



An Assessment of the Invasion of Rainy Lake, Voyageurs National Park, by Rainbow Smelt (*Osmerus mordax*)

1990–2002

Natural Resource Report NPS/VOYA/NRR—2019/1962



ON THE COVER

Marion Bay, Voyageurs National Park
NPS photo.

An Assessment of the Invasion of Rainy Lake, Voyageurs National Park, by Rainbow Smelt (*Osmerus mordax*)

1990–2002

Natural Resource Report NPS/VOYA/NRR—2019/1962

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Names and Acronyms Used in This Report

CPE Catch per unit of effort.

Fish species:

Common Name	Scientific Name	Family
Black Crappie	<i>Pomoxis nigromaculatus</i>	Centrarchidae
Burbot	<i>Lota lota</i>	Gadidae
Cisco	<i>Coregonus artedii</i>	Salmonidae
Emerald Shiner	<i>Notropis atherinoides</i>	Cyprinidae
Iowa Darter	<i>Etheostoma exile</i>	Percidae
Johnny Darter	<i>Etheostoma nigrum</i>	Percidae
Lake Whitefish	<i>Coregonus clupeaformis</i>	Salmonidae
Logperch	<i>Percina caprodes</i>	Percidae
Longnose Sucker	<i>Catostomus catostomus</i>	Catostomidae
Ninespine Stickleback	<i>Pungitius pungitius</i>	Gasterosteidae
Northern Pike	<i>Esox lucius</i>	Esocidae
Rainbow Smelt	<i>Osmerus mordax</i>	Osmeridae
Sauger	<i>Sander canadensis</i>	Percidae
Slimy Sculpin	<i>Cottus cognatus</i>	Cottidae
Smallmouth Bass	<i>Micropterus dolomieu</i>	Centrarchidae
Spottail Shiner	<i>Notropis hudsonius</i>	Cyprinidae
Tadpole Madtom	<i>Noturus gyrinus</i>	Ictaluridae
Trout-perch	<i>Percopsis omiscomaycus</i>	Percopsidae
Walleye	<i>Sander vitreus</i>	Percidae
White Sucker	<i>Catostomus commersoni</i>	Catostomidae
Yellow Perch	<i>Perca flavescens</i>	Percidae

MNDNR Minnesota Department of Natural Resources.

USGS U.S. Geological Survey.

YOY Young-of-the-year

Abstract

Exotic Rainbow Smelt (*Osmerus mordax*), which had been present since 1972 in the upper Rainy Lake watershed, first appeared in Rainy Lake in 1990. Based on studies conducted elsewhere it appeared their invasion might have a significant effect on the aquatic ecosystem of Rainy Lake and might exacerbate an existing mercury contamination problem since there was some evidence that the rate of mercury accumulation in top level predators accelerates if they switch to a smelt diet. There were four parts to this assessment of the effect of the smelt invasion: (1) sampling methods were identified and tested, (2) food habits analyses were conducted to determine how the smelt were fitting into the food web, (3) long-term monitoring data and bioenergetics modeling were used to assess the possible effect of the smelt on the growth and condition of Walleye (*Sander vitreus*) and Northern Pike (*Esox Lucius*), and (4) mercury concentrations in smelt and native prey species were compared, as were pre- and post-invasion concentrations in Walleye and Northern Pike. Smelt abundance rose rapidly, peaking in the mid-1990s at which time hydroacoustic analysis indicated the biomass was similar to levels in the Great Lakes. By the early 2000s smelt abundance had fallen significantly. Smelt occupied their characteristic position in the food web – feeding primarily on zooplankton, ichthyoplankton, and *Mysis diluviana* and other invertebrates and in turn being preyed on by larger piscivores. Diet overlap was significant between smelt and smaller Walleye and Sauger (<200 mm), suggesting competition might occur if shared resources became limited. Contrary to expectations, the smelt invasion did not appear to have contributed significantly to changes in growth and condition and bioaccumulation of mercury in Walleye and Northern Pike.

Introduction

Voyageurs National Park occupies a unique place in the National Park System in that over one-third of its total area is water-covered (34,603 ha) and over 95% of the park is only accessible by air and water. The park is dominated by four major water bodies: Rainy, Namakan, Sand Point and Kabetogama Lakes. The first three of these are binational waters shared with the Canadian province of Ontario. No longer pristine, these lakes and their fish stocks have been subjected to many of the same anthropogenic factors that have affected the nearby Great Lakes. Dam construction on the outlets of Rainy and Namakan Lakes in the early 1900s, and subsequent water management programs, have changed the natural hydrological regimen, which has negatively affected many components of the aquatic ecosystem, including some fish species (Chevalier 1977, Kallemeyn et al. 1993). The fish populations have been impacted by overfishing—initially by commercial fishing and more recently by sport fishing (Chevalier 1977, Cohen et al. 1993)—and by the introduction and invasion of exotic species. Current fish populations support important sport and commercial fisheries (including tribal subsistence fishing), but airborne mercury has entered the environment and made fish consumption advisories necessary (Sorensen et al. 1990).

The most recent perturbation was the invasion of Rainy and Namakan Lakes by Rainbow Smelt (*Osmerus mordax*). Rainbow Smelt (hereafter referred to as smelt), which colonized numerous areas in the upper Rainy Lake watershed after being accidentally introduced by humans (Franzin et al. 1994), first appeared in Rainy and Namakan Lakes in 1990. Based on studies conducted elsewhere, the smelt may have a significant effect on the park's aquatic ecosystem, and in particular, its cool- and cold-water fish species (Evans and Loftus 1987, Hrabik et al. 1998). Due to their intermediate trophic position—as consumers of zooplankton (including ichthyoplankton) and as prey for top predators—smelt have the potential to introduce a wide array of ecological impacts from both direct and indirect effects (Kerfoot and Sih 1987, Carpenter 1988). Another ramification of the establishment of smelt may be elevated mercury levels in piscivores. Mercury levels in Walleye (*Sander vitreus*) and Northern Pike (*Esox lucius*) may increase further if they switch from an indigenous forage fish diet to one of smelt (Mathers and Johansen 1985).

Monitoring programs for fish and other aquatic biota, invaluable in detecting changes in ecosystems and recognizing long-term trends, need to be designed so that careful consideration is given to the specific question(s) being addressed (Duffy et al. 1994). Traditional sampling techniques (gill nets, seines, trap nets, and electrofishing boom shocker) currently used in the fish monitoring programs on Rainy and Namakan lakes are most effective in demersal, epilimnetic, and littoral habitats. These methods are not effective for sampling fish such as the smelt that spend most of their life in the pelagic zone. The integration of combined hydroacoustic assessment and midwater trawling appears to be the most promising method for quantifying stock structure, distribution, changes in abundance, and other vital statistics of smelt as well as other members of the endemic pelagic fish community. These methods have proven effective in the Great Lakes (Argyle 1982, Heist and Swenson 1983, Brandt et al. 1991, Argyle 1992), as well as smaller lakes where smelt occur (Burczinsky et al. 1987, Kim and LaBar 1991). A pilot survey conducted in 1996 (Fleischer et al. 1996) demonstrated the

efficacy of the integration of acoustic and midwater trawl methods to assess the status of Rainbow Smelt in Rainy Lake.

Methods

Study Area

This study was conducted on Rainy Lake, with sampling coverage spanning both the Minnesota and Ontario portions of the South Arm of the lake. Rainy Lake, which covers 92,110 ha, is composed of three geographically distinct basins, the largest and deepest of which is the South Arm which is divided between Ontario (27,300 ha) and Minnesota (21,900 ha). About 67% of the Minnesota portion is located within Voyageurs National Park. The South Arm has maximum and mean depths of 49.1 m and 10.7 m, respectively.

Based on long term limnological monitoring, Rainy Lake is classified as mesotrophic, or of intermediate productivity (Kallemeyn et al. 2003). The lake is dimictic, with average mid-August epilimnion thicknesses of 12 to 13 m and temperatures from 18° C. to 23° C. Since 1983 average late summer hypolimnion temperatures have ranged from about 8° C. to 12° C. Hypolimnetic dissolved oxygen concentrations do not limit fish distributions since they exceed 5 mg/L throughout the summer. Light penetration is regulated more by stain or color associated with organic materials than by algal productivity (Kepner and Stottlemeyer 1988, Payne 1991). Water transparency as determined from Secchi disk readings averages about 2.7 m on Rainy Lake. Sampling with a LiCor quantum sensor showed that incident light is rapidly reduced, falling to about one percent at depths of 4 m and 0.06% at 8 m.

Water levels on Rainy Lake are controlled by a hydroelectric dam that was built in 1909. Since these are international waters, water level management is regulated by the International Joint Commission (IJC) through the International Rainy Lake Board of Control. Regulation of lake levels is based on “rule curves”, which are bands of lake elevations within which the water levels are to be maintained during normal operations throughout the year. In 2000, the IJC revised the rule curves in an attempt to reduce the adverse ecological affects associated with the 1970 rule curves.

Rainy Lake supports a coolwater recreational fisheries with Walleye and Northern Pike being the principal harvested species. Other important species in the fishery are Sauger (*Sander vitreus*), Smallmouth Bass (*Micropterus dolomieu*), and Black Crappie (*Pomoxis nigromaculatus*). Yellow Perch (*Perca flavescens*), Spottail Shiners (*Notropis hudsonius*), and several other cyprinid species are the primary prey species (Kallemeyn et al. 2003). The most common native coldwater species in the lakes are Lake Whitefish (*Coregonus clupeaformis*), Cisco (*C. artedi*), and Burbot (*Lota lota*).

Field Sampling

To increase sampling efficiency of the multiple gear types being used, the Minnesota portion of the South Arm of Rainy Lake was divided into six sampling blocks on the basis of major geographical features. Blocks I–III extended from the Ranier Rapids at the west end of the lake to the Brule Narrows while Blocks IV–VI included the Brule Narrows and the area from there to the Kettle Falls area. Trawl and gill net sampling was further stratified by depth zones, i.e. 0–9.9 m, 10–20 m, and >20 m. Bottom and midwater trawl hauls and hydroacoustic data collection were conducted on a 24-foot boat borrowed from the USGS (U.S. Geological Survey) Lake Superior Biological Station.

Temperature and dissolved oxygen profiles were taken biweekly with a Yellow Springs Instrument Model 51 B meter as part of an ongoing, long-term monitoring program (Kallemeyn et al. 2003).

Fry sampling

Reproduction of smelt was monitored from 1996 to 1998 on the South Arm of Rainy Lake with a larval fish sampler patterned after the horizontal ichthyoplankton tow-net system developed by Nester (1987). Fry sampling was conducted in late May and June using paired 0.5-m plankton nets with a conical ratio of 1:5 and with 363- μ m Nitex mesh. Five- to 10-minute tows were typically made at inshore locations at depths of 1 to 3 m. Volume of water filtered was determined with Model 2030 General Oceanics digital flow-meters attached to the net support frame. The total number of tows in the three years was 34, 35, and 40, respectively.

Smelt netting

The nets used by the Minnesota Department of Natural Resources (MNDNR) and in this study to sample smelt were 61-meter-long, multifilament, nylon gill nets consisting of two panels 30.5 $\times$ 1.8 m with bar mesh sizes of 9.5 and 12.7 mm (hereafter referred to as smelt nets). Each September from 1991 to 2002, the MNDNR made eight sets at fixed sites with these nets in conjunction with their annual experimental gill netting program. From 1996 through 2002, sampling was conducted with these nets in four of the sampling blocks as part of this study. From 1997 to 2002 smelt nets were only set at depths greater than 10 m since relatively few smelt were captured in the shallower waters in 1996. Sampling was successful in 6, 7, 6, and 8 of the 8 years in June, July, August, and September, respectively. Scales and otoliths were collected for ageing.

Bottom trawling

Bottom trawling was conducted monthly from June through September in 1995 and 1996 and from June through August in 1997. The 4.9-m (headrope) semi-balloon trawl was constructed with 38-mm mesh with a cod end liner of knotless nylon with 6.4-mm bar mesh. Each month we attempted to make two tows in each of the 10-m depth strata in five of the sampling blocks. Sampling was done at fixed sites in an attempt to minimize hang-ups on the numerous boulders and rock reefs that are present in the lake. Tows were made along the contour at approximately 2 to 2.5 km/hr for 10 minutes. Captured fish were placed in plastic bags and put on ice until they could be returned to the laboratory for processing.

Hydroacoustics/Midwater trawling

The principal sampling period for smelt was August and early September so that the young-of-the-year smelt had reached collectable sizes. Surveys were primarily done during daylight hours since initial sampling efforts demonstrated that the smelt were distributed throughout the water column during the day. This distribution is apparently due to poor light penetration resulting from the lake's humic water. Night samples were taken at a subset of the transects, however, to assess whether this pelagic distribution is applicable to other fish species (e.g., Cisco). To increase sampling efficiency, the major basins were divided into sampling blocks on the basis of major geographical features. Sampling transects within blocks were then selected randomly. All the line transects were arranged cross-contour. Geospatial data for each transect was recorded continuously with a Northstar global positioning system. Acoustic density estimates were stratified by 2-m vertical depth strata.

Midwater trawl tows targeted fish aggregations at depths and locations as indicated by the acoustics. Trawl samples were used to determine species composition and provide biological information and samples for target strength analyses. Fish collected in the midwater trawl were identified, measured, and weighed in species-aggregate. A Yellow Springs Instrument Model 51 B meter was used to measure temperature and dissolved oxygen levels. Readings were taken at one-meter intervals in the water column at every third to fourth transect.

A 7×7 m midwater trawl with 6-mm bar mesh in the cod end was used to collect fish for species and size verification. Trawling depth was obtained from a radio sonde unit attached to the trawl head rope. Tows were typically be 10 minutes long and were made at a speed of 2–3 meters per second.

Acoustic data was collected with a DT6000 BioSonics' Digital Transducer System with a 120- kHz split-beam transducer attached to a 7-m boat by a fixed frame mount. The system was calibrated to U.S. Navy standards by the manufacturer. Performance of the system was monitored by comparing the target strength of a reference tungsten carbide sphere with established values (Foote et al. 1987). Adjustments were made during the survey on the basis of the results of the comparisons.

