

# **Bioenergetics Modeling for Lake Trout and other Top Predators in Lake Champlain**



**Lake Champlain  
Basin Program**

Prepared by  
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for  
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TOP PREDATORS IN LAKE CHAMPLAIN

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#### Lake Champlain Basin Program Technical Reports

1. *A Research and Monitoring Agenda for Lake Champlain.* Proceedings of a Workshop, December 17-19, 1991, Burlington, VT. Lake Champlain Research Consortium. May, 1992.
2. *Design and Initial Implementation of a Comprehensive Agricultural Monitoring and Evaluation Network for the Lake Champlain Basin.* NY-VT Strategic Core Group. February, 1993.
3. (A) *GIS Management Plan for the Lake Champlain Basin Program.* Vermont Center for Geographic Information, Inc., and Associates in Rural Development. March, 1993.  
  
(B) *Handbook of GIS Standards and Procedures for the Lake Champlain Basin Program.* Vermont Center for Geographic Information, Inc. March, 1993.  
  
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4. (A) *Lake Champlain Economic Database Project. Executive Summary.* Holmes & Associates. March 1993.  
  
(B) *Socio-Economic Profile, Database, and Description of the Tourism Economy for the Lake Champlain Basin.* Holmes & Associates. March 1993  
  
(B) *Socio-Economic Profile, Database, and Description of the Tourism Economy for the Lake Champlain Basin. Appendices.* Holmes & Associates. March 1993  
  
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(D) *Conceptual Framework for Evaluation of Pollution Control Strategies and Water Quality Standards for Lake Champlain.* Anthony Artuso. March 1993.
5. *Lake Champlain Sediment Toxics Assessment Program. An Assessment of Sediment - Associated Contaminants in Lake Champlain - Phase 1.* Alan McIntosh, Editor, UVM School of Natural Resources. February 1994.  
  
*Lake Champlain Sediment Toxics Assessment Program. An Assessment of Sediment - Associated Contaminants in Lake Champlain - Phase 1. Executive Summary.* Alan McIntosh, Editor, UVM School of Natural Resources. February 1994.
6. (A) *Lake Champlain Nonpoint Source Pollution Assessment.* Lenore Budd, Associates in Rural Development Inc. and Donald Meals, UVM School of Natural Resources. February 1994.  
  
(B) *Lake Champlain Nonpoint Source Pollution Assessment. Appendices A-J.* Lenore Budd, Associates in Rural Development Inc. and Donald Meals, UVM School of Natural Resources. February 1994.

7. *Internal Phosphorus Loading Studies of St. Albans Bay. Executive Summary.* VT Dept of Environmental Conservation. March 1994.  
  
(A) *Dynamic Mass Balance Model of Internal Phosphorus Loading in St. Albans Bay, Lake Champlain.* Eric Smeltzer, Neil Kamman, Karen Hyde and John C. Drake. March 1994.  
  
(B) *History of Phosphorus Loading to St. Albans Bay, 1850 - 1990.* Karen Hyde, Neil Kamman and Eric Smeltzer. March 1994.  
  
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8. *Lake Champlain Wetlands Acquisition Study.* Jon Binhammer, VT Nature Conservancy. June 1994.
9. *A Study of the Feasibility of Restoring Lake Sturgeon to Lake Champlain.* Deborah A. Moreau and Donna L. Parrish, VT Cooperative Fish & Wildlife Research Unit, University of Vermont. June 1994.
10. *Population Biology and Management of Lake Champlain Walleye.* Kathleen L. Newbrough, Donna L. Parrish, and Matthew G. Mitro, Fish & Wildlife Research Unit, University of Vermont. June 1994.
11. (A) *Report on Institutional Arrangements for Watershed Management of the Lake Champlain Basin. Executive Summary.* Yellow Wood Associates, Inc. January 1995.  
  
(B) *Report on Institutional Arrangements for Watershed Management of the Lake Champlain Basin.* Yellow Wood Associates, Inc. January 1995.  
  
© *Report on Institutional Arrangements for Watershed Management of the Lake Champlain Basin. Appendices.* Yellow Wood Associates, Inc. January 1995.
12. (A) *Preliminary Economic Analysis of the Draft Plan for the Lake Champlain Basin Program. Executive Summary.* Holmes & Associates and Anthony Artuso. March 1995  
  
(B) *Preliminary Economic Analysis of the Draft Plan for the Lake Champlain Basin Program.* Holmes & Associates and Anthony Artuso. March 1995
13. *Patterns of Harvest and Consumption of Lake Champlain Fish and Angler Awareness of Health Advisories.* Nancy A. Connelly and Barbara A. Knuth. September 1995.
14. (A) *Preliminary Economic Analysis of the Draft Plan for the Lake Champlain Basin Program. Executive Summary - Part 2.* Holmes & Associates and Anthony Artuso. November 1995  
  
(B) *Preliminary Economic Analysis of the Draft Plan for the Lake Champlain Basin Program - Part 2.* Holmes & Associates and Anthony Artuso. November 1995
15. *Zebra Mussels and Their Impact on Historic Shipwrecks.* Lake Champlain Maritime Museum. January 1996.
16. *Background Technical Information for Opportunities for Action: An Evolving Plan for the Future of the Lake Champlain Basin.* Lake Champlain Basin Program. June 1996

17. (A) *Executive Summary. Economic Analysis of the Draft Final Plan for the Lake Champlain Management Conference.* Holmes & Associates and Anthony Artuso. July 1996  
  
(B) *Economic Analysis of the Draft Final Plan for the Lake Champlain Basin Management Conference.* Holmes & Associates and Anthony Artuso. July 1996
18. *Catalog of Digital Spatial Data for the Lake Champlain Basin .* Vermont Center for Geographic Information, Inc. September 1996.
19. *Hydrodynamic and Water Quality Modeling of Lake Champlain.* Applied Science Associates, Inc. July 1996.
20. *Understanding Phosphorus Cycling, Transport and Storage in Stream Ecosystem as a Basis for Phosphorus Management.* Dr. James P. Hoffmann, Dr. E. Allan Cassell, Dr. John C. Drake, Dr. Suzanne Levine, Mr. Donald W. Meals, Jr., Dr. Deane Wang. December 1996.
21. *Bioenergetics Modeling for Lake Trout and Other Top Predators in Lake Champlain.* Dr. George W. LaBar and Dr. Donna L. Parrish. December 1996.

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## Executive Summary

In this study, we used bioenergetics modeling to address the relationship of the top predators in Lake Champlain to the predominant prey, rainbow smelt *Osmerus mordax*, following the initiation of sea lamprey *Petromyzon marinus* control. Top predators include: lake trout *Salvelinus namaycush*, walleye *Stizostedion vitreum*, landlocked Atlantic salmon *Salmo salar* (LLS), rainbow trout *Oncorhynchus mykiss* (RT), and brown trout *Salmo trutta* (BT). The latter three species of predators are subsequently referred to as the 'SRB complex'. Study objectives were as follows:

1. Refine the bioenergetics models already built for lake trout and rainbow smelt by collecting dietary and habitat information currently not available for Lake Champlain and measure caloric content of Lake Champlain rainbow smelt at different times of the year and at different life stages.
2. Increase the diet data for Atlantic salmon and walleye and subsequently, to build bioenergetic models for each of them.
3. Measure rainbow smelt biomass in several areas of the lake during spring and late summer using hydroacoustic sampling.
4. Use the bioenergetic models, once developed, to predict the impacts of various fishery management scenarios on the Lake Champlain ecosystem.

The results showed that all of the listed predators feed extensively on rainbow smelt.

Hydroacoustic data on smelt population sizes indicate that smelt numbers were higher in 1990 than in 1994, which is during the time period of increasing survival of top predators resulting from sea lamprey control. Based on the bioenergetics modeling, under the worst-case scenario of maximum population sizes or stocking rates, maximum growth rates and

minimum mortality rates, the highest estimated total consumption of adult rainbow smelt >65 by all modeled predators is  $6.5 \times 10^9$  g, or 27% of the estimated standing crop of smelt. We conclude that because Atlantic salmon eat relatively more small smelt than lake trout and walleye, and because salmon don't live as long, the best way to effect a rapid change in prey consumption is to change stocking rates of the SRB complex.

## Introduction

Bioenergetic modeling is a tool available to resource managers and ecologists to help understand how fish grow. As a byproduct of that understanding, these models also have been extensively used to help understand predator/prey interactions and food web dynamics. As the name implies, bioenergetic modeling uses knowledge of the food habits and energy content of fish and their prey, predator metabolism and temperature of the habitat to model how changes in diet, population sizes or mortality rates affect fish growth. Some examples of their use include: estimation of feeding rates and host mortality for sea lamprey *Petromyzon marinus* (Kitchell and Breck 1980); a prediction that continued stocking of salmonids could mean a drastic decline in alewife *Alosa pseudoharengus* stocks, the principal prey species in Lake Michigan at the time (Stewart et al. 1981); and estimation of plankton consumption by alewife and subsequent effects (Stewart and Binkowski 1986; Hewett and Stewart 1989). Bioenergetics models have also been used to analyze contaminant uptake through the diet (Norstrom et al. 1976), to determine the effects of heating effluents on fish growth (Rice et al. 1983), to evaluate habitat choice (Wildhaber and Crowder 1990), to estimate prey availability (Stewart and Binkowski 1986; Hewett and Stewart 1989), to predict the impact of various global warming scenarios on fish populations (Hill and Magnuson 1990), and to estimate food consumption of various fish species (Hurley 1986; Carline 1987; Johnson et al. 1988; Wahl and Stein 1991).

During a sabbatical year (1991-92), one of the co-principal investigators (GL) developed bioenergetic models for Lake Champlain lake trout *Salvelinus namaycush* and rainbow smelt *Osmerus mordax*, using available data from Lake Champlain and, where not available, from fisheries literature. The specific objective was to predict changes in rainbow



smelt populations resulting from changes in rates of predation caused by increased survival and growth of lake trout after sea lamprey control. In this study (LaBar 1993), the models produced were used to predict changes in consumption of smelt and other prey by lake trout and the subsequent effects on rainbow smelt populations. These species were chosen because rainbow smelt are the most important prey and lake trout the most important salmonid predator in Lake Champlain. Lake trout will be significantly impacted by changes in rates of parasitism by sea lamprey.

State and federal fishery biologists predicted that following sea lamprey control, lake trout mortality should decrease by about 5%. Using that value, the model (LaBar 1993) predicted that after sea lamprey control, if stocking rates remained constant, lake trout stocks should be about 33% and 20% higher at the end of the third and fourth year after stocking, respectively, than they were before control. Peak population mass, however, was predicted to be nearly 70% higher in the post-control lake trout population. This would result in an increase of about 70% in cumulative consumption of both young and adult smelt and an 80% increase in *Mysis relicta* consumption. Similar changes are predicted to occur in lake trout consumption of yellow perch *Perca flavescens* and slimy sculpin *Cottus cognatus*.

Although the model (LaBar 1993) predicted a substantial increase in consumption of rainbow smelt by lake trout, the total annual mortality of rainbow smelt in the Main Lake was estimated to increase by only about 3% from 0.40 to 0.43. This increase in smelt mortality should result in a 15% decrease in smelt consumption of *Mysis*, a 16% decrease in consumption of small smelt by larger smelt and a 9% decrease in plankton consumption. Perhaps the most intriguing result from the modeling exercise was the prediction that because

of the increased consumption of smelt by lake trout, there would be a reduction in smelt cannibalism, which should result in essentially no net change in smelt stocks despite a 70% increase in consumption by their major predator. It must be remembered, however, that this model did not include predation by either walleye or the other salmonid predators.

However, there were several unknown factors which could change the model predictions. Growth rates of lake trout may change as sea lamprey parasitism diminishes; the change in lake trout growth rates will result in a change in their consumption of smelt. There were also some gaps in the diet data that needed to be filled in order to make the model prediction more reliable. For example, there was almost no dietary data on young lake trout. Data used in the model were taken from some scattered personal observations and from the literature on other bodies of water. For adult lake trout, data from Vermont Department of Fish and Wildlife (VTF&W) surveys corroborated those used in the model. Even winter-time data, although total numbers were small, supported model data. In winter, at least in management zone 2A (Figure 1), lake trout feed primarily on smelt. About 80% of the lake trout examined by creel census workers contained smelt > 76 mm long. The winter data also showed, however, that a few lake trout seemed to feed entrepreneurially; i.e., a few of them had large numbers of minnows in their stomachs. This phenomenon also needed to be explored, to determine if it needed to be incorporated into the model. Thermal regimes for young lake trout also needed to be determined, because growth is very responsive to temperature.

Continual estimates of standing stock or biomass, provided through hydroacoustic assessment are essential to understanding the total effect of predation on smelt. Although there is a long-term smelt monitoring program under way, using stepped-oblique mid-water

trawling, hydroacoustic assessment is the only way actual numbers of smelt stocks can be measured. The need for accurate population density information was vividly demonstrated during the modeling exercise. Without information on rainbow smelt population densities, the estimated 70% increase in consumption of smelt by lake trout could have been viewed with some alarm. However, because the hydroacoustic assessment showed that smelt stocks were very high, we were able to calculate that the increase in consumption by lake trout would not significantly reduce total numbers of smelt. The specific objectives were to:

1. refine the bioenergetics models already built for lake trout and rainbow smelt by collecting dietary and habitat information currently not available for Lake Champlain and measuring caloric content of Lake Champlain rainbow smelt at different times of the year and at different life stages;
2. increase the diet data for Atlantic salmon and walleye and subsequently, to build bioenergetic models for each of them;
3. measure rainbow smelt biomass in several areas of the lake during spring and late summer using hydroacoustic sampling;
4. use the bioenergetic models, once developed, to predict the impacts of various fishery management scenarios on the Lake Champlain ecosystem.

Of course lake trout aren't the only fish that depend on rainbow smelt for their food and rainbow smelt aren't the only food of top predators. Two other top predators for which bioenergetic models exist or can be adapted, and which are very important to fishery managers, are Atlantic salmon *Salmo salar* and walleye *Stizostedion vitreum*. The small amount of diet data available for Atlantic salmon and walleye indicates that they, too, feed on rainbow smelt (Kirn 1986). Our study was designed to supplement and update Kirn's (1986) data and then build bioenergetic models for these predators. By linking these top predator models, we can begin to understand a major portion of the food web dynamics in the lake.

## Methods

### Hydroacoustic Assessment

In mid-summer 1993, we acquired a Simrad EY 500 scientific sonar to carry out hydroacoustic assessment of fish stock size. The 200-kHz unit consists of a transducer, towed from the boat in a small v-fin towed body, and the echo sounder (Figure 2). The sounder is controlled from a portable computer, and information from the sounder is recorded and processed on the computer as well. Two types of surveys were carried out. Zigzag transects were surveyed in the Main Lake, starting at Burlington and continuing south to Barber Point (area 2B), and in the Inland Sea in June, 1994. Simultaneous echo-survey transects and midwater trawls were taken at the four standard rainbow smelt sampling stations (Shelburne Bay, outside Juniper Island in area 3B, Malletts Bay and the Inland Sea in area 5B; Figure 1) in August 1994.

Echo surveys were processed by the EP500 software program purchased with the sounder. Details on how the processing is carried out are found in Simrad (1993). When the surveys were processed by the software, analysis was also carried out by the same software. A minimum target strength of -60 dB was used as the smallest target to be included in the analysis. Results from this analysis were expressed in fish/ha, over the whole course of the transect, at depths from 3 m below the surface (the shallowest depth of the midwater trawl) to the maximum depth of the midwater trawl (40 m) in deep transects, or to two meters above the bottom on shallower transects. In addition to numbers of fish, the software analyzed target strength distribution in -3 dB increments, starting at -60 dB, expressing results as percent of targets in each target-strength category. Past midwater trawling has shown that almost all night-time pelagic fish are rainbow smelt (Kirn and LaBar

1991). Fewer than 1% of fish taken in midwater trawls are species other than rainbow smelt; an example of this small group would be lake whitefish *Coregonus artedii*. Furthermore, in all cases, fewer than 1% of the targets detected by the sounder had target strengths above -45 dB, and most were just above the bottom. A mean of only 1.6% of the echoes were in the -48 to -45 dB category. According to Love (1971), a signal of -45 dB would be generated by a fish of about 46 cm, much longer than even the largest smelt in Lake Champlain. Given the inherent variability around these data, the target strength frequency distributions and location in the water column of these larger echoes, when we extrapolated from the echo-data to estimate standing crop in the entire Main Lake, we used the entire estimated numbers per hectare, rather than attempting to adjust for non-smelt fishes.

