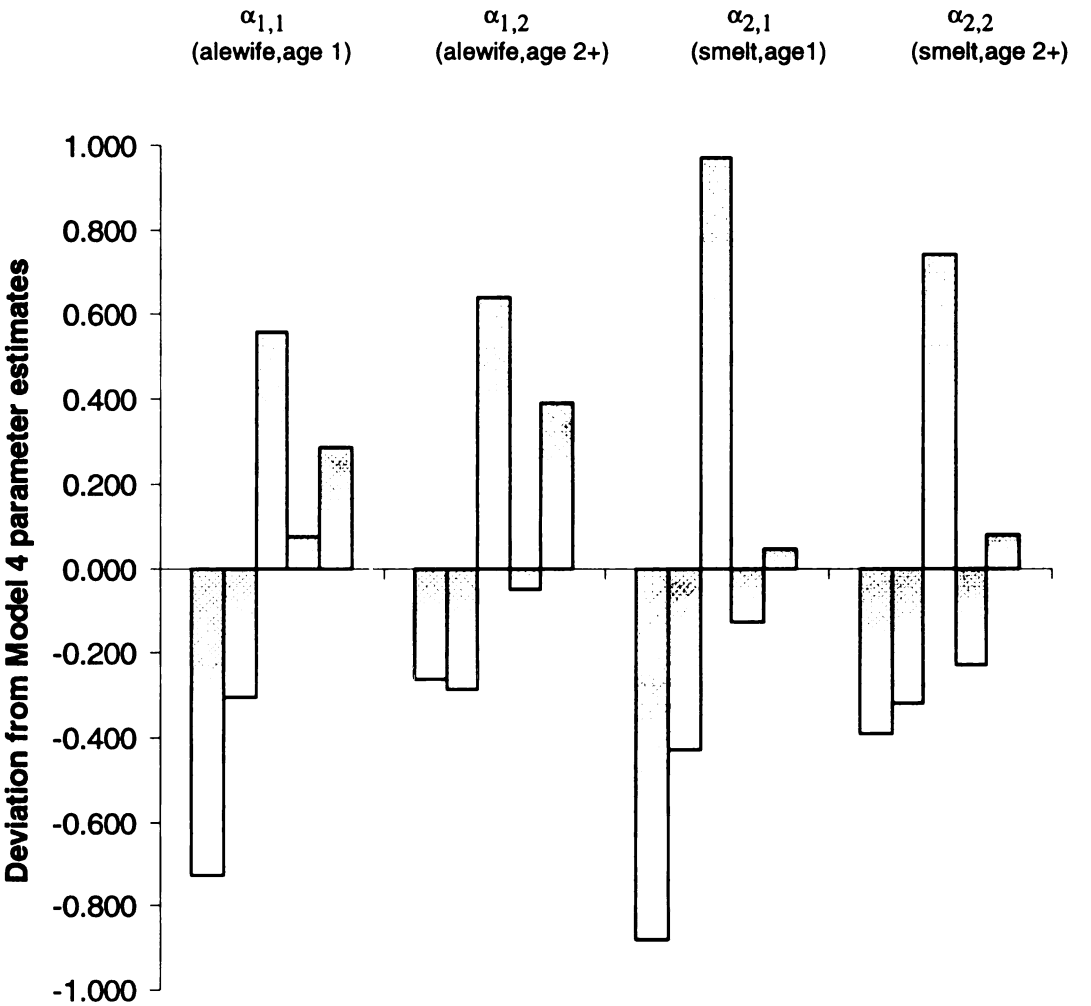


Figure 4.12– Sensitivity of estimated search rate parameters to fixing Cmax (first bar), increasing Cmax by 20% (second bar), decreasing Cmax by 20% (third bar), modifying size preference for weight of prey fish (fourth bar), and adjusting values to actual mid-year, day 182 (fifth bar). Each grouping represents one search rate parameter ($\alpha_{j,a}$) as defined in Table 4.5.

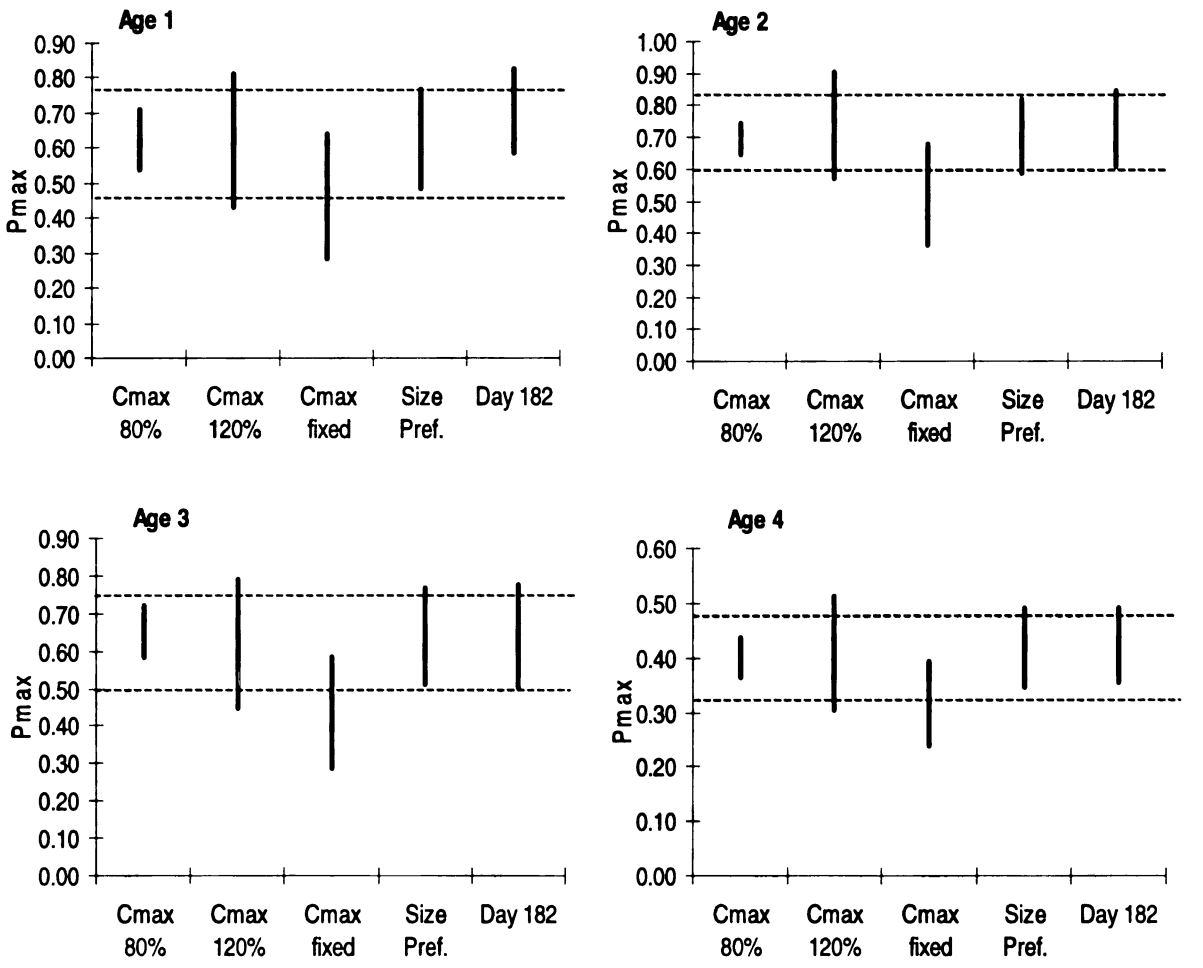


Figure 4.13– Results of the sensitivity analysis showing the minimum and maximum values of Pmax for each age. The lower level of each bar represents the minimum Pmax while the upper point represents the maximum value for each sensitivity analysis. The dashed lines represent the minimum and maximum values of Pmax estimated from Model 4 using the base values of all assumed constants (Table 4.3).

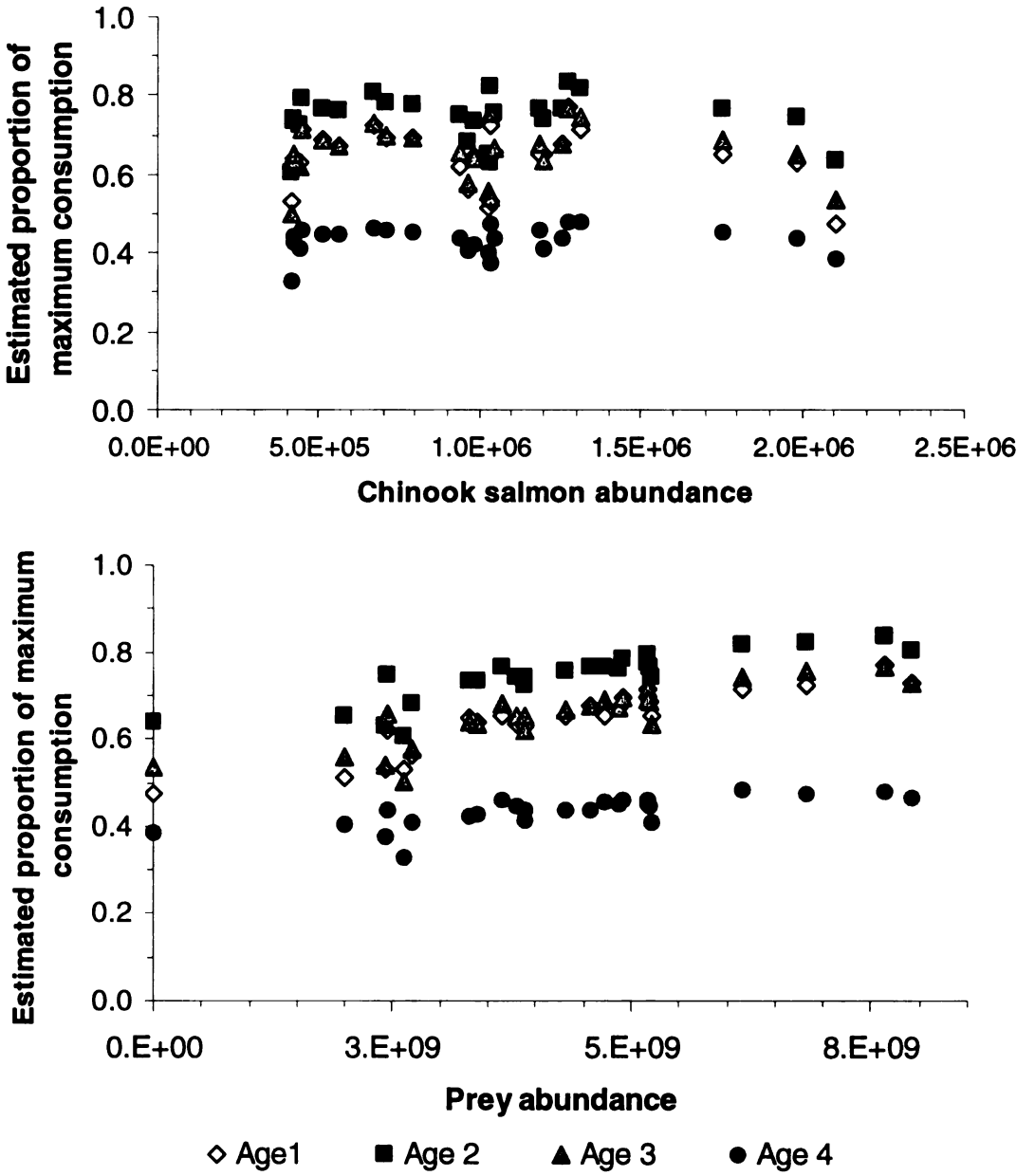


Figure 4.14 – Estimated proportion of maximum consumption (Pmax) related to chinook salmon abundance (top panel) and combined alewife and rainbow smelt abundance (bottom panel).

