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Bioenergetics of Walleye in Lake Oahe, South Dakota

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Bioenergetics of Walleye
in Lake Oahe, South Dakota

By

Scott D. Bryan

A thesis submitted in partial fulfillment
of the requirements for the Master of Science
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1995

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IN LAKE OAHE, SOUTH DAKOTA

This thesis is approved as a creditable and independent investigation by a candidate for the Master of Science degree and is acceptable for meeting the thesis requirements for this degree. Acceptance of this thesis does not imply that the conclusions reached by the candidate are necessarily the conclusions of the major department.

Dr. Walter G. Duffy — Date
Major Advisor

Dr. Charles G. Scalet — Date
Head, Department of Wildlife
and Fisheries Sciences

Dedicated to my best friend, my father, who
taught me to enjoy and appreciate the outdoors
and who has always been there for me,
through the good times and the bad.

ACKNOWLEDGMENTS

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ABSTRACT

BIOENERGETICS OF WALLEYE
IN LAKE OAHE, SOUTH DAKOTA

Scott D. Bryan

April 1995

The food habits, caloric density, and population dynamics of walleye *Stizostedion vitreum* were determined in 1993 and 1994 and combined with information on energetics and growth to determine the trophic interactions of walleyes in Lake Oahe, South Dakota. Monofilament gill nets were set at three depths in the water column (bottom, suspended, and surface) from May through September, 1994 to determine the effect of gill net placement on catch rates of walleyes. Catch per unit effort of walleyes was greater in bottom nets during July (5.2/net-h) than any other month or net location. In addition, 25- and 38-mm mesh sizes were effective for capturing walleyes between 320 and 490 mm.

High water levels and below average water temperatures allowed a cold-water prey fish, rainbow smelt *Osmerus mordax*, to occupy most of the water column throughout Oahe Reservoir in 1993. The fluctuating water levels and water temperatures have also had an influence on the food habits of walleyes. The relative importance (RI) index was used to compare walleye food habits in 1993 with those from a similar study of Lake Oahe conducted in 1991. Rainbow smelt had higher RI values than other prey in all regions of the reservoir during May to September, 1993. In 1991, rainbow smelt dominated the diet of walleyes only in the lower portion of the reservoir and diets were very diverse in the upper reaches.

Mean seasonal caloric density of mature walleyes (≥ age 3) showed distinct seasonal trends during May through September, 1994. Mean energy density was lowest during spring (1,820 cal/g) and highest during fall (1,960 cal/g). Immature walleyes (≤ age-2) showed no apparent seasonal trends in mean caloric density, but values differed among months. Changes in caloric density were also observed for rainbow smelt, lake herring *Coregonus artedi,* yellow perch *Perca flavescens,* and spottail shiners *Notropis hudsonius* among months. Age and seasonal differences exist in the energy density of fishes, and these factors need to be considered in energetics studies.

A bioenergetics model developed for walleyes in Lake Oahe was used to estimate predation on rainbow smelt, the primary forage species in the reservoir. Model estimates indicated that ages 1-6 walleyes in Lake Oahe would consume most of the rainbow smelt production, 8.639 x 10^9 g, over the course of one year. Potential changes in growth and consumption resulting from changing environmental conditions were then modeled. Model results suggested that growth of walleyes would increase slightly (20%) if the rainbow smelt population crashed and lake herring became established as a predominant prey species. However, growth of walleyes would decrease by as much as 50% if the rainbow smelt population declined due to an increase in water temperatures and a decrease in cold water habitat.

The use of bioenergetics modeling in Lake Oahe will allow biologists to address a wide variety of problems and concerns that may affect management decisions. This study demonstrated the importance of rainbow smelt in Lake Oahe as a forage fish. Management efforts need to be directed towards understanding this prey species to ensure the future of the walleye fishery.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

Introduction

Lake Oahe, the second largest reservoir on the Missouri River system, is located in north-central South Dakota and south-central North Dakota. Like many reservoirs in the midwest, the fish community in Lake Oahe is comprised of both introduced and indigenous sport fish. Walleye *Stizostedion vitreum* are endemic to the Missouri River, but originally they were not abundant (Benson 1968). However, they are now the most prolific sport fish in Oahe Reservoir (Wickstrom et al. 1993; Lott et al. 1994). Despite the importance of walleye in Lake Oahe, fluctuations in the harvest and declining natural reproduction have typified the fishery in recent years (Fielder 1990). To alleviate the problem of diminishing recruitment, the South Dakota Department of Game, Fish and Parks (SDGF&P) began stocking fry and fingerling walleyes in 1983 (Fielder 1992). In 1984, reduced daily harvest limits as well as minimum size limits were enacted on Lake Oahe in hopes of returning the walleye fishery to a more stable state, which to this point has been successful (Fielder 1990). Other popular resident sport fishes in Lake Oahe include northern pike *Esox lucius*, sauger *Stizostedion canadense*, channel catfish *Ictalurus punctatus*, and yellow perch *Perca flavescens*.

The closure of Oahe Dam resulted in the formation of cold water habitat and an opportunity for a new fishery to be established. In 1971, Lake Superior strain rainbow smelt *Osmerus mordax* were introduced into Lake Sakakawea, North Dakota. Rainbow smelt later escaped downstream to Oahe Reservoir and established a reproducing population by 1977 (Burczynski et al. 1987). To take advantage of this new habitat and prey base, SDGF&P began stocking a variety of coldwater predators. Lake trout *Salvelinus namaycush*, lake whitefish *Coregonus clupeaformis*, kokanee salmon *Oncorhynchus nerka*, steelhead trout *Oncorhynchus mykiss*, and brown trout *Salmo trutta* were all unsuccessfully introduced (Robert Hanten, SDGF&P, personal communication). In 1982, chinook salmon *Oncorhynchus tshawytscha* were introduced into Lake Oahe and subsequent stockings have created a popular sport fishery (Warnick 1987). In addition, a limited McConaughy strain rainbow trout *Oncorhynchus mykiss* fishery has been established in recent years (Duffy 1992). Lake herring *Coregonus artedii* were stocked (1984, 1988, 1990-1992) to provide a prey base with more stable population characteristics than rainbow smelt, but have not yet become established in the reservoir (SDGF&P, unpublished report).

The newly developed coldwater fishery peaked when over one million chinook salmon were stocked into the reservoir in both 1987 and 1988. This massive introduction of predators into the system put increased pressure on the rainbow smelt population. Condition and density of both chinook salmon and rainbow smelt decreased substantially in the following years and as a consequence, stocking of the salmon was reduced by as much as 80% (Marrone and Stout 1993).

The rapid decline in the smelt population and reductions in the size and growth of chinook salmon has been a cause for concern to reservoir managers and prompted the initiation of two research projects. The first project investigated the limnology of Oahe Reservoir to determine nutrient loading, the productivity of the lower trophic levels (Karnitz 1992), and the transfer of energy from lower trophic levels to forage fishes (Freiburger 1992; Sewell 1993). The second project, which is only partially completed, will provide information on seasonal survival, diet, growth, and energy requirements of walleyes, chinook salmon, and rainbow trout in Lake Oahe through bioenergetics modeling (Duffy 1992).

Although preliminary observations indicate that walleyes, chinook salmon, and rainbow trout may be competing for the same prey, trophic interactions between these three predators are poorly understood (Duffy 1992). Jackson (1992) reported that walleyes were utilizing rainbow smelt as a major prey item in the lower reaches of Oahe Reservoir. As the only established coldwater prey species available in Lake Oahe, rainbow smelt are also thought to be the predominant prey item for chinook salmon (Gary Marrone, SDGF&P, personal communication). Rainbow trout larger than

460 mm appear to be utilizing rainbow smelt, however invertebrates dominate their diet (Lynott et al., *in prep*). Because rainbow smelt are a major component of the diet of both walleyes and chinook salmon, continued stocking of either species could limit production of these predators through interspecific competition.

The purpose of this study was to determine the prey demand of walleyes for rainbow smelt, the primary forage species in Lake Oahe. Prey demand was estimated using a bioenergetics modeling approach. After demand was determined, potential changes in growth and consumption resulting from fluctuating environmental conditions were modeled. The first of these assumed water level management affected the reservoir's thermal regime, causing the rainbow smelt population to decline rapidly and forcing walleyes to feed on alternative prey, primarily yellow perch and spottail shiners *Notropis hudsonius*. The second simulation assumed that the rainbow smelt population collapsed following a period of high population density and intense intraspecific competition. I further assumed that lake herring became established in Oahe Reservoir at this time and that walleyes consumed lake herring, yellow perch and spottail shiners throughout the year.

Study Area

Lake Oahe was formed by the closure of Oahe Dam on the

Missouri River by the U.S. Army Corps of Engineers in August, 1958 (June 1976). The reservoir is one of six mainstem reservoirs on the Missouri River, extending from Pierre, located in central South Dakota, northward to the southern portion of North Dakota near Bismarck. Lake Oahe is federally operated as a multi-purpose reservoir, providing water storage for release during dry summer months to facilitate commercial barge traffic downstream, irrigation for the upper Great Plains, water for human consumption, hydroelectric power, and recreation (Riis 1985).

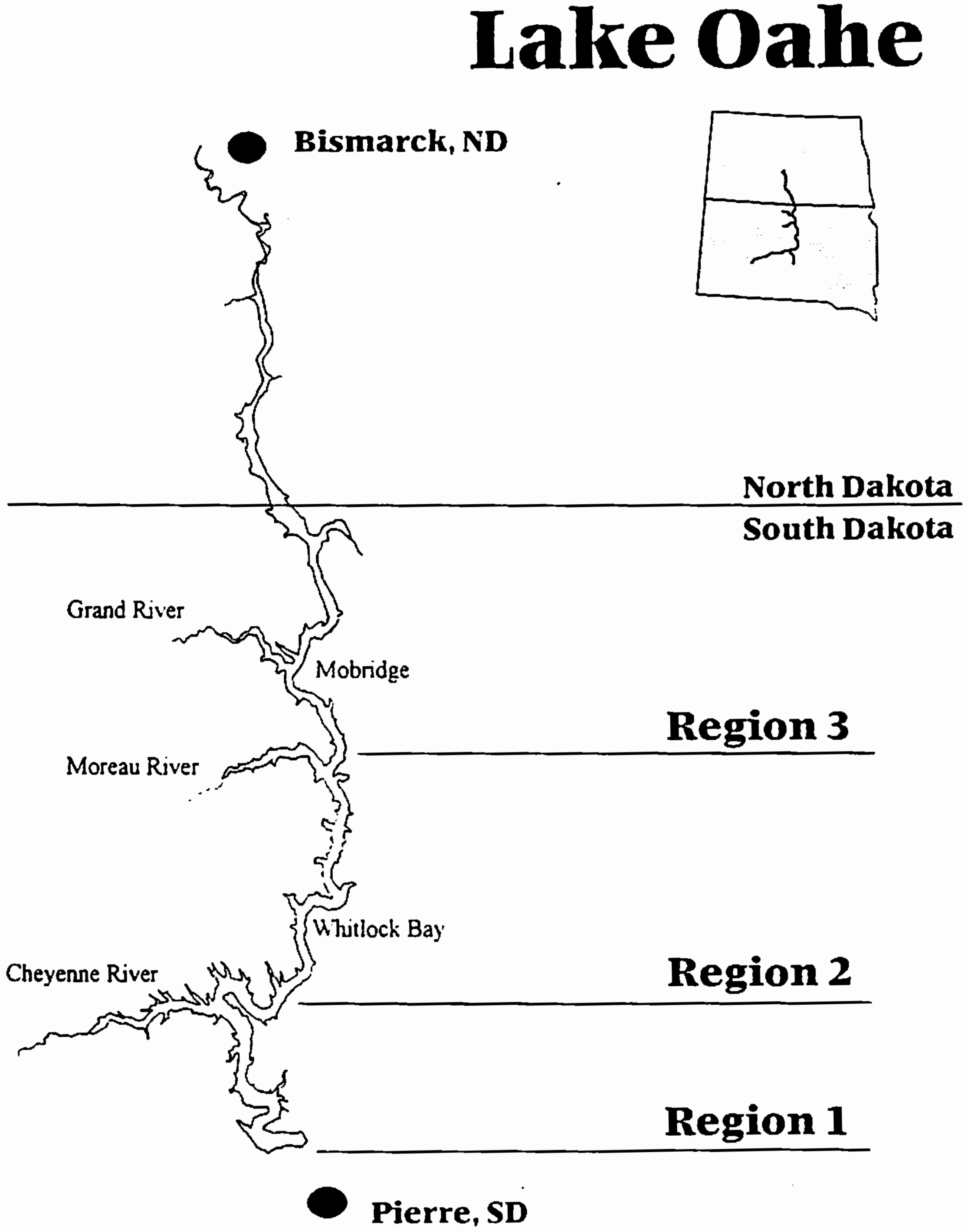
Lake Oahe, with a surface area of 1450 km^2 and a volume of 28.7 km^3 at full pool, is the fifth largest reservoir in the United States (Sveum 1988). Maximum depth of the lake is 66.8 m, mean depth is 19.2 m, and length at maximum pool is 370 km (Stone and Burczynski 1991). The reservoir reached full pool, 493.8 m above mean sea level, in December, 1967 and a minimum operating level has been established at 469.4 m above mean sea level (June 1976).

The damming of the Missouri River has changed its morphology in this reach from a silt laden river to a deep, oligotrophic, cold water reservoir (Duffy 1988). This new habitat created conditions suitable for a two-tiered fishery, capable of sustaining both warm and cold water fish species. Since the closure of Oahe Dam, the fish community has changed dramatically and productivity, as measured by fish growth, appears to have declined (Duffy 1988).