Acoustic data was analyzed using BioSonics' Visual Analyzer software. Acoustic-based estimates of abundance were derived from the application of a combined multi-beam/echo integration technique (Burczynski and Johnson 1986), where the measured in situ mean backscattering cross section of individual fish (Ehrenberg 1982) for the sampled area is used to scale the mean squared voltages. The theory of echo integration states that the density of fish in a given depth stratum is directly proportional to the average squared voltage at a time varied gain of $20 \log(R) + 2aR$, where R is range and a is the absorption coefficient (see Burczynski [1982] for a derivation and discussion of the theory of integration).

The echo reflecting power of a fish, commonly referred to as the target strength (TS), is the decibel equivalent of the target's backscattering cross section. Since the acoustic size range of fish is typically greater than -60 dB, a threshold voltage equivalent to a TS of -60 dB was used in the estimation of fish abundance. Estimates of fish abundance and biomass from individual transects was expanded to lake-wide estimates using the Voyageurs National Park geographic information system.

Standardized gill netting

Information on fish indices of abundance, size and age structure of populations, growth rates, and condition indexes was obtained from the experimental gill netting component of the MNDNR's Large Lake Assessment program (Wingate and Schupp 1985), which has been used on Rainy Lake since 1983. Each September, overnight gill net sets are made in Minnesota waters at 24 stations on Rainy Lake. Captured fish are identified, measured (total length, mm), and weighed (grams). Scales, otoliths, and/or cleithra are collected from game fish species for ageing.

Stomachs were routinely collected from fish caught in smelt nets, trawls, and experimental gill nets for food analysis. Additionally, in 1996 and 1997, overnight sets were made with experimental gill nets specifically to obtain stomachs for assessing predation by Walleye and other piscivores on smelt and to analyze Hg/trophic level relationships (Sorensen et al. 2001). The gill netting was done with

multifilament nylon nets 76 m long consisting of five panels 15.2 × 1.8 m with graded bar mesh sizes of 19 mm, 25 mm, 32 mm, 38 mm, and 51 mm. In 1996 two gill net sets were made in each of the 10-m depth strata in three of the sampling blocks on four occasions between late June and early October (N=72 gill net sets). Similar sampling in 1997 was done in two of the depth strata in three sampling blocks from late June through September (N=36 gill net sets). Stomachs removed from fish were either preserved in ethanol or kept on ice until they could be frozen in the laboratory.

To assess interactions of smelt with the zooplankton and zoobenthos communities as well as potential food-resource competition and diet overlap with Cisco and other native fish species, the pelagic zooplankton community was monitored in 1996. Zooplankton were collected biweekly from late May through September at four sites in Rainy Lake. Vertical net tows were made with a Hensen egg plankton net with a mouth diameter of 300 mm and 153-µm Nitex mesh. Vertical hauls were made from the bottom to the surface at all stations, with the depths ranging from 3 to 43 m. Additionally, tows were made from a depth of 10 m to the surface at two of the sites. Samples from two tows from each depth at each site were combined and preserved with Lugol's solution.

Laboratory protocol

In the laboratory, individual stomach contents were examined with a dissecting microscope and prey organisms were identified and enumerated. All items from individual taxa from all the fish in a monthly sample were then combined and a total dry weight was determined after the combined sample was dried for 24 hours at 100° C. For example, all smelt found in all the Walleye stomachs from a particular sampling method and period would be grouped together before being dried and weighed. Only those stomachs that contained food items were used for diet analysis.

Zooplankton samples and smelt and Cisco stomach contents collected in 1996 were analyzed at the USGS–Lake Michigan Ecological Station by Laurel Last. For the zooplankton analysis, a sample was initially adjusted to a fixed volume so that a 1-mL subsample would contain 300 to 400 organisms, after which a 1-mL aliquot was removed with a Hensen-Stempel pipette and placed in a rotary counting chamber for counting. Mature copepods and cladocerans were identified to species using a compound microscope and taxonomic keys prepared by Edmondson (1959), Balcer et al. (1984), Pennak (1989), and Thorp and Covich (1991). All copepod nauplii were counted only as nauplii while copepods were identified as cyclopoid or calanoid. Counts were converted to number of organisms per cubic meter with no adjustment for net efficiency.

Preserved stomachs from smelt and Cisco collected in 1996 were opened and flushed into a Petri dish for examination using a dissecting microscope. Only stomachs containing food were included in the diet analysis. All the organisms from young of the year fish and stomachs containing few food items were counted; food items from stomachs containing numerous organisms were subsampled. Due to the digestive degradation of zooplankton (*sensu* Bowen 1996), zooplankton counts were based on tails of copepods and heads of cladocerans, *M. relictus*, *Chaoborus*, and other invertebrates. Johannsen (1970) and Merritt and Cummins (1996) were used along with the keys used in the zooplankton analysis to identify food items.

Diet overlap between smelt and native fish species was examined using Schoener's (1970) index C_{xy} :

$$C_{xy} = 1 - 0.5 \left(\sum |p_{xi} - p_{yi}| \right)$$

Where p_{xi} is the proportion of resource i used by species x , and p_{yi} is the proportion of resource i used by species y . The index ranges between 0 (no overlap) and 1 (complete overlap) with values >0.6 being evidence of a significant overlap in resource use (Wallace 1981).

Ivlev's (1961) index of electivity was used to assess the degree that zooplankton species were selected by smelt and Cisco. The relationship is

$$E = (r_i - p_i)/(r_i + p_i)$$

Where r_i is the relative abundance of prey item i in the stomach contents, and p_i is the proportion of prey type i in the environment. Negative values indicate avoidance of prey, 0 = random selection, and positive values indicates active selection of prey.

Age and growth of fish were determined from scales, otoliths, and cleithra. Scales were pressed onto acetate slides and magnified impressions (40 $\times$) were examined with a microfiche reader. Annuli were identified, and scale radii and distances from the focus were measured. The Fraser-Lee method (DISBCAL software; Frie 1982) was used to back-calculate lengths at annuli. Otoliths and cleithra readings by two biologists provided verification of ages for Walleye and Northern Pike. Walleye otoliths were cracked into transverse sections, burned, and viewed with a dissecting microscope. Northern Pike cleithra were viewed whole and annuli counted.

Body condition of Walleye and Northern Pike caught in the MNDNR's annual standardized gill netting program was evaluated with the relative weight ($\underline{W}_r$) index (Wege and Anderson 1978). Relative weight ($\underline{W}_r$) is calculated as $\underline{W}/\underline{W}_s$, where $\underline{W}$ is the weight of an individual and $\underline{W}_s$ is a length-specific standard weight predicted by a length-weight regression constructed to represent the species. The standard weight equations used were:

$\log_{10}(\underline{W}_{s,g}) = -5.453 + 3.180 \log_{10}(L, \text{mm})$ for Walleye (Murphy et al. 1990), and

$\log_{10}(\underline{W}_{s,g}) = -5.437 + 3.096 \log_{10}(L, \text{mm})$ for Northern Pike (D. W. Willis published in Anderson and Neumann 1996).

The possible effect of smelt in the Walleye diet was also assessed by Dr. Brian Graeb, South Dakota State University, with a bioenergetics model. The analysis was conducted using caloric densities of Walleye (1+), smelt (1+), Cisco (1+), Yellow Perch (YOY and 1+), White Sucker (*Catostomus commersoni*, YOY), Spottail Shiner (YOY and 1+), and Black Crappie (YOY) collected from June through September 1997 from Rainy Lake by USGS Biological Station personnel. Laboratory analyses were conducted at the USGS Environmental Contaminants Research Center, Columbia, Missouri. For the analysis, fish meal samples weighing approximately 1 gram were placed into a pellet press and compressed, after which the pellet was removed and weighed. Samples were stored dessicated until used. Gross energy content was determined using an isoperibol oxygen bomb calorimeter (Parr Instrument 1241, Moline, Illinois). Twenty percent of the samples were run as duplicates.

Dr. Graeb modeled age-6 Walleye (starting weight 624 g) for one growing season using the following five different scenarios:

1. Baseline — water temperature at depth of 1 meter in 2003 which was the warmest summer; Diet data used was that recorded in 1996–1997 for Walleye in Rainy Lake. Smelt comprised 17% of the diet in those years.
2. All smelt diet — temperature and other data same as baseline but diet was changed to 100% smelt.
3. Cooler summer — same as baseline except temperatures at depth of 1 meter were changed to those in 2004, which was a much cooler summer.
4. Yellow Perch/Cisco diet — same as baseline except smelt were removed from the diet and replaced with an equal percentage of Yellow Perch and Cisco.
5. Temperature at depth of 10 m — same as baseline except using water temperatures at depth of 10 m.

Mercury

Data from long-term monitoring of mercury in fish for consumption advisories (programs by Minnesota and Ontario resource agencies) were used to assess whether the smelt invasion resulted in elevated mercury levels in Walleye and Northern Pike. Mercury concentrations in smelt and native invertebrate and fish organisms that may be preyed upon by Walleye and Northern Pike were determined by Sorensen et al. (2001).

Results and Discussion

Fishes Collected

A total of 21 fish species were collected, representing 12 of the 16 fish families known to occur in the waters of Rainy Lake. Twenty-one species were collected in the three years bottom trawling was conducted, 15 in the three years of midwater trawling, and 14 in the seven years smelt nets were set (Table 1). Rainbow Smelt, the target species, and Cisco were the predominant species in the midwater trawl and smelt nets while Trout-perch (*Percopsis omiscomaycus*) was dominant in the bottom trawl.

Fish Abundance and Distribution

Fry Sampling

Smelt typically migrate into streams for spawning, although shore spawning has been documented (Rupp 1965, MacCrimmon et al. 1983). Spawning normally occurs close to the ice-out time. From 1995 to 2002 on Rainy Lake, ice-out occurred within a day or two of the mean long-term ice-out day of 4 May in 5 of the 8 years. In 1998 and 2000, ice-out was 21 and 11 days earlier, respectively, than the long-term mean, and in 1996 was 15 days later. The rivers and streams entering Rainy Lake typically open up prior to lake ice-out so they were not accessible during the period when the smelt were most likely to have been spawning. Consequently, the exact time and location of spawning were not identified.

Ice out dates and egg incubation time were taken into consideration when deciding when to start fry sampling to assess smelt reproduction. Egg incubation time ranges from 2 to 4 weeks depending on temperature (Nellbring 1989), so fry sampling was initiated approximately that length of time after ice-out. In 1996, when ice-out was later than normal, the first net tows were not made until 7 June. Sampling started on 19 May 1997 (two weeks after ice-out) and on 27 May 1998 (almost six weeks after ice-out). Surface water temperatures at the time sampling started were approximately 13°C to 14°C in 1996 and 1998, but were only about 8°C in 1997. Smelt were captured on the first day of sampling in 1997 and 1998 and on 11 June in 1996. Sampling was continued for about two weeks all three years.

Smelt fry densities varied both temporally and spatially. Highest densities occurred in 1997 when the mean density for all blocks and sampling times was 5.12 fry/100 m³ (Table 2). The second highest density was in 1996 and the lowest in 1998. Densities were highest in both 1996 and 1997 in blocks IV and V that were located east of Brule Narrows. Smelt fry were 5–14 mm long. The observed densities, with the exception of those from blocks IV and V in 1997, were in a density range from Lake Michigan that was considered low (Tin and Jude 1983). The higher 1997 densities from blocks IV and V were near the lower edge of the range in densities reported from Lake Huron (O’Gorman 1984).

Table 1. Composition (%) of fish species caught in bottom and midwater trawl hauls and smelt nets in the South Arm of Rainy Lake, June–September, 1995–2002.

Species	Bottom trawl			Midwater trawl			Smelt nets						
	1995	1996	1997	1996	1997	1998	1996	1997	1998	1999	2000	2001	2002
Emerald Shiner	–	0.51	–	–	1.58	–	–	10.32	–	0.02	0.11	–	–
Spottail Shiner	0.94	1.56	–	–	–	0.02	0.27	0.25	–	0.02	0.11	–	–
Longnose Sucker	0.05	0.14	–	0.09	–	–	–	–	–	–	–	–	–
White Sucker	0.30	0.20	1.12	–	–	–	–	0.25	–	–	–	–	–
Tadpole Madtom	0.01	–	–	–	–	–	–	–	–	–	–	–	–
Northern Pike	–	0.07	0.14	–	0.06	–	–	–	–	–	0.05	0.06	0.20
Rainbow Smelt	3.75	2.30	1.68	49.48	43.53	18.54	64.58	46.68	36.14	31.82	25.69	8.10	1.40
Cisco	0.59	2.37	9.08	24.37	46.50	74.93	16.08	11.55	52.06	55.46	47.57	71.45	57.55
Lake Whitefish	0.15	0.10	5.03	0.09	0.67	0.73	–	0.25	1.29	–	0.28	1.54	–
Trout-perch	35.07	42.04	28.63	–	0.12	0.03	4.22	2.46	1.88	4.15	5.92	5.20	3.99
Burbot	2.26	3.75	12.43	1.22	0.30	–	0.82	1.23	0.67	0.53	0.28	1.06	3.13
Ninespine Stickleback	4.60	5.44	0.70	22.87	3.53	4.78	–	–	–	–	–	–	–
Slimy Sculpin	5.39	9.81	4.75	0.28	–	0.05	–	–	0.21	0.94	1.05	0.12	0.27
Smallmouth Bass	0.04	–	0.14	–	0.06	–	–	0.25	–	–	–	–	0.06

Table 1 (continued). Composition (%) of fish species caught in bottom and midwater trawl hauls and smelt nets in the South Arm of Rainy Lake, June–September, 1995–2002.