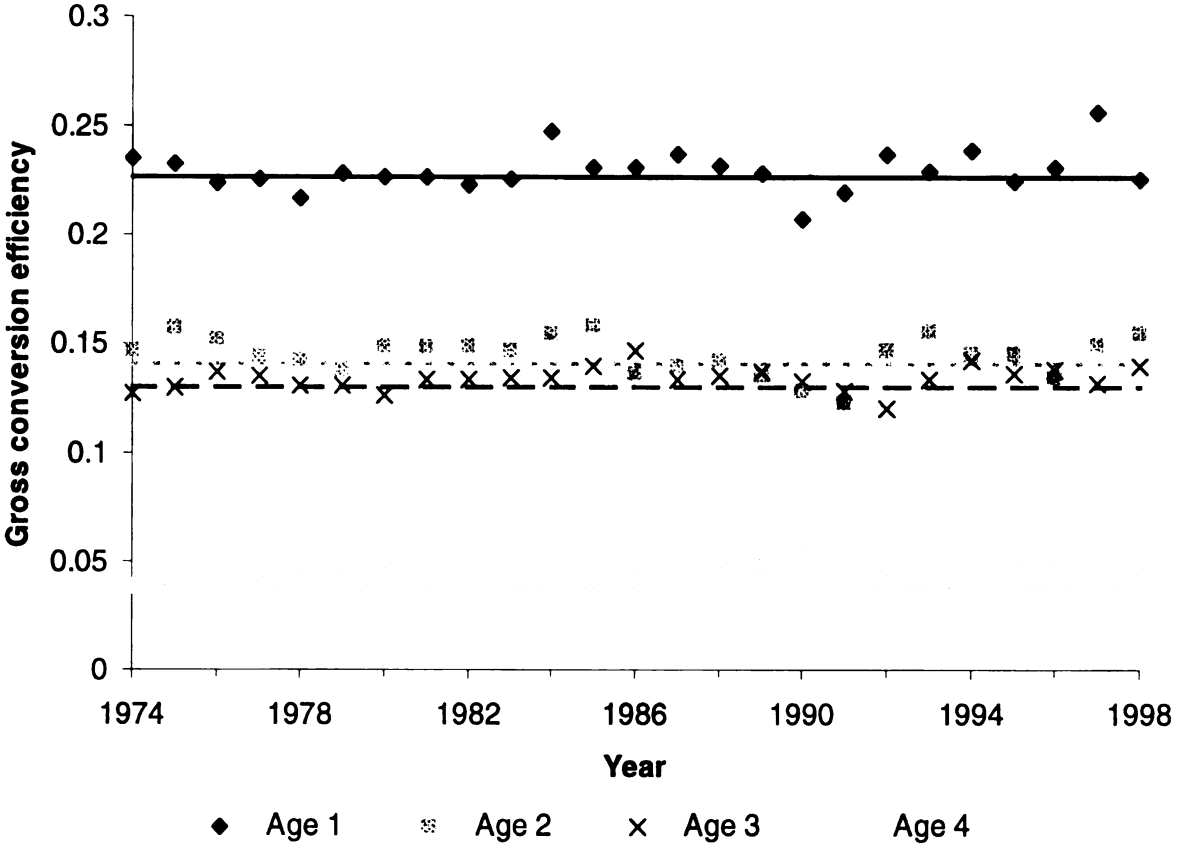


Figure 4-15 – Annual estimated gross conversion efficiency (calculated from bioenergetics models, Chapter 3 and Appendix B) for age 1-4 chinook salmon in the main basin of Lake Huron.

APPENDICES

Appendix A

Descriptive data for fish samples used in energy density analysis

This appendix describes the fish samples collected for use in the energy density analysis (Chapter 2) and presents descriptive statistics for these data. There were 707 fish collected in Lake Huron from June 11, 1996 to September 24, 1997. Various agencies (Michigan Department of Natural Resources, Chippewa/Ottawa Treaty Fishery Management Authority, Ontario Ministry of Natural Resources, and Biological Research Division-USGS) collected the fish throughout the year. Fish were measured for total length and weighed in the field, if possible. Individual whole fish were placed in plastic bags without water and frozen immediately or kept on ice until a freezer was available. Identification tags were placed with each fish to indicate the collector, site, time of day, date, length, and weight. We targeted for five fish in each size interval for each statistical district and month. Size intervals for predators were 100 mm (>100-200, >200-300, etc.) and 20 mm (>10-30, >30-50, etc.) for forage fish. An alternative procedure was sometimes used for forage fish since their small size did not always allow for accurate measurement of weight. Groups of small forage fish of the same species and from the same collection site were either sorted by size interval into separate bags or grouped together if the collector did not have time to sort by size class. An identification tag was placed in the bag with the same information outlined above. When possible, water was added to each bag so that fish were frozen in ice to minimize weight loss. Bags were frozen or placed on ice until a freezer was available.

To analyze regional differences, statistical districts were grouped into lake regions (Table A.1). Abbreviated species names (Table A.2) are used in this document when space on a table or figure was limited.

Samples of all key predator and prey species were obtained (see species list in Table A.2). However, there was incomplete coverage of months and statistical districts, resulting in missing months and regions for many species. Also, only a subsample of fish was processed in the bomb calorimeter to determine energy content. A linear regression of percent water on energy density was modeled from these samples and used to estimate the energy density of the remaining samples (see Chapter 2). Sample characteristics by month, statistical district, and gender are shown in Tables A.3 – A.5 for all samples and for those processed in the calorimeter. Table A.6 contains descriptive statistics (mean and standard deviation) for several key variables.

Mean energy density and mean percent water content of all samples by species are shown in Figure A.1. Only lake trout, chinook salmon, and burbot samples were obtained in all three regions of Lake Huron. Lake trout are known to reside in localized regional populations (Eshenroder et al. 1995) while burbot and chinook salmon may not. Regional differences in energy density were only found in the lake trout populations (Chapter 2).

Literature Cited

Eshenroder, R. L., N. R. Payne, J. E. Johnson, C. Bowen II, and M. P. Ebener. 1995. Lake trout rehabilitation in Lake Huron. Journal of Great Lakes Research 21 (Suppl. 1): 108-127.

Table A.1 – Number of samples from different statistical districts and lake regions. For the regional analysis of energy density, statistical districts were grouped to represent a particular lake region. The grouping of these statistical districts coincides with the regional lake trout populations.

Region	Statistical District	By Statistical District Frequency	Percent	By Region Frequency	Percent
North	MH1	145	20.51	145	20.51
Central	MH2	329	46.53	329	46.53
South	MH3	25	3.54	233	32.96
South	MH4	62	8.77		
South	MH5	24	3.39		
South	OH3	69	9.76		
South	OH4	43	6.08		
South	OH5	10	1.41		

Table A.2 – Species name abbreviations. These 3-letter codes are used in some tables and figures when the full species name did not fit into a table or figure.

Species	Type	Abbreviation
alewife	prey	ALE
bloater	prey	BLO
burbot	predator	BUR
chinook salmon	predator	CHS
lake trout	predator	LAT
rainbow smelt	prey	SME
sculpin	prey	SCU
stickleback	prey	STB
walleye	predator	WAE

Table A.3 -- Fish sample characteristics by month. Number of samples, N, are given as the total number of samples (top) and the number of samples processed in the bomb calorimeter (bottom, in parentheses).

Month	N	Alewife	Bloater	Burbot	Chinook salmon	Lake trout	Rainbow smelt	Sculpin	Stickle back	Walleye
Jan	22		9			4	9			
	(13)		(6)			(1)	(6)			
Mar	15		3	10		2				
	(3)		(3)							
Apr	1					1				
	(1)					(1)				
May	111		22	23	18	39	9			
	(52)		(16)	(14)	(14)	(6)	(2)			
Jun	217	72	2	44	15	53	31			
	(45)	(12)		(11)	(10)	(9)	(3)			
Jul	139	73			10	27	25	1	3	
	(34)	(10)			(7)	(5)	(9)		(3)	
Aug	111	35		3	40		32			1
	(17)	(4)			(8)		(5)			
Sep	39	1			9					29
	(18)				(7)					(11)
Oct	52			6	4	27				15
	(20)				(3)	(3)				(14)
Total	707	181	36	86	96	153	106	1	3	45
	(203)	(26)	(25)	(25)	(49)	(25)	(25)		(3)	(25)

Table A.4 – Fish sample characteristics by statistical district. Number of samples, N, are given as the total number of samples (top) and the number of samples processed in the bomb calorimeter (bottom, in parentheses).

Statistical District	N	Alewife	Bloater	Burbot	Chinook salmon	Lake trout	Rainbow smelt	Sculpin	Stickle back	Walleye
MH1	145		34	17	25	46	22	1		
	(64)		(25)		(22)	(9)	(8)			
MH2	329	161		21	44	50	49		3	1
	(62)	(21)		(11)	(8)	(9)	(10)		(3)	
MH3	25	1			4	15	3			2
	(7)	(1)			(1)	(1)	(2)			(2)
MH4	62			8	3		9			42
	(33)			(4)	(1)		(5)			(23)
MH5	24	5		1	5	13				
	(9)	(4)		(1)	(3)	(1)				
OH3	69	14	2	26	1	3	23			
	(1)				(1)					
OH4	43			8	9	26				
	(20)			(6)	(9)	(5)				
OH5	10			5	5					
	(7)			(3)	(4)					
Total	707	181	36	86	96	153	106	1	3	45
		(26)	(25)	(25)	(49)	(25)	(25)		(3)	(25)

Table A.5 -- Fish sample characteristics by gender. Number of samples, N, are given as the total number of samples (top) and the number of samples processed in the bomb calorimeter (bottom, in parentheses).

Gender	N	Alewife	Bloater	Burbot	Chinook salmon	Lake trout	Rainbow smelt	Sculpin	Stickle back	Walleye
F	133	0	0	35	21	56	0	0	0	21
				(14)	(17)	(12)				(14)
M	171	0	0	47	38	66	0	0	0	20
				(11)	(26)	(8)				(9)
U	403	181	36	4	37	31	106	1	3	4
		(26)	(25)	(0)	(6)	(5)	(25)	(0)	(3)	(2)
Total	707	181	36	86	96	153	106	1	3	45

Table A.6 – Descriptive statistics by lake region and month for all fish samples collected.

Means are shown with standard deviations in parentheses.

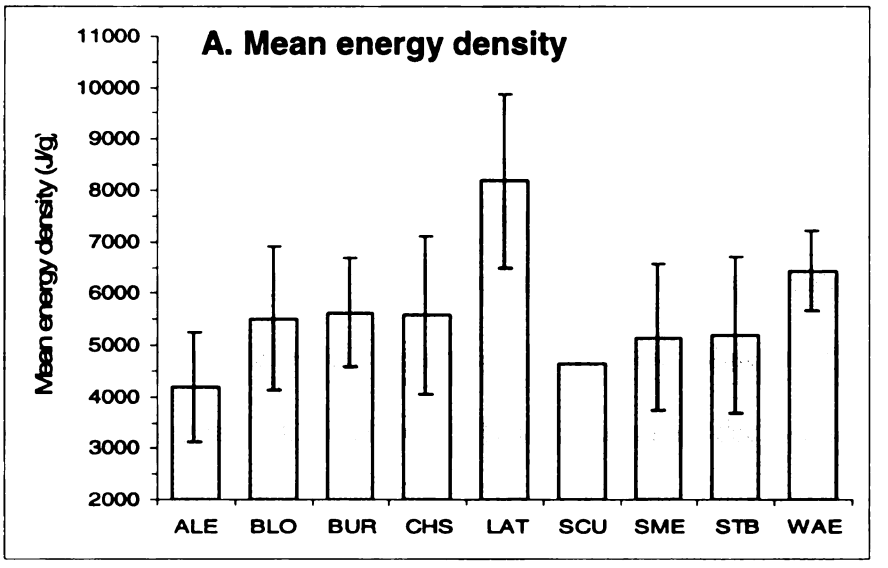
Species	Region	Month	N	Weight (kg)	Length (cm)	Percent water	Energy density J/g wet wt.
ALE	Central	6	57	0.017	12.215	82.5	3,755.4
				(0.02)	(4.03)	(3.06)	(843.1)
		7	73	0.013	11.127	81.8	3,935.2
				(0.01)	(3.58)	(3.51)	(966.4)
		8	30	0.017	12.432	77.9	5,009.5
				(0.01)	(3.21)	(4.27)	(1,174.6)
		9	1	0.010	10.600	78.8	4,764.3
	South	6	15	0.032	15.939	77.7	5,055.1
				(0.01)	(2.37)	(2.80)	(770.9)
		8	5	0.029	15.420	77.4	5,139.3
				(0.01)	(1.41)	(1.61)	(443.4)
BLO	North	1	9	0.139	25.025	78.1	4,965.5
				(0.06)	(2.80)	(5.70)	(1,567.3)
		3	3	0.127	22.367	77.8	5,043.4
				(0.06)	(4.76)	(3.02)	(830.7)
		5	22	0.142	26.167	74.5	5,948.8
				(0.06)	(3.16)	(4.61)	(1,269.2)
	South	6	2	0.325	25.650	81.9	3,900.2
				(0.04)	(1.06)	(0.41)	(113.8)
BUR	Central	6	19	1.518	54.653	75.7	5,842.3
				(0.72)	(8.82)	(3.76)	(1,302.3)
		8	2	0.830	43.600	76.0	5,760.8
				(0.95)	(17.54)	(0.07)	(24.3)
	North	3	10	1.521	51.790	75.8	5,823.9
				(0.29)	(5.98)	(2.79)	(965.2)
		5	1	0.249	32.800	82.2	3,587.5
		10	6	0.962	47.550	75.8	5,827.5
				(0.44)	(4.34)	(1.55)	(538.5)
	South	5	22	2.002	59.414	76.1	5,709.9
				(1.22)	(13.74)	(3.82)	(1,323.1)
		6	25	0.926	44.540	77.1	5,374.3
				(0.36)	(9.60)	(1.87)	(649.3)
		8	1	1.300	51.000	78.5	4,884.7