In order to account for the availability of habitat for smelt and salmonids, we assumed that smelt densities were uniform in all deep water (> 70 m) and all shallow water (< 45 m) habitat, and that intermediate depths had a uniform density equal to the mean density of deep and shallow habitats. We furthermore assumed that predator distribution was uniform in water deeper than 10 m. The surface area of the Main Lake is 68,200 ha, of which about 80% is deeper than 10 m.

To estimate the proportion of rainbow smelt stocks currently consumed by the three predators discussed here, we projected smelt standing crop determined by hydroacoustic assessment to the entire Main Lake. (Note: It is not possible to determine exact fish length from hydroacoustic information. Therefore, the hydroacoustic estimates include all post-larval rainbow smelt.) The assumptions used in this projection were the following:

1. Rainbow smelt are evenly distributed throughout each of the previously defined depth zones, at lake depths greater than 10 m. Our density estimates only

included smelt found between 3 and 40 m.

2. Numbers of rainbow smelt in Shelburne Bay are representative of numbers in areas of the Main Lake <45 m deep, and numbers at Juniper are indicative of numbers in areas >75 m. Areas between 45 and 75 m are assumed to have the average of Juniper and Shelburne.
3. The total surface area of the Main Lake was measured to be 710 km<sup>2</sup>, of which 80%, or 569 km<sup>2</sup> was deeper than 10 m.
4. Predators are evenly distributed throughout the zone, at lake depths >10 m.
5. Density estimates were based on an average of 1990 and 1994 hydroacoustic surveys.
6. All fish in the 3-m to 40-m depth range are rainbow smelt.
7. Mean weight of rainbow smelt is 20 g per fish.

### **Fish Collections**

Rainbow smelt. Rainbow smelt were collected from Malletts Bay, Inland Sea, and the Main Lake from May, August, and October 1993 in either mid-water or bottom trawls. After capture, fish were frozen on board the research vessel, and then stored at -10 °C in a walk-in freezer until processed.

Lake trout. A total of 332 lake trout were collected in 1993 with a bottom trawl at several sites in the Main Lake: 35 in May, 256 in August and 41 in October. Fish stocked in 1993 were frozen and taken to the laboratory, where stomachs were extracted and gut contents identified. Stomachs of larger fish were extracted on board the research vessel and preserved in formalin for later processing. Stomachs from winter-time angler-caught lake trout were analyzed by the Vermont Department of Fish and Wildlife and the data provided

to us.

Walleye and Atlantic salmon. From June to December in 1993, walleye and landlocked salmon were collected to obtain stomach contents for diet analysis (Table 1). On nine occasions during the summer, walleye and salmon were collected in gillnets ranging from 5.1 to 7.6 cm bar mesh. Lengths of netting for an overnight set ranged from 91 to 183 m for each mesh size with total meters set ranging from 183 to 549. Nets were generally set at sunset and retrieved at sunrise in areas where anglers were reporting catching either walleye or salmon or both species. We strived to set nets for no more than a 12-hour time period to obtain stomach contents in identifiable condition and also, to release fish alive. For walleye, 45% of those collected in gill nets were released alive. Water temperatures were recorded when the nets were set and again when nets were retrieved.

Upon removal from nets, fish were weighed to the nearest 100 g, total length recorded to the nearest millimeter, and scales removed for aging. On walleye, the second dorsal spine was also removed for aging, and on salmon, fin clips were recorded. Stomach contents from live fish were obtained by using a gastric lavage technique. Stomach contents were frozen immediately on dry ice. Dead fish were placed on ice for later work-up in the laboratory, which was done within two hours of retrieving nets. In addition to the above information, we were able to sex those fish not released.

We collected salmon during late October and early November while accompanying state fisheries biologists on electrofishing surveys. Of the 48 salmon collected electrofishing, 47 were released alive. In December, four salmon were collected by angling.

In the laboratory, fish stomach samples were thawed immediately prior to identifying contents. Fish prey items were measured, including total length (TL) and standard length

(SL). When those lengths were not available, backbone lengths (BB) were recorded. To express diet as a percent by weight of smelt, we developed a length-length regression, BB-TL (Figure 3). From the smelt work, a standard length-total length regression, SL-TL;  $r^2 = .95$ ; and, a length-weight regression (TL-Wt),  $r^2 = 0.90$ ; were available (G.W. LaBar, 1993 smelt trawls, unpublished data). For yellow perch, we used a backbone to total length regression developed by Knight et al. (1984) and a yellow perch total length to weight regression developed by LaBar and students in a University of Vermont (UVM) fish biology class.

### Bioenergetic Models

Bioenergetic models (Hewett and Johnson 1992) were used to estimate food consumption of lake trout, walleye, and the SRB complex, which is composed of Atlantic salmon (LLS), rainbow trout (RT) *Oncorhynchus mykiss*, and brown trout (BT) *Salmo trutta*. Inputs to the model included the following: growth rates, mortality rates, population sizes, food habits, caloric density of prey items, and water temperature where the fish are found through the year. Inputs for the SRB complex model are based on landlocked Atlantic salmon data. Inputs for lake trout were those used in LaBar (1993), except that population sizes were adjusted for various stocking rates and diets were adjusted based on the new dietary data. Because no bioenergetic model has been developed specifically for Atlantic salmon, we used the coho salmon model described by Hewett and Johnson (1992) to represent the SRB complex. The constants used in the walleye and SRB complex models are shown in Table 2. Those for lake trout were from LaBar (1993). Inputs for walleye and for the SRB complex are discussed below.



Caloric density of prey. We only analyzed caloric density of rainbow smelt > 65 mm. Caloric density for small smelt (<65 mm) was taken from Lantry (1991). Caloric density of yellow perch was taken from Hewett and Johnson (1992) and Craig (1977). Caloric density of small smelt and yellow perch was kept constant throughout the modeling exercise. For rainbow smelt > 65 mm, we analyzed fish of varying sizes from each area and season (Table 3). Pooled samples included 4-6 fish in a 10-mm size group.

To measure caloric density, fish were thawed in cold water, blotted dry, weighed (wet weight) and measured (total length). Guts were cleared of contents and fish were dried for 96 h @ 60 °C. Dry weight and percent dry weight were calculated for each fish. Each dried fish was ground in a Wiley Mill to a particle size of 0.5 mm. Fish in pooled samples were ground together. A sample of the ground material was weighed and then redried for 24 h @ 105 °C. The difference between the initial and final sample weights was calculated as moisture loss. Percent moisture and percent dry matter were then calculated.

Caloric values were determined using a Parr oxygen bomb calorimeter standardized by performing caloric determinations of benzoic acid pellets with a known heat of combustion. After 50 samples were run, the calorimeter was recalibrated and a new energy equivalent was calculated. Replicate samples were weighed (to the nearest 0.001 g) and placed in previously weighed crucibles. Subsequent to tissue preparation, caloric content was determined according to the Parr (1984) calorimeter manual. Fourteen samples were discarded because of incomplete combustion or an improper increase in temperature. The caloric values used in the walleye and SRB complex models are shown in Tables 4-5.

Growth Rates. Walleye growth rates were derived from fish collected during the course of the study. Aging of walleyes was effected by sectioning dorsal fin spines. After

mounting and sectioning, each spine was read by two people independently. Where there were disagreements, spines were read a third time. Where age disagreements were not sequential (e.g. 6,7,8) the sample was not used; only three were discarded. We calculated the 95% confidence interval of the weights at each age, and used the upper and lower bounds as the upper and lower values for the model (high and low weight estimates) (Table 6). We assumed that spawning commenced on April 1 each year, that each fish spawned each year, and that there was a 10% spawning weight loss. Colby et al. (1979) found female ovaries weighed between 16.3 and 24.1% of total body weight and male testes comprised 4.3% of body weight. Henderson and Nepszy (1994) also found female ovaries to weigh from 18-22% of total body weight. We therefore used the average between 4.3% (males) and 16.3% (females) because we did not have enough samples to run the model separately for males and females.

Atlantic salmon growth rates were provided by a consensus of fisheries biologists at the April 1994 bioenergetics workshop held at the University of Vermont. These growth rates came from fish collected during routine sampling by the New York Department of Environmental Conservation (NY DEC) and Vermont Department of Fish and Wildlife (VTF&W) (Table 7).

Mortality Rates. Two mortality rates for walleye were used: 0.30 and 0.50. According to available data, these rates most likely span the range of expected mortality for walleye (Newbrough et al. 1994).

Atlantic salmon mortality rates were taken from the UVM 1994 workshop, which were provided by a consensus of fishery biologists from NY DEC, VTF&W and the U.S. Fish and Wildlife Service (FWS).

Population sizes. Walleye population sizes (Table 8) for the model were derived by using mean population estimates for all years from three spawning locations (Poultney River, Great Chazy River and South Bay) (Newbrough et al. 1994). Each of these sites had enough mark and recaptures to calculate both Jolly-Seber and Bailey estimates. These two estimates for each site were averaged, then divided by either 0.4 or 0.8, which represented an upper and lower estimate on the proportion of the total walleye population that was represented by spawning populations in these areas. We note here that because of the migratory nature of walleye, these population estimates are for the entire lake. During the summer months, we know that walleye are frequently in the Main Lake area (Newbrough et al. 1994). Most of our information on walleye age and growth started at age 5; therefore, we began the model at that age and ran it for 15 cohorts ending at age 20. Thus, we ran the model twelve times for walleye, to factor in all combinations of population size, mortality, and growth.

Population sizes of the SRB complex were derived from the UVM workshop. These estimates accounted for current target rates and potential future stocking rates of the SRB complex (Table 9).

Diet. Diets used in the walleye (Table 10) and SRB complex (Table 11) models reflected food habits derived from our sampling (see Diets in Results Section). Lake trout diets (Table 12) were derived partially from our own sampling, especially of young lake trout, and in part from information from the long-term lake trout study carried out by VTF&W.

Diet information entered into the model is based on percent by wet weight, which was found by summing up all diet item weights for all fish in each month and summing item weights of each species. The summed weight of each item (prey species) was divided by

total weight to give percent by weight for each month.

Temperature. Temperatures (Table 13) were taken at the sampling sites for walleye and Atlantic salmon. We used the temperatures at the net depths for the models where we had that information. For periods of the year when we didn't have temperature data, we used literature values adjusted by the consensus of fisheries biologists at the April workshop.

## Results and Discussion

Hydroacoustic assessment. Hydroacoustic surveys in 1994 very closely reflected relative catches per unit of effort in various areas of the lake (Figure 4; Table 14). The Inland Sea had the highest estimated fish density, with a mean of 3551 fish/ha. Juniper density was estimated to be less than half that in the Inland Sea, and Malletts Bay and Shelburne Bay were intermediate (Table 15). Fish density in the Main Lake was substantially lower than in the four standard trawling sites, however, the estimate was derived from a single, long, zig-zag transect carried out in late June, rather than in August like the others.

Densities in 1994 were lower than smelt densities measured in 1990, using dual-beam acoustic equipment from Biosonics, Inc. In 1990, mean fish densities ranged from 7,100 fish/ha in the Inland Sea to 2,043 fish/ha at Juniper (Table 14). Catch rates in 1994 ranged from one-half those of 1990 at Shelburne Bay to the same catch rate in both years in Malletts Bay (Table 14). Hydroacoustic density estimates showed a similar range of change between 1990 and 1994, although the differences were not as pronounced in Shelburne Bay as for the catch data. Recent communication from Biosonics indicated that their values should be comparable to our more recent data, so the differences in fish density from 1990 to 1994 are

probably real differences. Also, changes in fish density estimated from hydroacoustic surveys parallel those in trawl catches. It is very possible that smelt populations in 1990 were at their apogee, however, only further study can verify it.

Diets. Of the 65 walleye collected in 1993, 37 contained identifiable prey (Table 16). Rainbow smelt were the overwhelming diet item and most smelt consumed were > 65 mm (Figure 5; Table 17). On July 9, yellow perch made a significant contribution to walleye diets (Table 16).

For landlocked salmon, we collected 90 fish of which 65 contained identifiable contents (Table 18). Essentially, smelt were the only prey item. In July, salmon ate mostly large (> 65 mm) smelt, but in October and November, only about half of the smelt consumed by salmon were > 65 mm (Tables 17 and 18).

Bioenergetic models. Earlier bioenergetic modeling for lake trout only (LaBar 1993) predicted that a projected 5% increase in lake trout survival after sea lamprey control would result in approximately a 70% increase in consumption of rainbow smelt (an increase from about  $700 \times 10^6$  g to  $1200 \times 10^6$  g) and a 3% increase in rainbow smelt annual mortality. Based on the modeling results, we predict that stocking 225,000 lake trout will result in a smelt consumption of  $1.4 \times 10^9$  g by lake trout (Table 19). For the SRB complex, biologists expect that mortality will decrease dramatically as sea lamprey control is effected, from 80% at the start of sea lamprey control, to an eventual 50% annual mortality rate. According to our models, that change will result in an increase of over 300% in total consumption of rainbow smelt by the SRB complex (Figures 6 and 7; Table 19), from  $1.4 \times 10^9$  g at stocking rates of 390,000 salmon per year and 80% mortality to  $4.8 \times 10^9$  g at the same stocking level and 50% mortality. Reductions in stocking rates are projected to result in a

nearly 1:1 reduction in estimated consumption by the SRB complex (Table 19); i.e., reducing the SRB complex by 20% would result in a reduction by 20% in their smelt consumption.

Atlantic salmon feed more preferentially on smaller smelt than do walleye and lake trout (Figure 8). Cumulative consumption by the SRB complex is therefore quite high for these smelt (Figures 9 and 10) as well as for large smelt (Figures 11 and 12).

Because the data on walleye population sizes, mortality and growth rates are not as reliable as the same data on lake trout and Atlantic salmon, we bracketed the likely consumption patterns. Total consumption rates of rainbow smelt projected for the 16 cohorts of walleye (ages 5-21) varied from a low of  $355 \times 10^6$  g per year for low population size, annual mortality rate of 50% and low growth, to  $1,315 \times 10^6$  g at high population size, 30% annual mortality and high growth rate (Figures 13-18; Table 20).

If we assume that walleye grow at an intermediate rate and that their annual mortality is between 30% and 50%, then annual consumption of rainbow smelt should lie between about  $1,200 \times 10^6$  g and  $375 \times 10^6$  g. Changes in mortality rates are very important in changing total consumption by walleye. The cumulative consumption curve for 50% annual mortality (Figure 15) reached an asymptote at about age 12, whereas for the 30% mortality model (Figure 16), the cumulative consumption curve continues to rise through age 19. The important difference is that there are many more older walleye in the 30% model than in the 50% model. Between age-7 and age-21, consumption increases 33% with mortality at 50%, but at 30% mortality, consumption increases more than 100% over the same age span. When the SRB complex and walleye consumption from bioenergetics modeling are compared, we find salmon having a much greater impact on the prey base than walleye (Figure 19).

Walleye consumption of yellow perch could be very important. At high weight, high population and low mortality, walleye are projected to eat more than  $40 \times 10^6$  g of yellow perch per year (Figures 17-18), which is about one-third the total estimated angler catch (more than 2 million perch weighing an average of 60 g each; B. Chipman, personal communication). Even the lowest estimate projects yellow perch consumption of more than  $10 \times 10^6$  g. It must be remembered, however, that this projection is based on very few samples.