Species	Bottom trawl			Midwater trawl			Smelt nets						
	1995	1996	1997	1996	1997	1998	1996	1997	1998	1999	2000	2001	2002
Black Crappie	0.31	0.44	–	–	–	–	–	–	–	–	–	–	–
Iowa Darter	–	0.03	–	–	–	–	–	–	–	–	–	–	–
Johnny Darter	19.93	21.54	3.21	–	–	–	–	–	–	–	–	–	–
Yellow Perch	23.24	3.92	7.12	0.09	0.12	0.16	10.35	4.91	1.13	0.10	0.39	0.06	–
Logperch	0.09	–	–	–	–	–	–	–	–	–	–	–	–
Sauger	2.28	3.15	8.80	–	–	0.02	2.59	2.70	1.00	3.19	11.24	6.91	16.23
Walleye	1.00	2.64	17.18	1.50	3.53	0.75	1.09	19.16	5.63	3.77	7.42	5.50	17.17
Total catch	7,791	2,957	716	1,067	1,645	6,294	734	407	2,399	3,954	1,806	1,692	1,503
Effort	136	106	84	34	66	75	57	31	70	72	72	54	72
# of species	18	18	14	9	11	10	8	11	9	10	11	10	9

The highest densities of fry in the net tows were members of the Percidae family (Table 2). In 1996, relatively high densities were captured in all the blocks except block VI, which was unexpected since that block includes the channels downstream from Kettle Falls where Walleye are known to spawn. Catches in that block were also very low in 1997, but in 1998 they were the highest of the three blocks where sampling occurred. Cisco were collected in most of the blocks but densities were usually low. Burbot were also collected in most of the blocks, with the highest densities occurring in 1998.

Table 2. Rainy Lake fry sampling 1996–1998 with fry densities converted to number per 100 m³. Others includes Trout-perch, catostomids, and centrarchids.

Year	# of tows	Total Volume (m ³)	Species	Block						Mean
				I	II	III	IV	V	VI	
1996	34	4870.71	Smelt	0.58	0.37	1.15	2.00	3.90	0.56	1.44
			Percids	19.49	125.57	92.58	29.98	64.14	0.00	38.16
			Cisco	0.22	7.07	8.07	1.20	1.81	0.00	1.38
			Burbot	0.62	0.83	3.07	0.00	1.45	1.13	0.92
			Others	0.91	0.00	0.00	0.00	0.10	0.60	0.55
1997	35	9891.51	Smelt	0.34	1.00	–	11.49	15.02	0.00	5.12
			Percids	19.14	3.55	–	0.88	0.63	0.05	6.89
			Cisco	1.12	0.91	–	3.99	0.76	0.59	1.57
			Burbot	1.75	2.37	–	2.50	11.45	7.84	4.67
1998	40	4210.29	Smelt	–	–	–	0.19	0.25	0.00	0.14
			Percids	–	–	–	5.00	5.54	9.22	6.46
			Cisco	–	–	–	0.05	0.13	0.44	0.19
			Burbot	–	–	–	12.29	33.34	9.44	15.34
			Others	–	–	–	0.44	0.39	0.07	0.32

Bottom trawling

Bottom trawling, despite being restricted to relatively smooth bottoms, had the most diverse catches with all 21 fish species collected in the three years of the study. The annual trawl catches varied widely, with the mean CPE (catch per unit of effort) falling from about 57 fish per haul in 1995 to 28/haul in 1996, and even further to 8.5/haul in 1997 (Table 3). Overall, the largest trawl catches occurred in hauls made at depths of less than 10 m (Table 3). This was particularly true in 1995 when there were relatively large catches of Yellow Perch, Johnny Darters, and Trout-perch. Trout-perch, which were also relatively abundant in the 10- to 20-m depth zone, remained the dominant species in 1996 and 1997.

Smelt comprised a relatively small portion of the bottom trawl catches. The proportion of the total catch comprised of smelt decreased from 3.8% in 1995 to 1.7% in 1997. Young of the Year (YOY) smelt were primarily caught at depths of less than 20 m, while the CPEs of adults were highest in the >20 m depth zone (Table 3). Spatially, 60% of the smelt were caught in the blocks east of Brule Narrows in 1995. In 1996 and 1997, 83% and 72% of the smelt were caught in those blocks, respectively.

Table 3. Bottom trawl fish catches (expressed as catch per unit of effort, CPE) from three depth zones in Rainy Lake, 1995–1997.

Fish species	1995			1996			1997		
	<10	10–20	>20	<10	10–20	>20	<10	10–20	>20
Rainbow Smelt 1+	1.40	0.10	0.42	0.00	0.37	1.17	0.10	0.07	0.21
Rainbow Smelt YOY	4.21	1.19	0.12	0.16	0.18	0.20	0.03	0.03	0.04
Walleye	1.02	0.60	0.00	1.00	1.05	0.0	1.17	2.93	0.00
Sauger	0.96	2.48	0.32	0.45	1.92	0.10	0.57	1.47	0.08
Yellow Perch	34.33	2.33	1.28	2.11	0.89	0.07	1.57	0.13	0.00
Johnny Darter	23.79	8.46	0.12	11.89	4.84	0.03	0.53	0.23	0.00
Iowa Darter	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00
Logperch	0.12	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Trout-perch	30.02	26.56	0.40	14.84	17.68	0.23	3.00	3.83	0.00
Slimy Sculpin	0.06	3.00	6.82	0.05	5.13	3.10	0.00	0.30	1.04
Tadpole Madtom	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Ninespine Stickleback	5.52	1.67	0.32	3.55	0.26	0.53	0.00	0.03	0.17
Burbot	0.00	0.15	4.22	0.00	0.13	3.53	0.00	0.00	3.71
Lake Whitefish	0.04	0.17	0.05	0.00	0.05	0.03	0.57	0.20	0.54
Cisco	0.02	0.75	0.22	0.03	1.45	0.47	1.13	0.57	0.58
White Sucker	0.06	0.29	0.02	0.03	0.13	0.00	0.10	0.17	0.00
Longnose Sucker	0.00	0.04	0.02	0.00	0.08	0.03	0.00	0.00	0.00
Black Crappie	0.46	0.04	0.00	0.21	0.13	0.00	0.00	0.00	0.00
Smallmouth Bass	0.06	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.04
Spottail Shiner	1.52	0.00	0.00	1.21	0.00	0.00	0.00	0.00	0.00

Table 3 (continued). Bottom trawl fish catches (expressed as catch per unit of effort, CPE) from three depth zones in Rainy Lake, 1995–1997.

Fish species	1995			1996			1997		
	<10	10–20	>20	<10	10–20	>20	<10	10–20	>20
Emerald Shiner	0.00	0.00	0.00	0.39	0.00	0.00	0.00	0.00	0.00
Northern Pike	0.00	0.00	0.00	0.06	0.00	0.00	0.03	0.00	0.00
Total	102.65	47.85	14.33	35.98	34.30	9.49	8.70	9.96	6.41
Number of hauls	48	48	40	38	38	30	30	30	24

Smelt nets

The number of fish species caught ranged from 8–11 over the seven years of sampling. Smelt was the predominant species caught in the smelt nets in 1996 and 1997, but Cisco became most abundant after that time (see Table 1). Together, these two dominant species typically accounted for 60% to 80% of the annual catch. Walleye, Sauger, Trout-perch, and Burbot were also commonly taken. The portion of the catches accounted for by the two Percid species was variable, ranging from 3.7% in 1996 to 33.4% in 2002.

Because of mesh selectivity, the majority of the smelt, Cisco, Walleye, and Sauger caught in the smelt nets were less than 200 mm long (Figure 1). The smelt ranged in age from 1 to 4 years, with ages 1 and 2 being predominant (Table 4). Young-of-the-year (YOY) smelt were not represented in the catches because they were invulnerable to the gear. Based on back calculated lengths, Walleye ages ranged from 1 to 2 years, with possibly some faster growing YOY appearing in the late summer catches. The majority of the Sauger were 2 or 3 years old, with possibly a few being 4 years old. Cisco were not aged but based on published growth data, most were probably 1 to 2 years old (Scott and Crossman 1973).

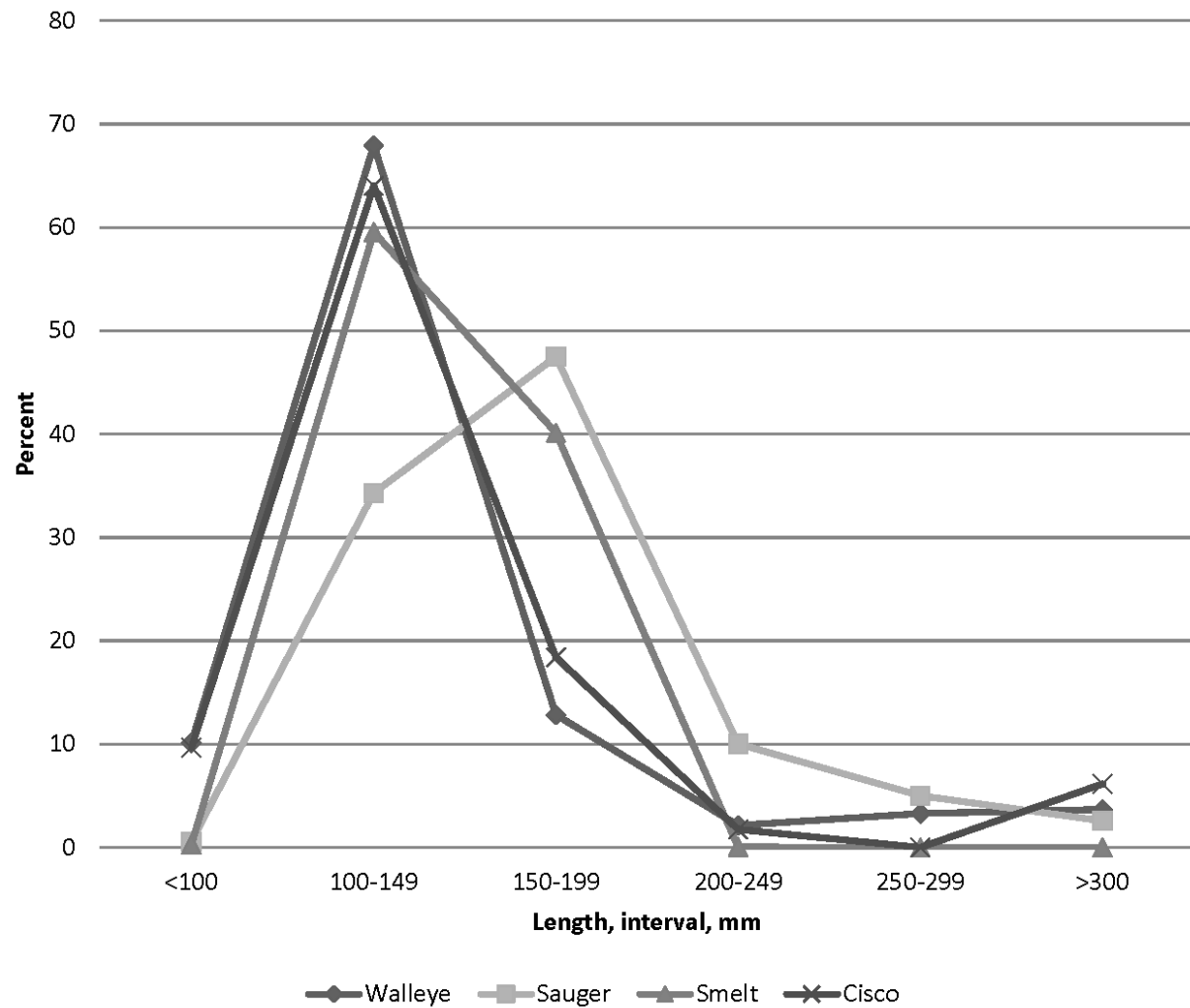


Figure 1. Length frequency distribution of Walleye, Sauger, Rainbow Smelt, and Cisco from smelt net catches used in food habit analyses, Rainy Lake.

Table 4. Catch per unit of effort (CPE) and age distribution of Rainbow Smelt in smelt nets set at depths >10m in Rainy Lake, 1996–2002.

Year	Month	# lifts	Depth (m)		CPE by age (yrs)			
			10–20	>20	1	2	3	4
1996	June	39	2.67	1.33	1.06	1.67	0.42	0
	August	6	14.33	31.67	7.40	14.57	1.03	0
	September	6	90.00	103.33	65.35	29.15	2.17	0
	TOTAL	51	–	–	9.92	6.10	0.47	0
1997	June	6	3.67	0.33	1.14	1.17	0.02	0
	July	5	1.00	21.67	4.03	7.11	0.03	0
	September	5	3.00	31.00	3.27	13.10	0.13	0
	TOTAL	16	–	–	3.30	7.87	0.08	0
1998	June	22	1.00	6.50	0.25	2.57	0.13	0
	July	24	8.00	4.25	2.99	3.01	0.08	0
	August	24	1.67	53.25	5.71	20.84	0.90	0.01
	TOTAL	70	–	–	3.20	8.85	0.34	0.02
1999	June	18	2.33	5.22	0.47	2.86	0.12	0
	July	18	17.00	13.11	6.71	7.99	0.36	0
	August	18	6.11	44.89	11.63	12.73	1.14	0
	September	18	12.67	38.44	9.34	14.49	1.58	0.03
	TOTAL	72	–	–	7.06	9.52	0.87	0.02
2000	June	18	1.78	10.78	0.61	5.33	0.33	0
	July	18	0.67	8.44	0.29	4.15	0.12	0
	August	18	0.89	29.00	4.52	8.75	1.62	0.05
	September	18	0.56	22.22	0.91	6.15	4.27	0.06
	TOTAL	72	–	–	1.59	6.08	1.59	0.03
2001	July	18	4.67	1.22	2.11	0.56	0.28	0
	August	18	1.56	3.44	0.83	1.50	0.17	0
	September	18	1.33	3.00	0.17	1.83	0.17	0
	TOTAL	54	–	–	1.05	1.30	0.19	0
2002	June	18	0.22	0.11	0.00	0.17	0.00	0
	July	18	0.00	0.00	0.00	0.00	0.00	0

Table 4 (continued). Catch per unit of effort (CPE) and age distribution of Rainbow Smelt in smelt nets set at depths >10m in Rainy Lake, 1996–2002.