Table A.6 continued

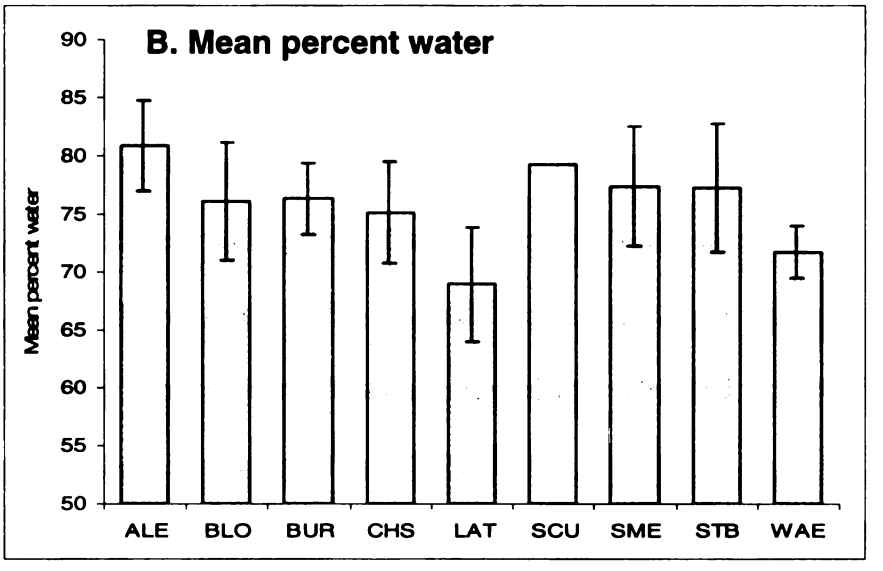
Species	Region	Month	N	Weight (kg)	Length (cm)	Percent water	Energy density J/g wet wt.
CHS	Central	6	7	1.702	39.386	75.7	5,393.3
				(2.21)	(23.41)	(7.45)	(2,583.0)
		7	5	1.454	33.560	77.5	4,748.0
				(2.61)	(27.83)	(4.92)	(1,704.3)
		8	31	0.790	31.244	76.8	4,989.6
				(1.63)	(17.94)	(1.81)	(626.3)
		10	1	1.700	54.600	75.1	5,592.4
	North	5	1	0.130	24.100	79.2	4,153.8
		6	2	4.830	58.100	72.3	6,543.1
				(5.69)	(33.80)	(1.97)	(682.2)
		7	5	3.112	56.060	73.1	6,292.4
				(3.81)	(29.21)	(3.72)	(1,287.9)
		8	9	1.230	47.911	75.4	5,472.6
				(0.60)	(7.45)	(1.84)	(637.9)
		9	8	2.540	60.105	74.6	5,762.3
				(1.44)	(13.48)	(2.66)	(920.3)
	South	5	17	2.051	53.324	71.6	6,795.8
				(1.86)	(17.27)	(4.70)	(1,627.3)
		6	6	1.046	29.483	78.0	4,589.7
				(1.74)	(28.03)	(8.17)	(2,830.2)
		9	1	1.600	46.100	73.0	6,328.0
		10	3	1.617	47.400	72.0	6,662.5
				(1.23)	(21.81)	(3.89)	(1,347.7)
LAT	Central	6	50	1.414	44.462	68.7	8,282.1
				(1.14)	(13.99)	(5.38)	(1,862.6)
	North	1	4	0.945	47.875	74.0	6,438.8
				(0.25)	(5.87)	(1.36)	(472.7)
		3	2	0.780	40.600	73.9	6,480.2
				(0.45)	(7.64)	(5.20)	(1,800.6)
		4	1	3.500	70.100	74.0	6,450.4
		7	27	0.842	39.983	70.7	7,581.2
				(0.47)	(7.83)	(4.68)	(1,621.5)
		10	12	1.539	49.583	71.9	7,156.8
				(1.11)	(12.31)	(5.07)	(1,755.4)
	South	5	39	2.098	56.667	68.0	8,525.6
				(1.25)	(14.18)	(3.16)	(1,094.3)
		6	3	0.787	39.767	71.8	7,204.5
				(0.41)	(5.13)	(1.19)	(412.3)
		10	15	3.009	64.093	63.9	9,937.5
				(0.95)	(7.14)	(3.23)	(1,120.5)

Table A.6 continued

Species	Region	Month	N	Weight (kg)	Length (cm)	Percent water	Energy density J/g wet wt.
SCU	North	7	1	0.001	5.000	79.3	4,635.5
SME	Central	6	5	0.013	14.330	74.8	5,870.5
				(0.01)	(1.67)	(4.19)	(1,151.7)
		7	22	0.005	8.186	80.5	4,285.8
				(0.01)	(3.27)	(6.95)	(1,911.4)
		8	22	0.004	8.340	77.7	5,055.2
				(<0.001)	(2.51)	(2.66)	(730.6)
	North	1	9	0.022	13.961	79.3	4,626.0
				(0.01)	(1.56)	(1.89)	(520.3)
		5	9	0.012	12.356	75.0	5,811.3
				(0.01)	(1.85)	(2.58)	(709.1)
		7	3	0.008	10.533	82.1	3,840.2
				(0.01)	(4.69)	(4.44)	(1,221.9)
		8	1	0.032	17.600	78.6	4,820.4
	South	6	26	0.097	20.898	74.8	5,855.2
				(0.05)	(5.52)	(5.58)	(1,533.4)
		8	9	0.008	11.763	76.5	5,404.3
				(<0.001)	(1.80)	(2.89)	(794.0)
STB	Central	7	3	0.002	6.867	77.2	5,194.2
				(<0.001)	(0.65)	(5.47)	(1,505.8)
WAE	Central	8	1	2.000	79.000	76.4	4,820.7
	South	9	29	1.441	49.903	71.4	6,571.6
				(0.83)	(8.64)	(2.21)	(766.7)
		10	15	1.333	49.239	72.2	6,279.4
				(0.54)	(6.56)	(1.92)	(666.1)



Species	%CV
ALE	25.665
BLO	25.207
BUR	18.803
CHS	27.429
LAT	20.706
SCU	0.000
SME	27.499
STB	28.991
WAE	11.987



Species	%CV
ALE	4.829
BLO	6.641
BUR	4.003
CHS	5.874
LAT	7.099
SCU	0.000
SME	6.653
STB	7.087
WAE	3.103

Figure A.1 – Mean energy density (A) and mean percent water (B) of each species collected with error bars representing one standard deviation. The percent coefficient of variation for each graphed variable is shown in the table on the right. Note, graphs use non-zero origin. Abbreviated species names are shown in Table A.2.

Appendix B

Parameter Values Used in Bioenergetics Models

This appendix describes the bioenergetics parameters I used in my implementation of the Wisconsin model (Hewett and Johnson 1995 Ver 3.0b) for each predator population in Lake Huron. These models included one for burbot in the main basin; one for chinook salmon in the main basin; three for lake trout corresponding to the northern, central, and southern regions of the main basin; and two for walleye, corresponding to Saginaw Bay and the region of the main basin south of Saginaw Bay. Some model values were obtained from the energy density analysis of Lake Huron species outlined in Chapter 2. Other values, such as water temperature and weight-at-age, were derived from published data. Physiological parameters supplied with the distributed version of the Wisconsin model were changed as needed to accommodate individual predator populations (Table B.7).

Simulation length

All bioenergetics models were run for 365 days. The first simulation day for burbot and lake trout was January 1st and July 1st respectively. Chinook salmon and walleye were each modeled in two time periods (see Growth section). For chinook salmon, the first day of simulation was January 1st for the pre-harvest period followed by a post-maturation period commencing on day 214. Age 4 chinook salmon were assumed to spawn and die on day 214 (August 2nd). Simulation of the walleye growth period

began on May 1st proceeded by the maintenance period beginning on day 153 (October 1st).

Actual and preferred water temperature

The seven bioenergetics models cover different portions of the main basin including: the entire main basin; the northern, central, and southern regions of the main basin; and Saginaw Bay. Water temperature information for each of these areas (Table B.1) was obtained from NOAA/GLERL reports (Grumblatt 1976; McCormick 1996; Nalepa et al. 1996; Johengen et al. 2000). In Saginaw Bay, inner bay data from 1994-1996 was used except for missing months January-March and November-December, which were estimated from 1993 Bay City data.

For bioenergetics models, the water temperature experienced by a predator was the actual water temperature unless it exceeded the preferred temperature (Table B.2). It was assumed that predators would reside in their preferred water temperature or in lower temperatures when the preferred temperature was not available. The preferred temperature of age 0 chinook salmon was 18oC, while age 1+ chinook salmon and lake trout preferred 11oC water (Stewart and Ibarra 1991). Burbot ages 1-3 preferred 12oC water while ages 4+ preferred 10oC water (Rudstam et al. 1995). Preferred temperature for all walleye age classes was set to 22oC (Kitchell et al. 1977).

Diet composition

Diet composition for each predator population was estimated from data provided by the Biological Research Division -- US Geological Survey; Chippewa/Ottawa Treaty

Fishery Management Authority; Michigan Department of Natural Resources; and Ontario Ministry of Natural Resources. Predator ages were grouped into age classes. Mean prey weights for each age class were estimated by summing all prey weights and dividing by the total number of prey samples weighed. Where data were absent, mean prey weights were set equal to adjacent age classes. Prey counts in each predator age class were multiplied by the mean prey weight resulting in an estimate of prey biomass consumed. The proportion of each prey item in the diet was determined by dividing prey biomass by total biomass of each predator age-class (Table B.3). When sufficient data were available, the proportion of each prey species consumed by weight in each year (1991-1999) was estimated. The mean across years became the proportion of each prey in the diet. In some instances, prey item counts and weights were pooled over the data time periods to provide a large enough sample size. With only three significant digits used to define the diet composition in the bioenergetics models, some rounding corrections were needed to adjust the values to sum to 1.0.

Prey Energy Density

In the Wisconsin model (Hewett and Johnson 1995 Ver 3.0b), energy density must be provided for each prey item identified in the diet composition. Prey energy density may be constant or vary by day. In Chapter 2, the energy density was estimated for the majority of prey items found in the diets of the key predators. Two diet items, invertebrates and "other fish", were not estimated with bomb calorimetry. For invertebrates, the mean energy density used in previous studies of Lake Michigan (Stewart et al. 1983; Rudstam et al. 1995) was used (Table B.4). In the diet composition,

"other fish" represent species not normally found in the open waters of Lake Huron or immature individuals of predator species. Here, the mean energy density for "other fish" used in previous studies (Cummins and Weychuck 1971 as used in Stewart et al. 1983; Stewart and Binkowski 1986) was used (Table B.4).

For the predominant prey species, regional and seasonal energy densities were determined from Lake Huron samples (Chapter 2). Some adjustments were made to these values to accommodate each predator population model. For bloater, two samples came from the southern region of the lake while all others came from the north. Data were insufficient to identify regional or seasonal differences in energy density, so the overall mean was used in bioenergetics models (Table B.4). For stickleback, the average of the three processed samples was used (Table B.4). Only one sculpin was analyzed from Lake Huron with an estimated energy density of 4636 J•g-1 wet weight. Because of this limited sample, the value used in the bioenergetics models (Table B.4) was an average of this value and those published by Cummins and Weychuck (1971, as used in LeBar 1993), and Rottiers and Tucker (1982).

Alewife energy density was found to vary by region and by month (Chapter 2). However, no samples were available from the northern region and there were insufficient samples from the central and southern regions to determine seasonal trends for each region. Differences in energy density between these two regions were minimal (Figure B.1-A). Therefore, regional differences in energy density are ignored in our bioenergetics models.