The Grand, Moreau, and Cheyenne rivers are major tributaries that enter the reservoir in South Dakota. These rivers, which drain the prairies of western South Dakota, are turbid and important sources of silt deposition and nutrient production in the reservoir (Nelson 1980).

For purposes of this study, only the South Dakota portion of Lake Oahe was considered, which consists of three distinct regions (Figure I.1). The upper region (Region 3), is riverine, shallow, turbid, and does not thermally stratify during summer months. The middle region (Region 2) is a transitional area that retains its mesotrophic riverine characteristics but becomes more lacustrine as it nears the lower region. The lower region (Region 1) is typified by cold, deep, oligotrophic water and the formation of a thermocline during summer months.

A wide variety of game and non-game fish species inhabit Oahe Reservoir. A total of 36 species were present between 1989 and 1993 (Lott et al. 1994). The primary sport fishes include walleye, northern pike, channel catfish, smallmouth bass *Micropterus dolomieu*, rainbow trout, and chinook salmon. Forage fishes include rainbow smelt, spottail shiners, yellow perch, emerald shiner *Notropis atherinoides*, and lake herring.



igure I.1. Map of Lake Oahe indicating sampling regions.

Chapter 1.

Catch Per Unit Effort and Length Distributions of Three Predatory Fishes Captured in Bottom, Surface, and Suspended Gill Nets

Introduction

Fisheries managers today are often charged with the task of quickly and accurately assessing the status of fish populations. This challenge becomes even more daunting in a climate of declining budgets and other resources. As a consequence, managers are continually searching for the most efficient method with which to obtain an adequate sample of a fishery.

Gill nets are among the most effective gear for collecting many species of fish (Carlander 1953) and they are the most widely used gear to sample fish populations in the United States and Canada (Gablehouse et al. 1992). Despite the extensive use of gill nets in North America, questions still remain about their effectiveness and the biases associated with their use.

Lagler (1978) defined mesh size selectivity as "a curve giving, for each size of fish, the proportion of the total population of that size which is caught in a unit operation of the gear". Mesh-size efficiency is the area under the selectivity curve (Regier and Robson 1966). There are, however, inherent biases associated with selectivity and efficiency that may result in descriptions of size structure, growth, and mortality that are not representative of the population (Hamley 1975). Possible solutions to the biases related to mesh size efficiency include the use of non-selective nets with several mesh sizes (Hubert 1983) and methods to correct for changes in catch efficiency of a mesh size by length group (McCombie and Fry 1960; Willis et al. 1985).

Hamley and Regier (1973) used direct estimates of gill net selectivity for walleyes and found that selectivity curves were bimodal, representing fish that were caught by wedging and tangling. Larger mesh sizes are typically more effective than smaller mesh sizes and their selectivity curves are taller. Selectivity, however, involves more than a single process and the exact definition is not obvious (Hamley 1975)

The techniques most commonly used to evaluate gill net catch data are length-frequency and catch-per-unit-effort (CPUE) analysis (Gablehouse et al. 1992). Fishes of a certain length range are most effectively captured by a specific mesh size (Willis et al. 1985). Therefore, simply determining the length distribution and the mean CPUE of a species of fish in each mesh size allows managers to determine the most effective mesh sizes for sampling specific sizes and species of fish. This method requires less time than analyzing mesh size selectivity and efficiency curves and still provides managers with the ability to monitor trends over time.

In addition to determining the CPUE of different mesh sizes, fisheries biologists must also take into account the most productive location in the water column to capture the desired sizes and species of fish. Although placement of gill nets varies with target species and habitat, the most common manner of deployment is the stationary bottom set (Hubert 1983). Gill nets set at or near the surface of the water (Biggins and Cressey 1973) or suspended (Von Brandt 1964) in the water column have also been used, but their effectiveness in capturing fishes has not been thoroughly reported.

The purpose of this study was to compare the CPUE and length distribution of walleyes, rainbow trout, and chinook salmon caught in bottom, surface, and suspended gill nets with a variety of mesh sizes.

Methods

Walleyes, chinook salmon, and rainbow trout were sampled at monthly intervals, from May through September 1994, using monofilament experimental gill nets. Bottom and surface nets were set near and perpendicular to shore in water ranging in depth from 3-18 m. Suspended nets were set at depths ranging from 4-31 m in water ranging from 15-55 m. Nets set on the bottom and surface had dimensions of 76 x

2.4 m and consisted of five 15.2 m panels with mesh sizes of 19, 25, 38, 57, and 76 mm (bar measure). The twine diameter was 0.28 mm for all mesh sizes. Nets suspended in the water column had dimensions of 76 x 6.1 m and consisted of five 15.2 m panels. Mesh sizes were 25, 38, 64, 76, and 89 mm (bar measure) with twine diameters of 0.28, 0.28, 0.33, 0.40, and 0.47 mm, respectively. All nets were hung on a one-half basis (Gebhards 1966).

The study area was restricted to the middle and lower regions of the reservoir (Figure I.1). Walleyes occupy the entire reservoir, are the predominant sport fish in the reservoir, and compose nearly 80% of the total fish harvest (Stone et al. 1994). A coldwater fishery, established through the stocking of chinook salmon and rainbow trout (Warnick 1987), exists only in the middle and lower regions of the reservoir.

Bottom, surface, and suspended gill nets were set 0.5 h before sunset. Nighttime gill net sets have been found to be most productive for the capture of rainbow trout (Smith 1959) and chinook salmon (Myrl Keller, Michigan Department of Natural Resources, personal communication). The walleyes, chinook salmon, and rainbow trout collected were also being used for a diet analysis; therefore, nets were pulled after 1-4 h to minimize digestion and regurgitation of prey. Nets were reset up to 3 times a night until sample size goals were reached for each species. If the sample size was not reached in one night, the nets were moved to another site in the same region of the reservoir. Sampling was conducted a maximum of four nights per region in each of the two regions each month.

Walleyes, chinook salmon, and rainbow trout were measured for total length (mm) and the mesh size that each fish was captured in was recorded. I did not differentiate between fishes caught by entanglement and body wedging. All fishes not used in diet analyses were released.

Fishes were placed into 10-mm length groups and length-frequency histograms were constructed for each mesh size and species. Mean CPUE was calculated on an fish/net-h basis. The mean CPUE of suspended nets was divided by 2.5 to standardize net area for data analysis because they contained 2.5 times the surface area of bottom and surface nets. Because the data were not normally distributed, mean CPUE and mean total length data were rank transformed before comparisons were made (Conover and Iman 1981). The ranked data were then evaluated using analysis of variance for unequal sample sizes. If a significant difference was detected, least squares means were used to test for significant differences among means. An *a posteriori* power analysis was used to determine the probability of not committing a type II error for comparisons that were nonsignificant (Zar 1984; Peterman 1990). The Statistical Analysis System (SAS; SAS Institute 1985) was used to calculate analysis of variance. Comparisons of mean CPUE among net locations were limited to the 25- and 38-mm mesh sizes common to each net. Small sample sizes prevented comparisons of CPUE in 76-mm mesh among nets. An alpha level of 0.05 was established *a priori* for all tests.

Results

Walleyes

We collected 1,234 walleyes in 704 h from May through September, 1994 (Table 1.1). The mean monthly CPUE for all nets combined differed significantly among months (Table 1.2). Mean CPUE for walleyes ranged from a high of 3.4/net-h in July to a low of 1.3/net-h in August with an overall mean in 1994 of 2.5/net-h.

The overall mean CPUE of walleyes in bottom nets was greater than that of surface or suspended nets (Table 1.3). Also, the mean CPUE was greater in surface nets than in suspended nets. The greatest mean catch rates were observed in the 38-mm mesh in all net locations and the net location x mesh size interaction was significant (P = 0.001).

The mean CPUE of bottom nets was greater than surface and suspended nets in all months (Figure 1.1). Catch rates in surface nets were greater than in suspended nets during May, June, and July. The mean CPUE of bottom nets increased from May (1.6/net-h) to a maximum of 5.2/net-h in July. Catch rates then declined substantially in August and

Table 1.1. Number of nets set, total hours nets were fished, and total catch of walleyes, chinook salmon, and rainbow trout in bottom, surface, and suspended monofilament gill nets in Lake Oahe, May-September 1994.

Net type	Number of nets	Total h	Walleye	Chinook Salmon	Rainbow Trout
Bottom	66	106.7	613	1	10
Surface	194	398.6	594	37	82
Suspended	44	199.0	27	147	8
Totals	304	704.3	1,234	185	100

Table 1.2. Mean monthly catch per unit effort (CPUE), and probabilities (*P*) of no difference among months for walleyes, chinook salmon, and rainbow trout captured by 25- and 38-mm mesh in monofilament gill nets in Lake Oahe, May-September 1994. Standard errors are in parentheses. Monthly mean CPUE having the same letters within rows are not significantly different by multiple-comparison analysis ($\alpha > 0.05$).

		Mean monthly CPUE (fish/net-h)					
Species	P	May	June	July	August	September	All Months
Walleye	0.002	2.41(0.40)^{a}	2.58(0.68)^{a}	3.44(1.00)^{a}	1.34(0.44)^{b}	3.21(0.90)^{a}	2.49(0.29)
Chinook Salmon	0.001	0.01(0.01)^{a}	0.07(0.02)^{bc}	0.43(0.29)^{b}	0.08(0.04)^{ac}	0.54(0.24)^{d}	0.16(0.06)
Rainbow Trout	0.012	0.22(0.04)^{a}	0.13(0.04)^{ab}	0.32(0.15)^{a}	0.07(0.03)^{b}	0.01(0.01)^{b}	0.17(0.03)

Table 1.3. Mean catch per unit effort (CPUE), probabilities (*P*) of no difference in net location, and power ($1 - \beta$) values by mesh size for walleyes, chinook salmon, and rainbow trout captured by 25- and 38-mm mesh and both mesh sizes combined in bottom, surface and suspended monofilament gill nets in Lake Oahe, May-September 1994. Standard errors are in parentheses. Mean CPUE having the same letters within rows are significantly different by multiple-comparison analysis ($\alpha > 0.05$).

Species Mesh Size	*P*	$1 - \beta$	Mean CPUE (fish/net-h) by net location Bottom	 Surface	 Suspended
Walleye					
25 mm	0.001	[x]	2.18(0.04)^{a}	0.43(0.08)^{b}	0.006(0.004)^{c}
38 mm	0.001	[x]	3.03(0.39)^{a}	0.55(0.10)^{b}	0.03(0.01)^{c}
Overall	0.001	[x]	2.61(0.28)^{a}	0.49(0.06)^{b}	0.02(0.01)^{c}
Chinook Salmon					
25 mm	0.001	[x]	0.00(0.00)^{a}	0.03(0.01)^{a}	0.11(0.04)^{b}
38 mm	0.001	[x]	0.00(0.00)^{a}	0.05(0.02)^{a}	0.12(0.02)^{b}
Overall	0.001	[x]	0.00(0.00)^{a}	0.04(0.01)^{a}	0.12(0.02)^{b}
Rainbow Trout					
25 mm	0.140	0.32	0.006(0.006)	0.05(0.01)	0.006(0.003)
38 mm	0.002	[x]	0.00(0.00)^{a}	0.12(0.03)^{b}	0.006(0.003)^{a}
Overall	0.004	[x]	0.003(0.003)^{a}	0.09(0.02)^{b}	0.006(0.002)^{ab}

[x] Not appropriate to calculate $1 - \beta$ if significant difference occurs (Peterman 1990).