Year	Month	# lifts	Depth (m)		CPE by age (yrs)			
			10–20	>20	1	2	3	4
2002 (continued)	August	18	0.67	0.44	0.33	0.23	0.00	0
	September	18	0.33	0.56	0.28	0.16	0.00	0
	TOTAL	72	–	–	0.15	0.14	0.00	0

MNDNR smelt catches from 1991 to 1995 were low, with CPEs ranging from 0.5 to 3.9 (Figure 2). The late summer smelt CPEs peaked in both the USGS and MNDNR net sets in 1996, after which they gradually declined so that by 2002, CPE was less than one fish per lift (Figure 2). USGS catches, which were usually lowest in June, typically peaked in late summer (Table 4). Other than in August of 1998, smelt CPEs were consistently higher in Blocks IV and VI, located east of Brule Narrows. MNDNR Cisco catches gradually declined from 1992 to 1995, after which they were variable. The initial USGS Cisco catches in 1996 and 1997 were less than 10 fish per lift, after which they rose to a peak of 40 in 1998 (Figure 2). From 2000 to 2002, they ranged from 16 to 23 per lift.

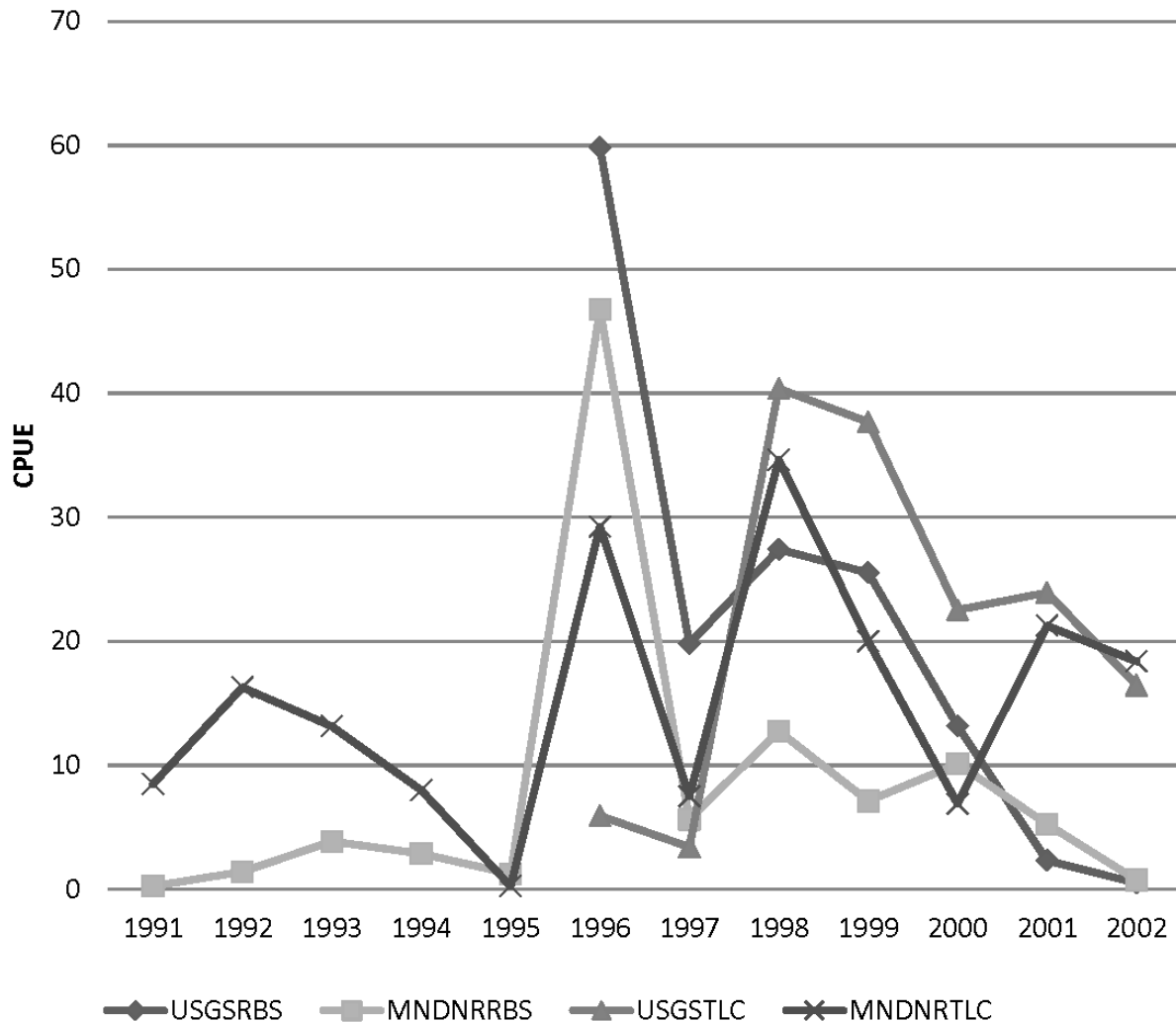


Figure 2. Catch per unit of effort of Rainbow Smelt (RBS) and Cisco (TLC) in USGS and MNDNR smelt net sets in August-September in Rainy Lake, 1991–2002.

Midwater trawling

The number of fish species caught ranged from 9 to 11 in the three years of midwater trawling (Table 5). The overall fish CPEs were 31.4 in 1996, 24.9 in 1997, and 83.9 in 1998. In 1996, smelt comprised 49.5% of the catch, Cisco 24.4%, and nine-spine stickleback 22.9%. In 1997, smelt and Cisco both comprised over 40% of the catch, while in 1998, about 75% of the catch was Cisco and 18% smelt (Table 5).

Midwater trawl catches contained both YOY and older smelt (Figure 3). Modal lengths of YOY increased from 30 mm in late June to 45 mm in late July to about 55 mm in mid-August of 1998. Similar growth of YOY occurred in 1996 and 1997.

Table 5. Midwater trawl fish catches (expressed as catch per unit of effort, CPE) from three depth zones in Rainy Lake, 1996–1998.

Fish species	1996			1997			1998		
	<10	10–20	>20	<10	10–20	>20	<10	10–20	>20
Rainbow Smelt 1+	0.57	21.88	39.00	2.22	10.94	0	1.65	2.00	1.00
Rainbow Smelt YOY	0.21	0.00	0.00	2.59	5.59	0	18.76	8.84	10.00
Walleye	0.29	0.65	0.33	1.69	0.12	0	0.59	0.68	0.00
Sauger	0.00	0.00	0.00	0.00	0.00	0	0.00	0.03	0.00
Yellow Perch	0.00	0.06	0.00	0.06	0.00	0	0.19	0.08	0.00
Trout-perch	0.00	0.00	0.00	0.06	0.00	0	0.00	0.05	0.00
Slimy Sculpin	0.00	0.00	1.00	0.00	0.00	0	0.00	0.08	0.00
Ninespine Stickleback	15.36	1.12	3.33	0.00	1.71	0	7.62	0.51	0.00
Burbot	0.00	0.53	1.33	0.00	0.15	0	0.00	0.00	0.00
Lake Whitefish	0.00	0.00	0.00	0.28	0.06	0	0.92	0.32	0.00
Cisco	0.21	12.59	14.33	17.50	6.03	0	71.27	52.59	133.00
Longnose Sucker	0.00	0.09	0.00	0.00	0.00	0	0.00	0.00	0.00
Smallmouth Bass	0.07	0.00	0.00	0.03	0.00	0	0.00	0.00	0.00
Spottail Shiner	0.00	0.00	0.00	0.00	0.00	0	0.03	0.00	0.00
Northern Pike	0.00	0.00	0.00	0.03	0.00	0	0.00	0.00	0.00
Emerald Shiner	0.00	0.00	0.00	0.81	0.00	0	0.00	0.00	0.00
Number of hauls	14	17	3	32	34	0	37	37	1

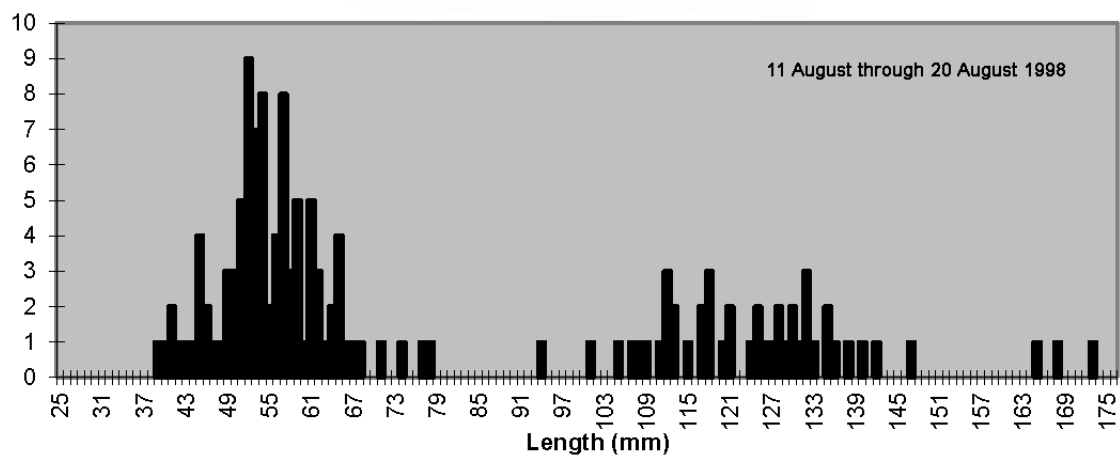
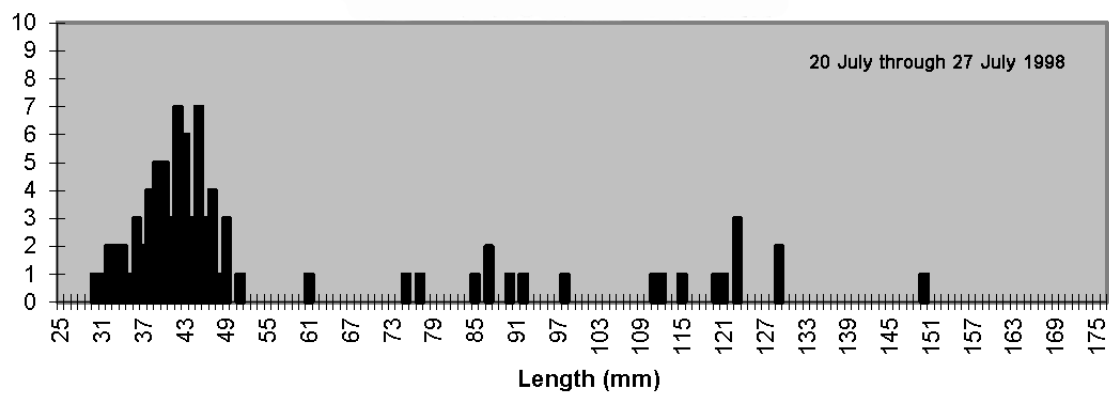
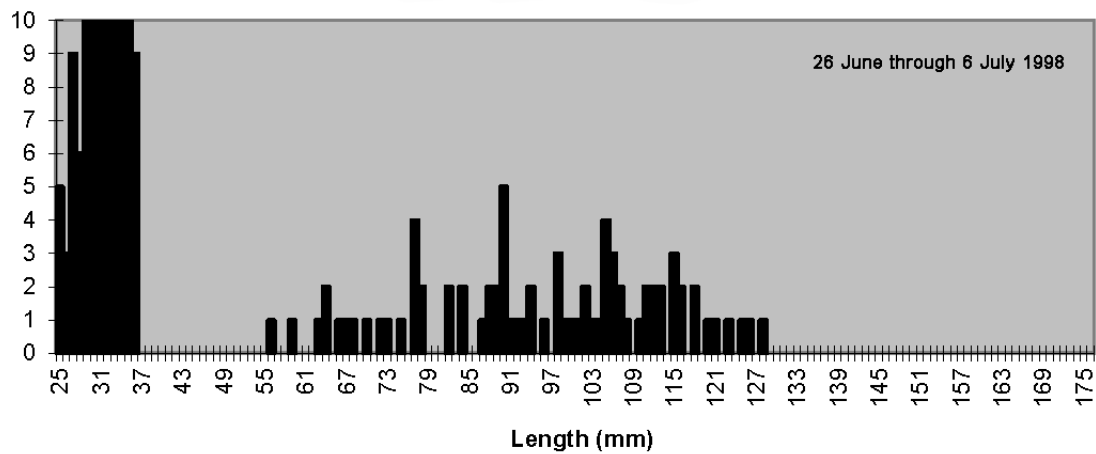


Figure 3. Length frequencies of Rainbow Smelt caught during three midwater trawl hauls in 1998.

Hydroacoustic/midwater trawling

Integrated hydroacoustic/midwater trawling data collection was only successful in 1996. Field sampling was carried out in 1997, but the resulting data were unuseable due either to equipment malfunction or inexperienced operator error. The 1996 results did show that the majority of the smelt were typically located in or immediately below the thermocline, with moderate concentrations down to about 20 meters. This distribution was probably the result of water temperatures in the epilimnion being about 20 degrees, which is two degrees higher than the 18 degrees commonly reported as the upper temperature limit for yearling and older smelt.

As was the case for the smelt nets and bottom trawl catches, while there was considerable variation in the smelt biomass estimates between blocks and transects, they were higher in the blocks east of Brule Narrows (Figure 4). In 1996, when the smelt population was apparently at its peak, the biomass in Rainy Lake was comparable to smelt biomasses in three of the Great Lakes and a Missouri River reservoir, Lake Oahe (Figure 5). The overall mean value for the 28 transects that were sampled in 1996 was 9.5 kg/ha which was within the ranges reported for Lakes Huron and Michigan.