While alewife energy density was found to vary by month, samples were collected only during the months of June through September. To determine energy

density for the missing months, energy density values from Hurley (1986), energy density averaged over size-classes from Rand et al. (1994), and energy density averaged over gender from Flath and Diana (1985) were used. First, monthly mean energy density for both the Lake Huron estimates and the published values were obtained. The Lake Huron means were consistently lower than the means of the published values (Figure B.1-B). The ratio of the Lake Huron energy density to the published values for the months of June, July, and August was found to be 0.791. This ratio was then applied to the mean monthly energy density of the published data to obtain estimates of alewife energy density for the missing months (Table B.4).

The energy density of rainbow smelt was found to vary seasonally but samples were available only from January and May through August (Figure B.2). Mean energy density in the month of July was lower than all other months sampled, but variability was high. Other studies have found that rainbow smelt energy density increases from May through October (Foltz and Norden 1977; Rand et al. 1994; Vondracek et al. 1996). Because energy densities of the Lake Huron samples were unusually low in July, these samples were removed from the following analysis of seasonal energy density patterns. The seasonal pattern of energy density in rainbow smelt was estimated in a similar fashion as described for alewife. Published energy density from Vondracek et al. (1996) and values averaged over size-classes from Rand et al. (1994) were averaged to obtain monthly values. In some cases, a gap of one month in these data was estimated by interpolation. Lake Huron rainbow smelt energy density was consistently higher than the published values, with a mean proportional difference of 1.148 (Figure B.2-B). This

proportion was applied to the literature means to get an adjusted estimate of rainbow smelt energy density for the missing months (Table B.4).

Predator Growth

Fish growth is represented by the change in weight from one time period to another. For lake trout and burbot, weight-at-age data provided starting and ending weights. The starting weight was approximated by the weight-at-age while the ending weight was set to the weight-at-age for the next older age. Weight-at-age estimates for burbot were obtained by fitting mean weights for ages 3 through 17 (McLeish et al., In preparation) to a von Bertalanffy curve. For all lake trout models, the mean weight-at-age was estimated from spring gill net surveys conducted by the Michigan Department of Natural Resources.

Walleye growth was divided into two periods – a growth period occurring between May and October and a maintenance period from November to April. During the maintenance period, weight was maintained at the October level except for gonadal development (Hurley 1986). Weight gain during this time was 12% of body mass, which was then lost during spawning. For the growth period, weight-at-age was estimated from 1985-1995 Lake Huron creel data and was used to identify starting and ending weights. The ending weight for the last age in the growth period was estimated as the same proportional increase experienced in the prior age. The ending weight for the growth period became the starting weight for the gonadal development period. The ending weight for this period was estimated as the starting weight plus the weight lost to spawning (Table B.5).

Chinook salmon growth was partitioned into pre-harvest and post-maturation time intervals. Weir return weight-at-age was available for two time periods: 1973-1981 and 1985-1999 (McLeish et al., In preparation) and harvest weight-at-age from 1985-1998. For the post-maturation interval, the mean weight-at-age was computed for each time period from the data (Bence and Dobiesz 2000). Back-calculating these weights to annulus formation produced weight-at-age estimates for the pre-harvest interval (Table B.5). For age 0 chinook salmon weight-at-annulus formation was assumed to be 4.54 g (Stewart and Ibarra 1991).

Predator spawning losses

Reproductive tissues are generated during the normal growth period and lost during spawning. In the Wisconsin bioenergetics model, a proportion of fish biomass is lost on a pre-defined spawning day. The models do not differentiate between male and female predators; therefore as recommended (Hewett and Johnson 1995), the gonadal tissue lost by males and females is averaged to produce the percent biomass lost during spawning. In all three lake trout models, an individual matured at age 6, losing 6.8% of their biomass on simulation day 118 (Stewart et al. 1983). Burbot began spawning at age 3, losing 11% of their biomass on simulation day 32 (Rudstam et al. 1995). Walleye matured at age 3, with an average loss of 12% of their body mass (Hurley 1986), occurring on day 365 between simulated periods of growth and gonadal development. Chinook salmon are semelparous and die after spawning. Adults matured at age 4, spawning on simulation day 214, when they were dropped from the model.

Predator Energy Density

The Wisconsin Model (Hewett and Johnson 1995 Ver 3.0b) uses a linear relationship to track changes in energy density as a fish grows. Two different relationships can be applied, one above and one below a specified weight threshold. To identify these relationships, predator weight was plotted against energy density to identify mass cutoff values. A single linear relationship was tested as the simplest model. The extra sums of squares test (Neter et al. 1996) was used to evaluate this reduced model against a model that included separate intercepts and slopes above and below a weight threshold, specific to each predator population. For burbot and walleye, no relationship between energy density and weight was evident; therefore, the overall mean energy density was used (Table B.6). For lake trout and chinook salmon, the relationship between energy density and weight was better estimated by two linear relationships. Each population had a unique mass cutoff, defined by the intersection of the two lines (Figure B.3). Values of the intercepts, slopes, and mass cutoffs were used as parameters (a1, b1, a2, b2, and mass cutoff) in the predator energy density equation in the Wisconsin model (Table B.7). Based on the results of Chapter 2, predator energy density was treated as not varying seasonally.

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Table B.1 – Estimated Lake Huron water temperatures on the frist day of each month, based on NOAA/GLERL reports (Grumblatt 1976; McCormick 1996; Nalepa et al. 1996; Johengen et al. 2000).

Month	Lakewide	North	Central	South	Saginaw Bay
Jan	1	1	1	1	3
Feb	1	0	0	2	3
Mar	1	0	1	3	4
Apr	4	1	3	6	7
May	8	7	8	9	11
Jun	11	12	11	11	19
Jul	19	19	19	20	22
Aug	20	19	20	22	23
Sep	15	14	15	16	19
Oct	12	10	11	14	12
Nov	8	8	8	8	6
Dec	3	3	2	2	4

Table B.2 – Water temperatures on the first day of each month as experienced by predators in Lake Huron during bioenergetics modeling. Estimated water temperatures are used (Table B.1) except when the preferred water temperature is exceeded. It was assumed that predators would reside in their preferred water temperature or in lower temperatures when the preferred temperature is not available. Shaded cells represent preferred water temperatures.

	Burbot		Chinook salmon		Lake Trout (North)	Lake Trout (Central)	Lake Trout (South)	Walleye (South)	Walleye (Saginaw Bay)
Date	Age 1-3	Age 4+	Age 0	Age 1+	Age 1+	Age 1+	Age 1+	Age 2+	Age 2+
Jan	1	1	1	1	1	1	1	1	3
Feb	1	1	1	1	1	0	2	2	3
Mar	1	1	1	1	1	1	3	3	4
Apr	4	4	4	4	1	3	6	6	7
May	8	8	8	8	7	8	9	9	11
Jun	11	10	11	11	11	11	11	11	19
Jul	12	10	18	11	11	11	11	20	22
Aug	12	10	18	11	11	11	11	22	22
Sep	12	10	15	11	11	11	11	16	19
Oct	12	10	12	11	10	11	11	14	12
Nov	8	8	8	8	8	8	8	8	6
Dec	3	3	3	3	3	2	2	2	4

Table B.3 – Diet composition of Lake Huron predators by age class. Values represent the proportion by weight of each prey item in the diet.

		Prey Species						
	Age Class	Alewife	Bloater	Invertebrate	Sculpin	Rainbow Smelt	Sticklebac k	Other fish
Burbot	1-3	0.156	0.000	0.474	0.227	0.136	0.003	0.004
	4-7	0.262	0.027	0.330	0.158	0.214	0.004	0.004
	8+	0.264	0.029	0.115	0.087	0.476	0.003	0.026
Chinook	0	0.111	0.000	0.000	0.002	0.479	0.001	0.408
Salmon	1	0.298	0.000	0.000	0.004	0.634	0.010	0.053
	2+	0.732	0.000	0.000	0.000	0.233	0.029	0.006
Lake trout	1-3	0.273	0.001	0.000	0.148	0.544	0.030	0.005
(North)	4-6	0.160	0.003	0.000	0.049	0.757	0.013	0.019
	7+	0.381	0.034	0.000	0.046	0.486	0.000	0.053
Lake trout	1-3	0.511	0.000	0.000	0.010	0.473	0.004	0.002
(Central)	4-6	0.556	0.000	0.000	0.001	0.439	0.003	0.001
	7+	0.768	0.005	0.000	0.001	0.222	0.000	0.004
Lake trout	1-3	0.512	0.000	0.000	0.006	0.478	0.001	0.003
(South)	4-6	0.555	0.000	0.000	0.000	0.443	0.001	0.001
	7+	0.836	0.000	0.000	0.001	0.129	0.000	0.034
Walleye	2-3	0.805	0.000	0.000	0.002	0.190	0.002	0.002
(South)	4+	0.598	0.000	0.000	0.003	0.378	0.000	0.021
Walleye	2-3	0.429	0.000	0.000	0.003	0.135	0.003	0.431
(Saginaw Bay)	4+	0.436	0.000	0.000	0.004	0.078	0.000	0.482

Table B.4 – Energy density of Lake Huron prey species used in this implementation of the Wisconsin model. Data were derived from samples collected in Lake Huron (see Chapter 2) except for invertebrates and "other fish", which were not sampled. Mean energy density for invertebrates (Cummins and Weychuck 1971; Stewart et al. 1983; Stewart and Binkowski 1986) and for "other fish" (Stewart et al. 1983; Rudstam et al. 1995) was derived from published values.

	Energy density estimated from Lake Huron samples					Energy density estimated from literature	
Month	Alewife	Bloater	Sculpin	Rainbow smelt	Stickleback	Invertebrates	Other fish
Jan	5695	5514	4997	4626	5194	4248	5153
Feb	4944	5514	4997	4970	5194	4248	5153
Mar	4257	5514	4997	5315	5194	4248	5153
Apr	5936	5514	4997	5563	5194	4248	5153
May	4549	5514	4997	5811	5194	4248	5153
Jun	4026	5514	4997	5858	5194	4248	5153
Jul	3935	5514	4997	5540	5194	4248	5153
Aug	5028	5514	4997	5146	5194	4248	5153
Sep	4566	5514	4997	6061	5194	4248	5153
Oct	6297	5514	4997	7065	5194	4248	5153
Nov	6142	5514	4997	5817	5194	4248	5153
Dec	6486	5514	4997	5221	5194	4248	5153

Table B.5 – Predator starting weights (grams) as used in the bioenergetics models. The ending weights were the starting weights for the next age class. For age 2 walleye, no value is given for the maintenance period since these represent immature individuals that are not spawning. Therefore, the end weight for age 2 walleye was the starting weight for age 3. For chinook salmon, starting weight for age 0 fish was used as in Stewart and Ibarra (1991).

	Burbot	Lake trout			Walleye	
Age		North	Central	South	Growth	Maintenance
1	391	45	45	56		
2	535	206	147	318	437	n/a
3	685	568	462	790	713	1040
4	835	1,028	957	1,399	1,040	1357
5	980	1,509	1,575	2,064	1,357	1721
6	1,120	1,961	2,232	2,724	1,721	2085
7	1,251	2,359	2,861	3,340	2,085	2411
8	1,373	2,694	3,443	3,891	2,411	2687
9	1,485	2,968	3,951	4,370	2,687	2908
10	1,587	3,188	4,390	4,777	2,908	3033
11	1,680	3,362	4,765	5,118	3,033	3080
12	1,764	3,499	5,085	5,400	3,080	3128
13	1,839	3,604	5,357	5,631		
14	1,906	3,686	5,578	5,819		
15+	2,018	3,749	5,757	6,208		

	Chinook salmon			
	1973-1981		*1982-1998*	
Age	Annulus formation	Fall spawning	Annulus formation	Fall spawning
0	4.54	238	4.54	196
1	572	1,739	458	1,242
2	3,073	4,791	2,160	3,401
3	7,128	8,823	4,865	5,956
4	9,361	10,378	6,324	7,136

Table B.6 – Regression results for the final model used for each predator. Predators with no mass cutoff showed no evidence of a relationship between weight and energy density. Predators with a mass cutoff value were best defined with one model below the cutoff and another above the cutoff (see Figure B4).

	R^2	F	df	p-value	Mass cutoff	Line intersection
Burbot	0.0111	0.94	1, 84	0.3347	n/a	n/a
Chinook salmon	0.3861	19.29	3, 92	<0.0001	4.0	2.98
Lake trout (North)	0.3414	7.26	3, 42	0.0005	1.5	1.51
Lake trout (Central)	0.6173	24.74	3, 46	<0.0001	1.5	1.33
Lake trout (South)	0.3502	9.52	3, 53	<0.0001	2.0	1.85
Walleye	0.0720	3.34	1, 43	0.0746	n/a	n/a

Table B.7 – Physiological parameters used in the Wisconsin bioenergetics models for Lake Huron predators. The equations (Eq) and parameters (e.g., CA, FA, etc.) refer to bioenergetics models as presented by Hewett and Johnson (1995).