The estimated standing crop of rainbow smelt in the Main Lake portion of Lake Champlain was  $24 \times 10^9$  g, based on the assumptions presented in the methods section. Under the scenario of maximum population sizes or stocking rates, maximum growth rates and minimum mortality rates, the highest estimated total consumption of rainbow smelt  $> 65$  mm by all modeled predators is  $6.5 \times 10^9$  g, or 27% of the standing crop. It must be recognized, however, that we were not able to include walleye younger than 5 years in the estimates of consumption. In addition, there is no information on standing crop of smelt  $< 65$  mm because they can not be reliably estimated by current hydroacoustic techniques. Given that younger, faster-growing fish typically consume more than older, slower-growing fish (LaBar 1993, for example), it is likely that our worst case scenario of smelt consumption by these three predator species is still low. It is impossible to come up with the real worst case scenario given that there are no data on these younger walleye. Unfortunately, given the uncertainty surrounding the walleye population, growth and mortality data, it is impossible to estimate how low the estimate of smelt consumption may be.

The lowest total smelt consumption by the three predators calculated by the models, occurs under low population or stocking numbers, low growth rates and high mortality.

Under these conditions, consumption of rainbow smelt  $> 65$  mm is estimated to be only  $1.4 \times 10^9$  g. However, for this to occur, mortality rates of Atlantic salmon would have to remain inordinately high, walleye populations would have to be much smaller than seems likely, and numbers of stocked lake trout would have to drop from 225,000 to 80,000. The first two of these scenarios are not likely. Therefore, estimated total consumption by the predators, once the effects of sea lamprey control have stabilized, will probably be about  $5 \times 10^9$  g, representing about 20% of the estimated standing crop of smelt  $> 65$  mm.

The total impact of top predators, post-sea lamprey control, on rainbow smelt is potentially dramatic. However, in the whole scheme of things, even the total consumption of small smelt by the SRB complex was surprisingly small. It has been known since 1985 (Kirn 1985) that Atlantic salmon rely more heavily on smaller smelt in their diet than do lake trout or walleye. Thus, because of that fact and because Atlantic salmon had fewer cohorts than either lake trout or walleye, it was assumed that effecting changes in consumption rates (Stewart et al. 1981) would be more rapid by changing salmon stocking rates than by changing lake trout stocking rates.

Atlantic salmon are eating relatively more small smelt than the other two predators and they also don't live as long. Therefore, the best way to effect a rapid change in prey consumption is to change stocking rates of the SRB complex. However, if the mortality rate of salmon stabilizes at about 50%, changing total consumption may not be as rapid as was previously thought. It will be very difficult to quickly effect change in predatory inertia of either lake trout or walleye; even after cessation of stocking of lake trout, there are several cohorts extant in the lake. Obviously, with walleye, the only control over numbers is through changes in regulation. Many times, changes in regulation are not particularly effective at changing harvest (and thus mortality) rates.



## Study Conclusions

1. Rainbow smelt are the major diet item of lake trout, walleye, and the SRB complex in Lake Champlain. However, sporadically, yellow perch may be a significant contribution to walleye diets.
2. Rainbow smelt numbers derived, from hydroacoustic assessment, appear to have declined from 1990 to 1994, however they may have been at their apogee in 1990; further study is necessary to verify this.
3. Based on bioenergetics modeling, under the worst-case scenario of maximum population sizes or stocking rates, maximum growth rates and minimum mortality rates, the highest estimated total consumption of rainbow smelt > 65 mm by all modeled predators is  $6.5 \times 10^9$  g, or 27% of the mean 1990-94 standing crop.
4. Because Atlantic salmon eat relatively more small smelt than lake trout and walleye, and because salmon don't live as long, we conclude that the best way to effect a rapid change in prey consumption is to change stocking rates of the SRB complex.

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Table 1. Numbers of walleye (WAL) and landlocked Atlantic salmon (ATS) collected in gill nets during 1993. Depth includes the range in lake depth at net site. Set values are depth where net was set. Missing values indicate net was set on the bottom. NM=bar mesh size. NL=net length.

Date	Location	Depth (m)		NM (cm)	NL (m)	WAL	ATS	
		Range	Set					
06/09	Shelburne Bay	7.6-15.2	-	15.3	46	0	0	
06/11	Shelburne Bay	5.5-12.5	-	11.4	36	2	0	
06/14	Shelburne Bay	5.5-13.7	-	11.4	36	0	0	
06/25	Converse Bay: Inside	9.1-9.4	-	5.1	91	4	1	
		9.4-10.4	-	6.4	91	8	0	
		10.4-12.2	-	7.6	91	0	0	
	Converse Bay: Outside	9.1-13.7	-	5.1	91	6	1	
		11.3-18.6	-	6.4	91	0	0	
		11.3-11.3	-	7.6	91	1	0	
	07/01	Shelburne Bay	11.3-15.2	4.3	5.1	183	7	19
			5.5-6.1	-	6.4	183	11	1
	07/09	Inland Sea: Mary Crest	3.0-8.2	-	6.4	91	9	0
8.2-9.8			-	7.6	91	1	0	
Inland Sea: Eagle Mt		14.9-21.3	4.6	5.1	91	2	0	
		14.9-21.3	4.6	6.4	91	1	0	
07/14	Inland Sea: Cowbanks	24.4-30.5	15.5	5.1	91	0	3	
		24.4-30.5	15.5	6.4	91	0	7	
07/14	Inland Sea: Mary Crest	3.0-3.7	-	7.6	91	1	0	
		2.4-6.4	-	6.4	91	5	0	
07/21	Shelburne Bay	19.2-21.3	15.5	6.4	183	0	1	
08/19	Inland Sea: Mary Crest	7.3-10.7	-	6.4	91	1	0	
		7.3-10.7	-	7.6	91	2	0	
08/19	Inland Sea: Cowbanks	24.4-30.5	18.3	5.1	91	0	1	
		24.4-30.5	18.3	6.4	91	0	3	
10/26	Inland Sea: Cowbanks	8.2-9.4	-	6.4	183	0	1	
		4.0-9.4	-	7.6	183	5	0	
Total Collected						65	38	

Table 2. Parameter values used in walleye and SRB complex bioenergetic models.

Parameter	Walleye	SRB Complex
Intercept for metabolism (RA)	0.0108	0.00264
Metabolism versus weight coefficient (RB)	-0.2	-0.217
Metabolism versus temperature coefficient (RQ)	2.1	0.06818
Metabolism versus swimming speed coeff. (RTO)	27.0	0.0234
Upper temperature bound on maximum consumption, $C_{max}$ (RTL)	-	25.0
Intercept for weight dependence of swimming speed above cutoff temperature (RK1)	-	1.0
Slope for weight dependence of swimming speed (RK4)	-	0.13
Intercept of swimming speed versus temperature and weight below RTL (ACT)	1.0	9.7
Coefficient of water temperature dependence of swimming speed below RTL (BACT)	-	0.0405
Specific dynamic action (SDA)	0.172	0.172
Intercept for maximum consumption at 0°C (CA)	0.25	0.303
Weight-dependence coefficient for $C_{max}$ (CB)	-0.27	-0.275
Temperature-dependence coefficient for $C_{max}$ (CQ)	2.3	5.0
Optimum water temperature, °C (CTO)	22.0	15.0
Temperature at which consumption ceases, °C (CTM)	28.0	18.0
Temperature at which dependence is CK4 of maximum, °C (CTL)	-	24.0
Temperature-dependence value for increasing portion of temperature dependence curve (CK1)	-	0.36
Temperature-dependence value for decreasing portion of temperature dependence curve (CK4)	-	0.01
Intercept for portion of consumed food egested (FA)	0.158	0.212
Coefficient for egestion versus temperature (FB)	-0.222	-0.222
Coefficient for egestion versus feeding level (FG)	0.631	0.631
Intercept for proportion of consumed food excreted (UA)	0.0253	0.0314
Coefficient for excretion versus temperature (UB)	0.58	0.58
Coefficient for excretion versus feeding level (UG)	-0.299	-0.299
Consumption model	Kitchell <sup>a</sup>	T&L <sup>c</sup>
Respiration model	Kitchell <sup>a</sup>	Stewart <sup>d</sup>
Egestion model	Elliot <sup>b</sup>	Mixed Diet

a Kitchell et al. (1977).

b Elliot (1976).

c Thornton and Lessem (1978).

d Stewart et al. (1983).

Table 3. Seasonal caloric values of rainbow smelt sampled during 1993.

No. of Fish	Location	Mean Total Length (mm)	Mean Wet Weight (g)	Mean Dry Weight (g)	Mean cal/g wet weight	Standard deviation (wet cal/g)
<u>May</u>						
1	Inland Sea	139	8.8	1.7532	903.15	4.38
1	Inland Sea	141	9.4	1.7532	941.70	4.38
1	Main Lake	145	24.3	4.2143	965.67	2.87
5	Main Lake	152	16.7	3.5684	996.95	13.25
1	Main Lake	164	18.5	4.2050	1045.20	3.65
1	Main Lake	179	25.3	5.1223	1062.16	4.02
1	Malletts Bay	126	8.8	1.5264	858.27	2.06
1	Malletts Bay	127	8.0	1.3674	852.44	2.56
1	Malletts Bay	132	10.1	1.7039	872.95	3.75
<u>August</u>						
1	Inland Sea	120	8.3	1.7100	1061.45	8.03
1	Inland Sea	130	10.5	2.1523	1140.68	9.16
5	Inland Sea	136	11.0	2.3111	1103.51	13.08
1	Main Lake	125	19.3	4.0413	1153.95	1.20
6	Main Lake	139	11.1	2.3831	1145.52	9.28
1	Main Lake	155	29.3	6.2130	1168.82	0.45
1	Malletts Bay	120	7.9	1.3831	896.35	3.75
5	Malletts Bay	130	9.3	--	956.36	4.61
5	Malletts Bay	139	11.1	1.9938	954.41	13.76
<u>October</u>						
1	Inland Sea	122	8.9	1.9603	1194.81	2.26
5	Inland Sea	123	8.9	1.8321	1154.72	10.37
1	Inland Sea	132	10.8	1.9622	1019.79	2.12
1	Main Lake	127	11.4	2.4000	1188.10	7.92
4	Main Lake	150	20.2	4.3635	1347.27	25.31
1	Main Lake	143	15.3	3.2504	1258.36	10.03
1	Main Lake	156	22.9	5.3176	1446.87	12.02
1	Main Lake	185	33.6	8.3660	1365.39	9.78
1	Malletts Bay	102	5.2	0.8580	919.80	2.55
1	Malletts Bay	105	6.0	1.2578	1113.16	2.12
1	Malletts Bay	115	6.6	1.2736	856.80	6.08



Table 4. Seasonal caloric values (cal/g wet weight) of smelt and yellow perch used in walleye bioenergetics model. Values for smelt >65mm were obtained from Lake Champlain samples using time-weighted averages (Table 3) . These values did not include smelt collected from the Inland Sea. Caloric values for smelt <65mm taken from Lantry (1991).

Day of model year <sup>a</sup>	Smelt >65mm	Smelt <65mm	Yellow Perch
1	976	673	1242
62	1131	673	1242
138	1245	673	1242
214	976	673	1242
365	976	673	1242

<sup>a</sup> Model year began June 1.

Table 5. Seasonal caloric values (cal/g wet weight) of smelt used in landlocked Atlantic salmon bioenergetics model. Values for smelt >65mm were obtained from Lake Champlain samples using time-weighted averages (Table 3) . These values did not include smelt collected from the Inland Sea. Caloric values for smelt <65mm taken from Lantry (1991):

Day of model year <sup>a</sup>	Smelt >65mm	Smelt <65mm
1	976	673
62	1131	673
138	1245	673
214	976	673
365	976	673

<sup>a</sup> Model year began June 1.

Table 6. Walleye weights used in bioenergetics model.

Cohort	Lower 95% weight interval (grams)	Median weight (grams)	Upper 95% weight interval (grams)
5	1429	1728	2090
6	1480	1757	2090
7	1541	1787	2090
8	1580	1817	2090
9	1636	1848	2100
10	1686	1879	2100
11	1737	1911	2100
12	1772	1943	2122
13	1826	1976	2143
14	1863	2010	2165
15	1895	2044	2219
16	1910	2078	2253
17	1920	2113	2322
18	1929	2149	2392
19	1939	2185	2465
20	1920	2222	2553

Table 7. Landlocked Atlantic salmon weights used in bioenergetics model.

Cohort	Start Weight (grams)	End Weight (grams)
1	60	860
2	860	1750
3	1750	2300
4	2300	2800
5	2800	3200
6	3200	3600

Table 8. Walleye population estimates used in bioenergetics model.

Cohort	High Population Estimate Mort=0.3	Low Population Estimate Mort=0.3	High Population Estimate Mort=0.5	Low Population Estimate Mort=0.5
4	165651	82825	275444	137722
5	115955	57978	137722	68861
6	81169	40584	68861	34431
7	56818	28409	34431	17215
8	39773	19886	17215	8608
9	27841	13920	8608	4304
10	19489	9744	4304	2152
11	13642	6821	2152	1076
12	9549	4775	1076	538
13	6685	3342	538	269
14	4679	2340	269	134
15	3275	1638	134	67
16	2293	1146	67	34
17	1605	802	34	17
18	1123	562	17	8
19	786	393	8	4
20	551	275	4	2
Total	550884	275440	550884	275442

Table 9. Population of SRB Complex at three annual mortality rates.

Cohort	Initial Pop 390,000	Initial Pop 360,000	Initial Pop 300,000	Initial Pop 210,000
<u>Annual Mortality=0.8</u>				
1	390000	360000	300000	210000
2	78000	72000	60000	42000
3	15600	14400	12000	8400
4	3120	2880	2400	1680
5	624	576	480	336
Total	487344	449856	374880	262416
<u>Annual Mortality=0.65</u>				
1	390000	360000	300000	210000
2	136500	126000	105000	73500
3	47775	44100	36750	25725
4	16721	15435	12863	9004
5	5852	5402	4502	3151
6	2048	1891	1576	1103
Total	598896	552828	460691	322483
<u>Annual Mortality=0.5</u>				
1	390000	360000	300000	210000
2	195000	180000	150000	105000
3	97500	90000	75000	52500
4	48750	45000	37500	26250
5	24375	22500	18750	13125
6	12188	11250	9375	6563
Total	767813	708750	590625	413438

Table 10. Proportion (wet weight) of smelt and yellow perch in walleye diets.

Day of model year	Smelt > 65mm	Smelt < 65mm	Yellow Perch
1	0.994	0.006	0.0
31	0.740	0.003	0.257
61	1.000	0.0	0.0
148	1.000	0.0	0.0
365	0.994	0.006	0.0

Table 11. Proportion (wet weight) of smelt in landlocked Atlantic salmon diets.

Day of model year	Smelt > 65mm	Smelt < 65mm
1	0.995	0.005
61	1.000	0.0
122	0.655	0.345
153	0.569	0.431
183	0.321	0.679
273	1.000	0.0
365	1.000	0.0

Table 12. Proportion (wet weight) of various dietary items in lake trout diets, used in the bioenergetics model.

Day of Model Year	Zooplankton	Smelt		Mysis	White Perch	Yellow Perch	Sculpin
		> 65mm	< 65mm				
Cohort 1-2							
1	36	0	23	40	0	0	1
31	11	86	0	3	0	0	0
62	7	92	0	1	0	0	0
93	5	66	3	26	0	0	0
113	34	35	20	8	3	0	0
365	36	0	23	40	0	0	1
Cohorts 3-10							
1	2	73	0	1	0	7	17
30	2	88	0	1	0	4	5
61	2	88	0	1	0	4	5
365	2	73	0	1	0	7	17

Table 13. Water temperatures used in walleye and SRB Complex bioenergetics models.

Walleye Day of model year	Water Temperature (°C)	Salmon Day of model year	Water Temperature (°C)
1	14.0	1	15.0
25	14.0	30	15.0
30	14.0	61	16.0
39	19.0	92	15.0
44	21.5	123	10.0
79	22.8	153	9.0
148	11.2	184	6.0
164	9.3	215	5.0
184	6.0	243	4.0
215	5.0	274	4.0
243	4.0	304	6.0
274	4.0	335	14.0
304	6.0	365	15.0
334	10.0		
365	14.0		

Table 14. Catch per 55-min midwater trawl (CPUE  $\pm$  SE) and density of fish ( $\pm$  SD) estimated from hydroacoustic assessment at four sampling sites in Lake Champlain in 1990 and 1994.