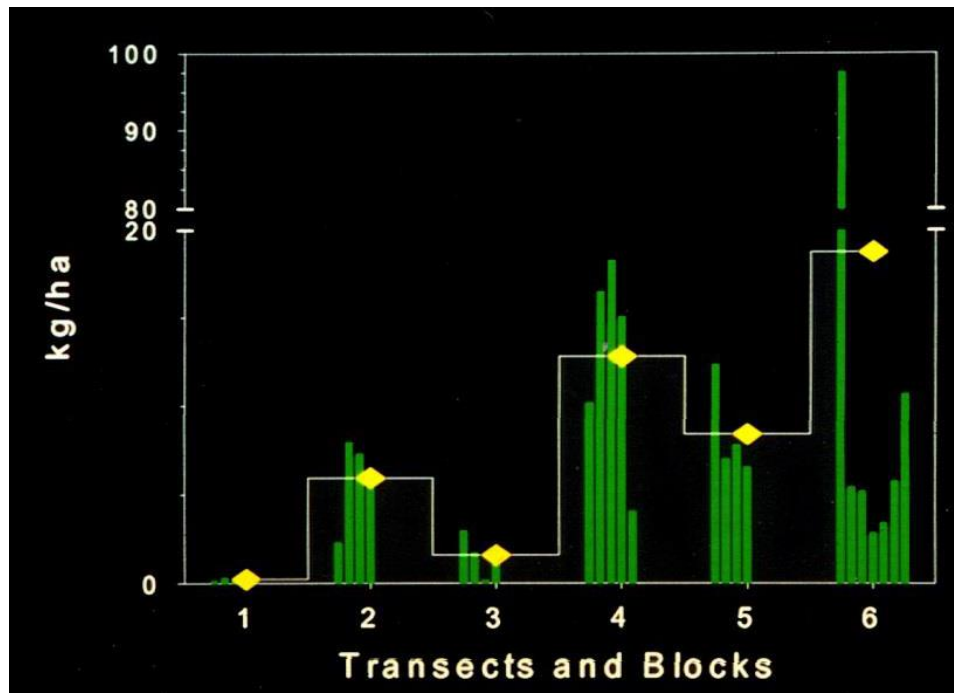


Figure 4. Estimated Rainbow Smelt densities from six sampling blocks in Rainy Lake, 1996.

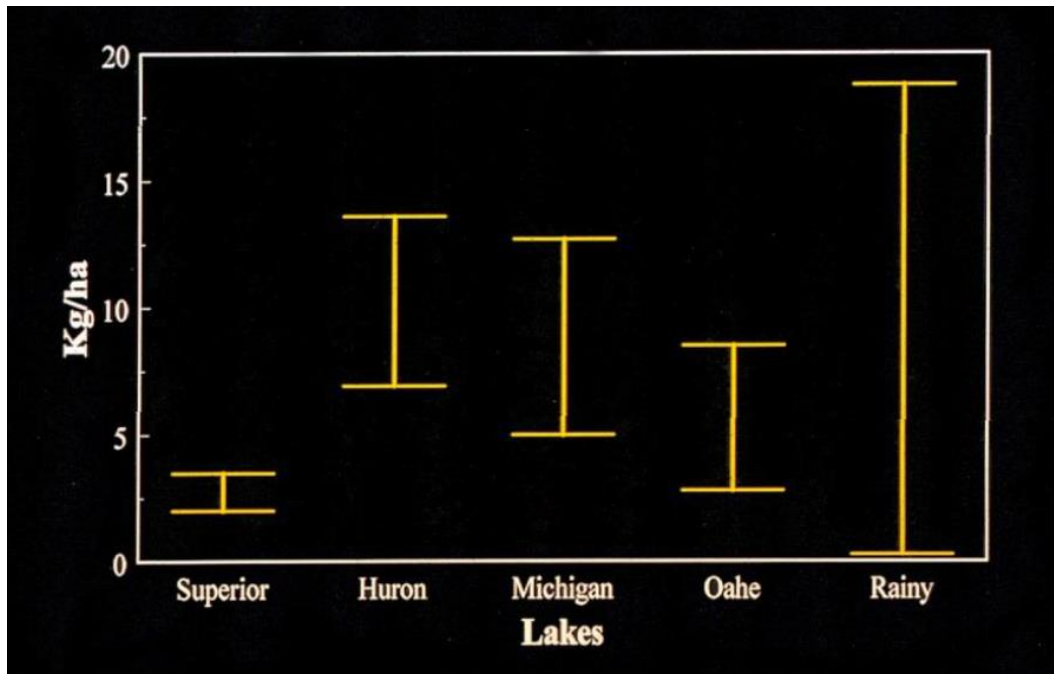


Figure 5. Comparison of Rainbow Smelt biomass for three of the Great Lakes (Superior, Huron, Michigan), Lake Oahe (a reservoir of the Missouri River), and Rainy Lake.

Table 6. Total length (mm) distribution of Rainbow Smelt at time of capture in smelt nets, Rainy Lake, June through September 1996, 2000, 2001, by age group. Weighted mean length calculated using midpoint of length intervals.

Length Interval (mm)	June			July			August				Sept				Months Combined			
	1	2	3	1	2	3	1	2	3	4	1	2	3	4	1	2	3	4
100–109	2	0	0	12	1	0	5	1	0	0	5	0	0	0	24	2	0	0
110–119	29	0	0	36	1	0	43	5	0	0	57	0	0	0	165	6	0	0
120–129	13	7	0	4	4	0	32	2	0	0	31	11	0	0	80	24	0	0
130–139	3	13	0	4	10	0	10	13	0	0	13	23	0	0	30	59	0	0
140–149	2	32	0	0	31	0	3	17	0	0	0	46	0	0	5	126	0	0
150–159	0	30	1	0	41	0	0	43	4	0	0	52	1	0	0	166	6	0
160–169	0	16	5	0	35	3	0	59	5	0	0	137	20	0	0	247	33	0
170–179	0	5	2	0	9	5	0	13	11	0	0	11	35	0	0	38	53	0
180–189	0	0	2	0	2	1	0	6	8	0	0	0	19	0	0	8	28	0
190–199	0	0	1	0	0	1	0	1	3	1	0	0	4	1	0	1	9	2
200–209	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0
Total	49	103	11	56	134	11	93	160	31	1	106	280	79	1	304	677	130	2
Weighted mean length	–	–	–	–	–	–	–	–	–	–	–	–	–	–	119.6	158.0	175.3	195.0

Rainbow Smelt Life History

Rainbow Smelt growth

The length distribution of YOY smelt collected in midwater trawl hauls did not overlap the length distribution of older smelt. In 1998, modal lengths of YOY smelt increased from 29–37 mm in early July to 42–45 mm in late July to 52–57 mm in mid-August (see Figure 3). During those same time periods, total lengths of the smallest yearling or older smelt were 55, 61, and 93 mm, respectively.

The length ranges of age-1 and age-2 smelt overlapped as did the latter with the length range of age-3 fish (see Table 6). Differences between the modal length intervals of age-1 and age-2 smelt ranged from 30 to 50 mm, while differences between the age-2 and age-3 groups were only 10 to 20 mm. The mean total lengths of age-1, -2, and -3 smelt from Rainy Lake—120, 158, and 175 mm, respectively—were generally within 10 mm of total lengths of freshwater smelt in Gull Lake, Michigan (Burbidge 1969) and Lake Sakakawea, North Dakota (Berard 1978). The oldest smelt observed in Rainy Lake was 4 years old.

Rainbow Smelt length-weight relationship

The general length-weight relationship for smelt was established by pooling the data from fish collected in all the sampling equipment. The length-weight equation for 1997 was $\text{Log } W (\text{weight, g}) = -5.7699 + 3.2524 \text{ Log } L (\text{length, mm})$. For 1998, it was $\text{Log } W = -5.8271 + 3.2740 \text{ Log } L (\text{length, mm})$. Weights calculated with these formulas were generally similar to those in some other smelt populations, an exception being in the Miramichi River (New Brunswick, Canada) where smelt were much heavier at comparable lengths (Table 7).

Rainbow Smelt as predators

Young of the year — Midwater trawl collections in August and September of 1996 contained 29 YOY Rainbow Smelt, 24 of which had food items in their stomachs. In 1998, midwater trawls in June through August contained 75 YOY Rainbow Smelt, 73 of which had prey organisms in their stomachs. The diet in both years was dominated by copepods and cladocerans (Table 8). In 1996, the zooplankton that occurred most frequently in the stomachs were the copepods *Limnocalanus macrurus* and *Diaptomus sicilis* and the cladoceran *Daphnia galeata mendotae*. (Table 8). Together, those three organisms comprised 64% of all the organisms in the YOY Rainbow Smelt stomachs. Other organisms found in the stomachs in 1996 were *Mysis relicta*, *Chaoborus* spp., ostracods, and the amphipod *Pontoporeia affinis*. In 1998, copepods occurred in 97% of the stomachs and comprised 71% of all the organisms in the YOY stomachs.

1+ Rainbow Smelt — In August–September of 1996, stomachs of 115 1+-year-old Rainbow Smelt collected by midwater trawling and in smelt nets contained food items (Table 8). The most frequently occurring food items were *Mysis relicta*, the copepod *Limnocalanus macrurus*, and *Chaoborus* spp. Numerically, the predominant organisms in the diet were *Chaoborus* spp., *Daphnia galeata mendotae*, *Limnocalanus macrurus*, and *Mysis relicta*.

Table 7. Comparison of estimated weights (g) of Rainbow Smelt from Rainy Lake (1997, 1998); Gull Lake, Michigan (Burbidge 1969); Parker River, Massachusetts (Murawski and Cole 1978); Miramichi River, New Brunswick, Canada (McKenzie 1958); and Lake Oahe, South Dakota (Burczynski et al. 1987).

Length (mm)	Rainy Lake		Gull Lake	Parker River	Miramichi River	Lake Oahe
	1997	1998				
20	0.03	0.03	0.06	0.02	–	0.04
30	0.11	0.10	0.19	0.09	–	0.15
40	0.28	0.26	0.44	0.22	–	0.35
50	0.57	0.54	0.84	0.47	–	0.69
60	1.03	0.99	1.45	0.87	–	1.21
70	1.70	1.64	2.28	1.47	–	1.94
80	2.63	2.53	3.38	2.30	6.0	2.90
90	3.86	3.72	4.79	3.41	7.6	4.15
100	5.43	5.26	6.54	4.86	10.9	5.71
110	7.41	7.18	8.66	6.70	13.6	7.63
120	9.83	9.55	11.20	8.97	17.3	9.94
130	12.75	12.42	13.97	11.74	22.9	12.67
140	16.22	15.82	17.66	15.06	28.8	15.86
150	20.31	19.83	21.65	18.99	35.5	19.60
160	25.05	24.50	26.20	23.58	43.4	23.78
170	30.51	29.88	31.33	28.91	52.3	28.59
180	36.74	36.03	37.09	35.03	64.2	34.00
190	43.80	43.01	43.52	42.00	75.9	40.06
200	51.76	50.87	50.64	49.90	90.1	46.81

Based on Ivlev's (1961) index of electivity, zooplankton species selected by Rainbow Smelt were the copepods *Epischura lacustris* and *Limnocalanus macrurus*, and the cladocerans *Leptodora kindtii* and *Daphnia galeata mendotae* (Table 9). These zooplankters were relatively large, with lengths generally ranging from 1.5 to 2.5 mm. Lengths of the *Chaoborus* sp. and *Mysis relicta* ranged from 6–10 mm and 2–5 mm, respectively.

Stomachs analyzed from 1996 to 1998 included Rainbow Smelt collected from both midwater trawl hauls and smelt nets. The most frequently occurring organisms in the stomachs from trawl hauls were copepods, cladocerans, *Mysis relicta*, and *Chaoborus* (Table 10). Based on the number of organisms, the zooplankters were predominant (Table 10). *Mysis relicta*, copepods, and, in 1996, *Chaoborus* sp. occurred most frequently in fish from the smelt net catches (Table 10). As was the case in the fish

from the trawl hauls, copepods and cladocerans were numerically predominant except in 1998 when *Mysis relicta* was most abundant. Fish occurred in 8% to 13% of the stomachs during the three years. Although smelt, percids, and coregonids were observed in the smelt stomachs from smelt nets, most of the fish remains in the stomachs were unidentifiable. This is a common occurrence when fish are gill netted, particularly with overnight sets. Other factors that may have caused consumption of Cisco and lake whitefish to be underestimated were: (1) ice late into the spring precluded sampling when larvae and fry of the fall spawning Cisco and lake whitefish were likely most abundant, and (2) rapid digestion of their embryos and larvae (1–2 hours) (Crowder 1980).

Table 8. Stomach contents of young of the year and age 1+ Rainbow Smelt (RBSYOY, RBS1+) and Cisco from Rainy Lake (1996), as percent frequency of occurrence (FOO) and percent of total number of organisms (#).