	Consumption		Respiration		Egestion/ Excretion		Predator energy density		Spawning loss	
Burbot	*Eq*	*2*	*Eq*	*2*	*Eq*	*1*	*Eq*	*1*		
	CA	0.099	RA	0.01	FA	0.17	Joule den	5630	% lost	0.11
	CB	-0.195	RB	-0.17	FB	0			Loss day	32
	CQ	2.41	RQ	1.88	FG	0				
	CTO	13.7	RTO	21	UA	0.09				
	CTM	21	RTM	24	UB	0				
	CTL	0	RTL	0	UG	0				
	CK1	0	RK1	0						
	CK4	0	RK4	0						
Chinook salmon	*Eq*	*3*	*Eq*	*1*	*Eq*	*3*	*Eq*	*2*		
	CA	0.303	RA	0	FA	0.212	PA1	4566		
	CB	-0.275	RB	-0.22	FB	-0.222	PB1	0.877		
	CQ	5	RQ	0.07	FG	0.631	Mass cutoff	2982		
	CTO	15	RTO	0.02	UA	0.0314	PA2	7182		
	CTM	18	RTM	0	UB	0.58	PB2	0		
	CTL	24	RTL	25	UG	-0.299				
	CKA	0.36	RK1	1						
	CKB	0.01	RK4	0.13						
			ACT	9.7						
			BACT	0.04						
			SDA	0.17						
Lake trout (north)	*Eq*	*1*	*Eq*	*1*	*Eq*	*3*	*Eq*	*2*		
	CA	0.059	RA	0			PA1	5302		
	CB	-0.307	RB	-0.3	FA	0.212	PB1	2.285	% lost	0.068
	CQ	0.123	RQ	0.06	FB	-0.222	Mass cutoff	1509	Loss day	118
			RTO	0.02	FG	0.631	PA2	8752		
			RTM	0	UA	0.0314	PB2	0		
			RTL	11	UB	0.58				
			RK1	1	UG	-0.299				
			RK4	0.05						
			ACT	11.7						
			BACT	0.04						
			SDA	0.17						

Table B.7 continued.

	Consumption		Respiration		Egestion/ Excretion		Predator energy density		Spawning loss	
Lake trout	*Eq*	*1*	*Eq*	*1*	*Eq*	*3*	*Eq*	*2*		
	CA	0.059	RA	0	FA	0.212	PA1	5787	% lost	0.068
(central)	CB	-0.307	RB	-0.3	FB	-0.222	PB1	2.431	Loss day	118
	CQ	0.123	RQ	0.06	FG	0.631	Mass cutoff	1325		
			RTO	0.02	UA	0.0314	PA2	8196		
			RTM	0	UB	0.58	PB2	.614		
			RTL	11	UG	-0.299				
			RK1	1						
			RK4	0.05						
			ACT	11.7						
			BACT	0.04						
			SDA	0.17						
Lake trout	*Eq*	*1*	*Eq*	*1*	*Eq*	*3*	*Eq*	*2*		
	CA	0.059	RA	0	FA	0.212	PA1	6429	% lost	0.068
(south)	CB	-0.307	RB	-0.3	FB	-0.222	PB1	1.784	Loss day	118
	CQ	0.123	RQ	0.06	FG	0.631	Mass cutoff	1849		
			RTO	0.02	UA	0.0314	PA2	9427		
			RTM	0	UB	0.58	PB2	0		
			RTL	11	UG	-0.299				
			RK1	1						
			RK4	0.05						
			ACT	11.7						
			BACT	0.04						
			SDA	0.17						
Walleye	*Eq*	*2*	*Eq*	*2*	*Eq*	*2*	*Eq*	*1*		
	CA	0.25	RA	0.01	FA	0.158	Joule den	6435		
(Southern	CB	-0.27	RB	-0.2	FB	-0.222				
region	CQ	2.3	RQ	2.1	FG	0.631				
and	CTO	22	RTO	27	UA	0.0253				
Saginaw	CTM	28	RTM	32	UB	0.58				
Bay)	CTL	0	RTL	0	UG	-0.299				
	CK1	0	RK1	0						
	CK4	0	RK4	0						

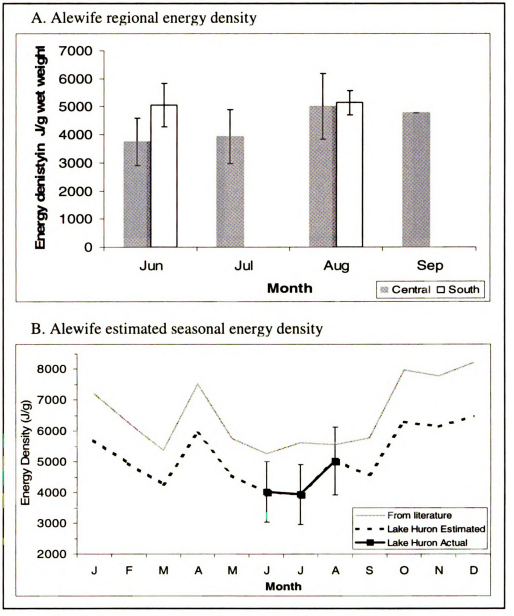


Figure B.1 – Alewife seasonal energy density in $J \bullet g^{-1}$ wet weight. Samples were available from June through September but only from the central and southern regions (A). To approximate a seasonal energy density pattern, missing months were estimated as the proportional difference from published values of alewife energy density from other Great Lakes (B).

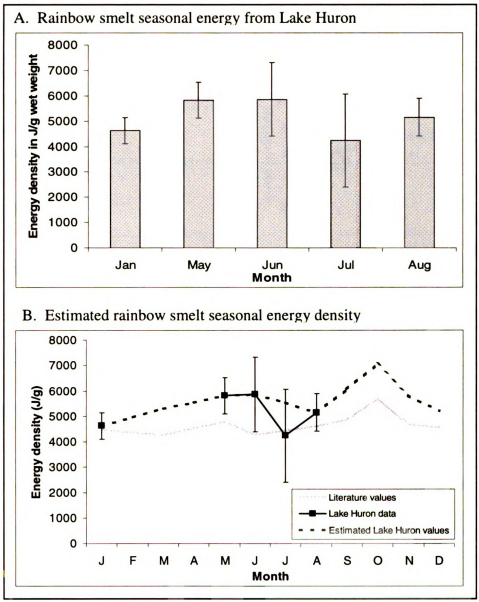
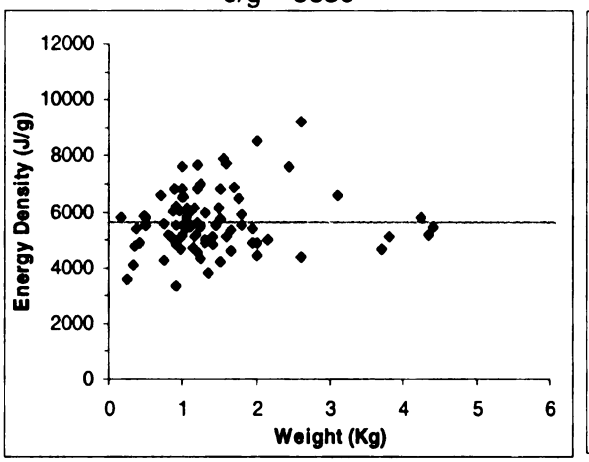


Figure B.2 – Rainbow smelt seasonal energy density in $J \bullet g^{-1}$ wet weight. Samples were available for Janurary and from May through August; samples from all lake regions were pooled (A) as results from Chapter 2 showed no significant differences between regions. To approximate a seasonal energy density pattern, missing months were estimated as the proportional difference from published values of rainbow smelt energy density from other Great Lakes (B).

Figure B.3 – Linear relationships between predator weight and energy density used in this implementation of the Wisconsin model. Where two different relationships were employed, the mass cutoff separating the two lines is indicated below the title.

Burbot

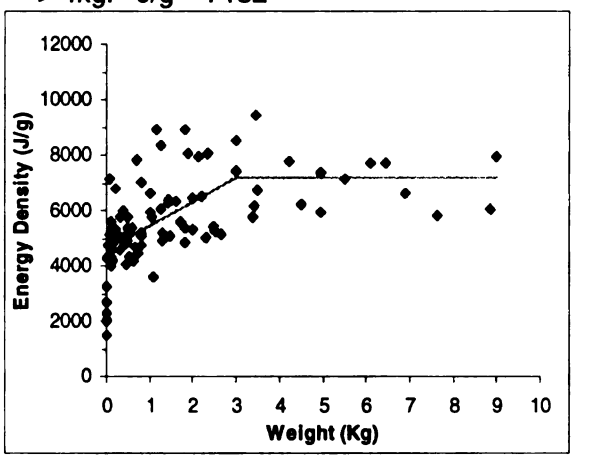
J/g = 5630



Chinook Salmon

<= 4Kg: J/g = 4566 + 877 Weight

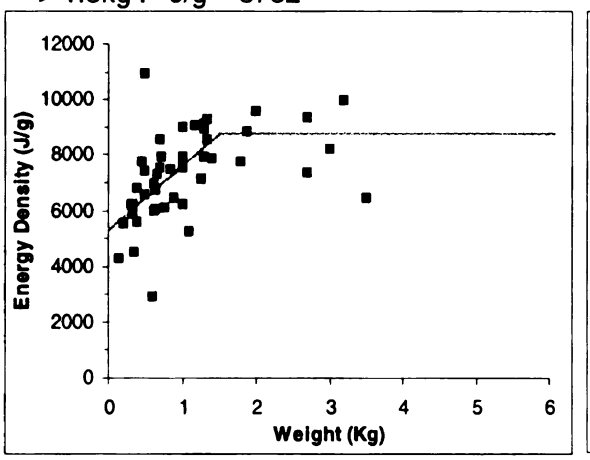
> 4kg: J/g = 7182



Lake trout (North)

<= 1.5Kg : J/g = 5302 + 2285 * Weight

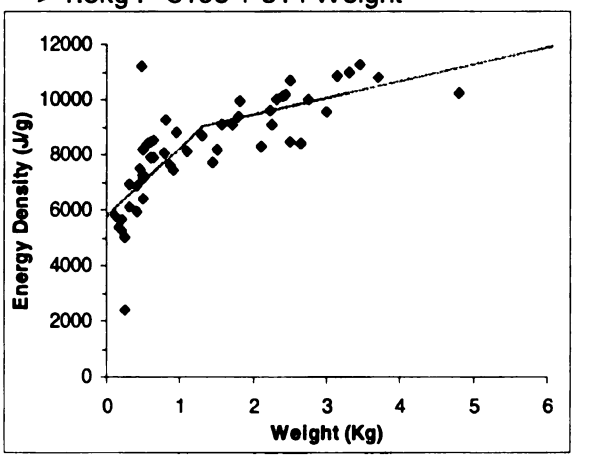
> 1.5kg : J/g = 8752



Lake trout (Central)

<= 1.5Kg : J/g = 5787 + 2431 Weight

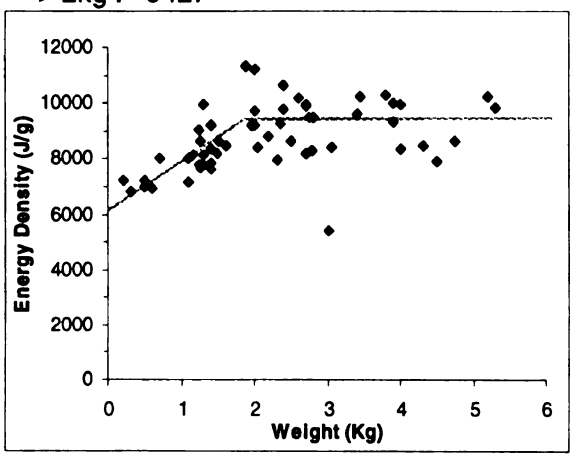
> 1.5kg : 8196 + 614 Weight



Lake trout (South)

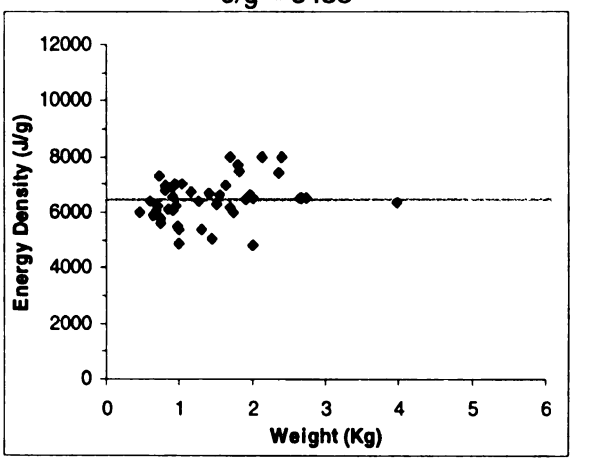
<= 2Kg : J/g = 6148 + 1784 Weight

> 2kg : 9427



Walleye

J/g = 6435



Appendix C

Data and Assumptions Used for Projections of Consumption

To estimate future consumption by the key predators, several assumptions were made regarding mortality rates, weight-at-age, diet composition, and GCE, during the projection period, 1999 – 2020. Models of the key predators included one for burbot in the main basin; one for chinook salmon in the main basin; three for lake trout corresponding to the northern, central, and southern regions of the main basin; and two for walleye, corresponding to Saginaw Bay and the region of the main basin south of Saginaw Bay. This appendix describes the assumptions and default values used to project consumption. A summary of the assumptions is given in Table C.1 while a more detailed description is given below.