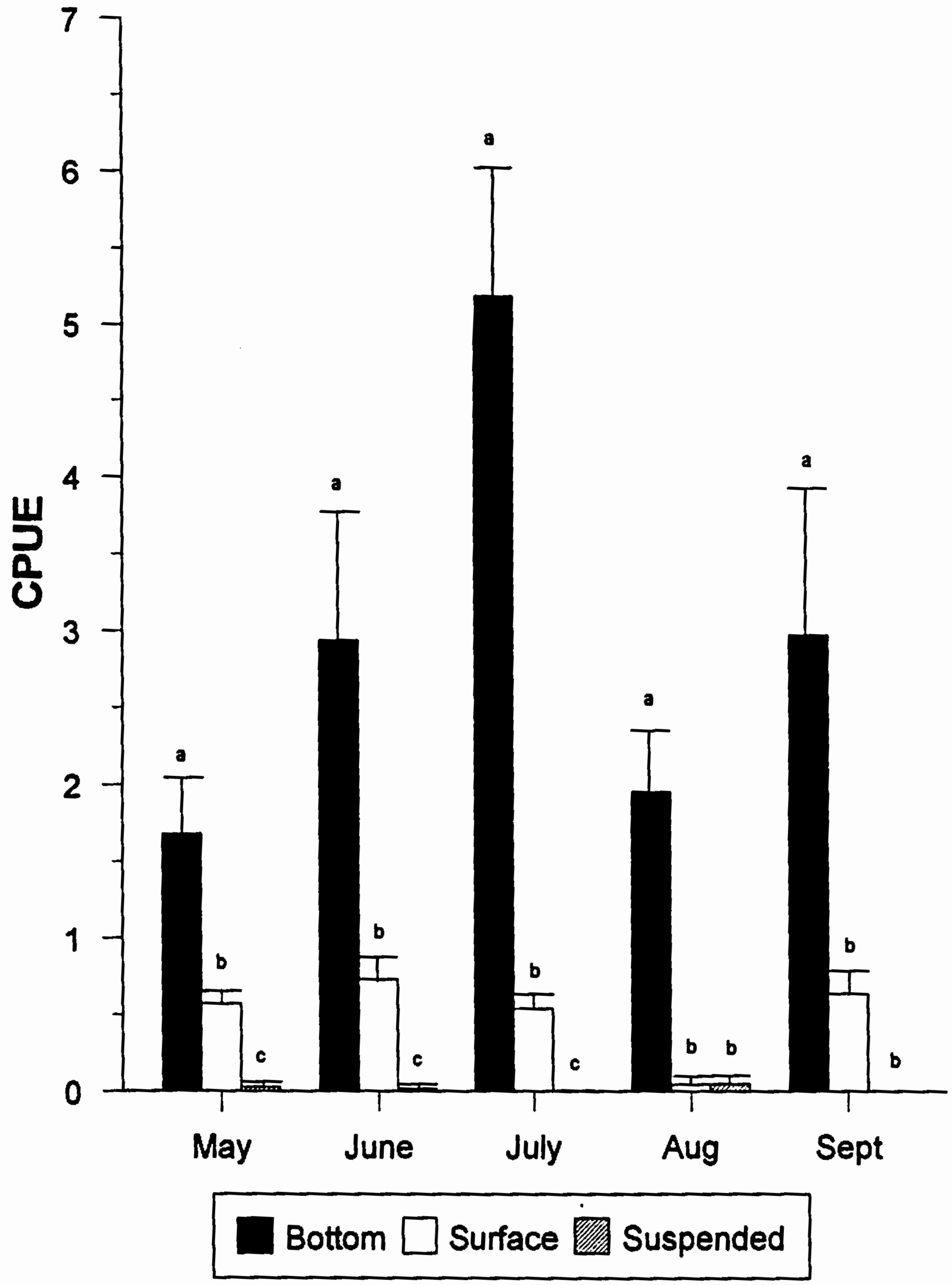


Figure 1.1. Mean monthly catch per unit effort (fish/net-h) for walleyes captured in 25- and 38-mm mesh of bottom, surface, and suspended monofilament gill nets in Lake Oahe, May-September 1994. Bars represent one standard error. Mean catch rates with the same letter are not significantly different within each month ($\alpha > 0.05$).

increased again in September. Mean CPUE in surface nets ranged from 0.04/net-h during August to 0.7/net-h during June. The mean CPUE of suspended nets was low each month, ranging from 0.0 to 0.04/net-h.

Mean total length of walleyes collected in 1994 in all mesh sizes ranged from 405 mm in bottom nets to 512 mm in suspended nets (Table 1.4). The mean total length of walleyes captured in the 25-mm mesh of suspended nets was greater than bottom and surface nets. There was no statistical difference in the mean total lengths of walleyes captured in 38-mm mesh among net locations ($P = 0.12$). The low power value (0.39) may indicate that the sample size of walleyes in the 38-mm mesh was too small for among net comparisons.

Few fish lengths that differ from the mode by more than 20% are caught in gill nets (Baranov 1948). My data are consistent with this observation (Figure 1.2). Three hundred and thirty-one walleyes were captured in the 25-mm mesh. Of which, 68 (20.5%) were < 20% and 24 (7.2%) were > than 20% of the modal length of 410 mm. The modal length for the 38-mm mesh was the same as the 25-mm mesh, which may indicate the presence of an especially abundant year-class. Of the 477 walleyes captured in the 38-mm mesh, only five (1.0%) were < 20% and 72 (15.1%) were > 20% of the modal total length.

able 1.4. Mean total length (TL), probabilities (P) of no difference among net locations, and power (1 - β) values by mesh size for walleyes, chinook salmon, and rainbow trout captured in bottom, surface, and suspended monofilament gill nets in Lake Oahe, May-September 1994. Standard errors are in parentheses. Mean TL having the same letters within a row are not significantly different by multiple-comparison analysis ($\alpha > 0.05$).

pecies Mesh Size	*P*	1 - β	Mean TL (mm) by net location Bottom	 Surface	 Suspended
alleye					
25 mm	0.020	[x]	376.3(77.3)[a]	392.7(66.5)[b]	506.7(135.0)[c]
38 mm	0.121	0.39	433.7(62.9)	431.9(55.9)	459.3(49.2)
All meshes	0.001	[x]	404.8(101.5)[a]	426.3(82.2)[b]	512.1(93.7)[c]
hinook Salmon					
25 mm	0.844	[y]	[z]	312.7(157.9)	306.7(129.6)
38 mm	0.601	[y]	[z]	523.8(217.5)	429.5(96.2)
All meshes	0.652	[y]	459.0(----)	419.8(217.4)	413.5(154.7)
Rainbow Trout					
25 mm	0.423	[y]	[z]	321.7(84.7)	352.5(145.6)
38 mm	0.038	[x]	189.0(----)[a]	397.6(56.9)[b]	405.3(39.6)[b]
All meshes	0.013	[x]	259.0(111.7)[a]	395.1(97.9)[b]	360.4(108.9)[ab]

[x] Not appropriate to calculate 1 - β if significant difference occurs (Peterman 1990).

[y] 1 - β could not be calculated because error mean square was higher than model mean square.

[z] No data collected.

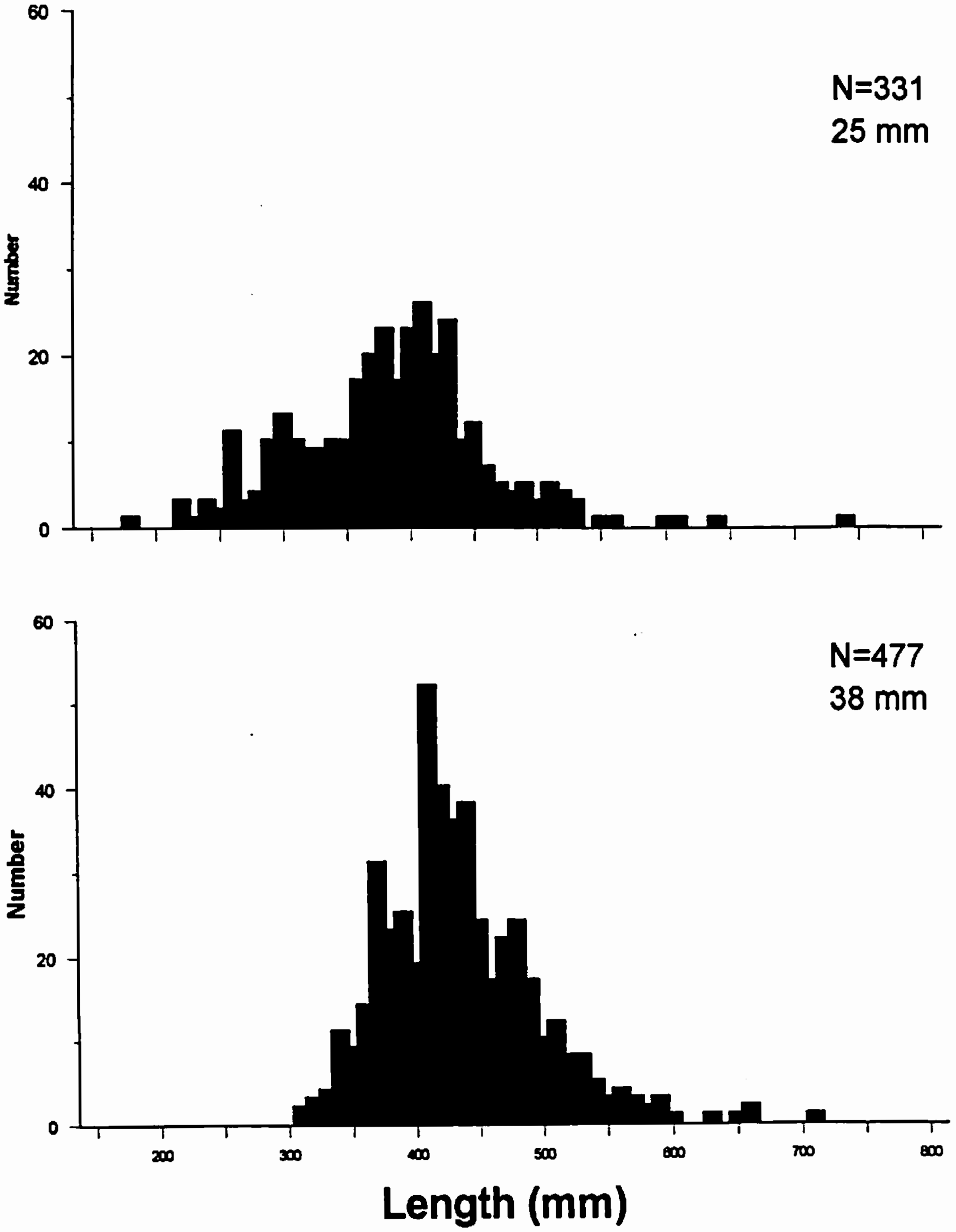


Figure 1.2. Length distribution of walleyes captured in 25- and 38-mm mesh of monofilament gill nets in Lake Oahe, May-September 1994.

Chinook salmon

One hundred eighty-five chinook salmon were captured during the sampling period (Table 1.1). Mean monthly CPUE for all nets combined differed among months (Table 1.2). Mean catch rates ranged from 0.01/net-h in May to 0.5/net-h in September with an overall mean CPUE of 0.2/net-hour. The overall mean CPUE in September was greater than all other months sampled. Catch rates of chinook salmon in July were also about three times greater than the overall mean CPUE in 1994.

The mean CPUE of chinook salmon in suspended nets was greater than in bottom or surface nets (Table 1.3). Mean CPUE of chinook salmon in the suspended nets was greater in 38-mm mesh than in 25-mm mesh ($P = 0.001$). There was no significant difference ($P = 0.12$) in mean catch rates between bottom and surface nets even though only one chinook salmon was captured in bottom nets. Power values were low (≤ 0.40) for the 25- and 38-mm mesh sizes in bottom and surface nets, indicating that the sample size of chinook salmon was too low for an accurate analysis.

Catch rates for chinook salmon captured in suspended gill nets increased from May to August (Figure 1.3). Mean CPUE of chinook salmon was greater in suspended nets than in bottom or surface nets during all months except May and September. Mean CPUE of chinook salmon in suspended nets peaked in August (0.3/net-h).

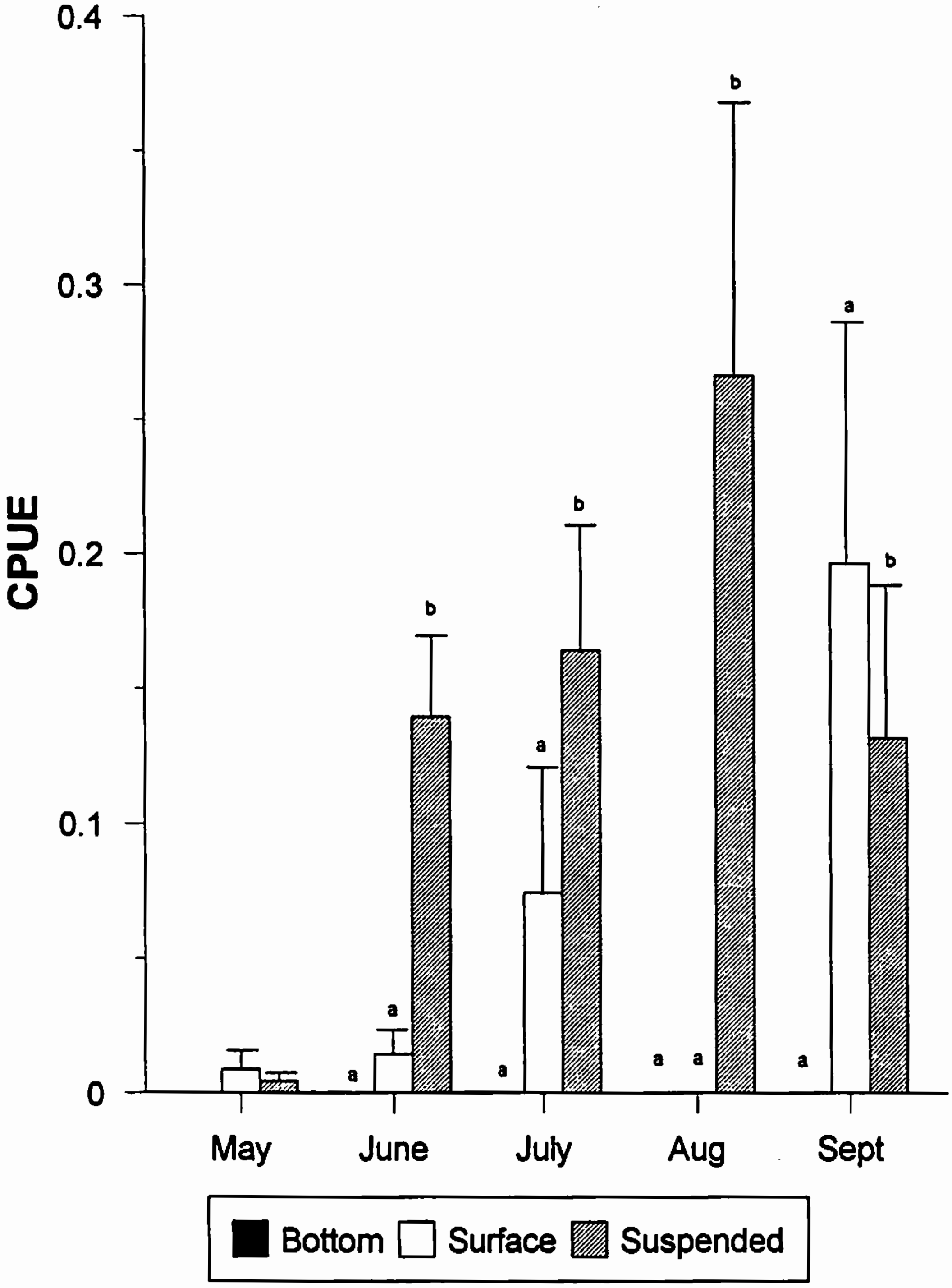


Figure 1.3. Mean monthly catch per unit effort (fish/net-h) for chinook salmon captured in 25- and 38-mm mesh of bottom, surface, and suspended gill nets in Lake Oahe, May-September 1994. Bars represent one standard error. Mean catch rates with the same letter are not significantly different within each month ($\alpha > 0.05$)

Mean total length of chinook salmon captured in 1994 was 413 mm in suspended nets and 420 mm in surface nets (Table 1.4). Because only one salmon (459 mm) was collected in the bottom nets, this net location was not considered in the mean length comparisons. Chinook salmon caught in the 25- and 38-mm meshes of the surface nets had a greater mean total length than those caught in the same meshes of suspended nets, but differences were not significant ($P > 0.65$). Sample sizes of chinook salmon were probably too small for an accurate analysis because power values could not be calculated due to high error mean squares.