Food Items		RBSYOY		RBS1+		Cisco	
Group	Taxa	FOO	#	FOO	#	FOO	#
Aquatic Insects	Hemiptera	0	0	0.87	0.02	0	0
	Ephemeroptera	0	0	8.70	1.13	5.88	0.26
	Trichoptera	0	0	0.87	0.02	0	0
	<i>Chaoborus</i> sp.	8.33	1.30	45.22	26.82	37.25	1.92
	Chironomidae	0	0	5.22	0.14	21.57	0.39
	Other Diptera	0	0	7.83	0.48	0	0
Zooplankton	Copepoda – Immature Calanoida	25.00	3.90	14.78	1.04	0	0
	Copepoda – Adult Calanoida – <i>Diaptomus sicilis</i>	54.17	12.12	6.96	0.43	10.78	0.82
	Copepoda – Adult Calanoida – <i>Diaptomus minutus</i>	0	0	3.48	0.10	1.96	0.03
	Copepoda – Adult Calanoida – <i>Diaptomus oreonensis</i>	8.33	0.87	5.22	0.22	1.96	0.03
	Copepoda – Adult Calanoida – <i>Limnocalanus macrurus</i>	62.50	34.63	42.61	12.58	17.65	4.93
	Copepoda – Adult Calanoida – <i>Epischura lacustris</i>	12.50	3.46	13.91	16.07	5.88	1.12
	Copepoda – Immature Cyclopoida	12.50	5.19	8.70	2.09	0	0
	Copepoda – Adult Cyclopoida – <i>Cyclops bicuspidatus thomasi</i>	12.50	10.82	5.22	1.01	17.65	2.56
	Copepoda – Adult Cyclopoida – <i>Cyclops vernalis</i>	0	0	0.87	0.02	0	0
	Copepoda – Adult Cyclopoida – <i>Meoscyclops americanus</i>	0	0	0.87	0.02	0	0
	Copepoda – Adult Cyclopoida – <i>Mesocyclops edax</i>	0	0	2.61	0.07	13.73	0.56
	Copepoda – Adult Cyclopoida – <i>Mesocyclops albidus</i>	0	0	0	0	2.94	0.07
	Copepoda – Adult Cyclopoida – <i>Tropocyclops prasinus mexicanus</i>	0	0	2.61	0.17	0	0

Table 8 (continued). Stomach contents of young of the year and age 1+ Rainbow Smelt (RBSYOY, RBS1+) and Cisco from Rainy Lake (1996), as percent frequency of occurrence (FOO) and percent of total number of organisms (#).

Food Items		RBSYOY		RBS1+		Cisco	
Group	Taxa	FOO	#	FOO	#	FOO	#
Zooplankton (continued)	Cladocera – <i>Daphnia</i> spp.	16.67	2.60	20.87	7.89	61.76	50.97
	Cladocera – <i>Daphnia retrocurva</i>	0	0	4.35	0.22	6.86	0.05
	Cladocera – <i>Daphnia galeata mendotae</i>	29.17	17.32	23.48	17.08	62.75	9.86
	Cladocera – <i>Bosmina longirostris</i>	4.17	0.43	6.96	0.96	14.71	0.72
	Cladocera – <i>Eubosmia coregoni</i>	0	0	0	0	1.96	0.02
	Cladocera – <i>Leptodora kindtii</i>	0	0	5.22	0.26	18.63	0.96
	Cladocera – <i>Diaphanosoma leuchtbergianum</i>	8.33	3.03	2.61	0.07	0	0
	Cladocera – <i>Holopedium gibberum</i>	4.17	1.30	5.22	0.26	16.67	16.19
	Other Cladocerans	0	0	7.83	0.24	4.90	0.06
Other organisms	<i>Mysis relicta</i>	8.33	0.87	71.30	9.60	16.67	1.04
	Amphipoda	8.33	0.87	11.30	0.41	9.80	0.95
	Ostracoda	4.17	0.87	0	0	1.96	0.06
	Pelecypoda	0	0	0	0	9.80	0.30
	Fish	0	0	5.22	0.55	0	0
	Hydracarina	0	0	0	0	8.82	0.13
	Hirudinea	0	0	0	0	0.98	0.10
Sample Size	–	24	231	115	4,157	102	34,202

Table 9. Composition of adult crustacean zooplankton (ZP) in Rainy Lake compared to the proportion (%) found in Rainbow Smelt and Cisco stomachs, June–October 1996. Ivlev Electivity Index, the degree to which zooplankton species were selected by smelt and Cisco, is also shown (see calculation on page 7).

Zooplankton Category	Scientific Name	ZP	Smelt		Cisco	
		%	%	Ivlev	%	Ivlev
Copepoda – Adult Calanoida	<i>Diaptomus sicilis</i>	3.31	0.87	-0.58	2.16	-.21
	<i>Diaptomus ashlandi</i>	0.04	0	0	0	0
	<i>Diaptomus minutus</i>	3.06	0.19	-0.88	0.08	-.95
	<i>Diaptomus oreonensis</i>	4.77	0.44	-0.83	0.07	-.97
	<i>Limnocalanus macrurus</i>	3.56	25.39	+0.75	13.00	+0.57
	<i>Epischura lacustris</i>	0.04	32.43	+1.00	2.95	+0.97
Copepoda – Adult Cyclopoida	<i>Cyclops bicuspidatus thomasi</i>	2.30	2.04	-0.06	6.74	+0.49
	<i>Cyclops vernalis</i>	0	0.05	0	0	0
	<i>Meoscyclops americanus</i>	0	0.05	0	0.19	0
	<i>Mesocyclops edax</i>	3.00	0.15	-0.90	1.47	-0.34
	<i>Mesocyclops albidus</i>	0	0	0	0	0
	<i>Tropocyclops prasinus mexicanus</i>	2.81	0.34	-0.78	0	0
Cladocera	<i>Daphnia retrocurva</i>	5.08	0.44	-0.84	0.12	-0.95
	<i>Daphnia galeata mendotae</i>	13.13	34.47	+0.45	26.01	+0.33
	<i>Daphnia longiremis</i>	0.17	0	0	0	0
	<i>Bosmina longirostris</i>	23.41	1.94	-0.85	1.90	-0.85
	<i>Eubosmia coregoni</i>	0	0	0	0.06	0
	<i>Leptodora kindtii</i>	0.03	0.53	+0.89	2.52	+0.98
	<i>Polyphemus pediculus</i>	0.43	0	0	0	0
	<i>Diaphanosoma leuchtbergianum</i>	26.79	0.15	-0.99	0	0
	<i>Holopedium gibberum</i>	3.74	0.53	-0.75	42.73	+0.84
	<i>Chydorus spaaericus</i>	3.70	0	0	0.09	-0.95
	<i>Ceriodaphnia lacustris</i>	0.63	0	0	0	0
Sample size	–	13,934	2,060	–	12,976	–

Table 10. Comparison of stomach contents of Age-1+ Rainbow Smelt collected in midwater trawl hauls (MWT) and smelt nets (SN) from Rainy Lake, 1996–1998, as percent frequency of occurrence (FOO) and percent of total number of organisms (#).

Organism	1996 MWT		1996 SN		1997 MWT		1997 SN		1998 MWT		1998 SN	
	FOO	#	FOO	#	FOO	#	FOO	#	FOO	#	FOO	#
Cladocera	45.95	68.79	26.92	11.14	37.86	12.46	1.40	1.20	61.50	51.50	4.60	30.70
Copepoda	56.76	17.09	53.85	40.42	87.38	84.25	39.40	83.20	69.20	45.80	4.60	11.80
Amphipoda	10.81	0.35	6.41	0.23	2.91	0.06	7.00	3.10	0	0	5.70	2.10
<i>Mysis relicta</i>	83.78	10.90	58.97	8.69	48.54	0.48	50.70	8.30	29.20	1.40	90.00	51.10
<i>Chaoborus</i> sp.	24.32	2.79	52.56	36.25	16.50	2.71	8.50	2.70	35.40	1.30	5.70	3.30
Chiromidae	0	0	1.28	0.03	1.94	0.02	2.80	0.10	0	0	0	0
Other Diptera	0	0	16.67	0.84	0	0	0	0	0	0	0	0
Ephemeroptera	0	0	14.10	1.58	0.97	0.01	2.80	0.10	0	0	0	0
Trichoptera	0	0	1.28	0.03	0	0	0	0	0	0	0	0
Hemiptera	2.70	0.09	0	0	0	0	0	0	0	0	0	0
Unidentified invertebrates	0	0	0	0	0	0	1.40	0.001	1.50	0.01	1.10	0.10
Percidae	0	0	1.28	0.03	0	0	0	0	3.10	0.02	0	0
Rainbow Smelt	0	0	5.13	0.37	0	0	0	0	0	0	0	0
Coregonidae	0	0	0	0	0	0	1.40	0.40	0	0	0	0
Unidentified Fish	0	0	6.41	0.37	0.97	0.01	8.50	0.80	0	0	7.40	1.00
Sample size	37	1,147	78	2,979	103	11,658	71	1,689	65	9,370	349	5,234

From 1999 through 2002, all smelt collected for stomach analysis came from overnight smelt net sets. During this period, *Mysis relicta* was the dominant organism in the smelt stomachs based on frequency of occurrence, the number of organisms, and weight of organisms in all four years (Table 11). Fish remains were identified infrequently.

Table 11. Food habits of yearling and older Rainbow Smelt (*Osmerus mordax*) collected in smelt nets from Rainy Lake, June through September, 1999–2002. Percent frequency of occurrence (FOO) is based on number of stomachs with food. Percent number (#) and weight is based on the total number and weight (grams) of organisms in the sample. “tr” = trace amount.

Food Items	1999			2000			2001			2002		
	FOO	#	weight	FOO	#	weight	FOO	#	weight	FOO	#	weight
Cladocera	1.90	5.82	0.18	0	0	0	1.40	0.13	0.01	14.3	65.01	25.00
Copepods	0.80	3.27	0.15	0	0	0	0	0	0	21.4	1.42	tr
Amphipods	15.40	6.25	3.73	0.40	0.12	0.03	0	0	0	0	0	0
<i>Mysis relicta</i>	80.30	64.42	84.43	98.70	98.46	98.19	83.30	76.94	61.79	85.70	32.62	75.00
<i>Chaoborus</i>	25.10	18.88	5.67	0	0	0	1.40	0.13	tr	0	0	0
Diptera	1.00	0.30	tr	0	0	0	15.30	21.89	3.78	7.10	0.95	tr
Ephemeroptera	1.20	0.21	0.62	0	0	0	0	0	0	0	0	0
Other Invertebrates	0.40	0.05	tr	0.20	0.03	0.04	1.40	0.26	0.04	0	0	0
Fish – Percids	0	0	0	0.20	0.09	0.18	1.40	0.13	29.56	0	0	0
Fish – Coregonids	0.20	0.12	2.01	0	0	0	0	0	0	0	0	0
Fish – Burbot	0.60	0.05	1.05	0.20	0.01	0.04	0	0	0	0	0	0
Fish – Unidentified	1.90	0.63	2.14	2.40	0.28	1.52	4.20	0.52	4.82	0	0	0
Sample size	482	5,806	5.13	543	7,662	8.31	72	772	0.83	14	423	0.08

Rainbow Smelt as prey

While the overnight sets of smelt nets and experimental gillnets caused large portions of the fish remains in stomachs to be unidentifiable, smelt were identified in Walleye, Northern Pike, Sauger, and Burbot stomachs. Predation on smelt by these species has also been commonly observed in other lakes and reservoirs (Evans and Loftus 1987). From 1996 through 2002, 638 of 1,121 stomachs from Walleye and Sauger caught in smelt nets contained food items. However, smelt were only positively identified in five of these fish, the majority of which, as previously indicated, were less than 200 mm long.

The majority of the predators captured in the experimental gillnets, due to the mesh selectivity, were larger fish. Stomachs of Walleye and Northern Pike captured in experimental gillnets in 1996 and 1997 showed that the two piscivores were preying on smelt. Smelt was the predominant identifiable fish species in the Walleye stomachs based both on the frequency of occurrence and the number of prey items (Table 12). While smelt was the most numerous food item in Northern Pike stomachs in 1996, Cisco occurred more frequently in both 1996 and in 1997 and was the most abundant in 1997 (Table 12). Although fish remains were commonly observed in Sauger stomachs, the proportion that could be identified as smelt was not as large as that observed for Walleye (Table 12). Mysis relicta was the dominant organism in the Sauger stomachs. One smelt was identified in one of the 117 Burbot stomachs examined in 1996.

In 2002, stomachs from 119 Walleye and 52 Northern Pike caught by the MNDNR in their annual fall gill netting survey were examined. While unidentified fish remains were present in 42% of the Walleye stomachs and in 33% of the Northern Pike stomachs, no smelt were identified.

Rainbow Smelt diet overlap with other fish species

Stomach analyses were conducted for Cisco, Walleye, Sauger, and several smaller fish species to assess the possible extent of diet overlap with smelt.

Cisco food habits — Cisco used for stomach analyses were collected in smelt nets (n=53), experimental gillnets (n=31), and a midwater trawl (n=18) in 1996. The 102 Cisco containing food ranged in total length from 94 to 375 mm, 70 of which were less than 200 mm long. All but four of the Cisco longer than 200 mm were caught in experimental gill nets.

Cladocerans were the most frequently observed and most numerous food items in the Cisco stomachs (see Table 8). In total, cladocerans comprised over 78% of all the food items in the Cisco stomachs. *Daphnia* that could not be identified to species comprised over 50% while the six cladoceran species that were identified comprised another 27.8%. While *Daphnia galeata mendotae* occurred most frequently, *Holopedium gibberum* was numerically most abundant.

Table 12. Prey of Walleye, Sauger, and Northern Pike as percent frequency of occurrence (FOO based on stomachs with food) and percent of the number of prey items (#) from fish captured in experimental gillnets in the South Arm of Rainy Lake, June–September, 1996–1997.

Stomach contents	<i>Walleye 1996</i>		<i>Walleye 1997</i>		<i>Sauger 1996</i>		<i>Sauger 1997</i>		Northern Pike 1996		Northern Pike 1997	
	FOO	#	FOO	#	FOO	#	FOO	#	FOO	#	FOO	#
Fish – Rainbow Smelt	17.2	15.9	10.9	16.9	5.8	5.8	9.2	3.3	17.1	26.2	4.3	3.3
Fish – Ninespine Stickleback	2.6	2.2	1.7	1.7	6.7	2.3	6.9	2.2	0	0	8.7	6.7
Fish – Yellow Perch	2.6	1.9	0.8	0.6	3.8	2.0	0	0	7.3	10.0	0	0
Fish – Cisco	0.7	0.3	4.2	2.8	0	0	0	0	22.0	16.2	26.1	20.0
Fish – Spottail Shiner	0.7	0.3	0	0	0	0	0	0	0	0	0	0
Fish – Sauger	0	0	0	0	0	0	0	0	7.3	3.8	0	0
Fish – Burbot	0	0	0	0	0	0	1.1	0.4	7.3	3.8	4.3	3.3
Fish – Troutperch	0	0	0	0	0	0	0	0	2.4	3.8	0	0
Fish – Johnny Darter	0	0	0.8	2.8	0	0	1.1	0.4	0	0	0	0
Fish – White Sucker	0	0	0.8	0.6	0	0	0	0	0	0	0	0
Fish – Sculpin	0	0	0.8	1.1	1.0	0.4	1.1	0.4	0	0	0	0
Fish – Walleye	0	0	0	0	0	0	0	0	0	0	8.7	10.0
Fish – Emerald Shiner	0	0	0	0	1.0	0.4	0	0	0	0	4.3	3.3
Fish – Smallmouth Bass	0	0	0	0	0	0	0	0	0	0	4.3	3.3
Fish – Unidentified fish	69.5	45.7	57.1	42.9	56.7	23.4	47.1	18.0	29.3	18.8	39.1	40.0

Table 12 (continued). Prey of Walleye, Sauger, and Northern Pike as percent frequency of occurrence (FOO based on stomachs with food) and percent of the number of prey items (#) from fish captured in experimental gillnets in the South Arm of Rainy Lake, June–September, 1996–1997.