Mortality rates

Natural mortality rates, excluding sea lamprey-induced mortality, for the projection period were constant (Table C.2) and set to the value used in the last year of the assessment models (Bence and Dobiesz 2000).

Several types of fishing mortality were applied during the projection period depending on the predator species. Southern walleye and burbot used a single source of fishing mortality that was set to the value of the last year of the assessment models; for Saginaw Bay walleye the average of the last three years was used (Table C.3). All three lake trout models and the chinook salmon model (Bence and Dobiesz 2000) contained commercial and recreational fishing mortality calculated as the product of selectivity and

fishing intensity (Table C.3). Fishing mortality for projections in the southern lake trout model used constant selectivity from the last year of data and set fishing intensity to the average of the last three years. For northern and central lake trout, selectivity and fishing intensity were allowed to vary over time during pre-projection years. Both variables were set to the average of the last three years for estimation of fishing mortality in projected years.

The chinook salmon population model (Bence and Dobiesz 2000) operates with two time periods within a year consisting of the first seven months, then a "pulse" harvest and maturation process, followed by the remainder of the year. The harvest and maturation proportions (Table C.4) were set to the estimates for the last year in the assessment model (Bence and Dobiesz 2000).

Sea lamprey induced mortality was applied to the burbot model and all three lake trout models (Table C.5). For the projection period, this mortality source was adjusted by a scaling factor (Schleen et al. 2002) intended to reflect the reduction of sea lamprey abundance resulting from treatment of the St Marys River (Table C.6).

Weight-at-age

For northern and southern lake trout, burbot, and Saginaw Bay and southern region walleye, weight-at-age did not change over time in the assessment models (Bence and Dobiesz 2000). These constant values were used for the projection period (Table C.7). However, weight-at-age varied over time for chinook salmon and central lake trout during the pre-projection period. The value for the projection period was the average of the last three years used in the assessment model (Table C.7).

Diet and gross conversion efficiency

Diet composition (Table C.8) and gross conversion efficiency (Table C.9) were assumed constant for estimates of recent and projected consumption. Diet composition was estimated from agency-collected data (Appendix C). Gross conversion efficiency was estimated from bioenergetics models of each predator population (Appendix C).

Recruitment

During the projection period, recruitment in each year was attributed to natural reproduction and/or stocking, varying by predator species. Burbot and southern walleye recruitment was due exclusively to natural reproduction and was held constant during the projection period (Table C.10). Neither of these populations was stocked during the projection period.

A constant number of wild recruits was used for walleye in Saginaw Bay (Table C.10). The number of walleye stocked into Saginaw Bay varied during 1999 and 2001 of the projection period and was constant after 2002 to the end of the projection (Table C.10).

Constant wild recruitment and number of stocked fish were used for chinook salmon recruitment during the projection period (Table C.10). The number of stocked fish represents a 20% reduction in chinook salmon stocking which began in 1999.

Lake trout natural recruitment was set to zero for projections. Recruitment from stocking lake trout in each lake region was obtained using a movement matrix (Table C.11) and a stocking table (Table C.12). The movement matrix defines the proportion of

fish stocked at each stocking location that recruit to each lake region. The stocking table lists annual numbers of fish stocked in each stocking location. The matrix product of the stocking table and the movement matrix is a matrix containing the annual number of recruits in each lake region. After the number of recruits per region was estimated, a post-stocking survival rate of 0.7399 was applied to the recruits in the southern region only.

Size regulations

Size regulations in the recreational fishery (Table C.13) were used in the northern and central lake trout models during the projection period. Recreational mortality rates (Table C.3) were multiplied by a factor (Table C.16) to adjust for hooking mortality experienced by fish smaller than the minimum size limit in a given year. The adjustment factor was estimated by

$$x_{a,y} = p_{a,y} + (1 - p_{a,y}) \times h$$

where $x_{a,y}$ is the age- and year-specific adjustment factor that will be applied to recreational fishing mortality rates; $p_{a,y}$ is the age- and year-specific proportion of fish that are larger than the minimum size limit; and h is a constant hooking mortality of 0.15. The proportion of fish above a specific size limit

$$p_{a,y} = 1 - Z(s_y, \mu_a, \sigma_a)$$

was determined using a cumulative normal distribution with an age-specific mean (μ_a) and standard deviation (σ_a) derived from a von Bertalanffy growth model, where sy is a

year-specific size limit. Mean length (μ_a) was estimated using von Bertalanffy growth parameters (Table C.14) for northern and central lake trout models. The standard deviation (σ_a) was estimated by multiplying the age-specific mean length by a constant coefficient of variation of 0.15 (Table C.15).

Literature Cited

Bence J. R. and N. E. Dobiesz. 2000. Estimating forage fish consumption by predators in Lake Huron. Great Lakes Fishery Commission Project Completion Report. Available for download at http://www.glfc.org/research/cap.htm .

Schleen, Larry P., Christie, Gavin C., Heinrich, John W., Bergstedt, Roger A., Young, Robert J., Morse, Terry J., Lavis, Dennis S., Bills, Terry D., Johnson, James E., Ebener, Mark P. in press. Development and implementation of an integrated program for control of sea lampreys in the St. Marys River. Journal of Great Lakes Research, SLIS II Special Issue.

Table C.1 -- Assumptions used during the projection period. These are default assumptions in the Consumption Projection Model software but the user may change them.

Item	Assumptions / Settings during projection
Natural mortality rates	Constant during projection period. set to the value used in the last year of the assessment models. Excludes sea lamprey-induced mortality.
Fishing mortality	
Southern and Saginaw Bay walleye & burbot	Constant during projection period. Single source of fishing mortality is set to the value of the last year of data.
Chinook salmon and northern, central, and southern lake trout	Commercial and recreational fishing mortality included. Constant during projection period. Value set to last year of assessment data
Sea lamprey-induced mortality Burbot and northern, central, and southern lake trout	Used in projection period only. Sea lamprey-induced mortality from assessment model is adjusted by a scaling factor to reflect reduction of sea lamprey abundance from treatment of the St Marys River.
Maturation proportion for chinook salmon	Set to the estimates for the last year in the assessment model
Weight-at-age	Constant during projection period.
Diet composition and GCE	Constant during projection period.
Stocking	
Lake trout	One stocking table Cy lake region used for all lake trout populations. When used in conjunction with movement matrix, recruitment data will be changed.
All other species	Constant during projection period.
Movement matrix for lake trout	Constant during projection period. One movement matrix used for all lake trout populations. Works with lake trout stocking table.
Size regulations for lake trout	
Lake trout only	Recreational fishery: 20" in 2001, 22" in 2003, 24" in 2005
Natural recruitment	Constant during projection period.

Table C.2 – Natural mortality rates used in projections of consumption.

Age	Burbot	Chinook salmon	Lake trout North	Lake trout Central	Lake trout South	Walleye Bay	Walleye South
0		1.3048					
1	0.6663	0.3000	0.4983	0.5631	0.4168		
2	0.3184	0.1000	0.2282	0.2087	0.1911	0.3190	0.2900
3	0.1716	0.1000	0.2282	0.2087	0.1911	0.3190	0.2900
4	0.1235	0.1000	0.2282	0.2087	0.1911	0.3190	0.2900
5	0.1077	0.1000	0.2282	0.2087	0.1911	0.3190	0.2900
6	0.1025		0.2282	0.2087	0.1911	0.3190	0.2900
7	0.1008		0.2282	0.2087	0.1911	0.3190	0.2900
8	0.1003		0.2282	0.2087	0.1911	0.3190	0.2900
9	0.1001		0.2282	0.2087	0.1911	0.3190	0.2900
10	0.1000		0.2282	0.2087	0.1911	0.3190	0.2900
11	0.1000		0.2282	0.2087	0.1911	0.3190	0.2900
12	0.1000		0.2282	0.2087	0.1911	0.3190	0.2900
13	0.1000		0.2282	0.2087	0.1911		
14	0.1000		0.2282	0.2087	0.1911		
15+	0.1000		0.2282	0.2087	0.1911		

Table C.3 – Fishing mortality used in projections of consumption.

	Fishing mortality			***Commercial mortality***			***Recreational mortality***		
	Burbot	Walleye		Lake trout			Lake trout		
Age		Bay	South	North	Central	South	North	Central	South
0									
1	0.0110			0.0009	0.0002	0.0007	0.0001	0.0001	0.0005
2	0.0192	0.0000	0.2061	0.0015	0.0006	0.0024	0.0002	0.0002	0.0012
3	0.0306	0.0965	0.4724	0.0102	0.0027	0.0119	0.0014	0.0016	0.0100
4	0.0320	0.0965	0.4061	0.1389	0.0119	0.0509	0.0117	0.0219	0.0992
5	0.0292	0.0965	0.2549	0.6842	0.0298	0.1061	0.0477	0.0764	0.3220
6	0.0350	0.0965	0.2977	0.8685	0.0335	0.0956	0.0681	0.0798	0.3735
7	0.0387	0.0965	0.2623	0.8360	0.0229	0.0614	0.0710	0.0635	0.3594
8	0.0400	0.0965	0.3052	0.7321	0.0124	0.0360	0.0713	0.0413	0.3350
9	0.0401	0.0965	0.3484	0.5496	0.0061	0.0204	0.0713	0.0218	0.3054
10	0.0414	0.0965	0.5133	0.3310	0.0028	0.0114	0.0713	0.0099	0.2716
11	0.0436	0.0965	0.5739	0.1613	0.0013	0.0064	0.0713	0.0042	0.2349
12	0.0481	0.0965	0.4785	0.0688	0.0006	0.0037	0.0713	0.0017	0.1974
13	0.0500			0.0277	0.0003	0.0022	0.0713	0.0007	0.1612
14	0.0500			0.0112	0.0002	0.0014	0.0713	0.0003	0.1282
15+	0.0500			0.0048	0.0001	0.0009	0.0713	0.0002	0.0995

Table C.4 – Fishing and maturation proportions for chinook salmon used in projections of consumption. The chinook salmon model operates with two time periods within a year consisting of the first seven months (prior to a "pulse" harvest and maturation process) followed by the remainder of the year.

	Chinook salmon proportion	
Age	*Harvest*	*Maturation*
0	0	0
1	0.0328	0.0417
2	0.0929	0.0947
3	0.3320	0.3975
4	0.3320	0.7071
5	0.3320	1.0000

Table C.5 – Sea lamprey-induced mortality for lake trout and burbot used in projections of consumption, before applying the scaling factor (Table C.6).

	Burbot	Lake trout		
Age		North	Central	South
1	0.0057	0.0000	0.0000	0.0000
2	0.0057	0.0164	0.0121	0.0862
3	0.0190	0.1293	0.0853	0.2632
4	0.0981	0.2615	0.1918	0.3551
5	0.1203	0.3459	0.2742	0.3805
6	0.0809	0.3864	0.3216	0.3842
7	0.1795	0.4032	0.3472	0.3832
8	0.2937	0.4095	0.3614	0.3816
9	0.3476	0.4117	0.3697	0.3802
10	0.3520	0.4123	0.3748	0.3793
11	0.4134	0.4122	0.3782	0.3786
12	0.5326	0.4119	0.3804	0.3781
13	0.8489	0.4116	0.3820	0.3777
14	1.0000	0.4114	0.3831	0.3775
15+	1.0000	0.4114	0.3831	0.3775

Table C.6 – Sea lamprey-induced mortality scaling factor for projection periods. After 2015 the last value of 0.1601 was used for all other years.