The length distribution of chinook salmon caught in the 38-mm mesh shows that few fish with a total length differing from the mode by more than 20% were collected (Figure 1.4). This may be misleading, however, due to the small sample size as explained above. Of the 67 chinook salmon captured in the 38-mm mesh, nine (13.4%) were < 20% and 10 (14.9%) were > 20% of the modal total length of 430 mm. The lengths of chinook salmon caught in the 25-mm mesh is more widely distributed than the 38-mm mesh. Fifty-six chinook salmon were captured in the 25-mm mesh, of which none (0%) were < 20% and 17 (26.1%) were > than 20% of the modal total length of 240 mm.

Rainbow trout

We collected 100 rainbow trout in 704 h of gill

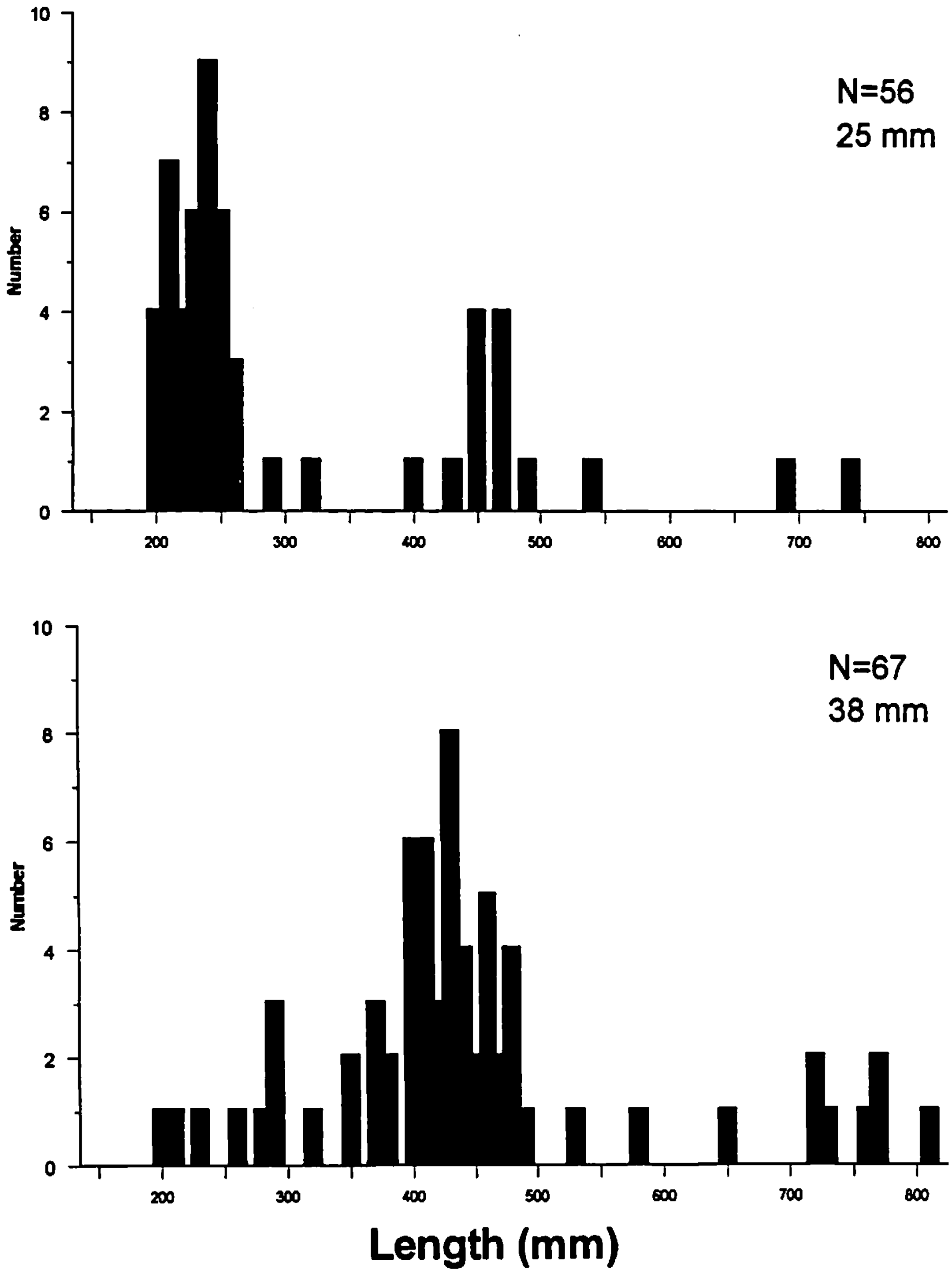


Figure 1.4. Length distribution of chinook salmon captured in 25- and 38-mm mesh of monofilament gill nets in Lake Oahe, May-September 1994.

netting during May through September, 1994 (Table 1.1). Monthly mean CPUE during May and July were greater than during August and September (Table 1.2). Mean CPUE was highest during July while the mean CPUE was lowest during September. Overall mean CPUE was only 0.2/net-h for the entire sampling season.

The mean CPUE of surface nets was greater than in bottom nets, and similar to that of suspended nets (Table 1.3). Highest catch rates of rainbow trout were observed in the 38-mm mesh of surface nets and they were greater than that in 38-mm mesh of suspended or bottom nets. Mean CPUE in 25-mm mesh did not differ significantly among net locations; however, a low power value (0.3) may indicate that the sample size was too small for an accurate analysis.

The mean CPUE of rainbow trout in surface nets peaked in July (0.2/net-h) and was higher than all other months and net locations (Figure 1.5). Catch rates were low in suspended nets until September when mean CPUE was greater than in surface and bottom nets. Rainbow trout were only captured in bottom nets during May.

Mean total lengths of rainbow trout captured in 1994 ranged from 259 mm in bottom nets to 395 mm in surface nets (Table 1.4). There was no significant difference in the mean total length of rainbow trout captured in the 25-mm mesh of surface and suspended nets, but power analysis could not be performed due to a high error mean square. Both the

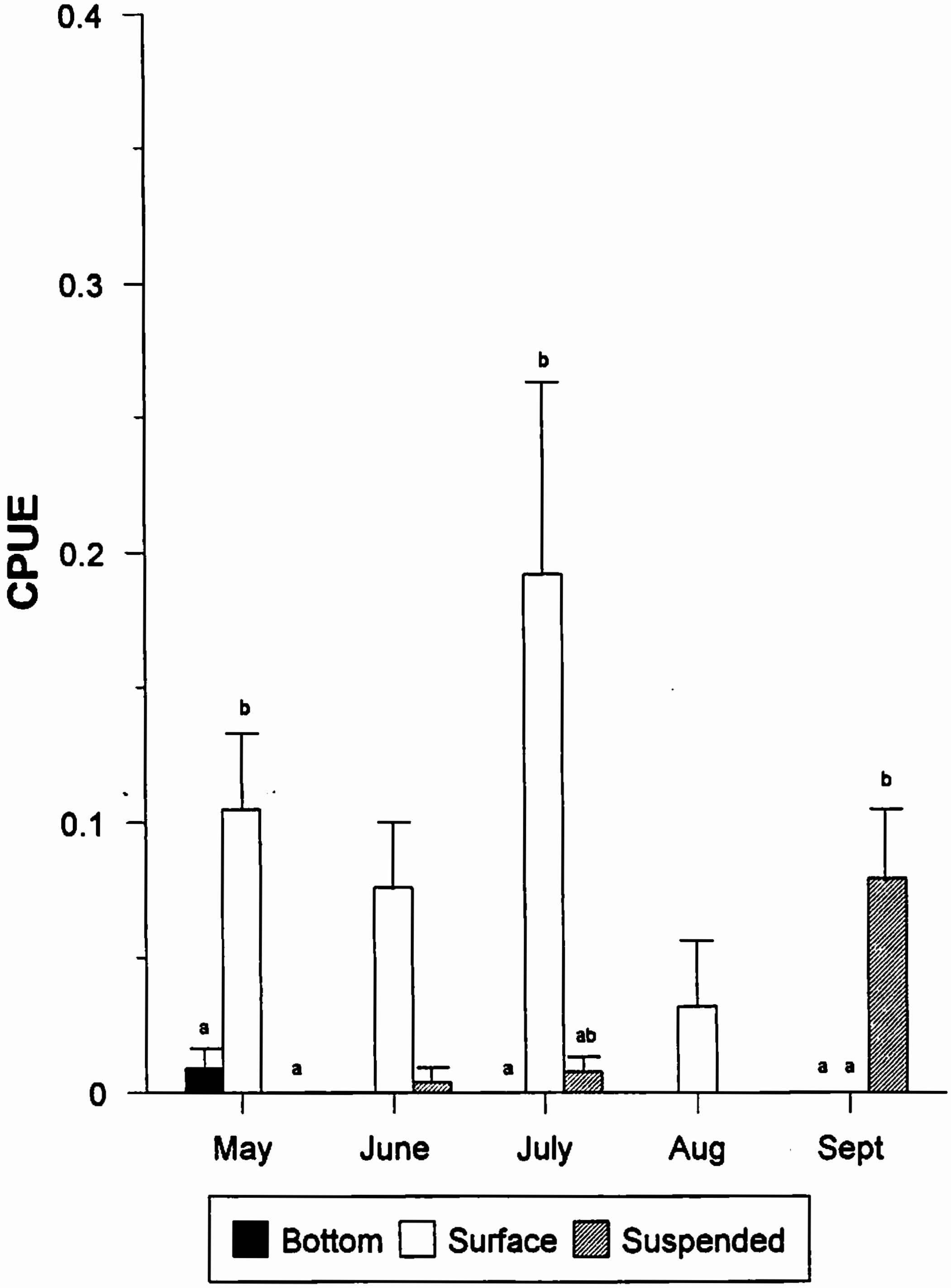


Figure 1.5. Mean monthly catch per unit effort (fish/net-h) for rainbow trout captured in 25- and 38-mm mesh of bottom, surface, and suspended monofilament gill nets in Lake Oahe, May-September 1994. Bars represent one standard error. Mean catch rates with the same letter are not significantly different within each month ($\alpha > 0.05$).

surface and suspended nets captured significantly larger rainbow trout than the bottom nets in 38-mm mesh. When all mesh sizes were combined, surface nets caught significantly larger fish than bottom nets.

Sample size was inadequate to distinguish a true mode for rainbow trout captured in 25-mm mesh and there were no distinct peaks or valleys in the length-frequency histogram (Figure 1.6). The 43 rainbow trout captured in the 38-mm mesh had a modal length of 380 mm. Of those 43 fish, three (7.0%) were < 20% and five (11.6%) were > 20% of the mode.

Discussion

Walleyes

In general, bottom nets had greater mean catch rates than either surface or suspended nets and the 38 mm mesh was the most effective mesh for capturing a large number of walleyes. More walleyes were caught during July in bottom nets than during any other month. Surface nets were most effective during June, and although catch rates were always low, the greatest mean CPUE of suspended nets was during August.