Stomach contents	Walleye 1996		Walleye 1997		Sauger 1996		Sauger 1997		Northern Pike 1996		Northern Pike 1997	
	FOO	#	FOO	#	FOO	#	FOO	#	FOO	#	FOO	#
Invertebrates – Ephemeroptera	5.3	3.2	21.8	24.9	6.7	7.8	9.2	4.8	2.4	1.2	4.3	3.3
Invertebrates – Chironomidae	0.7	0.3	0.8	1.7	0	0	1.1	0.4	0	0	0	3.3
Invertebrates – <i>Mysis relicta</i>	6.0	26.3	0.8	0.6	13.5	53.3	21.8	66.5	0	0	0	0
Invertebrates – Crayfish	1.3	1.0	2.5	2.3	1.9	0.8	0	0	7.3	13.8	4.3	0
Invertebrates – Amphipods	1.3	1.0	0.8	1.1	1.0	0.4	1.1	0.4	0	0	0	0
Invertebrates – Copepods	0.7	0.3	0	0	1.9	3.1	0	0	0	0	0	0
Invertebrates – Miscellaneous	3.3	1.6	0	0	0	0	9.2	3.3	0	0	0	0
Unidentified	3.3	1.6	0	0	6.7	0.3	0	0	0	0	0	0
Stomachs examined	250	0	246	0	261	0	258	0	82	0	258	0
Stomachs with food	151	0	119	0	104	0	87	0	41	0	87	0

Based on Ivlev's (1961) index of electivity, zooplankton species selected by Cisco were the copepods *Epischura lacustris* and *Limnocalanus macrurus* and the cladocerans *Leptodora kindtii* and *Daphnia galeata mendotae* (see Table 9). These relatively large zooplankters were the same species selected by the smelt. *Holopedium gibberum*, another large cladoceran, was also selected by Cisco.

In addition to actively selecting several of the same zooplankton species, 19 separate food items occurred in both the Cisco and smelt stomachs (Table 8). Despite this, the Schoener Index value based on the numbers or organisms was only 0.34, suggesting low diet overlap between the two species.

Walleye and Sauger food habits — Food of Walleye and Sauger caught in overnight smelt net sets in 1998, 2000, and 2001 included crustaceans, insects, *Mysis relicta* and other invertebrates, and fish (Table 13). Most food items were <200 mm long. In 1998, fish were observed in approximately half of the Walleye stomachs containing food. However, in the majority of the cases the remains could not be identified to species. Other organisms that occurred in more than 10% of the Walleye stomachs in 1998 were *Mysis relicta*, amphipods, and cladocera. In 2000 and 2001, *Mysis relicta* occurred in over 70% of the Walleye stomachs, while copepods occurred in over 10%. The predominant organisms in the Walleye stomachs based on the number of food items were the copepods, cladocerans, and *Mysis relicta*.

Fish were present in over 40% of the Sauger stomachs in 1998 and 2001, but as was the case for the Walleye, most could not be identified to species (Table 13). *Mysis relicta* was the most frequently occurring and most abundant invertebrate in the Sauger stomachs except in 1998 when copepods were more abundant.

Smelt, Walleye, and Sauger captured in the smelt nets utilized many of the same food items. Schoener Index values comparing Walleye and Sauger diets to the smelt diet based on frequency of occurrence exceeded 0.6 in both 2000 and 2001 (Table 13). The index value was also >0.6 based on the number of organisms in smelt and Sauger stomachs in all three years. These values indicated significant overlap and suggest that competition may possibly occur if resources became limiting.

Yellow Perch, Johnny Darter, Trout-perch, Slimy Sculpin, and Burbot food habits — Stomach analyses for these five native species showed that they utilized many of the same food items as smelt (Table 14). Cladocerans and copepods were most abundant in the two percid species as was the case for the smelt. The most abundant organisms for the other three species were amphipods, which comprised a very small portion of the smelt diet. Schoener Index values comparing the diets of these species to the smelt diet ranged from 0.10 to 0.54 indicating little diet overlap.

Rainbow Smelt effect on growth and condition of Walleye and Northern Pike — Walleye and other piscivores switching to a smelt diet have commonly been found to exhibit increased growth (McCaig, and Mullan 1960, Jones et al. 1994). However, that did not appear to be the case in Rainy Lake based on back-calculated lengths of Walleye from the pre- and post-smelt invasion periods. Mean back calculated lengths of age-1 to age-6 male and female Walleye were generally less in the years

following the smelt invasion of Rainy Lake (Table 15). The differences in length, however, were not significantly different.

The bioenergetics model using caloric and temperature data from Rainy Lake as well as studies elsewhere suggest that condition of Walleye would increase if they switched to a smelt diet. Caloric densities of smelt were greater than those of Yellow Perch, Cisco, Spottail Shiner, and other fish

Table 13. Prey of Rainbow Smelt (RBS), Walleye (WAE), and Sauger (SAR) as percent frequency of occurrence (FOO based on stomachs with food) and percent of the number of prey items (#) from fish captured in smelt nets in the South Arm of Rainy Lake, June–September, 1998, 2000–2001.

	1998 RBS		1998 WAE		1998 SAR		2000 RBS		2000 WAE		2000 SAR		2001 RBS		2001 WAE		2001 SAR	
Food Items	FOO	#	FOO	#	FOO	#	FOO	#	FOO	#	FOO	#	FOO	#	FOO	#	FOO	#
Cladocera	4.6	30.7	13.3	55.6	18.2	69.0	0.0	0.0	2.3	11.0	0.0	0.0	1.4	0.1	0.0	0.0	0.0	0.0
Copepods	4.6	11.8	9.2	3.7	0.0	0.0	0.0	0.0	11.4	20.9	1.0	0.1	0.0	0.0	14.6	61.0	0.0	0.0
Amphipods	5.7	2.1	19.4	23.3	0.0	0.0	0.4	0.1	5.7	0.5	0.4	0.0	0.0	0.0	1.8	0.1	0.0	0.0
<i>Mysis relicta</i>	90.0	51.1	28.6	13.7	45.5	28.9	98.7	99.5	71.6	47.0	19.4	95.1	83.3	76.9	76.4	38.2	67.7	89.7
<i>Chaoborus</i>	5.7	3.3	9.2	1.1	0.0	0.0	0.0	0.0	15.9	18.7	5.8	2.4	1.4	0.1	0.0	0.0	1.6	0.9
Diptera	0.0	0.0	1.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	15.3	21.9	1.8	0.1	1.6	0.2
Ephemeroptera	0.0	0.0	6.1	0.3	0.0	0.0	0.0	0.0	3.4	0.3	1.4	0.1	0.0	0.0	0.0	0.0	0.0	0.0
Other invertebrates	1.1	0.1	0.0	0.0	0.0	0.0	0.2	0.1	2.3	0.2	1.2	0.1	1.4	0.3	3.6	0.1	3.2	0.3
Fish	7.4	1.0	48.0	2.2	54.6	2.1	2.8	0.4	14.8	1.4	11.6	2.2	5.6	0.6	12.7	0.1	41.9	8.9
Stomachs with food	349	–	98	–	11	–	543	–	83	–	208	–	72	–	55	–	62	–
# food items	–	5,234	–	3,070	–	519	–	7,662	–	1,317	–	2,440	–	772	–	1,650	–	582
RBS with WAE*	0.30	0.52	–	–	–	–	0.60	0.48	–	–	–	–	0.76	0.39	–	–	–	–
RBS with SAR*	0.39	0.61	–	–	–	–	0.79	0.96	–	–	–	–	0.65	0.78	–	–	–	–
WAE with SAR*	0.63	0.71	–	–	–	–	0.78	0.51	–	–	–	–	0.72	0.25	–	–	–	–

* Diet overlap was examined using Schoener's Index (see equation on page 16).

Table 14. Comparison of the food habits of Rainbow Smelt with those of five native fish species based on the proportion of the number of food items (#) observed in the stomachs, Rainy Lake 1996. Smelt food habit data from analysis conducted by L. Last. Diet overlap between Rainbow Smelt and each native fish species was examined using Schoener's Index (see equation on page 16).

Food items	Rainbow Smelt	Yellow Perch	Trout-perch	Johnny Darter	Slimy Sculpin	Burbot
Cladocerans	0.2692	0.9384	0.1244	0.4709	0.0610	0
Copepods	0.3389	0.0341	0.0582	0.2097	0.0037	0
Amphipods	0.0041	0.0024	0.4442	0.0636	0.7449	0.7171
<i>Mysis relicta</i>	0.0960	0.0125	0.0013	0.0014	0.0370	0.0630
<i>Chaoborus</i> sp.	0.2682	0.0002	0.0148	0.0447	0.0074	0
Chironomids	0.0014	0.0008	0.2085	0.1502	0.1072	0.0746
Other insects	0.0166	0.0072	0.0202	0.0108	0.0240	0.1260
Ostracods	0	0	0.1298	0.0392	0.0148	0.0010
Misc. Invertebrates	0	0.0028	0	0.0068	0	0.0126
Percidae	0	0.0001	0	0	0	0
Ninespine stickleback	0	0.0001	0	0	0	0.0019
Other fish	0.0055	0	0	0.0027	0	0.0039
Stomachs with food	115	85	259	112	145	25
Number of food items	4,157	8,702	2,974	739	541	1,032
Schoener's index	–	0.33	0.22	0.54	0.13	0.10

Table 15. Analysis of variance comparison of mean lengths of Northern Pike and Walleye in Rainy Lake pre- and post-invasion by Rainbow Smelt. Standard error is shown in parentheses.

Species	Sex	Age	df	Pre-mean Length, mm	Post-mean Length, mm	F	P
Northern Pike	M	1	1,20	222.98 (8.50)	233.34 (8.50)	0.7428	0.399
	M	2	1,18	377.61 (9.13)	406.83 (9.13)	5.1164	0.036
	M	3	1,16	469.51 (10.74)	489.13 (10.74)	1.6673	0.215
	M	4	1,14	527.66 (11.37)	530.89 (11.37)	0.0403	0.844
	F	1	1,20	233.36 (8.58)	246.20 (7.83)	1.2217	0.282
	F	2	1,18	393.50 (12.61)	421.54 (11.41)	2.7194	0.116
	F	3	1,16	490.55 (16.25)	519.88 (14.53)	1.8105	0.197
	F	4	1,14	551.36 (21.88)	597.21 (19.29)	2.4700	0.138
Walleye	M	1	1,22	102.65 (3.15)	103.72 (3.15)	0.0575	0.813
	M	2	1,20	183.25 (5.79)	174.67 (5.79)	1.0970	0.307
	M	3	1,18	258.52 (7.03)	245.53 (7.03)	1.7064	0.208
	M	4	1,16	323.89 (9.18)	311.68 (9.18)	0.8843	0.361
	M	5	1,14	383.12 (10.38)	368.95 (10.38)	0.9316	0.351
	M	6	1,12	431.89 (14.08)	426.68 (14.08)	0.0685	0.798
	F	1	1,22	102.74 (3.03)	101.91 (3.03)	0.0349	0.854
	F	2	1,20	183.80 (5.57)	172.76 (5.57)	1.9613	0.177
	F	3	1,18	259.39 (6.76)	242.14 (6.76)	3.2584	0.088
	F	4	1,16	324.56 (9.62)	308.29 (9.62)	1.4298	0.249
	F	5	1,14	374.55 (11.18)	368.95 (11.18)	0.1254	0.729
	F	6	1,12	403.41 (9.37)	388.16 (9.37)	1.3261	0.272

species preyed upon by Walleye (Table 16). Modeling results showed that the weight of age-6 Walleye at the end of a warm growing season would be greater with an all smelt diet than that projected for the baseline in which smelt comprised 17% of the Walleye diet (Figure 6). Even if the smelt portion of the Walleye diet was maintained at 17%, cooler water temperatures would result in larger increases in the estimated weight of the Walleye. Replacing the smelt with Cisco and Yellow Perch reduced the Walleye's estimated weight below that obtained under the baseline conditions.

Table 16. Caloric densities (kilocalories/gram) of Walleye, Rainbow Smelt, and common prey fishes captured in Rainy Lake, 1997. Densities for Walleye are means calculated from analysis of individual fish, while densities for other species are from composite samples. Number (#) of fish used to calculate the mean or in the composite sample is also shown.