Area	Mean CPUE		Density (fish/ha)	
	1990	1994	1990	1994
Shelburne Bay	740 $\pm$ 4	381 $\pm$ 74	2704 $\pm$ 220	2231 $\pm$ 862
Juniper	191 $\pm$ 4	126 $\pm$ 5	2043 $\pm$ 560	1484 $\pm$ 371
Malletts Bay	465 $\pm$ 62	460 $\pm$ 47	2800 $\pm$ 80	2803 $\pm$ 404
Inland Sea	1628 $\pm$ 36	977 $\pm$ 118	7100 $\pm$ 700	3551 $\pm$ 1516

Table 15. Mean fish density (fish/ha) estimated by hydroacoustic surveys at five sites in Lake Champlain in 1994. SD=Standard deviation. N=number of transects.

Site	N	Density	SD	CPUE	SD
Shelburne Bay	8	2231	862	381	196
Juniper	4	1484	371	126	9
Malletts Bay	6	2803	404	460	133
Inland Sea	10	3551	1516	977	316
Main Lake	13	461	344	---*	—

\*Main Lake hydroacoustic data was acquired only in June. Midwater trawling was carried out in August.



Table 16. Walleye numbers collected and numbers of empty stomachs during 1993. YP=yellow perch, EPH=Ephemeroptera, CHI=Chironomidae.

Date	Number of fish collected	Number of empty stomachs	Smelt (mm)		YP	EPH	CHI
			> 65	< 65			
6/11	2	0	2	0	0	3	0
6/25	19	4	42	1	0	0	1
7/1	17	10	28	0	0	0	0
7/9	13	5	27	0	5	0	0
7/14	6	5	1	1	0	0	0
8/19	3	1	3	0	0	0	0
10/26	5	3	12	0	0	0	0
Total	65	28	115	2	5	3	1

Table 17. Number and sizes of rainbow smelt found in walleye (WAL) and salmon (ATS) stomachs collected during 1993.

Length Class(mm)	Month											
	June		July		Aug		Oct		Nov		Dec	
	WAL	ATS	WAL	ATS	WAL	ATS	WAL	ATS	WAL	ATS	WAL	ATS
20-29	-		1	-	-	-	-	2		1		-
30-39	-		-	-	-	-	-	1		-		-
40-49	-		-	-	-	-	-	7		12		3
50-59	-		-	-	-	-	-	12		76		22
60-69	1		1	3	1	-	-	15		55		22
70-79	3		7	10	1	-	2	20		40		3
80-89	8		11	17	-	-	2	6		33		3
90-99	9		11	23	-	-	-	-		2		-
100-109	1		10	19	-	-	-	-		-		-
110-119	-		4	6	1	1	1	-		2		-
120-129	-		8	6	-	1	1	-		1		-
130-139	5		4	5	-	-	5	1		-		-
140-149	7		-	2	-	-	-	-		-		-
150-159	3		-	-	-	-	1	-		-		-
160-169	2		-	-	-	-	-	-		-		-
170-179	4		-	-	-	-	-	-		-		-
180-189	1		-	-	-	-	-	-		-		-
190-199	1		-	-	-	-	-	-		-		-

Table 18. Landlocked Atlantic salmon numbers collected and numbers of empty stomachs during 1993. EPH=Ephemeroptera, CHI=Chironomidae, TRI=Trichoptera.

Date	Number of fish collected	Number of empty stomachs	Smelt (mm)		EPH	CHI	TRI
			> 65	< 65			
6/25	2	2	0	0	0	0	0
7/1	20	3	71	1	1	0	1
7/14	10	1	17	0	0	0	0
7/21	1	0	2	0	0	0	0
8/19	4	1	2	0	0	0	1
10/26	1	0	1	0	0	0	0
10/27	18	9	34	29	0	2	0
11/3	1	0	2	6	0	0	0
11/8	29	8	102	112	1	0	0
12/9	4	1	14	39	0	0	0
Total	90	25	245	187	2	2	2

Table 19. Cumulative consumption of all smelt by lake trout and other salmonids at various stocking and mortality rates. For lake trout, the mortality rates were 0.40 for cohorts 1-10 and 0.30 for cohorts 11-15. For the other salmonids, the model used five cohorts at the 0.80 mortality rate and six cohorts for the other mortality rates. Lake trout data are from LaBar (1993).

Lake Trout				SRB Complex				
Stocking rates	Consumption (g X 10 <sup>6</sup> )			Stocking rates	Consumption (g X 10 <sup>6</sup> )			Mortality Rate
	<65mm	>65mm	Total		<65mm	>65mm	Total	
225,000	175	1,229	1,404	390,000	258	1,135	1,393	.80
180,000	140	983	1,123	360,000	238	1,048	1,286	.80
130,000	102	710	812	300,000	198	873	1,071	.80
110,000	86	600	686	210,000	139	611	750	.80
80,000	62	437	499	390,000	475	2,185	2,660	.65
				360,000	439	2,017	2,456	.65
				300,000	365	1,681	2,046	.65
				210,000	255	1,177	1,432	.65
				390,000	834	3,975	4,809	.50
				360,000	770	3,669	4,439	.50
				300,000	642	3,057	3,700	.50
				210,000	450	2,140	2,590	.50

Table 20. Cumulative consumption of smelt (>65mm) by walleye at two mortality rates, two population sizes, and three growth rates. The number of smelt (<65mm) consumed by walleye were too rare to be included in the analyses.

Mortality rate	Population size	Growth	Consumption (g X 10 <sup>6</sup> )
0.5	High	High	820
0.5	High	Medium	710
0.5	High	Low	650
0.5	Low	High	405
0.5	Low	Medium	370
0.5	Low	Low	355
0.3	High	High	1,315
0.3	High	Medium	1,100
0.3	High	Low	1,050
0.3	Low	High	660
0.3	Low	Medium	590
0.3	Low	Low	530

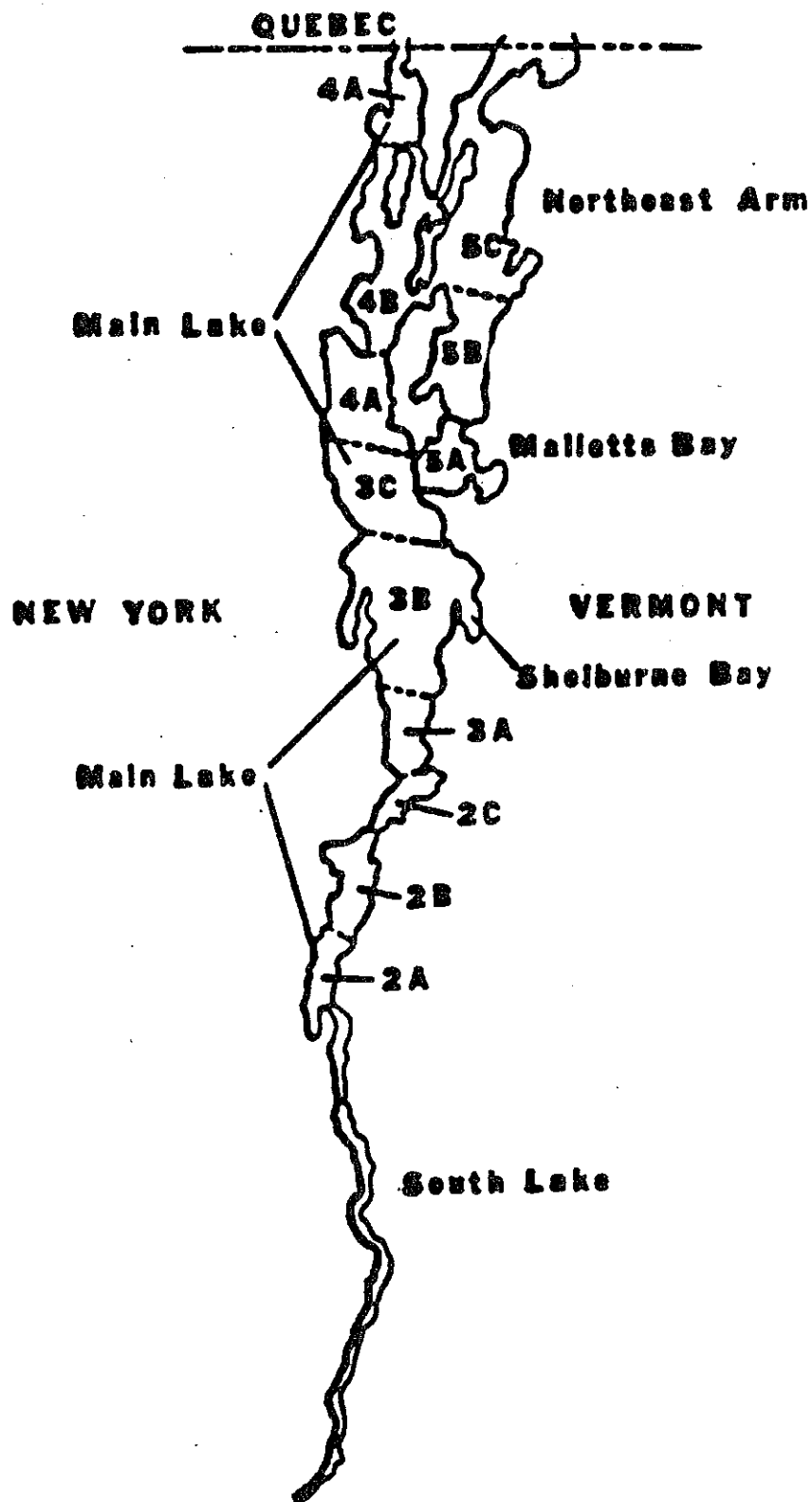


Figure 1. Lake Champlain, showing fisheries management zones.

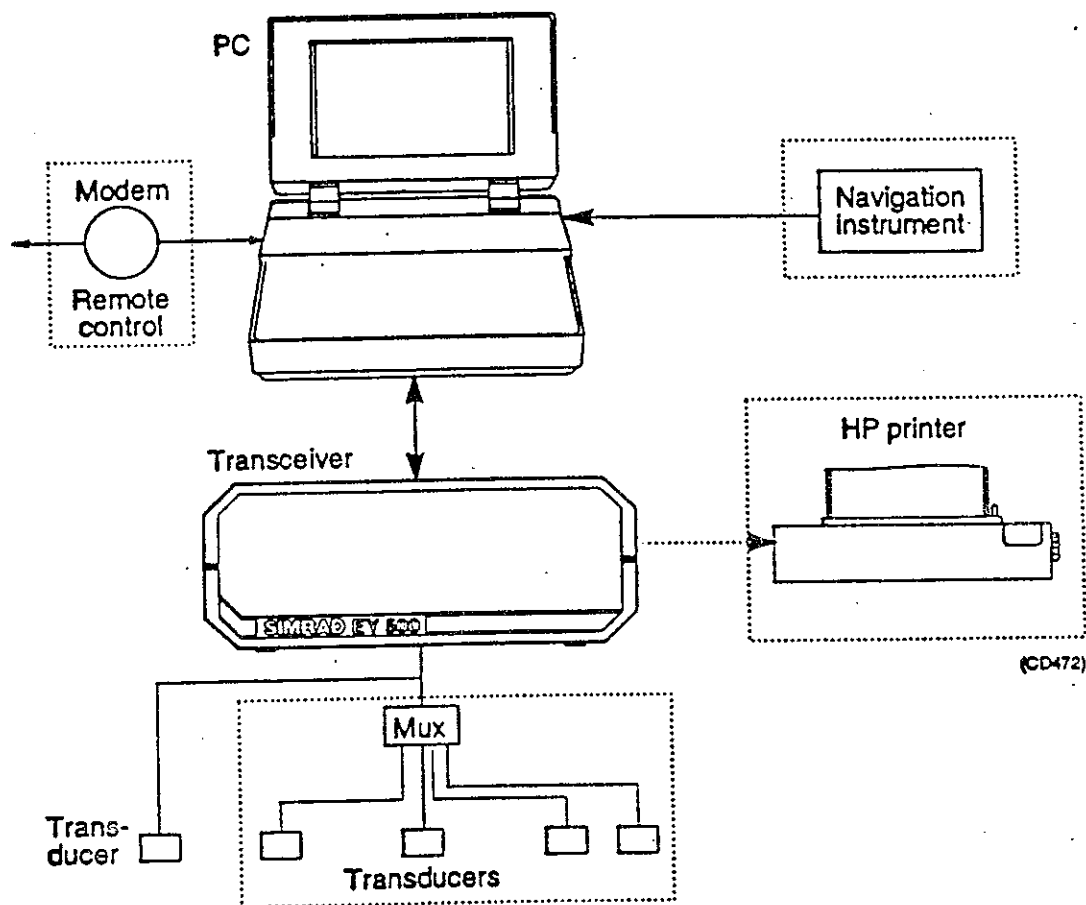


Figure 2. Schematic diagram of Simrad EY 500 hydroacoustic assessment system (taken from Simrad Owner's Manual).

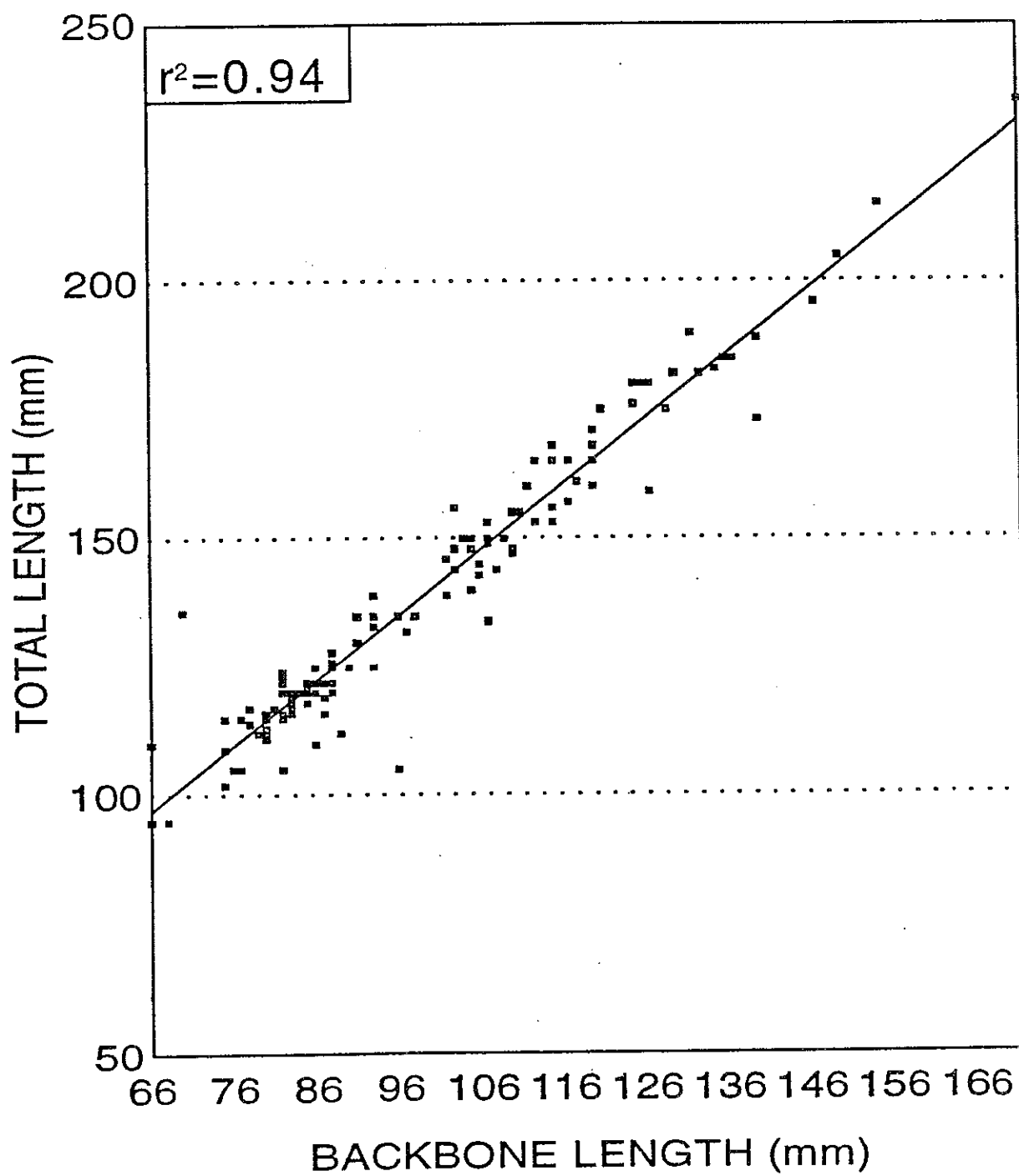


Figure 3. Relationship of total length to backbone length in rainbow smelt collected in 1993 trawls.