Schupp (1978) found seasonal variation in walleye catch rates by sport anglers, with higher returns in the spring and autumn, and lowest in July. Similar variations in catch data from gill nets were found in Norris Reservoir, Tennessee (Fitz and Holbrook 1978) and Lake Sakakawea, North

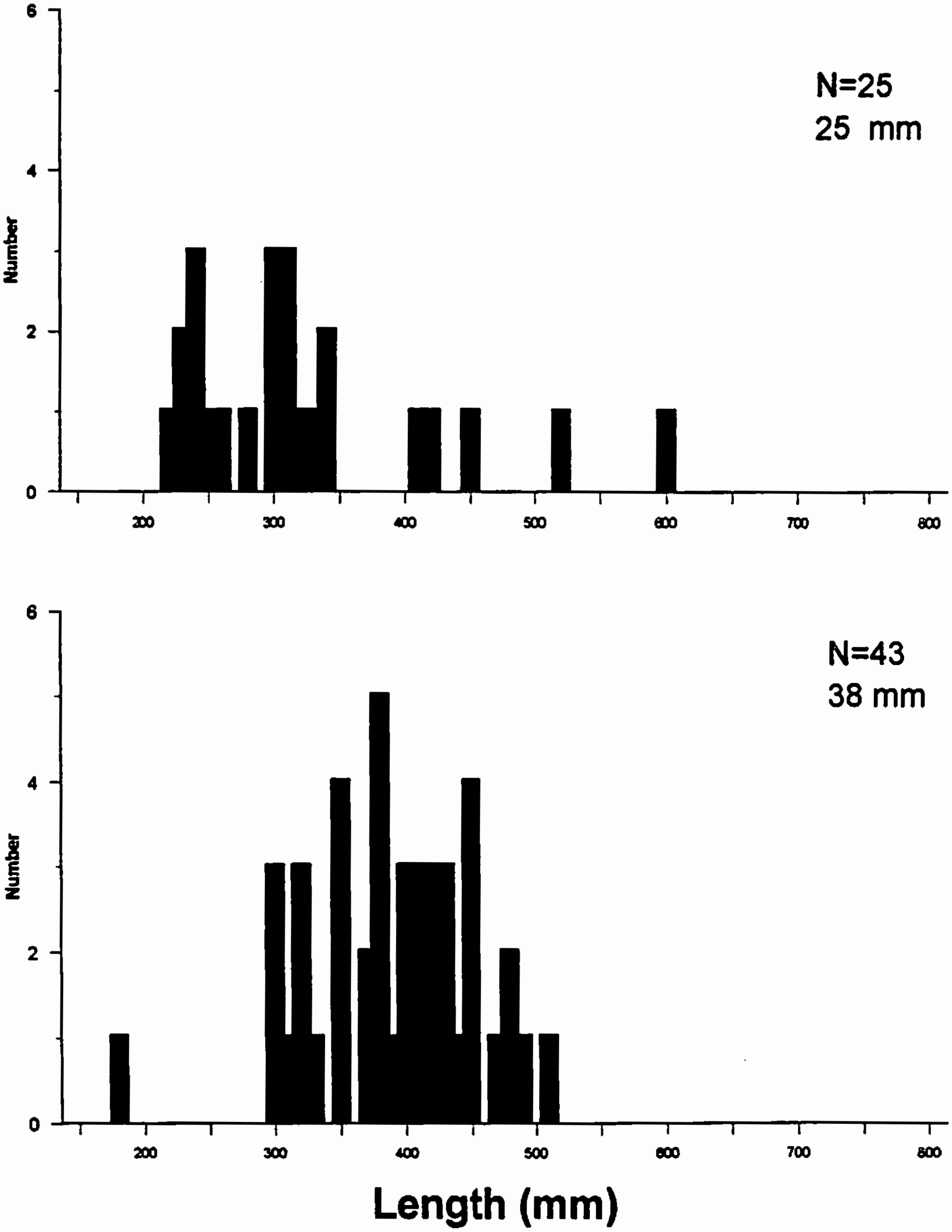


Figure 1.6. Length distribution of rainbow trout captured in 25- and 38-mm mesh of monofilament gill nets in Lake Oahe, May-September 1994.

Dakota (Mero and Willis 1992). Guy and Willis (1991) used trap nets and found high catch rates of walleyes in July and lower catch rates in May and September in Lake Madison, South Dakota. They suggested that percid behavior in unstratified natural lakes differs from that in stratified lakes and reservoirs. Temperatures and food availability are affected by the formation of a thermocline which alters the movement of predator species. Data from Lake Oahe, however, are more similar to that of unstratified natural lakes. This is possibly due to the wide distribution of prey fishes, especially rainbow smelt, in Lake Oahe.

The overlap between the two mesh sizes along with the relatively narrow length range of fish captured suggests that the 25- and 38-mm meshes are very effective for collecting walleyes between 320 mm and 490 mm. Walleyes caught in suspended nets were larger than those caught in either bottom or surface nets, suggesting that larger walleyes may be found in deeper waters.

Chinook Salmon

Mean CPUE for chinook salmon was greatest in suspended nets and catch rates were greater in the 38-mm than the 25-mm mesh size. Mean CPUE was greatest in suspended nets in August and surface nets had greater catch rates than other nets in September. Similarly, Aadland (1987) found that catch rates of chinook salmon captured in suspended monofilament gill nets in Lake Sakakawea, North Dakota increased steadily from June to August. Greater mean catch rates at the surface during September are probably due to increased activity during the fall spawning run (Scott and Crossman 1973).

Larger chinook salmon were caught in surface nets than in suspended nets, but differences were not significant. The length distribution data are skewed to the right of the mode, suggesting that chinook salmon greater than 20% of the modal total length may be more susceptible to tangling than wedging in the 25- and 38-mm mesh sizes. This is especially true in the later summer months as spawning male chinook salmon develop a kype that tangles more easily in the smaller mesh sizes.

Rainbow Trout

Low catch rates of rainbow trout in Lake Oahe during 1994 can be attributed to a small population size in the reservoir (< 100,000 stocked per year; Marrone and Stout 1993). Overall, surface nets had the greatest mean catch rates when sampling rainbow trout. The greater catch rates of rainbow trout observed in surface nets than in suspended or bottom nets, particularly during summer, was probably the result of fish feeding on wind blown terrestrial insects on or near the water surface (Keller et al. 1989; Lynott *in prep*).

Again, the greatest mean CPUE was observed in the 38-mm mesh of all net locations. The mean CPUE of surface nets was greatest during July, while in suspended nets it was greatest during September. Experimental netting and commercial harvests in Lake Ontario captured few rainbow trout during summer (Haynes et al. 1986). In the same study, anglers reported increased rainbow trout harvests during summer near the surface. My results may be more similar to the angler results than the netting studies in Lake Ontario because I sampled at the water surface.

The length distribution of rainbow trout captured in 25- and 38-mm mesh sizes were within those ranges reported by Smith (1959) from lakes in New Zealand. I found the 38-mm mesh to be effective for sampling fish between 300 and 455 mm and that surface nets caught larger fish than bottom or suspended nets. However, the relatively small total catch made determination of length distribution patterns difficult.

Year class strength could bias length-frequency data in a one-time sample (Neumann and Willis 1994). Lake Oahe was sampled over an extended period of time and my results, therefore, should indicate the overall effectiveness of the 25- and 38-mm mesh sizes. Seasonal growth of walleyes, chinook salmon, and rainbow trout assured that various sizes of fishes were susceptible to capture at different times of the year.

My data indicate that mean catch rates of walleyes, chinook salmon, and rainbow trout in Lake Oahe are susceptible to specific gill net locations and mesh sizes. These results should aid biologists in selecting the correct mesh sizes and placement of experimental gill nets when sampling walleyes, chinook salmon, and rainbow trout.

Chapter 2.

Effects of Changing Environmental Conditions on the Food Habits of Walleyes in Lake Oahe, South Dakota

Introduction

Water level management has long been used as a method of meeting management objectives for different species of fish (Willis 1986). Many of these management objectives deal with spawning, recruitment, and growth of young-of-the-year sport fish. Changing water levels also influence the distribution and abundance of prey fishes. Large drawdowns that concentrate prey fishes can increase predator foraging and growth by creating an environment where prey are more vulnerable to predators (Bennett 1962; Aggus 1979). However, growth of fishes may decrease after prolonged drawdown as concentrations of prey diminish and the production of most invertebrates and small fishes declines (Ploskey 1986). The vulnerability of a pelagic prey species may be unaffected by a drawdown (Lantz et al. 1967).

Water-level changes also effect primary productivity which can greatly influence responses at higher trophic levels (Ploskey 1986). Phytoplankton, as well as zooplankton, are indirectly affected by such factors as nutrient levels or light limitations resulting from water-level fluctuations (Jones and Bachmann 1978). Periphyton production is directly affected by low water levels which causes the periphyton to desiccate and die (Benson and Cowell 1967).

Rapidly rising waters that flood terrestrial areas temporarily increase supplies of aquatic invertebrate prey and of prey fishes that seek refuge from opportunistic predators (Applegate and Mullan 1967). Spring flooding of vegetation apparently is favorable for spawning and provides abundant food for the young largemouth bass *Micropterus salmoides* (Willis 1986). Flooding of terrestrial vegetation has also been associated with increased growth of walleye, northern pike, common carp *Cyprinus carpio*, smallmouth buffalo *Ictiobus bubalus*, goldeye *Hiodon alosoides* and other species of fish (Elrod and Hassler 1971; Nelson 1974; Strange et al. 1982).

Water level fluctuations also influence the thermal regime of reservoirs, which influences the distribution of game fishes and their prey. The summer distribution of rainbow smelt is normally controlled by water temperature in Lake Oahe and smelt were found in stratified portions of the reservoir where water temperatures ranged from 5 to 14°C. (Burczynski et al. 1987). Heist and Swenson (1983) found that rainbow smelt in the Great Lakes occupied temperatures ranging from 6-16°C and were associated with the lake bottom during the day and moved upward at night, apparently for feeding. Optimum temperature for growth of yellow perch was 28°C and they consistently occupy temperatures between

20°C and 29°C in the summer (Hokanson 1977). Shiners *Notropis* spp. associate with temperatures ranging from 19°C to 27°C (Jobling 1981).

Walleye populations are affected by many variables, of which water temperature is extremely important (Armour 1993). When surface temperatures in northern lakes exceeded 22.2°C, walleyes retreated from shallow waters over reefs and bars along the shoreline to deeper and cooler waters (Eddy and Underhill 1974). Walleyes seemed to avoid temperatures above 24°C in May-August during reservoir stratification in Norris Reservoir, Tennessee and even utilized hypoxic water when temperatures exceeded 24°C (Fitz and Holbrook 1978). However, Kimsey (1958) observed that walleyes were successful in an unstratified lake (Clear Lake, Iowa) where summer temperatures sometimes exceeded 27°C. Growth of walleyes is also apparently limited to temperatures above 6°C (Hokanson 1977).

Walleyes are opportunistic predators that prey on a variety of fish species (Lyons and Magnuson 1987; Vigg et al. 1991; Jackson 1992; Mero 1992). In water bodies where rainbow smelt or yellow perch are available, walleyes appear to select these species as prey (Swenson 1977; Lyons and Magnuson 1987; Jackson 1992; Mero 1992) However, prey distribution varies both temporally and spatially (Kelso 1973; Knight et al. 1984; Mero 1992) and the diet of walleyes often consists primarily of aquatic insects during portions of the year (Kelso 1973; Swenson 1977; Johnson et al. 1988; Mero 1992). Since these temporal changes in diet are also associated with changes in thermal regime, climatic variation may influence the annual diet of walleyes. Understanding how climatic variation contributes to walleye dietary shifts will aid in managing this species.

Since 1991, the environmental conditions in central South Dakota have changed substantially. Instead of the normal high summer temperatures and low levels of precipitation, the area has experienced below average temperatures, near record rainfall, and heavy snows. With these variations in the climate and environment, changes in the aquatic community could be expected.

The purpose of this investigation was to evaluate the food habits of walleyes in Lake Oahe during 1993, a year of record high precipitation and below average air temperatures, and 1994, when water levels remained high and temperatures were moderate. To illustrate the influence of prey species distribution on the diet of walleyes, the 1993 data is compared with that of Jackson (1992) which were collected during a year when reservoir water elevation was low and air temperatures were higher than in both 1993 and 1994.

Methods

Walleyes were collected monthly from May to September in both 1993 and 1994, and in January and February, 1994 with experimental bottom, surface, and suspended monofilament gill nets. Gill net dimensions are described in Chapter 1. Only age 1 and older were collected due to ineffective mesh sizes for age 0 walleyes. From May to September, gill nets were set 0.5 h before sunset and fish were removed every 2 h until fifteen adults and fifteen juvenile walleyes were collected. In January and February, gill nets were set for 24 h under the ice. Gill nets were set for a total of 774 h in 1993, in which 1,195 walleyes were captured and 438 were retained for diet analyses. In 1994, gill nets were set for 1,416 h and 1,243 walleyes were captured. Of those, 467 were kept for diet analyses (Appendix A.1). Upon capture, walleyes were weighed (g) and measured for total length (mm). Each fish was placed on ice to slow digestive processes until they could be taken to the field laboratory. At the field laboratory, the entire digestive tract was removed from each walleye and preserved in 10% formalin. Later, both invertebrate prey and prey fishes were enumerated and total length (mm) and wet weight (g) recorded. Partially digested prey were identified based on structures resistant to digestion. Prey digested beyond recognition were placed into an unidentifiable category.

Prey species were captured using multifilament gill nets (2.4 m x 61 m) with bar mesh sizes of 10, 13, 16, and 19 mm. Modified fyke (6 mm) nets were also used to collect prey fish. Although relative densities of prey were not determined, presence or absence of prey species was documented.

Water temperature and depth at sampling sites were determined each sampling date using a Scout Model multi-probe water quality sensor (Hydrolab Inc., Austin, Texas). Water temperature and water level data from 1991 were provided by the U.S. Army Corps of Engineers, Pierre, South Dakota.

Food habits of walleyes were analyzed using the relative importance (RI) index (George and Hadley 1979). The relative importance index is calculated as follows:

$$RI=\frac{AI_a}{\sum_{a-1}AI_a}$$

where AI_a = (percent of all prey items ingested that are taxa a) + (percent occurrence of taxa a in the diet) + (percent of the diet mass represented by taxa a). The relative importance index ranges from 0 to 100 with 100 being most important. The index decreases the importance of prey eaten in large quantities by few fish and increases the importance of prey eaten in small quantities by many fish. Relative importance values were evaluated each month in each region. Since Jackson (1992) only collected data for adult walleyes in August, diet comparisons of adult walleyes were made only during that month.