Year	Scaling Factor
1998	1.0000
1999	1.0142
2000	0.8146
2001	0.4461
2002	0.5090
2003	0.4317
2004	0.3439
2005	0.3068
2006	0.2623
2007	0.2289
2008	0.2065
2009	0.1937
2010	0.1789
2011	0.1702
2012	0.1639
2013	0.1610
2014	0.1602
2015	0.1601

Table C.7 – Predator weight-at-age (kg) used in projections of consumption. Burbot weight-at-age was obtained from a von Bertalanffy growth model fitted to Michigan Department of Natural Resources (MDNR) data. Lake trout weight-at-age was obtained from MDNR spring gill new surveys. Walleye weight-at-age was estimated from 1985-1995 Lake Huron creel data. Both the Saginaw Bay and southern region walleye populations used the same weight-at-age values.

	Burbot	Chinook		Lake trout		Walleye
Age		salmon	North	Central	South	
0		0.23				
1	0.39	1.02	0.05	0.05	0.06	
2	0.54	2.68	0.21	0.17	0.32	0.44
3	0.68	5.00	0.57	0.66	0.79	0.71
4	0.83	7.03	1.03	0.90	1.40	1.04
5	0.98	8.60	1.51	1.31	2.06	1.36
6	1.12		1.96	2.03	2.72	1.72
7	1.25		2.36	2.74	3.34	2.08
8	1.37		2.69	3.45	3.89	2.41
9	1.48		2.97	4.02	4.37	2.69
10	1.59		3.19	4.47	4.78	2.91
11	1.68		3.36	4.78	5.12	3.03
12	1.76		3.50	5.00	5.40	3.08
13	1.84		3.06	5.33	5.63	
14	1.91		3.69	5.57	5.82	
15+	2.02		3.75	5.72	6.07	

Table C.8 – Diet composition for the projection period.

		Prey Species						
	Age Class	Alewife	Bloater	Invertebrate	Sculpin	Rainbow Smelt	Stickleback	Other fish
Burbot	1-3	0.156	0.000	0.474	0.227	0.136	0.003	0.004
	4-7	0.262	0.027	0.330	0.158	0.214	0.004	0.004
	8+	0.264	0.029	0.115	0.087	0.476	0.003	0.026
Chinook	0	0.111	0.000	0.000	0.002	0.479	0.001	0.408
Salmon	1	0.298	0.000	0.000	0.004	0.634	0.010	0.053
	2+	0.732	0.000	0.000	0.000	0.233	0.029	0.006
Lake trout	1-3	0.273	0.001	0.000	0.148	0.544	0.030	0.005
(North)	4-6	0.160	0.003	0.000	0.049	0.757	0.013	0.019
	7+	0.381	0.034	0.000	0.046	0.486	0.000	0.053
Lake trout	1-3	0.511	0.000	0.000	0.010	0.473	0.004	0.002
(Central)	4-6	0.556	0.000	0.000	0.001	0.439	0.003	0.001
	7+	0.768	0.005	0.000	0.001	0.222	0.000	0.004
Lake trout	1-3	0.512	0.000	0.000	0.006	0.478	0.001	0.003
(South)	4-6	0.555	0.000	0.000	0.000	0.443	0.001	0.001
	7+	0.836	0.000	0.000	0.001	0.129	0.000	0.034
Walleye	2-3	0.805	0.000	0.000	0.002	0.190	0.002	0.002
(South)	4+	0.598	0.000	0.000	0.003	0.378	0.000	0.021
Walleye	2-3	0.429	0.000	0.000	0.003	0.135	0.003	0.431
(Saginaw Bay)	4+	0.436	0.000	0.000	0.004	0.078	0.000	0.482

Table C.9 – Age-specific gross conversion efficiencies used during the projection period.

	Burbot	Chinook salmon	Lake trout			Walleye	
Age			North	Central	South	Sag Bay	South
0		0.316					
1	0.078	0.254	0.215	0.171	0.218		
2	0.066	0.171	0.195	0.192	0.175	0.168	0.185
3	0.083	0.079	0.148	0.156	0.139	0.174	0.189
4	0.082	0.066	0.118	0.130	0.116	0.154	0.173
5	0.077		0.105	0.114	0.105	0.151	0.170
6	0.072		0.108	0.111	0.110	0.142	0.160
7	0.068		0.092	0.095	0.094	0.129	0.147
8	0.069		0.081	0.084	0.085	0.118	0.135
9	0.066		0.072	0.076	0.077	0.107	0.123
10	0.064		0.066	0.069	0.070	0.092	0.106
11	0.062		0.060	0.064	0.065	0.079	0.091
12	0.060		0.056	0.060	0.061	0.079	0.092
13	0.058		0.053	0.056	0.057		
14	0.057		0.051	0.053	0.072		
15+	0.054		0.042	0.055	0.063		

Table C.10 – Number of recruits assumed for projection period.

Predator Population	Natural Recruitment	Stocking
Burbot	1,137,604	0
Chinook	953,791	2,976,465 US waters 2,578,305 Canadian waters 398,160
All lake trout populations	0	Determined by stocking matrix (Tables C.11 and C.12)
Southern walleye	366,421	0
Saginaw Bay walleye	389,434	1,006,377 in 1999 1,106,000 in 2000 645,951 in 2001 1,000,000 fish from 2002 to the end of the projection.

Table C.11 – Lake trout movement matrix used during the projection period. This matrix defines the percent of fish stocked in each stocking location that become resident in each lake region.

Stocking location	Lake region		
	North	Central	South
DI	0.973	0.013	0.014
MH1	0.720	0.229	0.051
MH2	0.349	0.548	0.103
MH3	0.097	0.355	0.548
MH4	0.000	0.132	0.868
MH5	0.000	0.000	1.000
MH6	0.000	0.000	1.000
OH3	0.349	0.548	0.103
OH4	0.000	0.132	0.868
SFBYR	0.048	0.091	0.861

Table C.12 – Lake trout stocking matrix used during the projection period. This matrix identifies the number of fish stocked at each location by year. Values after 2001 are estimates of the numbers to be stocked. No stocking was reported in MH6, OH3, or OH4 during the projection period.

	Stocking locations						
Year	DI	MH1	MH2	MH3	MH4	MH5	SFBYR
1999	130,000	141,055	216,900	68,210	195358	18,600	360,000
2000	130,000	147,371	226,612	71,264	204,106	0	360,000
2001	130,000	279,000	183,000	0	51,000	48,000	360,000
2002	130,000	279,000	338,000	134,334	134,333	134,333	0
2003	130,000	279,000	338,000	134,334	134,333	134,333	0
2004	130,000	279,000	338,000	134,334	134,333	134,333	0
2005	130,000	279,000	338,000	134,334	134,333	134,333	0
2006	130,000	279,000	338,000	134,334	134,333	134,333	0
2007	130,000	279,000	338,000	134,334	134,333	134,333	0
2008	130,000	279,000	338,000	134,334	134,333	134,333	0
2009	130,000	279,000	338,000	134,334	134,333	134,333	0
2010	130,000	279,000	338,000	134,334	134,333	134,333	0
2011	130,000	279,000	338,000	134,334	134,333	134,333	0
2012	130,000	279,000	338,000	134,334	134,333	134,333	0
2013	130,000	279,000	338,000	134,334	134,333	134,333	0
2014	130,000	279,000	338,000	134,334	134,333	134,333	0
2015	130,000	279,000	338,000	134,334	134,333	134,333	0
2016	130,000	279,000	338,000	134,334	134,333	134,333	0
2017	130,000	279,000	338,000	134,334	134,333	134,333	0
2018	130,000	279,000	338,000	134,334	134,333	134,333	0
2019	130,000	279,000	338,000	134,334	134,333	134,333	0
2020	130,000	279,000	338,000	134,334	134,333	134,333	0

Table C.13 – Lake trout recreational fishery minimum size limits during the projection period.

Year	Size limit in Inches	mm
2001	20	508.0
2002	20	508.0
2003	22	558.8
2004	22	558.8
2005	24	609.6
2006	24	609.6

Table C.14 – The von Bertalanffy growth model parameters used to estimate length-at-age (mm) for northern and central lake trout during the projection period.

	L_∞	K	t_0	CV
Northern lake trout	767.1	0.209	0.00608	0.15
Central lake trout	892.8	0.175	-0.1026	0.15

Table C.15 – Actual mean length (mm) and standard deviation used to estimate the adjustment factor on recreational fishing mortality for northern and central lake trout during the projection period.

	Northern lake trout		Central lake trout	
Age	Mean length	Standard deviation	Mean length	Standard deviation
1	144.20	21.630	157.16	23.573
2	261.93	39.290	275.63	41.344
3	357.41	53.612	375.02	56.253
4	434.85	65.227	458.41	68.761
5	497.65	74.647	528.37	79.255
6	548.58	82.287	587.06	88.058
7	589.88	88.482	636.30	95.444
8	623.38	93.506	677.60	101.641
9	650.54	97.581	712.26	106.839
10	672.57	100.886	741.34	111.200
11	690.44	103.566	765.73	114.859
12	704.93	105.739	786.19	117.929
13	716.68	107.502	803.36	120.504
14	726.21	108.931	817.77	122.665
15	733.94	110.091	829.85	124.477

Table C.16 – Size limit adjustment factor on recreational fishing mortality of northern and central region lake trout. The recreational fishing mortality (Table C.3) is multiplied by the adjustment factor to simulate the effect of hooking mortality related to the enforcement of the minimum size limit regulations during the projection period.

Northern lake trout

Age	2001	2002	2003	2004	2005	2006
1	0.15	0.15	0.15	0.15	0.15	0.15
2	0.15	0.15	0.15	0.15	0.15	0.15
3	0.1521	0.1521	0.1501	0.1501	0.15	0.15
4	0.2614	0.2614	0.1744	0.1744	0.1531	0.1531
5	0.5281	0.5281	0.3254	0.3254	0.2068	0.2068
6	0.7357	0.7357	0.533	0.533	0.3448	0.3448
7	0.8492	0.8492	0.6917	0.6917	0.5	0.5
8	0.9077	0.9077	0.7918	0.7918	0.6248	0.6248
9	0.9388	0.9388	0.8525	0.8525	0.7132	0.7132
10	0.9563	0.9563	0.8897	0.8897	0.7737	0.7737
11	0.9668	0.9668	0.9134	0.9134	0.8151	0.8151
12	0.9734	0.9734	0.929	0.929	0.8439	0.8439
13	0.9778	0.9778	0.9397	0.9397	0.8643	0.8643
14	0.9808	0.9808	0.9472	0.9472	0.8791	0.8791
15	0.9829	0.9829	0.9526	0.9526	0.89	0.89

Central lake trout

Age	2001	2002	2003	2004	2005	2006
1	0.15	0.15	0.15	0.15	0.15	0.15
2	0.15	0.15	0.15	0.15	0.15	0.15
3	0.1577	0.1577	0.1505	0.1505	0.15	0.15
4	0.3501	0.3501	0.2113	0.2113	0.1619	0.1619
5	0.6612	0.6612	0.4479	0.4479	0.2798	0.2798
6	0.843	0.843	0.682	0.682	0.4891	0.4891
7	0.924	0.924	0.8229	0.8229	0.6686	0.6686
8	0.9595	0.9595	0.897	0.897	0.786	0.786
9	0.9762	0.9762	0.9359	0.9359	0.8569	0.8569
10	0.9848	0.9848	0.9572	0.9572	0.8996	0.8996
11	0.9894	0.9894	0.9696	0.9696	0.926	0.926
12	0.9922	0.9922	0.9771	0.9771	0.9429	0.9429
13	0.9939	0.9939	0.982	0.982	0.9542	0.9542
14	0.9951	0.9951	0.9852	0.9852	0.9619	0.9619
15	0.9959	0.9959	0.9875	0.9875	0.9673	0.9673

Appendix D

Survey instrument and descriptive analysis of results

Introduction

While an increasing number of computer programs have become available for modeling fisheries (e.g., CAGEAN, Wisconsin Bioenergetics model of Hewett and Johnson 1995, and Breck 1998), natural resource management has generally lagged behind private corporations in implementing user-friendly computer interfaces. Such was the case with the "No Name" (J. Bence, unpublished data) model, which projected consumption by key predators in Lake Huron using multiple linked spreadsheets. However, projecting consumption under multiple management scenarios was cumbersome and prone to errors common to spreadsheet structure (i.e., copying cells). To simplify the process of projecting consumption and improve the model interface for fishery managers, the spreadsheet version of the consumption model was recreated as a user-friendly computer program . The resulting Consumption Projection Model (CPM) provides an easy-to-use interface that allows the creation of multiple management scenarios and comparisons between them.