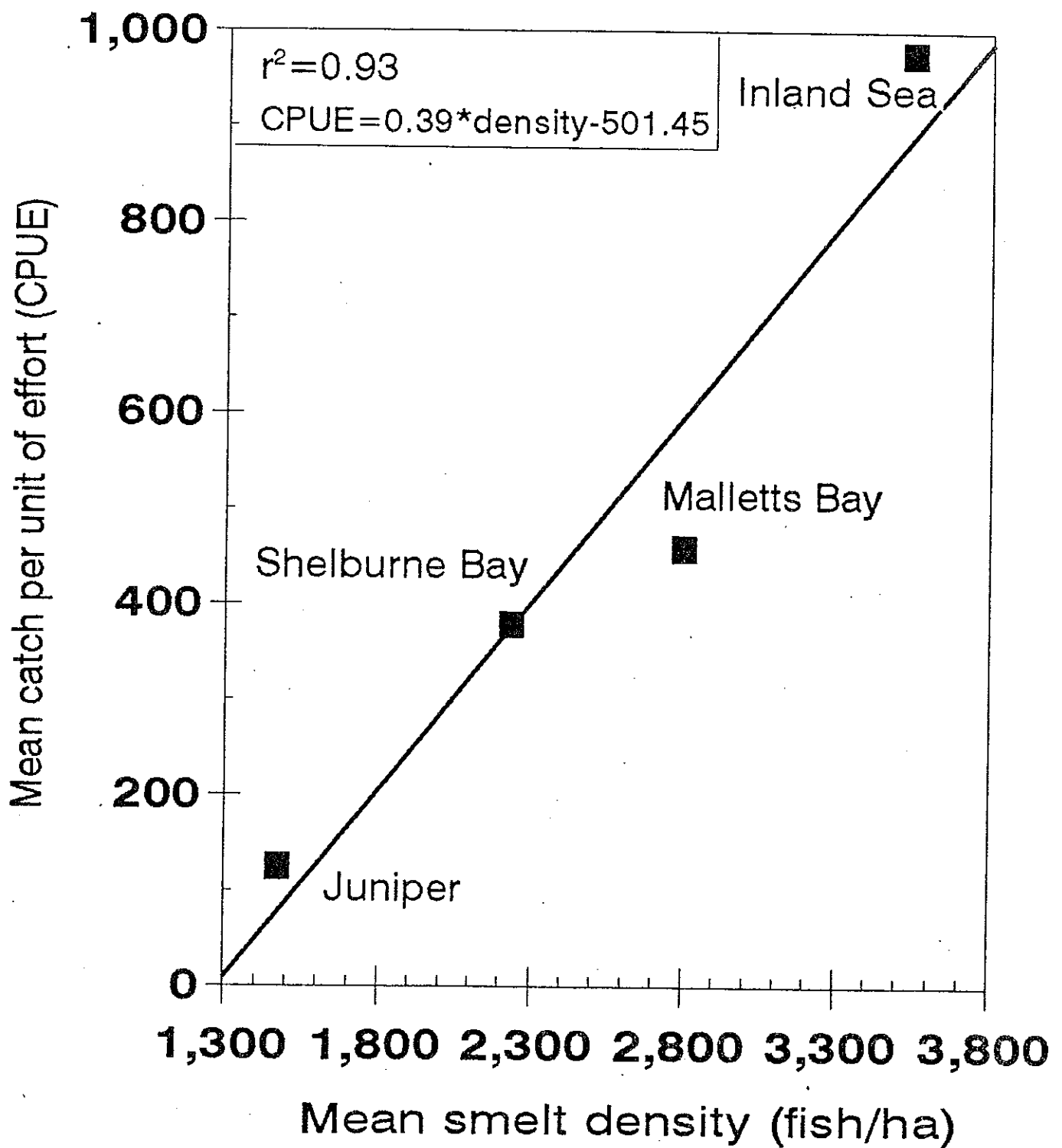


Figure 4. Relation of mean catch per unit of effort of smelt in midwater trawls to mean smelt density estimated by hydroacoustic assessment at the four standard trawling sites on Lake Champlain in 1994.

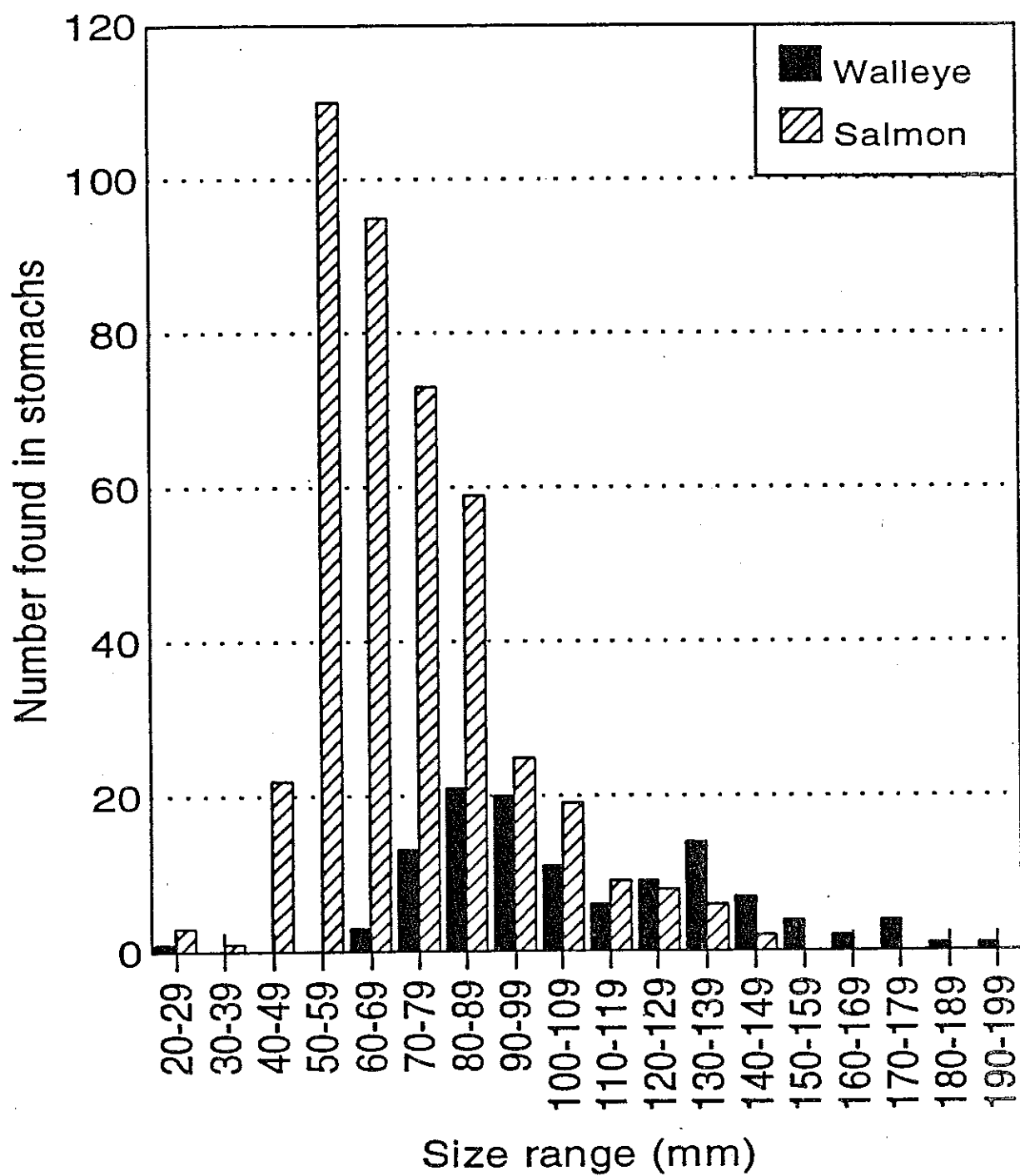


Figure 5. Length distribution of rainbow smelt found in walleye and Atlantic salmon stomachs collected in 1993 from the main Lake portion of Lake Champlain.

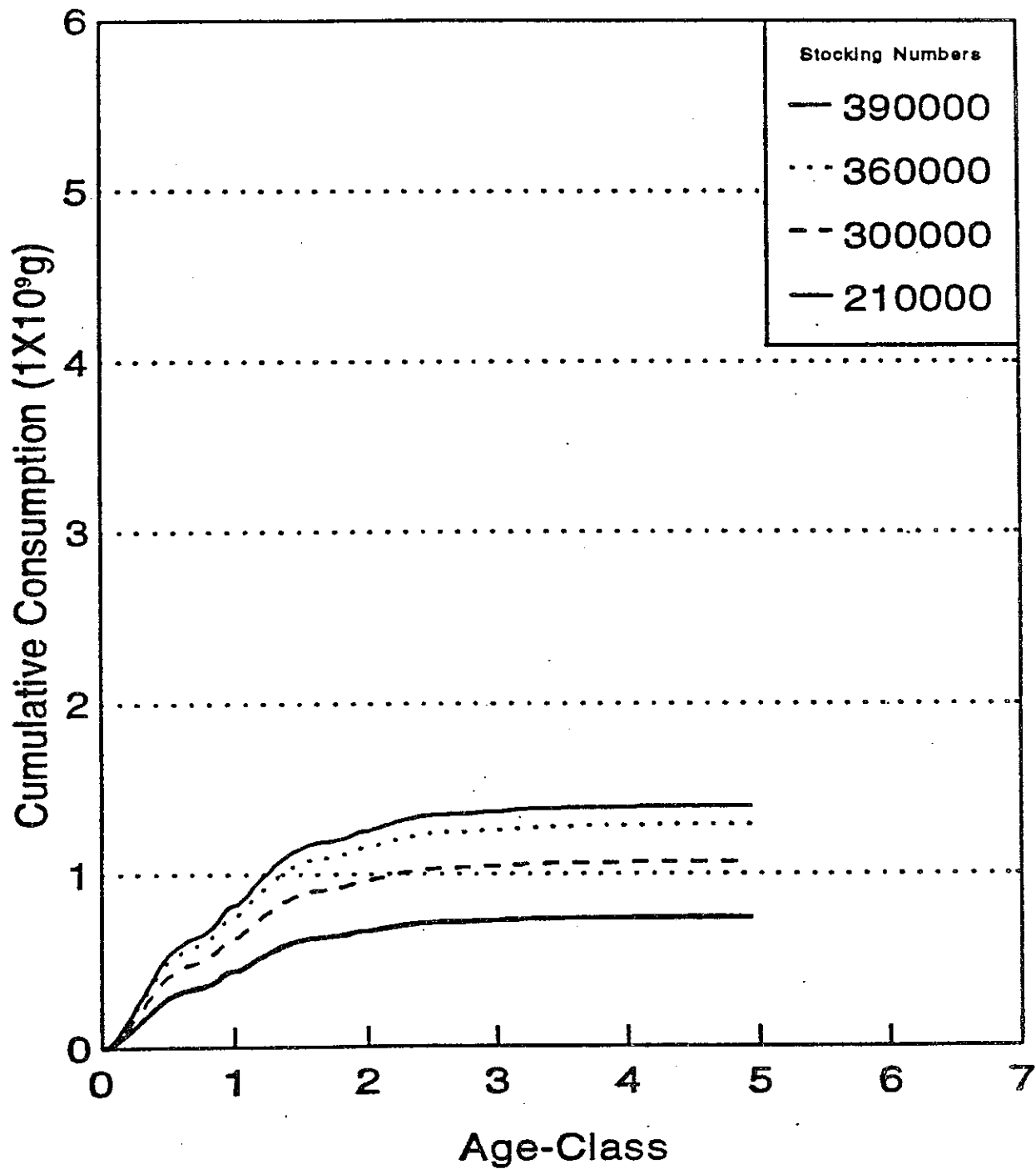


Figure 6. Cumulative consumption of rainbow smelt by the SRB complex at various stocking levels, an annual mortality rate of 0.80 and 5 cohorts estimated by bioenergetic models. (Note: in this and all subsequent figures where appropriate, consumption figures refer only to the Main Lake portion of the lake.)

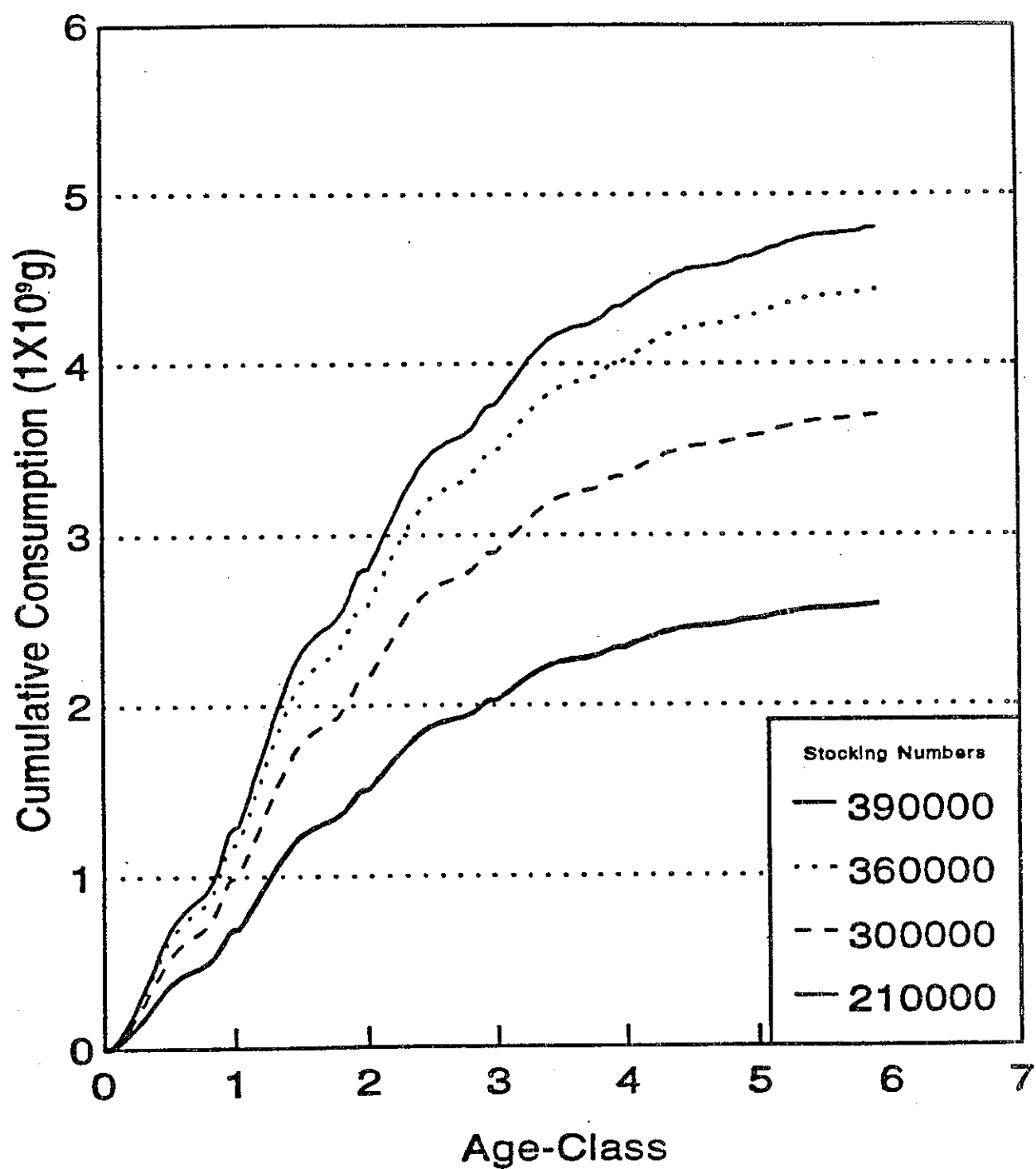


Figure 7. Cumulative consumption of rainbow smelt by the SRB complex at various stocking levels, an annual mortality rate of 0.50 and 6 cohorts estimated by bioenergetic models.