Jackson (1992) collected walleye stomach samples during the annual fish population survey conducted by the SDGF&P in August, 1991. Walleyes were collected in multifilament gill nets (91.4 m x 1.8 m) at nine stations throughout the South Dakota portion of Lake Oahe. Nets were fished overnight (24 h) at each station. A total of 1,402 walleyes were sampled from the nine sites on Lake Oahe in August, 1991; of these, 346 contained identifiable prey and were used in RI calculations.

Heavy rains and runoff from the snowpack caused reservoir volumes to increase substantially in 1993 (U.S. Army Corps of Engineers, personal communication). Flooding on the lower Missouri River resulted in minimal discharge from Oahe Dam during the summer months, further contributing to the volume of water in the reservoir during 1993 (Figure 2.1). Cooler air temperatures and greater reservoir volume in 1993, compared with 1991, influenced the thermal structure of the reservoir.

Water temperatures were cooler in 1993 than in 1991, especially in June and July (Figure 2.2). In 1991, a thermocline formed at about 21 m in August (Jackson 1992), which restricted the movement of some cold water fish species. In 1993, no thermocline was established and coldwater fish, such as rainbow smelt, were able to use the entire water column over a greater portion of the reservoir. Thus, cooler water temperatures in 1993 effectively

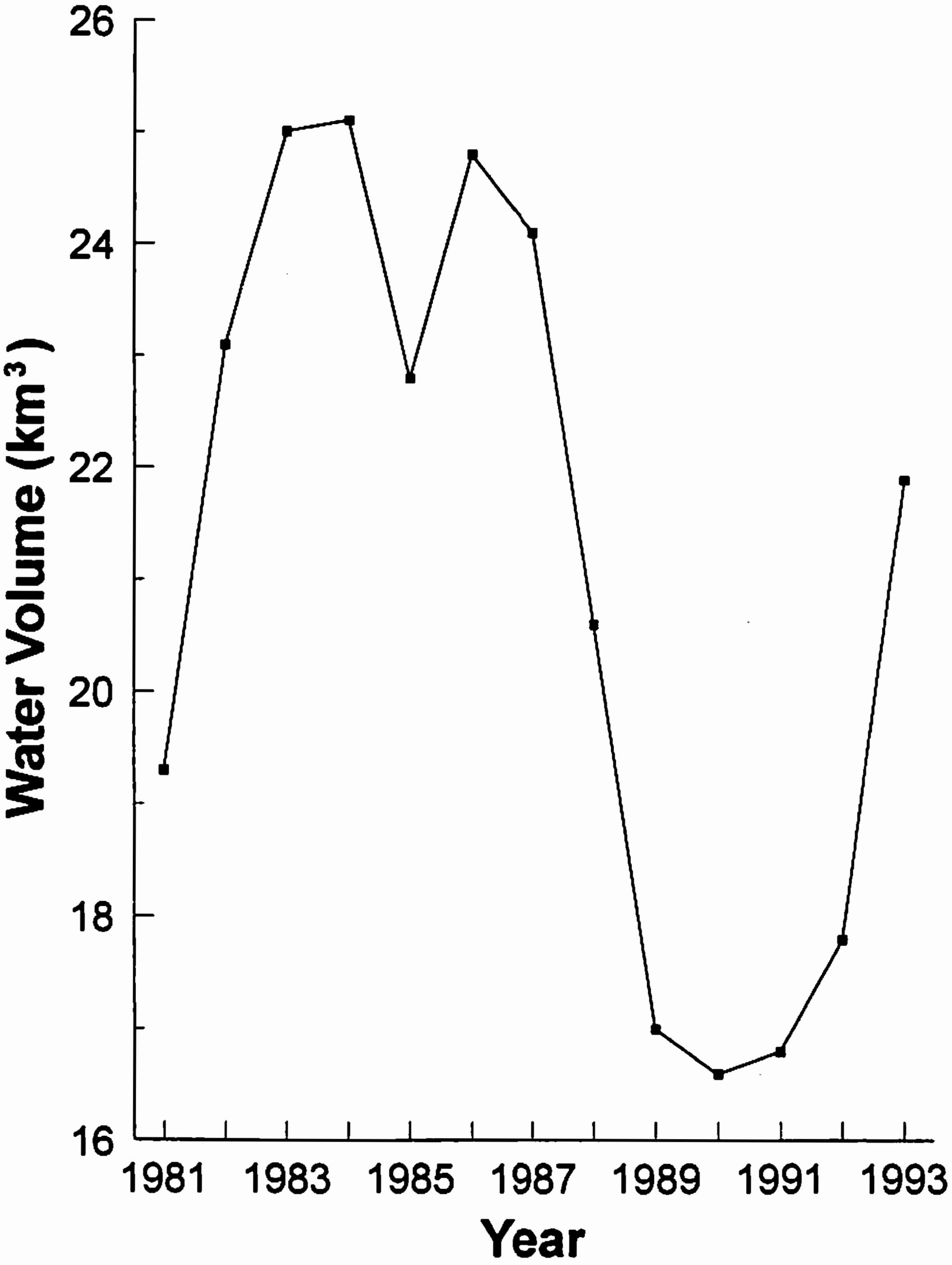


Figure 2.1. Lake Oahe reservoir water volumes during 1981-1993 (based on annual averages from the U.S. Army Corps of Engineers, Pierre, South Dakota).

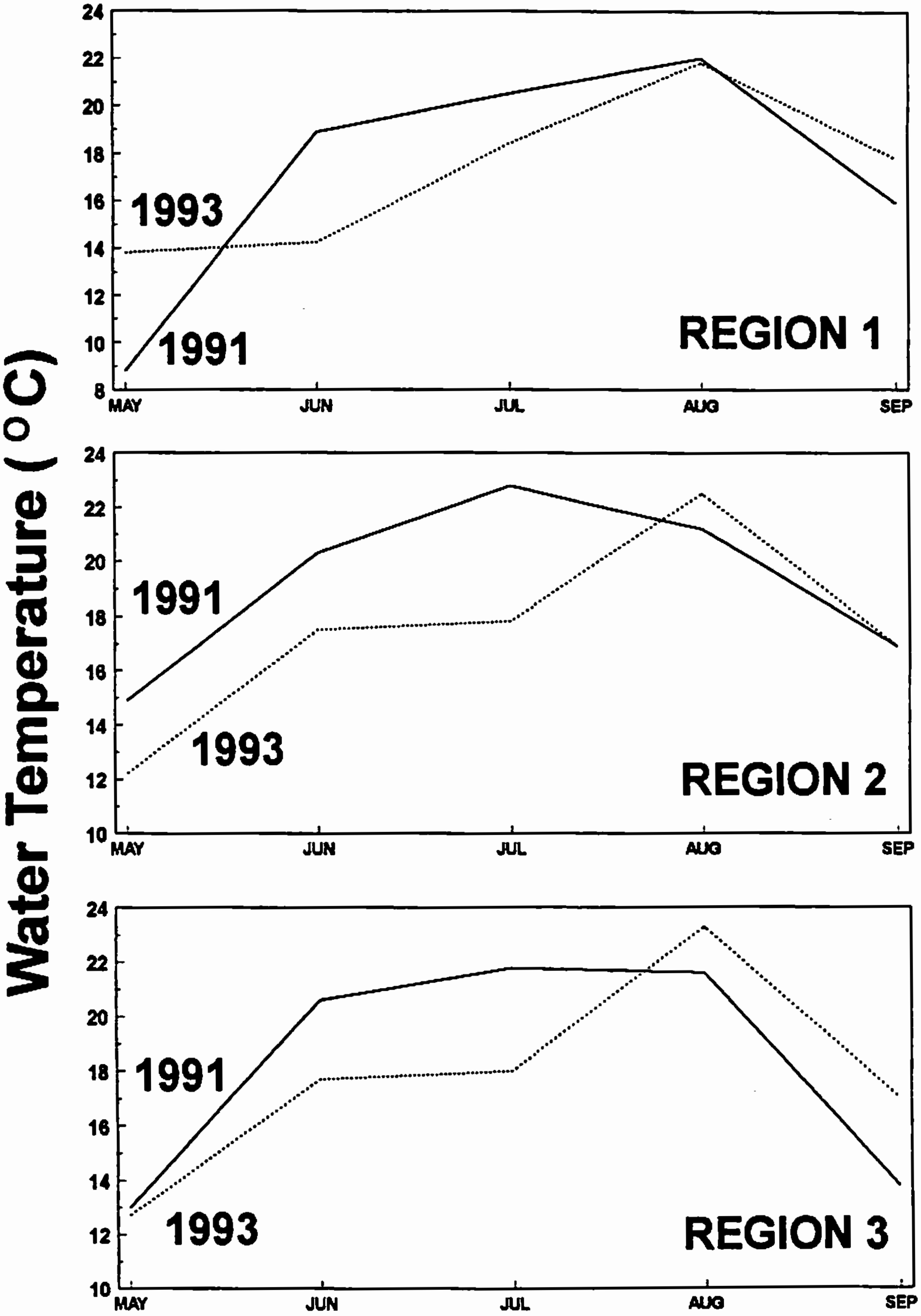


Figure 2.2. Monthly average surface water temperatures in the three sampling regions of Lake Oahe, during 1991 and 1993.

creased the habitat area available to many of the predator d prey fish species in the reservoir.

Results

Water levels, temperatures, and food habits in 1994 re similar to those in 1993, therefore only 1993 values re used in the comparisons. Relative importance values of ey items during 1994 are summarized in Appendix A.1.

Prey fishes available to walleyes varied between years d among regions of the reservoir (Table 2.1). In 1993 and 94, rainbow smelt were abundant in all three regions of e reservoir. Spottail shiners and yellow perch were mmon and only one freshwater drum was captured. In 1991, ckson (1992) collected a variety of prey fishes throughout e reservoir including rainbow smelt, yellow perch, ottail shiners, freshwater drum *Aplodinotus grunniens*, ite bass *Morone chrysops*, and white crappie *Pomoxis* *nularis*. However, in 1991, rainbow smelt were collected low numbers in region 2 and none were captured in region

Relative importance of fish was highest in all three gions of the reservoir during 1991 and 1993 (Figure 2.3). wever, in 1991, the importance of rainbow smelt decreased bstantially from region 1 to region 2 and no rainbow smelt re consumed by walleyes in region 3. Yellow perch, erald shiners, spottail shiners, white bass, white

Table 2.1. Prey fishes captured in small mesh gill nets during August 1991, 1993, and 1994 in Lake Oahe.

Region	1991[a]	1993	1994
1	Rainbow smelt Yellow perch White bass Freshwater drum White crappie Spottail shiner	Rainbow smelt Yellow perch Spottail shiner	Rainbow smelt Yellow perch Spottail shiner Emerald shiner
2	Rainbow smelt Yellow perch Spottail shiner Freshwater drum White crappie White bass	Rainbow smelt Yellow perch Spottail shiner	Rainbow smelt Yellow perch Spottail shiner
3	Yellow perch Spottail shiner Freshwater drum White crappie White bass	Rainbow smelt Spottail shiner Freshwater drum	Rainbow smelt Spottail shiner

[a] Obtained from Jackson (1992)

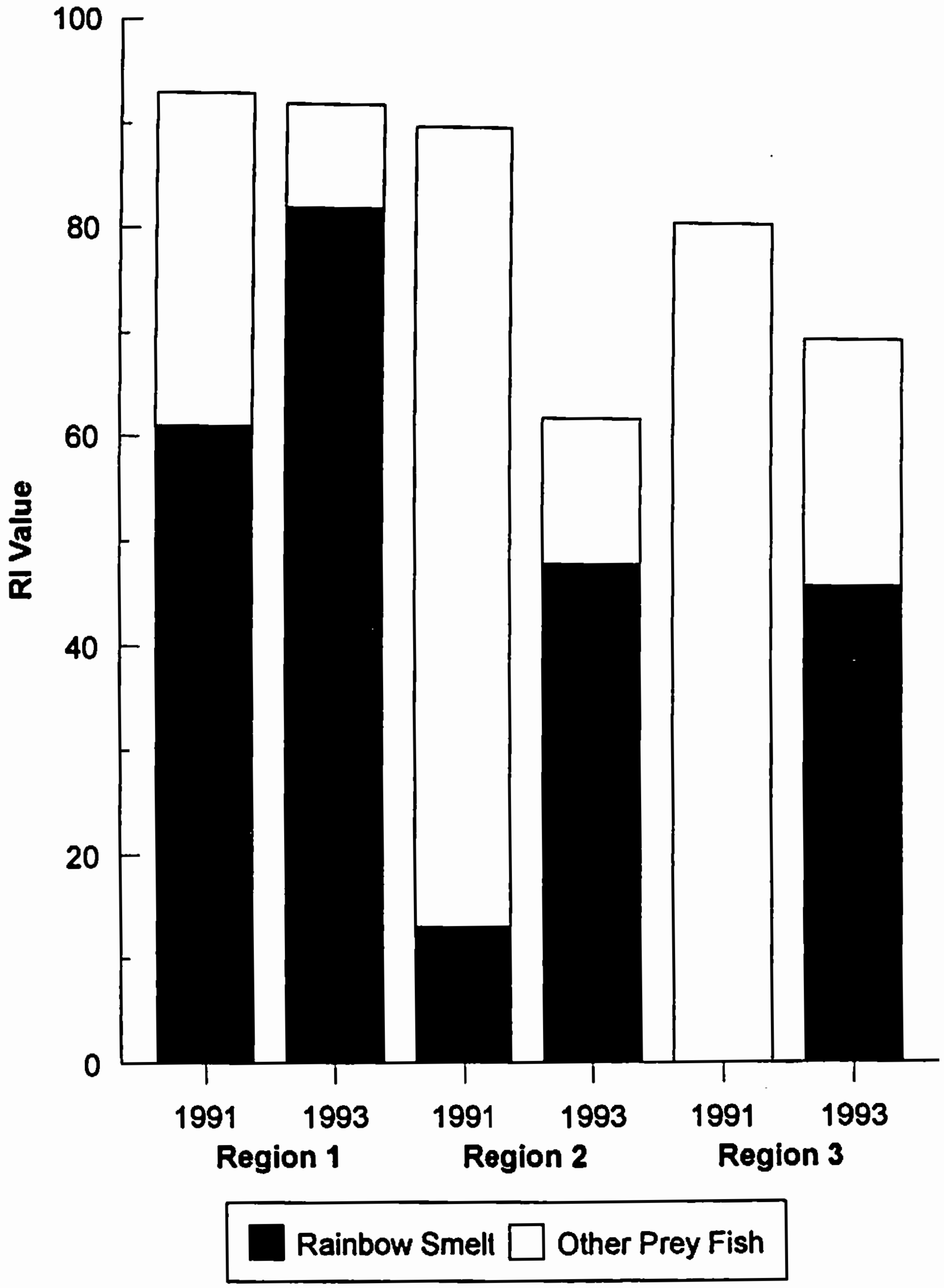


Figure 2.3. Relative importance (RI) values of prey fishes consumed by walleyes in 1991 (Jackson 1992) and 1993 in Lake Oahe.

crappies and freshwater drum dominated walleye diets in regions 2 and 3. In 1993, rainbow smelt RI values were higher than those of other prey throughout the sampling period in all three regions of the reservoir (Table 2.2).