Species, age	June		July		August		September	
	#	Kcal/gm	#	Kcal/gm	#	Kcal/gm	#	Kcal/gm
Walleye, 1+	10	4998	10	4971	—	—	10	4637
Rainbow Smelt, 1+	5	4861	5	5347	5	5498	5	5330
Cisco, 1+	—	—	5	4461	5	5043	7	4853
Yellow Perch, YOY	10	4516	10	4571	20	4469	20	4390
Yellow Perch, 1+	5	4423	5	4382	10	4224	5	4173
Spottail Shiner, YOY	23	4533	14	4633	13	4522	20	5041
Spottail Shiner, 1+	—	—	10	4499	10	4733	6	5059
White Sucker, YOY	—	—	8	4362	9	4416	1	4244
Black Crappie, YOY	—	—	5	4387	5	4386	20	4635

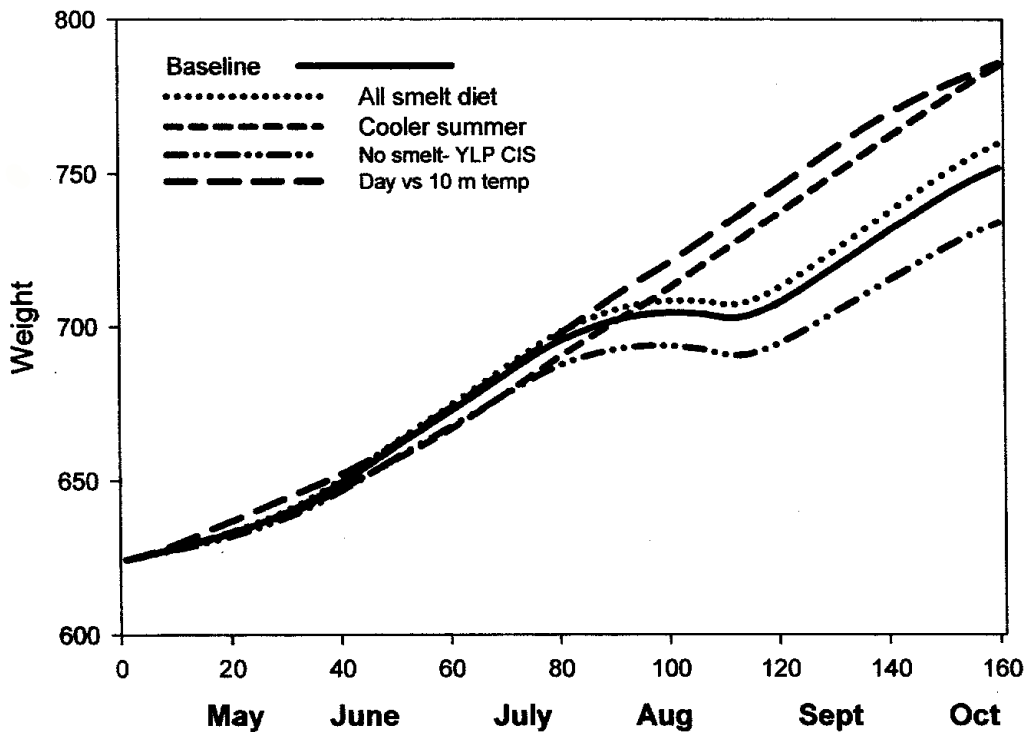


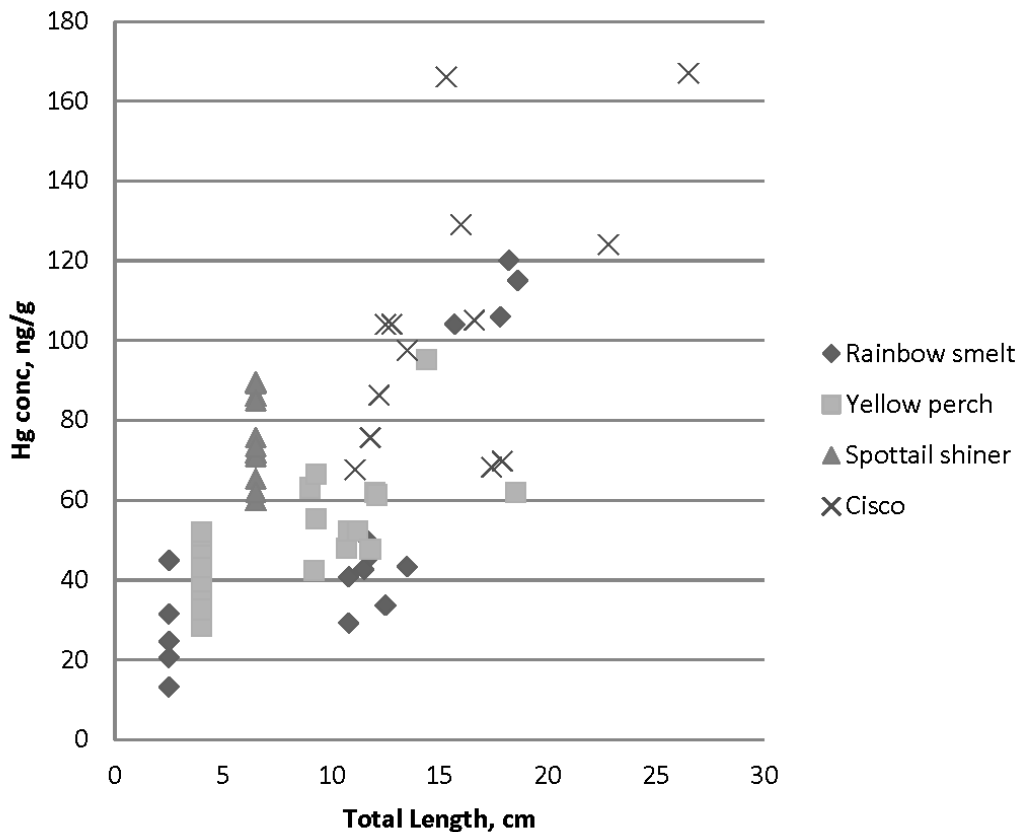
Figure 6. Comparison of bioenergetics model predictions of weight of age-6 Walleye for one growing season under various temperatures and diets, including with and without Rainbow Smelt.

Relative weights of Walleye—rather than increasing, as the bioenergetics modeling results suggested would happen—generally decreased following the smelt invasion. The mean W_r pre-invasion of 100 was significantly higher than the post-invasion value of 89 (ANOVA, $F = 39.38$, $P < 0.000$, $df = 1,19$). One potential explanation for why Walleye growth and condition did not respond as expected to the smelt invasion could be the rapid decline from their peak abundance, thereby reducing their availability as prey. Another factor that may have contributed to the declining growth rates and relative weights was an increased abundance of adult Walleyes. The mean index of relative year-class strength for Rainy Lake Walleye based on experimental gill net CPE for each year-class at ages 2, 3, and 4 was 83.6 for pre-smelt invasion year classes (1978–1989) and 133.8 for post-invasion year classes (1990–2002). This may have increased intraspecific competition and contributed to the slower growth and lower relative weights. Walleye growth within Wisconsin lakes was found to be density dependent with asymptotic length, growth rate, and body condition all changing with density (Sass et al. 2004).

Comparison of mean back-calculated growth rates for ages 1 to 4 Northern Pike generally increased after the smelt invasion (see Table 15). However, the differences in length from the pre- and post-invasion periods were not significantly different. Relative weights, however, were significantly lower after the smelt invasion (ANOVA, $F = 12.51$, $P = 0.002$, $df = 1,19$).

Rainbow Smelt effect on Walleye recruitment — Smelt introductions or invasions have been found to negatively affect Walleye recruitment in some instances, particularly in smaller lakes and reservoirs. Jones et al (1994) and Johnson and Goettl (1999) reported declines in YOY Walleye in Horsetooth Reservoir, Colorado, after smelt were introduced. YOY Walleye densities were lower in invaded lakes than in uninvaded lakes in Wisconsin (Mercado-Silva et al. 2007). The surface area of the Colorado reservoir and all but one of the Wisconsin lakes was $< 1,000$ ha. Although YOY Walleye densities were not specifically measured in Rainy Lake, the fact that strong above average Walleye year-classes were produced in 7 of the 12 years following the smelt invasion indicates the smelt had little or no effect on recruitment.

Rainbow Smelt effect on mercury concentrations in Walleye and Northern Pike — A concern stemming from the Rainbow Smelt invasion was that changes in the food web assemblage might result in dietary changes that could increase mercury concentrations in Walleye and Northern Pike, species for which consumption advisories already existed in Rainy Lake. In order to investigate this, baseline data for food web linkages and mercury concentrations for various organisms were collected from Rainy Lake in 1996 and 1997 (Sorensen et al. 2001). Although stable isotope analysis indicated that the trophic position of smelt was elevated relative to those of other prey fish, mercury concentrations generally were not. Mercury concentrations in smelt were actually lower than those of Yellow Perch, Spottail Shiner, and Cisco up to a length of about 120 mm (Figure 7). Above that length, concentrations in smelt were similar to those in Cisco but were higher than in Yellow Perch.



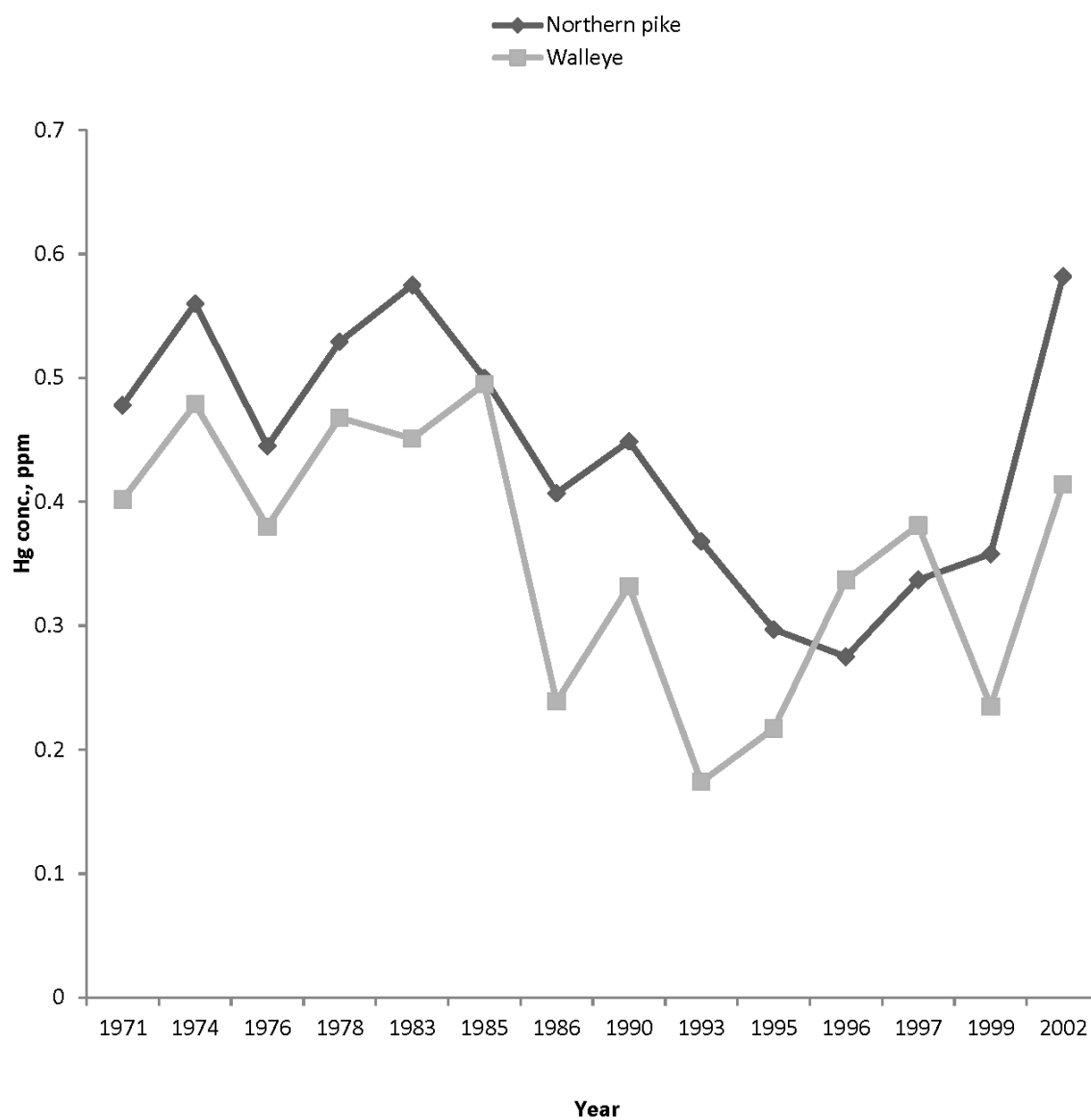


Figure 8. Estimated total mercury (Hg) concentrations in 55-cm Northern Pike and 39-cm Walleye from Rainy Lake, 1971–2002.

Conclusions

The smelt invasion in Rainy Lake generally has not resulted in some of the ecological effects that were predicted based on previous studies of invasions and introductions. The smelt exhibited a characteristic invasive pattern, building to high numbers by the mid-1990s, which then gradually fell to significantly lower, more consistent numbers throughout the late 1990s and early 2000s. Smelt reproduction apparently did occur every year, but there was some variation in year-class strength, as expected. The smelt occupied their characteristic position in the food web, feeding primarily on zooplankton (including ichthyoplankton) and other invertebrates and in turn being preyed upon by larger predators such as Walleye and Northern Pike. Diet overlap was significant between smelt and smaller Walleye and Saugee, suggesting competition could occur if shared resources became limited. Growth and condition of the predators decreased rather than increasing, as was thought might occur. Based on N-isotope analyses, the trophic position of smelt was elevated relative to the native forage species Cisco, Yellow Perch, and Spottail Shiner. However, mercury concentrations in smelt were similar to those in the native fish species of similar sizes. It was not clear what effect preying on smelt had on mercury concentrations in Walleye and Northern Pike. Because of the threat mercury poses to human health via the consumption of contaminated fish, further studies should be conducted to clarify the role smelt may play in the bioaccumulation of mercury by Walleye, Northern Pike, and other native piscivores.

Further efforts will be required to assess the long-term implications of the smelt invasion in Rainy Lake. Regular lake-wide observations will be needed to obtain estimates of smelt abundance and biomass to determine if the species has become a well-established member of the fish community. If so, monitoring and studies will continue to be needed to assess the smelt's effect on other members of the fish community and aquatic organisms. Unfortunately, these assessments will have to continually overcome the handicap provided by the limited information that was available for many members of the aquatic community prior to the smelt invasion.

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