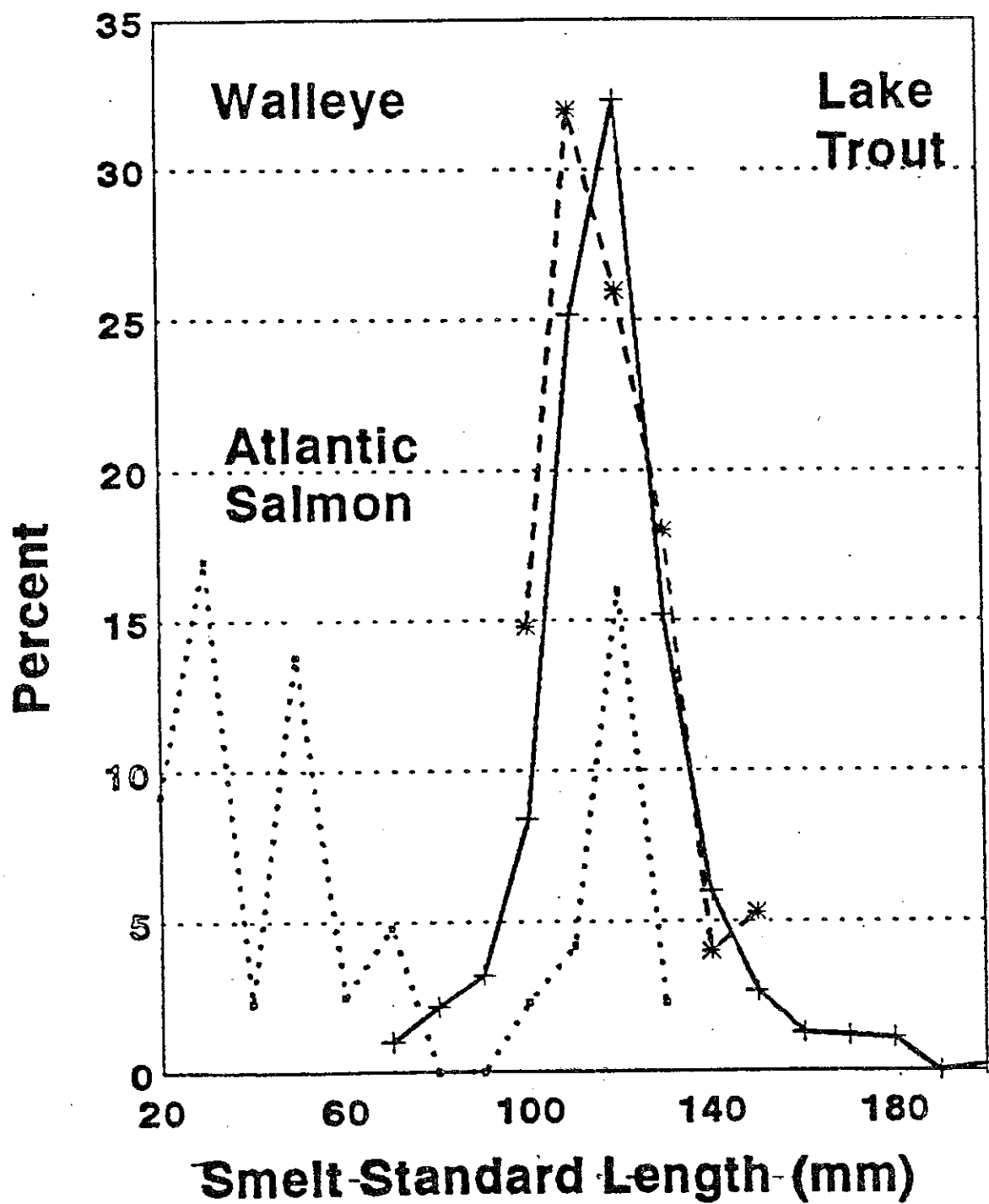


Figure 8. Length frequency distribution of rainbow smelt found in Atlantic salmon, walleye, and lake trout stomachs (from Kirn 1986).

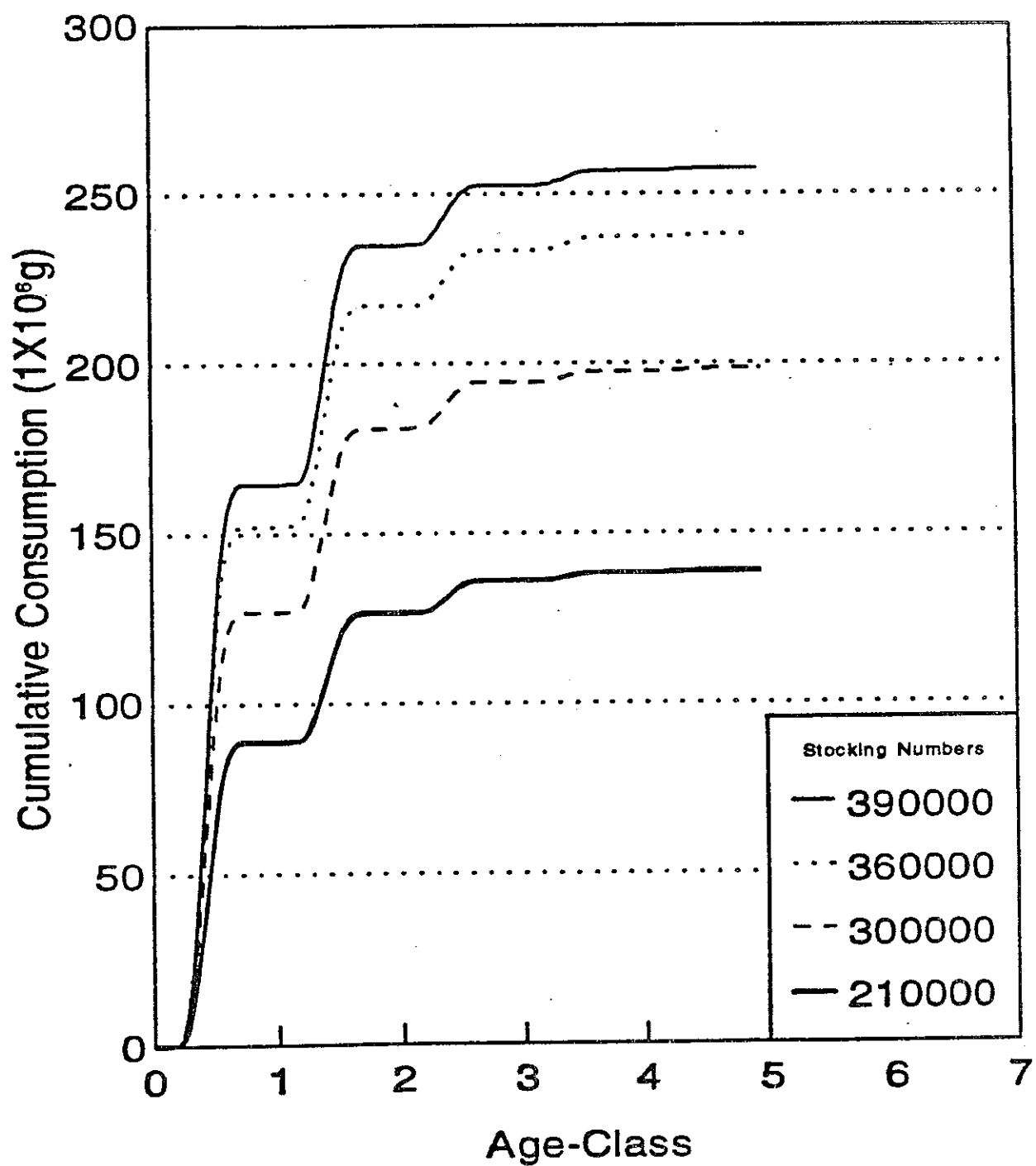


Figure 9. Cumulative consumption of rainbow smelt <65 mm by the SRB complex at various stocking levels, an annual mortality of 0.80 and 5 cohorts, estimated by bioenergetic models.

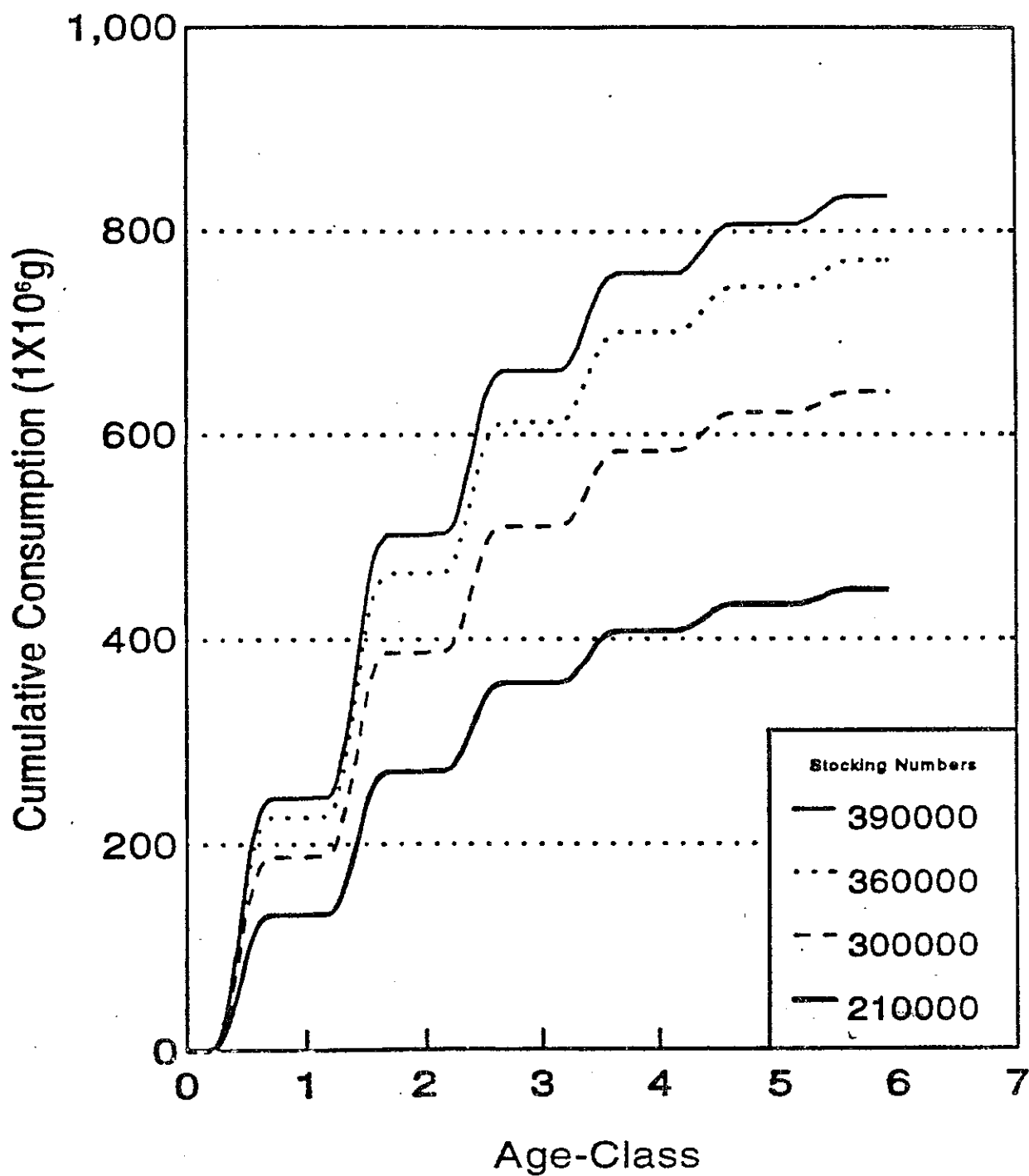


Figure 10. Cumulative consumption of rainbow smelt < 65 mm by the SRB complex at various stocking levels, an annual mortality of 0.50 and 6 cohorts, estimated by bioenergetic models.

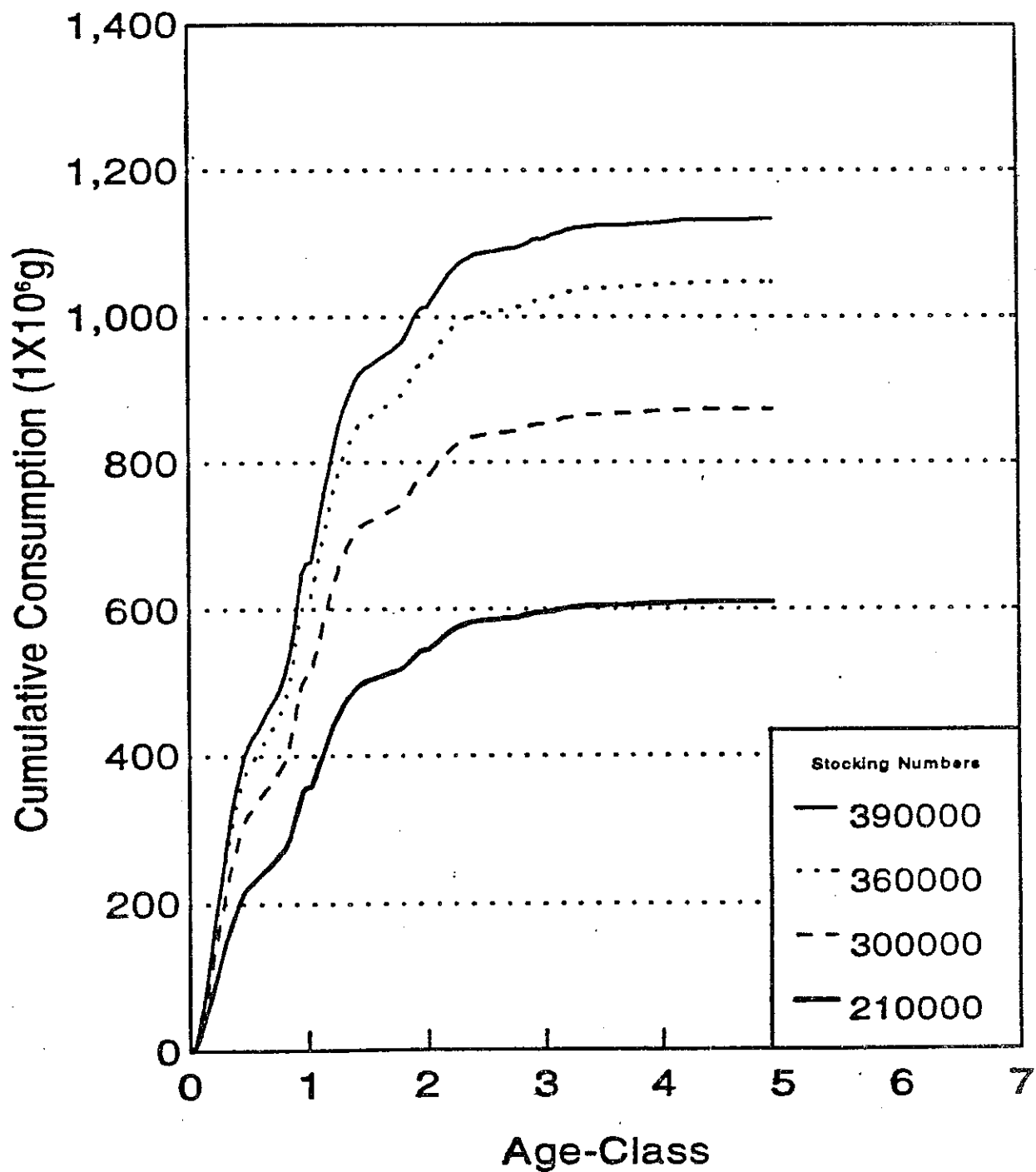


Figure 11. Cumulative consumption of rainbow smelt >65 mm by the SRB complex at various stocking levels, an annual mortality of 0.80 and 5 cohorts, estimated by bioenergetic models.