The RI values of macroinvertebrates, especially ephemeroptera and chironomidae, increased from region 1 to region 3 during both years, but were of greater importance in 1993 than in 1991. Predation by walleyes on zooplankton in Lake Oahe was sporadic and, for the most part, insignificant in all regions both in 1991 and 1993.

Discussion

The high relative importance values for fishes in the diet of walleyes in this study is consistent with the findings of others (Lyons and Magnuson 1987; Vigg et al. 1991; Jackson 1992; Mero 1992). During 1991, the formation of a strong thermocline restricted the movement of rainbow smelt. As a result, walleyes were only able to exploit rainbow smelt in the lower region of the reservoir and parts of the middle region. Unusually high water levels and low temperatures in 1993 allowed rainbow smelt to move throughout the entire reservoir. Although water temperatures were slightly higher in 1994, which allowed the formation of a weak thermocline, rainbow smelt still occupied the entire water column in all three regions of Lake Oahe. Because walleyes are opportunistic feeders, they

Table 2.2. Percent frequency of occurrence, biomass (g), and relative importance (RI) of prey consumed by walleyes collected in Lake Oahe, May-September, 1993.

				Rainbow Smelt			Other Prey Fish[a]			Unidentifiable Fish			Invertebrates[b]		
Month	Region	N	% MT[c]	% Freq.	Biomass	RI	% Freq.	Biomass	RI	% Freq.	Biomass	RI	% Freq.	Biomass	RI
MAY	1	30	10.0	22.0	315.7	83	0.0	---	--	6.7	0.8	4	20.0	0.9	13
	2	40	5.0	70.0	702.2	56	15.0	336.7	17	25.0	4.8	12	32.5	3.6	15
	3	25	20.0	36.0	144.6	51	4.0	4.4	3	12.0	2.4	7	56.0	1.7	39
JUN	1	30	23.3	43.3	223.5	71	6.7	15.1	6	30.0	3.4	23	0.0	---	--
	2	25	72.0	24.0	63.2	91	0.0	---	--	4.0	<0.1	9	0.0	---	--
	3	21	33.3	23.8	127.1	50	0.0	---	--	19.0	0.8	13	47.6	1.9	37
JUL	1	29	41.1	41.4	116.9	70	3.4	4.4	5	33.3	2.7	25	0.0	---	--
	2	33	36.4	24.2	100.4	51	3.0	3.8	4	33.3	3.9	29	8.0	0.9	16
	3	28	32.1	57.1	221.6	74	3.6	44.4	8	0.0	---	--	17.9	0.6	18
AUG	1	31	19.4	71.0	377.8	82	0.0	---	--	12.9	9.0	10	12.8	0.6	8
	2	32	50.0	15.6	49.0	48	0.0	---	--	12.5	0.2	14	31.3	1.3	38
	3	29	17.2	31.0	245.0	46	10.3	35.3	9	24.1	8.3	15	48.0	2.4	30
SEP	1	26	19.2	69.2	149.8	73	0.0	---	--	34.6	6.0	27	0.0	---	--
	2	28	7.1	82.1	475.1	89	3.6	11.6	3	3.6	3.0	6	3.6	0.2	2
	3	31	51.6	22.6	141.8	67	3.2	3.7	4	22.6	0.4	25	3.2	0.1	4

[a] Other prey fish includes chinook salmon, yellow perch, spottail shiners, and freshwater drum.
[b] Invertebrates includes ephemeridae, chironomidae, and zooplankton.
[c] Percent of stomachs collected that were empty.

were able to take advantage of this shift in prey distribution and utilize rainbow smelt in throughout the reservoir. Other prey fishes such as yellow perch, white crappies, and freshwater drum, which Jackson (1992) found to be important in walleye diets in 1991, were not important during 1993 or 1994.

Invertebrates were not a substantial part of the diet of walleyes in Lake Oahe during 1993 or 1994, but they were more important in region 3 than either of the other two regions. The importance of invertebrates, especially of ephemerids, was probably related to their abundance in the upper region.

The population size of rainbow smelt in Lake Oahe is cyclical and could decline precipitously over a one-two year period (unpublished data, SDGF&P, Pierre). A drawdown of reservoir water levels, coupled with warm water temperatures, could accelerate the collapse of the rainbow smelt population by reducing the availability of suitable habitat. Periods of reduced abundance of rainbow smelt may directly result in competition (Forney 1977) between walleyes and other predator species in Lake Oahe, such as chinook salmon, rainbow trout, and northern pike.

The results of this investigation demonstrated how environmental conditions can affect the distribution of a prey species and influence the food habits of a predator species. Although water level management by fisheries biologists on Lake Oahe is nearly impossible due to water use objectives by the U.S. Army Corps of Engineers, it becomes necessary to consider the trends that appear to be occurring (Figure 2.1) and adjust management practices accordingly. Rising water levels in recent years, after a period of dry years, has apparently resulted in a wider distribution of an important prey species, rainbow smelt. Higher stocking rates of top-level predators should coincide with these high water years. When water levels begin to decrease, a gradual decrease in stocking rates might prevent a collapse of the rainbow smelt population.

Chapter 3

Caloric Density of Three Predatory Fishes and Their Prey in Lake Oahe, South Dakota

Introduction

The popularity of bioenergetics modeling in recent years has raised awareness of the importance of determining seasonal caloric densities of fishes and their prey. Caloric density of predators and prey can significantly affect model computations of consumption, production, and conversion efficiency (Hewett and Johnson 1992).

Energy density of freshwater fishes varies with sex, body size, and season (Meakins 1976) as well as feeding rate, and activity level (Soofiani and Hawkins 1985). Variations in caloric values reflect the incorporation of different materials into tissue and the physiological changes during the life of a fish, thereby, invalidating the use of fixed energy values for the production and energetics of freshwater fishes (Meakins 1976). Despite this, several studies have assumed constant and equivalent energy values for both predators and prey when modeling fish energetics (Kitchell et al 1977; Stewart et al 1983; Rice and Cochran 1984; Bevelhimer et al. 1985).

Seasonal changes in caloric density of predators and prey can be significant (Soofiani and Hawkins 1985), even though the energy density of both trophic groups may be equal (Rottiers and Tucker 1982). In West Blue Lake, Manitoba, the caloric density of walleyes was lowest during spring and greatest during fall (Kelso 1973). The increase in energy density coincided with seasonal growth patterns. Rainbow smelt similarly undergo a period of energy storage prior to overwintering and spawning in Lake Michigan (Foltz and Norden 1977), as do most spring spawning fishes (MacKinnon 1972; Flath and Diana 1985; Rand et al. 1994). Dygert (1990) observed that it may be a disadvantage to spawn during spring because peak energy demands for gonad development come at a time when food resources are at a minimum. Evolutionally, however, spawning during spring when the potential to replace expended energy exists would provide a survival advantage over fall spawning, after which the fish might have to survive six months before regaining energy.

Energy density of fishes is influenced by age and the composition of tissues. Fishes that exhibit slow growth have significantly higher lipid and caloric concentrations than those growing faster (Gill and Weatherley 1984). Caloric density of salmonids in Lake Michigan doubled over their lifespan (Stewart 1980). As fish size increases, lipids constitute an increasing percentage of body weight. Therefore, the caloric density of the fish also increases (Weatherley and Gill 1983). Kelso (1973) also found that increased energy density in walleyes was probably due to fat reserves.

The purpose of this study was to determine seasonal differences in the caloric density of mature and immature walleyes, chinook salmon, and rainbow trout, as well as a variety of potential prey fishes in Lake Oahe, South Dakota. The data from this investigation can then be used to model seasonal energetics of freshwater fish.

METHODS

Walleyes, chinook salmon, and rainbow trout were collected during January, May, July, and September, 1994, using experimental monofilament gill nets. Gill nets were set on the bottom, at or near the surface, and suspended in the water column. Gill net dimensions are described in Chapter 1. Shoreline seines (30 x 1.8 m, 6 mm mesh) and small mesh gill nets (30 x 1.8 m; 9 and 13 mm mesh sizes) were used to capture prey fishes and age-0 fishes. Gill nets were set 1 h before sunset and fishes were removed every 2 h. Nets were reset up to three times each night until sample size goals were met or a maximum of 10 nights each month.

Rainbow smelt were collected in a separate study during May through September, 1991 using monofilament gill nets with dimensions of 22.9 x 1.3 m consisting of either 10 or 13 mm mesh size (bar measure). Gill nets were set just after dawn and smelt were removed every 3 h until sampling was complete in early evening. Rainbow smelt were also captured during the spawning run in early April with a 9 mm mesh dip net.

Upon capture, all fishes were immediately measured for total length (mm) and placed on ice until the fish could be frozen. In the lab, gut contents were stripped from the digestive tract of the predators to insure that the caloric density of the predator was not affected by prey in the stomach. Five immature (ages 1 and 2) and five mature (≥ age-3) walleyes, chinook salmon, and rainbow trout were frozen for caloric analysis each month. Also, up to five individuals of each prey species were frozen each month for caloric analysis. During 1991, up to 24 rainbow smelt were frozen each month to determine energy density.

All fishes were slowly thawed in cool water, as extremes in temperatures may cause denaturation of proteins (Streitwieser et al. 1992). Fishes were then measured for total length (mm) and wet weight (g). Large fishes (≥ 200 mm) were sectioned and coarsely ground using a Hobart Model 4146 meat grinder (Hobart Corp., Troy, Ohio). These coarsely ground fish, along with fishes < 200 mm, were homogenized using a Black and Decker model HC20 mincer/chopper (Black and Decker, Inc., Shelton, CT). Three subsamples (3-5 g wet weight) from each fish were placed into Dynalab model 2678 polyethylene bags (Dynalab Corp., Rochester, New York) and frozen at -22°C. Subsamples of all fishes except rainbow smelt were then freeze-dried for 24 h to a dry weight of approximately one gram. Rainbow smelt were homogenized and oven-dried at 60° C for 24 h. Two subsamples from each smelt were retained for caloric analysis.

Caloric density of all fishes was measured from subsamples using a Parr Model 1261 Calorimeter and standard methodologies (Parr Instrument Co. 1990). Corrections were made for burnt fuse wire and nitric acid formation during each run, but a sulfur correction was omitted. All values are reported as cal/g wet weight. Seasonal differences in caloric density were evaluated using analysis of variance. Least-squares means was used to determine differences among means. The Statistical Analysis System (SAS; SAS Institute 1985) was used for statistical tests. Fishes captured in January were not used due to complications with calorimetry techniques. Caloric values for rainbow smelt captured on 29 May and 10 June were combined because of the proximity of the sampling dates. Prey species that were not captured during each sampling period were not included in seasonal trend analysis.

RESULTS

Predatory Fishes

Seasonal mean caloric density of immature and mature walleyes exhibited different patterns during May through

September (Figure 3.1). Mean energy density of large walleyes was lowest during May and increased through September. The increase in energy density during this period (14.9%) corresponded with observed seasonal growth patterns. Caloric density of immature walleyes was greater during May (1,413 cal/g) than during July ($P = 0.0002$, df = 2) or September ($P = 0.004$, df = 2). Immature walleyes collected during July had the lowest mean caloric density observed (1,082 cal/g) during the study. Mean caloric density of mature walleyes was greater than immature walleyes ($P = 0.0016$, df = 2) during all months.

Caloric density of large (> 315 mm) and small (< 315 mm) chinook salmon also differed, but less than walleyes (Figure 3.2). Seasonally, caloric density of large chinook salmon increased during May through September. Mean caloric density was lowest during May ($P = 0.001$, df = 2) and increased 27.8% over the period. Seasonal patterns in mean caloric density of small chinook salmon were not apparent and there were no differences in caloric density among months. Mean energy density was lowest during May, increased during July, and decreased during September. Mean caloric density of large chinook salmon was greater than that of small chinook salmon in July ($P = 0.0234$, df = 1) and September ($P = 0.0001$, df = 1).