Objectives

The CPM was intended to improve upon the function and design of the previous spreadsheet model. To evaluate the effectiveness of the CPM, I conducted a half-hour

training session, then asked participants to complete a survey (Figure D-1) designed to determine the usefulness and ease-of-use of the CPM. Satisfaction with new features, such as the Windows interface, error messages, and help facilities, was also examined. The test subjects were stakeholders concerned with piscivore stocking and fishery management in Lake Huron, including managers in state, tribal, and provincial fisheries management agencies. Differences in management styles and objectives of these agencies need to be reflected in the CPM computer program to accommodate individual agency needs. Several questions requiring a written response were used (Figure D-1) to elicit these differences.

CPM Training Session

A training session was conducted during the July 2002 Lake Huron Technical Committee (LHTC) meeting in Gore Bay, Ontario. CPM was loaded onto laptop computers brought by each participant. A 10-minute presentation that reviewed the consumption model and how the program works preceded the training session. This was followed by 20 minutes of hands-on demonstration and training on the use of CPM. A baseline and a modified scenario were demonstrated while users followed along on their laptops. Due to time limitations, other program capabilities such as plot ranges, scenario information, and integrated help were not demonstrated.

At the end of the demonstration and a short question-and-answer period, the participants were given the survey (Figure D-1) and asked to complete it before the end of the meeting the next day. Since participants had limited training time to use CPM, they were asked to use the program on their own during the remainder of the meeting and

encouraged to ask questions regarding its operation. Participants returned completed surveys to a third party who placed them in an envelope. Survey responses to the first section were tabulated (Table D.1) and written responses to the second part were reviewed and summarized.

Survey Instrument

The survey (Figure D-1) contained two types of questions. The first page contained statements about the overall utility of the new computer program. It contained three subsections: usefulness, ease-of-use, and general issues. Participants used a 5-point response scale to indicate disagreement (value=1) through agreement (value=5) with each statement. The purpose of the response-scale questions was to determine the level of satisfaction participants gained from using the program. To measure the usefulness of CPM, respondents were asked if the new program would enhance job performance and be useful in their daily jobs. The ease-of-use section evaluated the CPM operation and user interface. The general section evaluated the CPM program vs. the "No Name" model as well as several other different aspects of the program (e.g., look-and-feel, help facility, error messages, etc.). [*Note, the CPM program was originally named Consume and that name is used in the survey instruments (Figure D.1 and Table D.1). It refers to the same computer program.*]

The second page contained questions that prompted respondents to identify the parts that worked and those that did not. The written responses were important for gathering auxiliary information about user satisfaction with the functionality built into the new computer program. They also served as a method of identifying important functions

that would be considered as additions to the CPM before the final version of the computer program was distributed. Detailed input from the users of the new program was important since only cursory surveying of potential users was done prior to creating the program. In addition, this feedback helped determine whether user expectations of the new program were met or not, and identify areas needing improvement.

Survey responses

There were approximately 12 participants in the training session. Since all of the LHTC meeting attendees were not required to participate, those with less interest in this topic may not have taken an active role in the hands-on training. Each participant received a survey; eight surveys were returned. Surveys were later tallied and summarized (Table D.1). One participant did not answer any items in the Usefulness section.

Usefulness

All answers, with the exception of one, to statements in this section received marks of 3 or higher indicating that the participants believe the CPM program will be useful in their job (Table D.1). The majority of answers in this section (22 of 28) were 4s or 5s indicating that the CPM was perceived as useful for fishery managers.
The last statement in this section, "Consume [CPM] has all the functions and capabilities I need", received some of the lowest scores and had the highest variation between scores. Scores ranged between 2 and 5, with a mean of 3.57. In the written section, many respondents noted functions they would like to see added to the CPM. Users generally

agreed that the program provides an important service in their jobs, but some additional functions would be helpful.

Ease Of Use

In this section, 38 of 40 answers rated the ease-of-use as 4 or higher (Table D.1). Overall, the CPM interface and methodology was easy to understand and users acquired sufficient information to operate the basic functions of the program in one short training session. This attests to the difficulty of setting up multiple scenarios and retrieving graphical output from the "No Name" model. The fourth statement, "Organization on the screens is clear", elicited the highest scores, with all participants giving it the highest mark of 5. All other statements in this section sought to determine whether the program was easy to use even with minimal training; 30 of 32 answers to these statements were scored as 4 or 5. It seems that the interface is clear and users find it understandable and easy to use but the process of using CPM and creating a scenario may be somewhat cumbersome or not well documented. The lack of sufficient training may have influenced these results.

General Usage

These statements sought to evaluate many different aspects of the program and, unlike the previous two sections, each question response will be discussed separately. In the first statement, respondents found the interface pleasing with all answers scoring 4 or higher (Table D.1). The CPM was rated as a big improvement over the "No Name" model (7 of 8 respondents scored it as 5) in the second statement. Most respondents did

not have sufficient time to try out other functions of CPM such as the help facility. Therefore, 5 out of 8 respondents rated the third statement concerning the use of the Help facility as "not applicable." The limited time to use the program before returning the survey most likely played a role in the number of "not applicable" answers (3 of 8) to the statement concerning the clarity of error messages. Two of the 5 scored answers were lower than 4, which may indicate a problem with how the CPM identifies errors it encounters. The CPM installation program was not available for all Windows® versions, so I manually installed the CPM on each participant's laptop prior to the training session. Since the users could not perform the installation themselves, half of the respondents (4 of 8) scored the statement about ease of installation as "not applicable". All respondents scored the last question related to overall satisfaction with the CPM as 4 or 5, indicating the CPM was generally perceived as easier to use than the "No Name" model.

Written Responses

The purpose of the open-ended questions in this section was to determine which CPM features the users liked and did not like, and to obtain feedback on improvements to the CPM that users would like to see. A summary of responses to the four questions are given below:

1. *Are there things that need to be changed or that did not work as predicted?*

   There were seven responses to this question. Four respondents indicated they could not respond to this question due to lack of time with the program and three respondents indicated no change was needed. One respondent indicated a "few minor bugs" were detected but did not list them.

2. *Are there things about Consume that you did not like?*

Six participants responded to this question. Four respondents indicated that there was nothing they did not like about the program. One respondent indicated that more time was needed to evaluate the program while another gave suggestions about improving the interface and updating parameters.

3. *Are there things in Consume that worked well or better than the spreadsheet model?*

Six of the seven respondents thought that CPM was an improvement over the previous spreadsheet implementation of the model. The seventh respondent indicated insufficient time to use the program to evaluate the CPM. Four respondents commented that the graphics and visualization were the important improvements. Others noted that the automation was the major advance over the spreadsheet version.

4. *Are there additional features that would make this program more useful to you or your job?*

Six participants responded to this question; two indicated more time was needed to evaluate the program. Suggestions for additional features by other respondents included (1) estimation and projection of sea lamprey induced mortality by species; (2) documentation describing the source of data used in the model; (3) providing standard pre-run scenarios depicting commonly used management actions; and (4) manual and documentation.

Conclusion

Clearly, survey respondents felt that the CPM computer program was an improvement over the "No Name" spreadsheet version and provided a better user interface. Most respondents agreed that the CPM was easy to use but several respondents noted some additional features that would make the program more useful. Many of these features will be added to the final version of the CPM. In particular, a hardcopy manual will be provided and some standard pre-defined scenarios will be created. These additions should enhance the usefulness and ease-of-use of the CPM.

Similarly, there were problems with the CPM installation process that prohibited users from installing the program themselves or scoring the statement concerning ease of installation. A dependable installation process is necessary to insure that distributed copies of the CPM can be installed on any Windows computer. Further, a working installation process for computer programs is considered a norm. The software package used to create this installation process could not accommodate all versions of Windows operating systems. It will be abandoned in lieu of a more complete software package that supports all versions of Windows.

While generally quite satisfied with the CPM, users needed more time to work with the program before responding. In scoring the statements on the first page of the survey, a number of answers were marked "not applicable". Responses to the open-ended questions on page two often showed that users had insufficient time using the CPM to evaluate it. These scores and comments point to the need for users to spend more time using the CPM and to become acclimated to it. Also, some of these responses may be attributed to the brevity of the training session. A longer, in depth training session, which

includes more hands-on examples and exploration of other features available in the CPM, might have addressed these concerns.

Literature Cited

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Dobiesz N.E. 2003. Computer Projection Model (installable software and documentation included). Available for download at the anonymous FTP site at glpd.fw.msu.edu in the directory CPM V1.0.

Hewett. S. W. and B. L. Johnson. 1995. Fish Bioenergetics Model 3. University of Wisconsin Sea Grant Institute, WIS-SG-91-250.

Table D.1. Answers to survey questions. The number of answers is shown in bold.

Statement to be evaluated by respondent	*Disagree >>>> Agree*						*Total*
	1	*2*	*3*	*4*	*5*	*N/A*	Answers
USEFULNESS							
Using Consume would enhance my effectiveness on the job				**5**	**2**		7
Using Consume would make it easier to do my job			**1**	**5**	**1**		7
Consume would provide an important service I need in my job			**1**	**4**	**2**		7
Consume has all the functions and capabilities I need		**1**	**3**	**1**	**2**		7
EASE OF USE							
Learning to use Consume was easy				**4**	**4**		8
Consume is simple to use				**6**	**2**		8
I find it easy to get Consume to do what I want it to do			**1**	**6**		**1**	8
Organization of information on the screens is clear					**8**		8
It was easy to define a scenario and run a projection				**5**	**3**		8
GENERAL							
The interface is pleasant				**4**	**4**		8
The program is an improvement over the spreadsheet models				**1**	**7**		8
It was easy to find the information I needed in help files			**1**		**2**	**5**	8
Error messages clearly identified how to fix problems		**1**	**1**	**3**		**3**	8
Installing Consume on my computer was easy					**4**	**4**	8
Overall, I am satisfied with this program				**4**	**4**		8

Figure D.1. Questionnaire for evaluating the program Consume

Instructions:
Please rate your use of the Consume program. Respond to each item by filling in the circle that best describes your experience using the program. For items that are not applicable, use N/A.

Confidentiality
Your responses to this survey are completely confidential. Your privacy will be protected to the maximum extent allowable by law. By completing and returning this form, you indicate your voluntary agreement to participate in this survey. This research is supported by Federal Aid grant F-80-R-2.

If you have questions or concerns regarding your rights as a study participant, or are dissatisfied at any time with any aspect of this study, you many contact—anonymously, if you wish—Ashir Kumar, Chair of the University Committee on Research Involving Human Subjects (UCRIHS) by phone: (517) 355-2180, fax: (517) 353-2976, email: ucrihs @msu.edu or regular mail: 246 Administration Bldg., East Lansing, MI 48824.

	Disagree >>>> Agree					
USEFULNESS	1	2	3	4	5	N/A
Using Consume would enhance my effectiveness on the job	O	O	O	O	O	O
Using Consume would make it easier to do my job	O	O	O	O	O	O
Consume would provide an important service I need in my job	O	O	O	O	O	O
Consume has all the functions and capabilities I need	O	O	O	O	O	O
EASE OF USE	1	2	3	4	5	N/A
Learning to use Consume was easy	O	O	O	O	O	O
Consume is simple to use	O	O	O	O	O	O
I find it easy to get Consume to do what I want it to do	O	O	O	O	O	O
Organization of information on the screens is clear	O	O	O	O	O	O
It was easy to define a scenario and run a projection	O	O	O	O	O	O
GENERAL	1	2	3	4	5	N/A
The interface is pleasant	O	O	O	O	O	O
The program is an improvement over the spreadsheet models	O	O	O	O	O	O
It was easy to find the information I needed in help files	O	O	O	O	O	O
Error messages clearly identified how to fix problems	O	O	O	O	O	O
Installing Consume on my computer was easy	O	O	O	O	O	O
Overall, I am satisfied with this program	O	O	O	O	O	O

Please continue on the next page. ☞

OTHER COMMENTS

Are there things that need to be changed or that did not work as predicted? (Please specify)

Are there things about Consume that you did not like? (Please specify)

Are there things in Consume that worked well or better than the spreadsheet model? (Please specify)

Are there additional features that would make this program more useful to you or your job? (Please specify)

Before the end of this meeting, please return this questionnaire to Jim Bence.