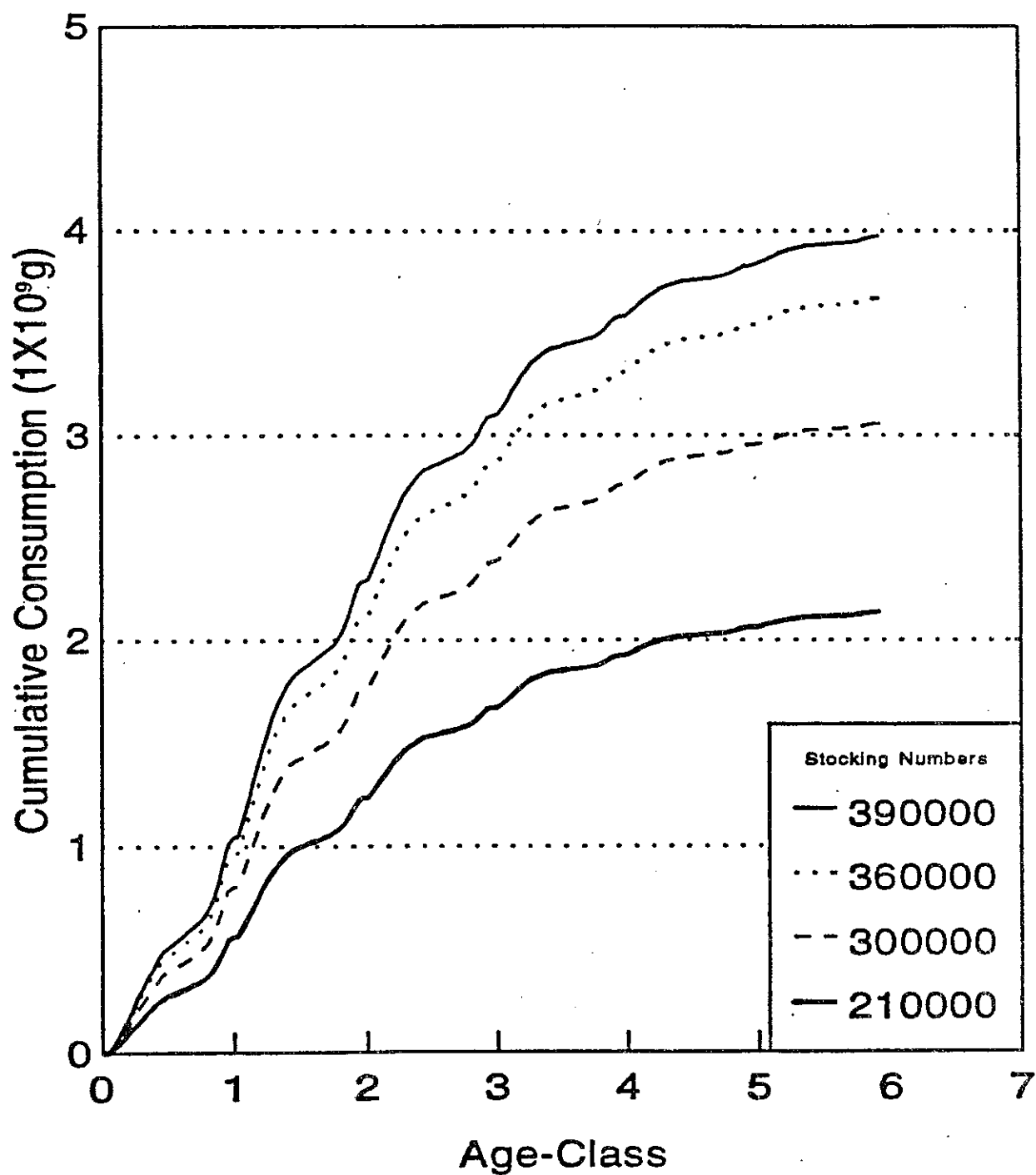


Figure 12. Cumulative consumption of rainbow smelt >65 mm by the SRB complex at various stocking levels, an annual mortality of 0.50 and 6 cohorts, estimated by bioenergetic models.

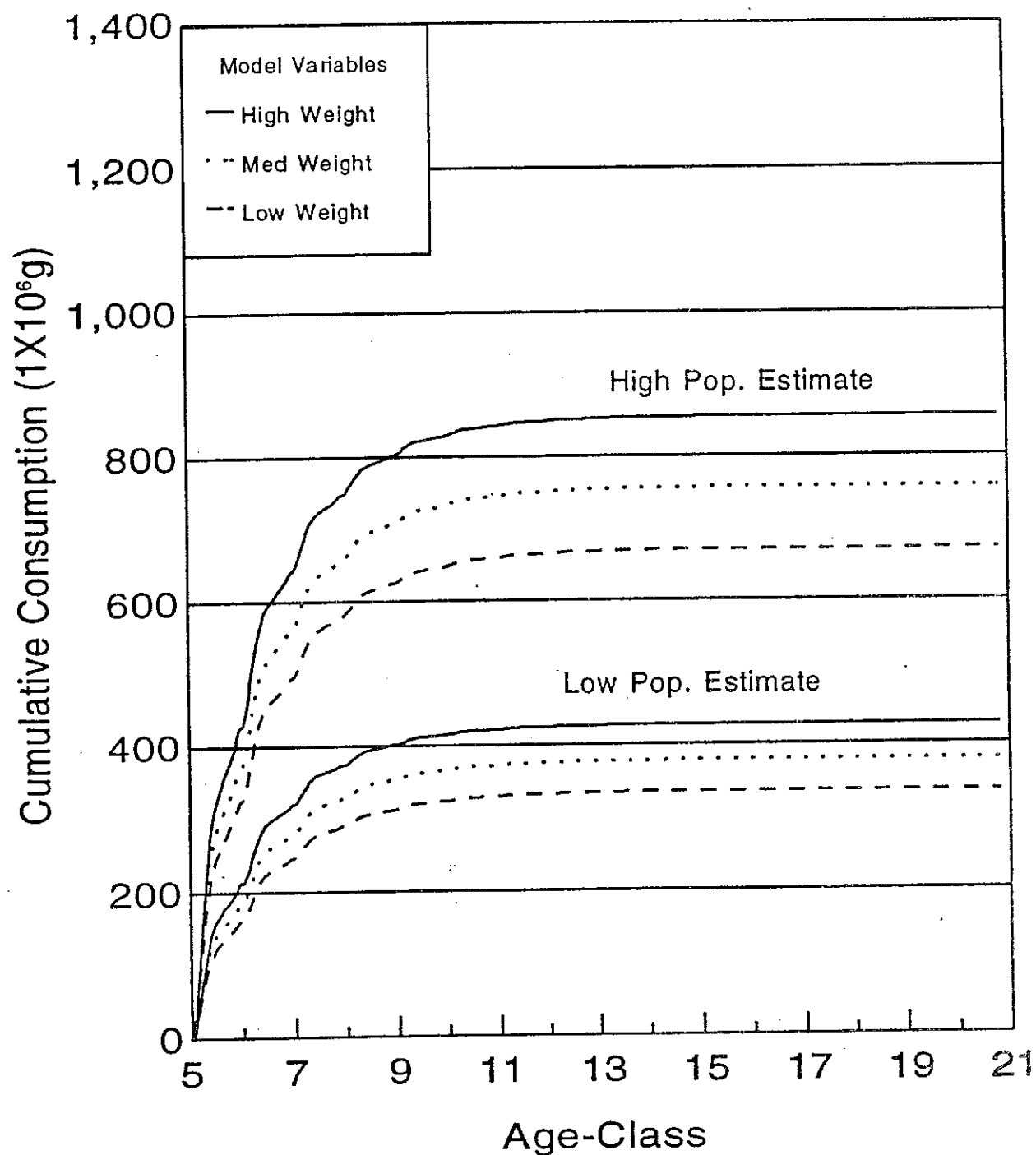


Figure 13. Cumulative consumption of all prey by walleye at high, medium and low growth rates, high and low population sizes, and annual mortality of 0.50, estimated by bioenergetic models.

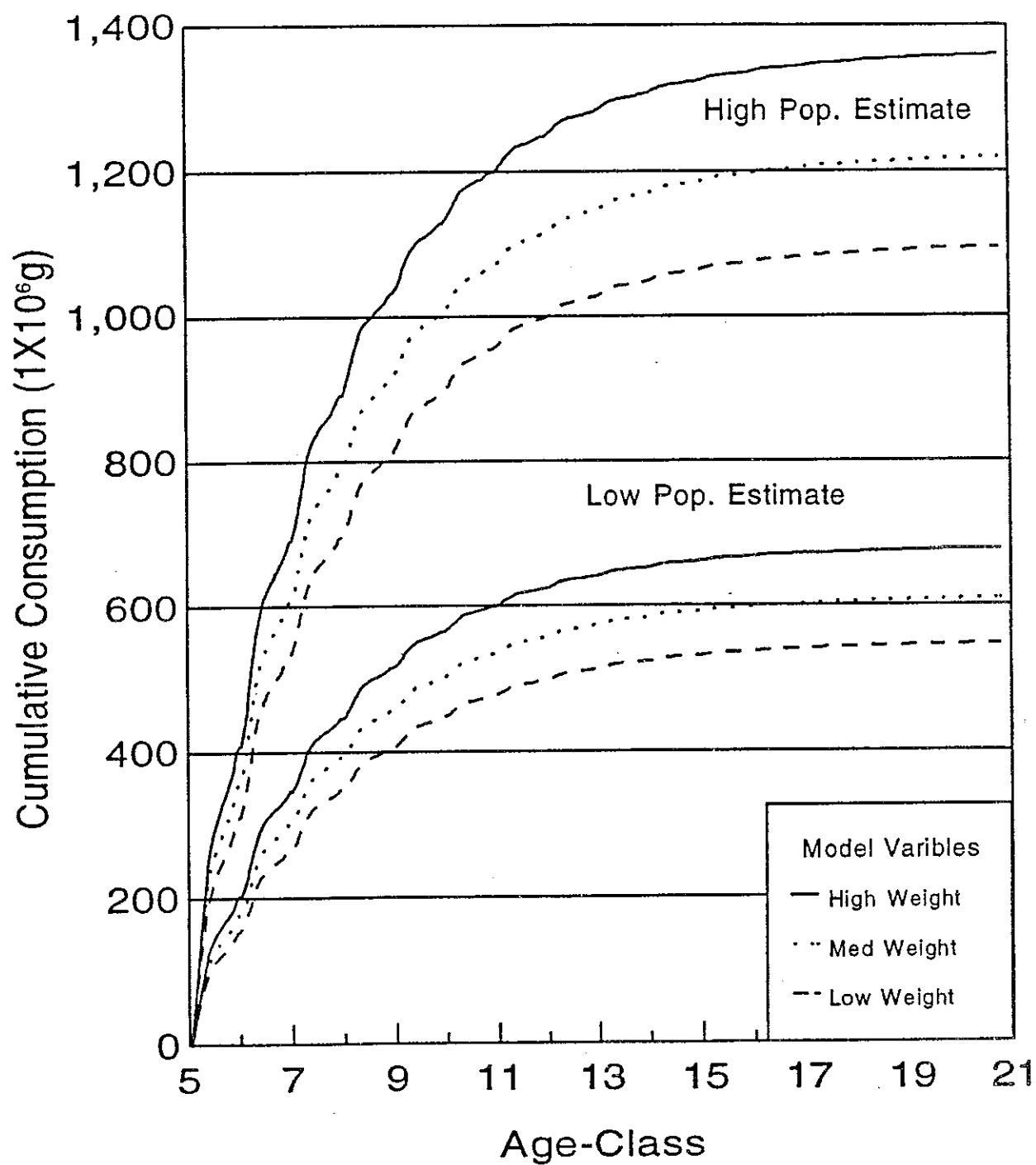


Figure 14. Cumulative consumption of all prey by walleye at high, medium and low growth rates, high and low population sizes, and annual mortality of 0.30, estimated by bioenergetic models.

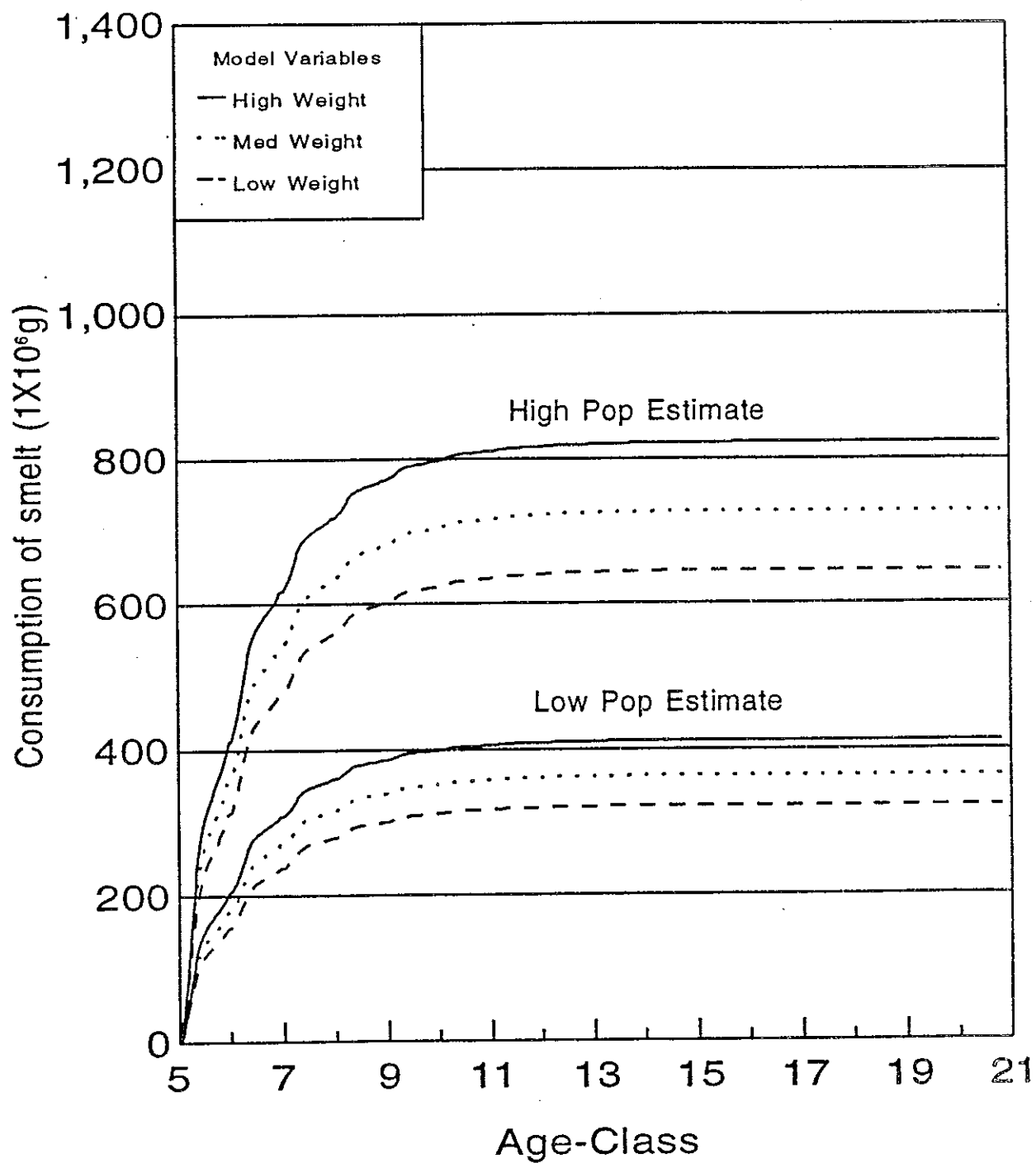


Figure 15. Cumulative consumption of rainbow smelt by walleye at high, medium and low growth rates, high and low population sizes, and annual mortality of 0.50, estimated by bioenergetic models.

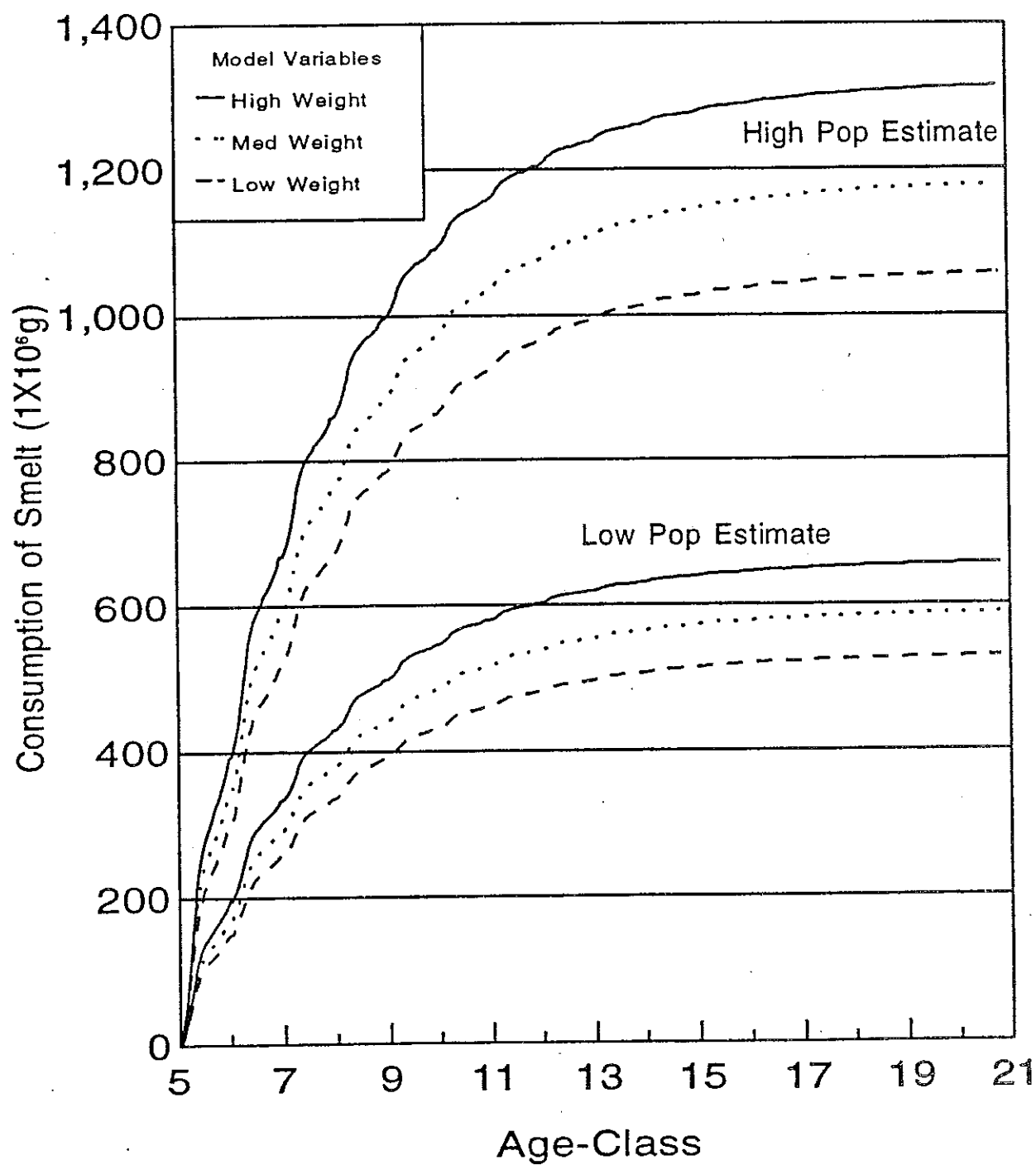


Figure 16. Cumulative consumption of rainbow smelt by walleye at high, medium and low growth rates, high and low population sizes, and annual mortality of 0.30, estimated by bioenergetic models.

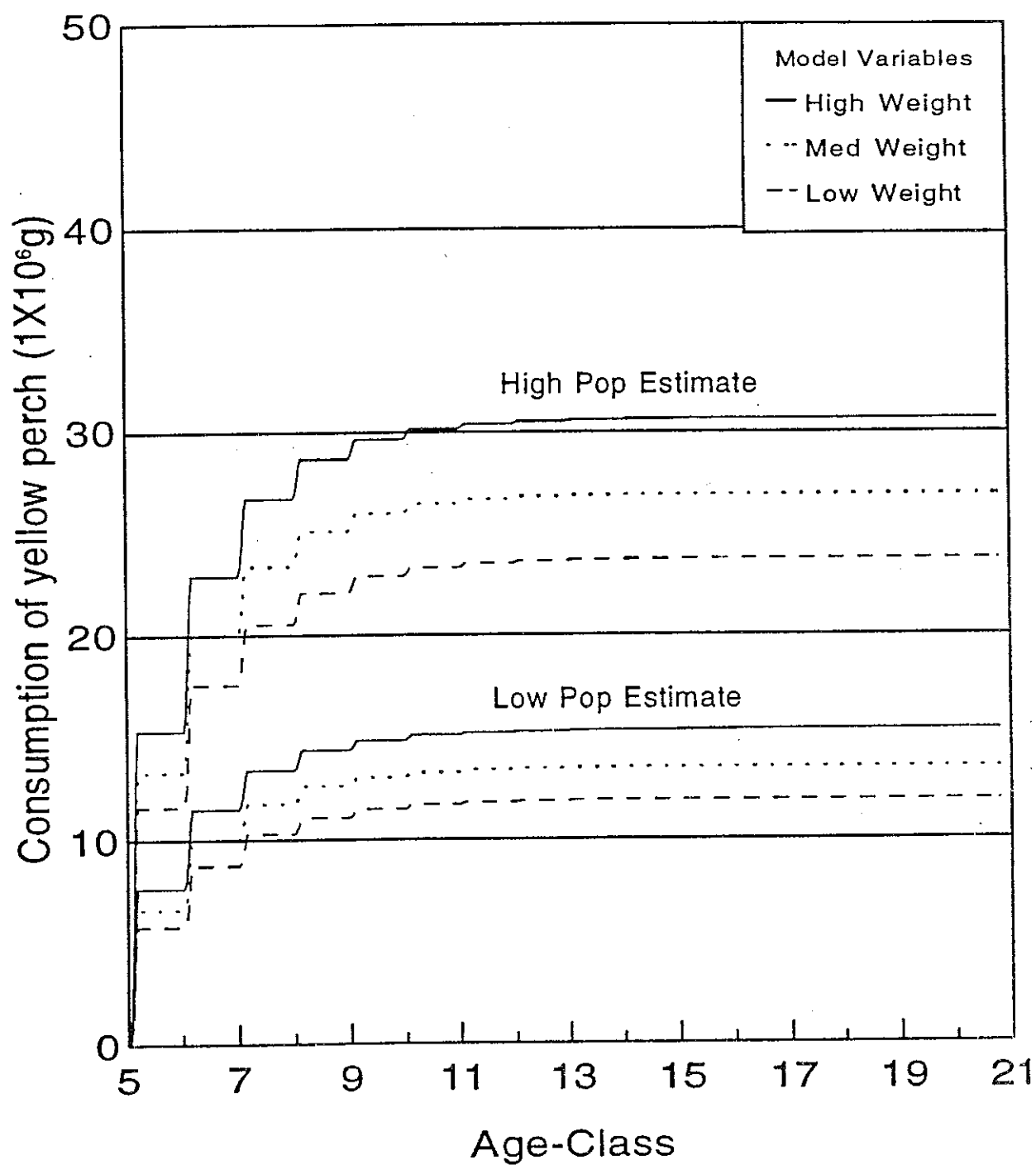


Figure 17. Cumulative consumption of yellow perch by walleye at high, medium and low growth rates, high and low population sizes, and annual mortality of 0.50, estimated by bioenergetic models.

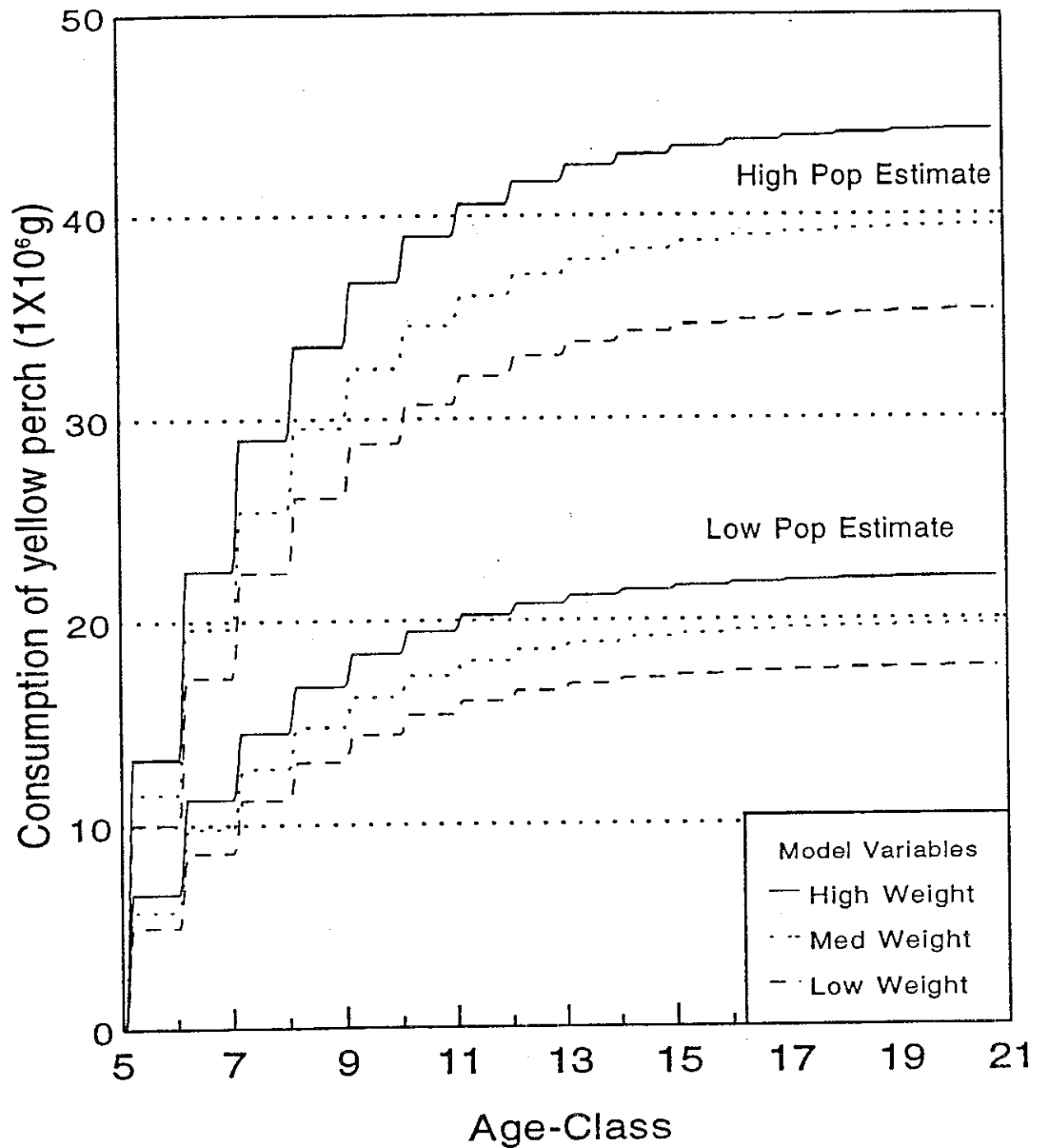


Figure 18. Cumulative consumption of yellow perch by walleye at high, medium and low growth rates, high and low population sizes, and annual mortality of 0.30, estimated by bioenergetic models.

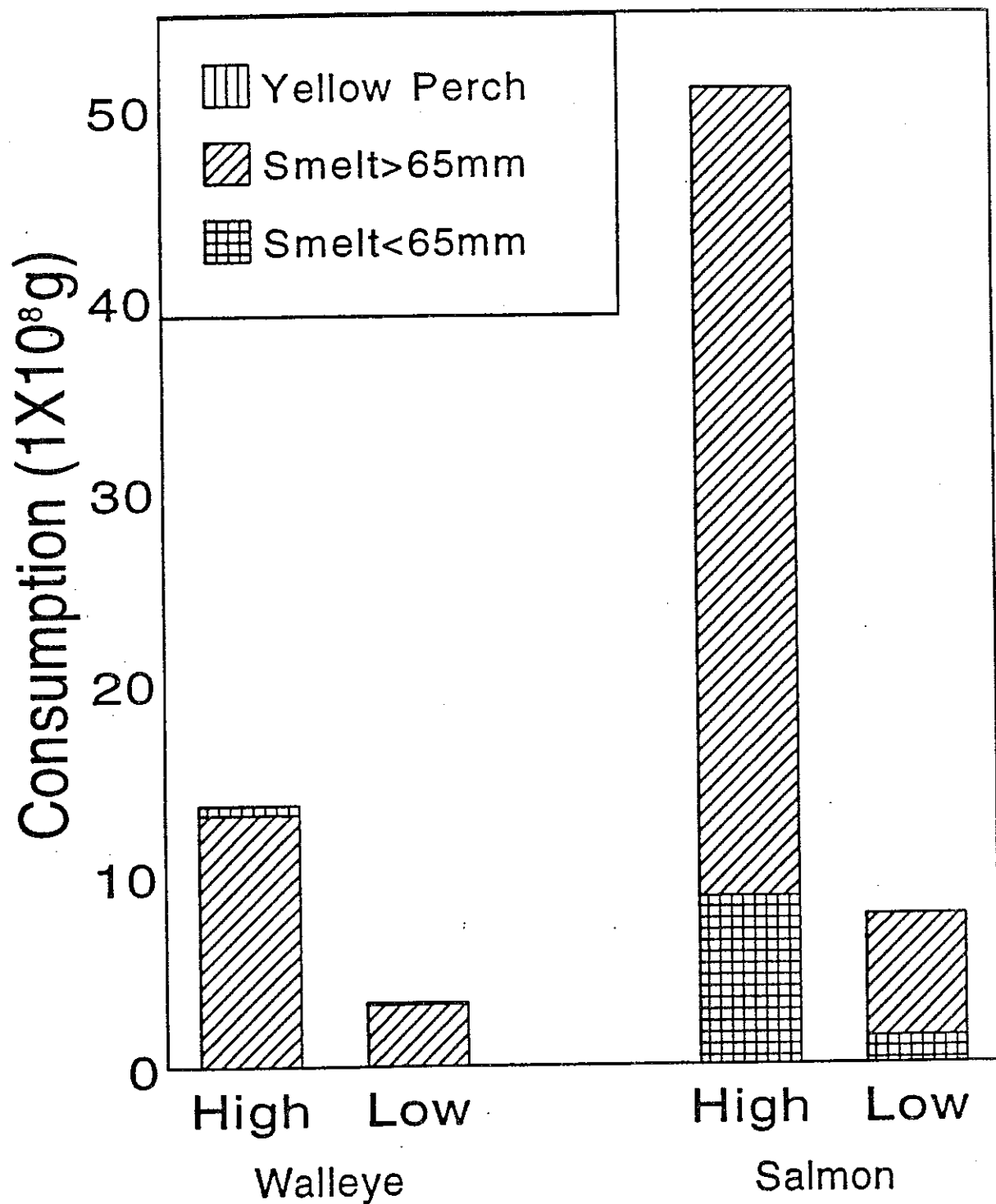


Figure 19. Total consumption of yellow perch, and small (< 65 mm) and large (> 65 mm) rainbow smelt by walleye and the SRB complex under high and low population sizes (see text for specifics of how high and low population estimates were derived).