Seasonal mean caloric density of rainbow trout increased during May through September (Figure 3.3). Mean

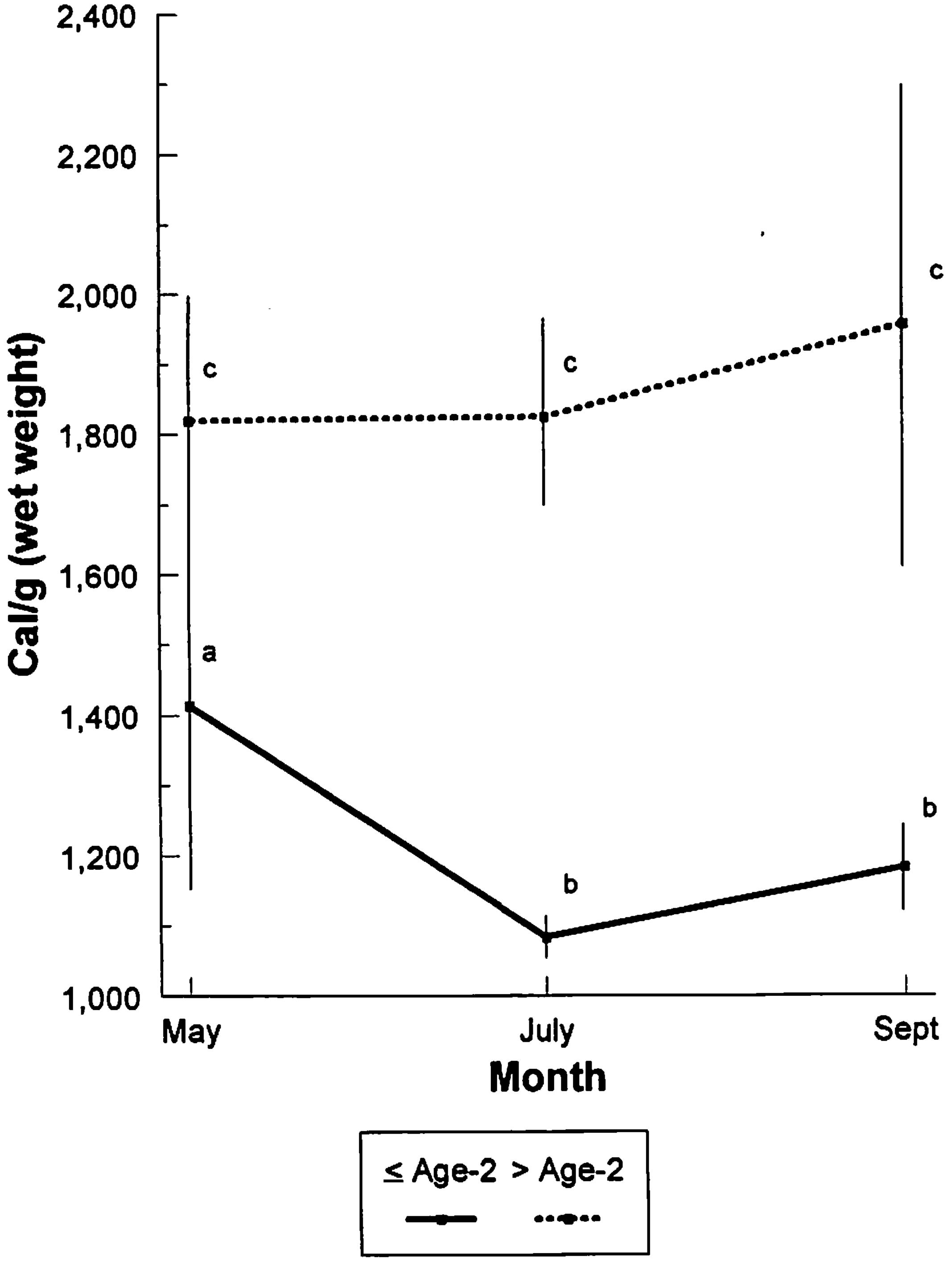


Figure 3.1. Mean seasonal caloric density (cal/g wet weight) of mature and immature walleyes during May through September, 1994 in Lake Oahe. Vertical lines represent one standard deviation. Mean caloric densities with the same letters are not significantly different (α=0.05).

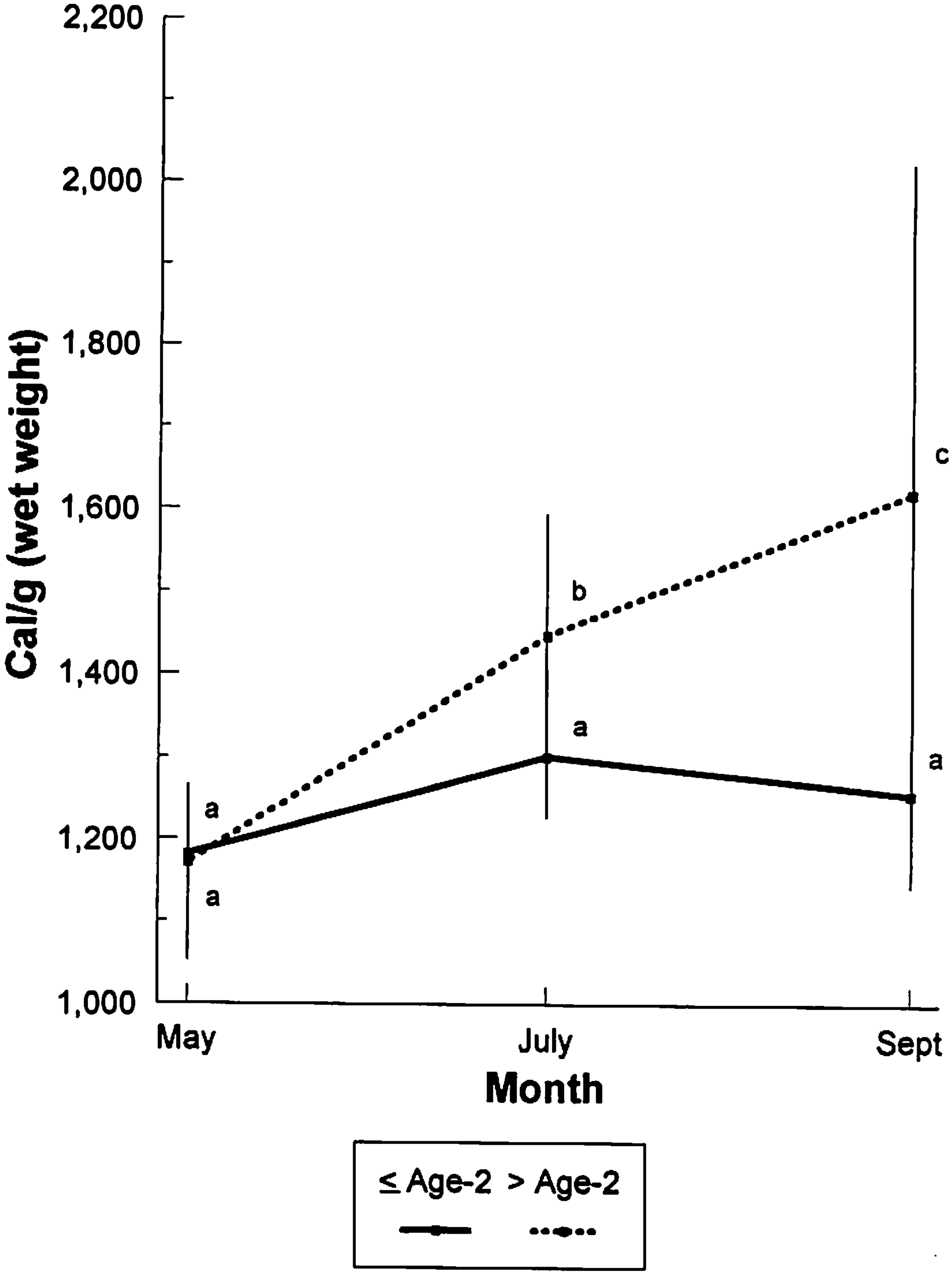


Figure 3.2. Mean seasonal caloric density (cal/g wet weight) of mature and immature chinook salmon during May through September, 1994 in Lake Oahe. Vertical lines represent one standard deviation. Mean caloric densities with the same letters are not significantly different ($\alpha=0.05$).

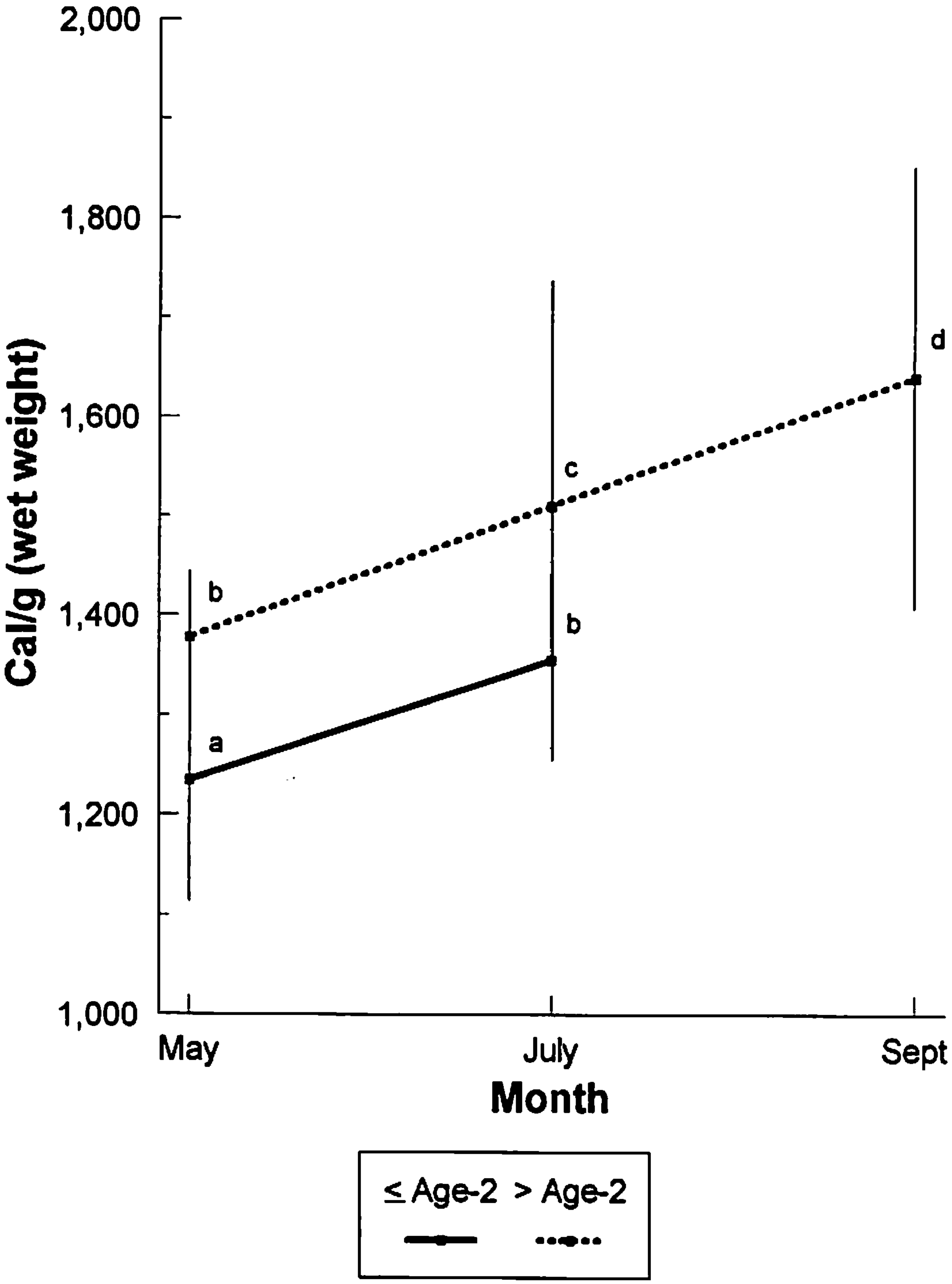


Figure 3.3. Mean seasonal caloric density (cal/g wet weight) of mature and immature rainbow trout during May through September, 1994 in Lake Oahe. Vertical lines represent one standard deviation. Mean caloric densities with the same letters are not significantly different ($\alpha=0.05$).

energy density of mature fish ranged from 1,378 cal/g during May to 1,642 cal/g during September, a 16% increase. Caloric density of mature fish collected during September was greater than during May (*P* = 0.0001, df = 2) and July (*P* = 0.033, df = 2). Mean caloric density of immature rainbow trout also increased during May through July. There were no immature rainbow trout captured in September, so seasonal patterns could not be identified. No significant differences between mean caloric density of mature and immature rainbow trout were observed among months.

Prey fishes

Rainbow smelt are the primary prey fish for walleyes (Bryan et al. 1995), chinook salmon (Tracy Hill, South Dakota State University, personal communication) and rainbow trout (Lynott et al., *in prep*) in Lake Oahe. Mean caloric density of rainbow smelt (75-177 mm) was greatest during July and decreased through the rest of the summer (Figure 3.4). Among-month comparisons were significant (*P* = 0.0001, df = 4).

Mean caloric density of lake herring (190-415 mm) was higher than all other prey fish, showing a seasonal increase from 1,799 cal/g during May to 2,304 cal/g during September (Figure 3.4). Mean caloric density of lake herring did not differ among months (*P* = 0.1840, df = 2).

Other important prey fishes in Lake Oahe include yellow

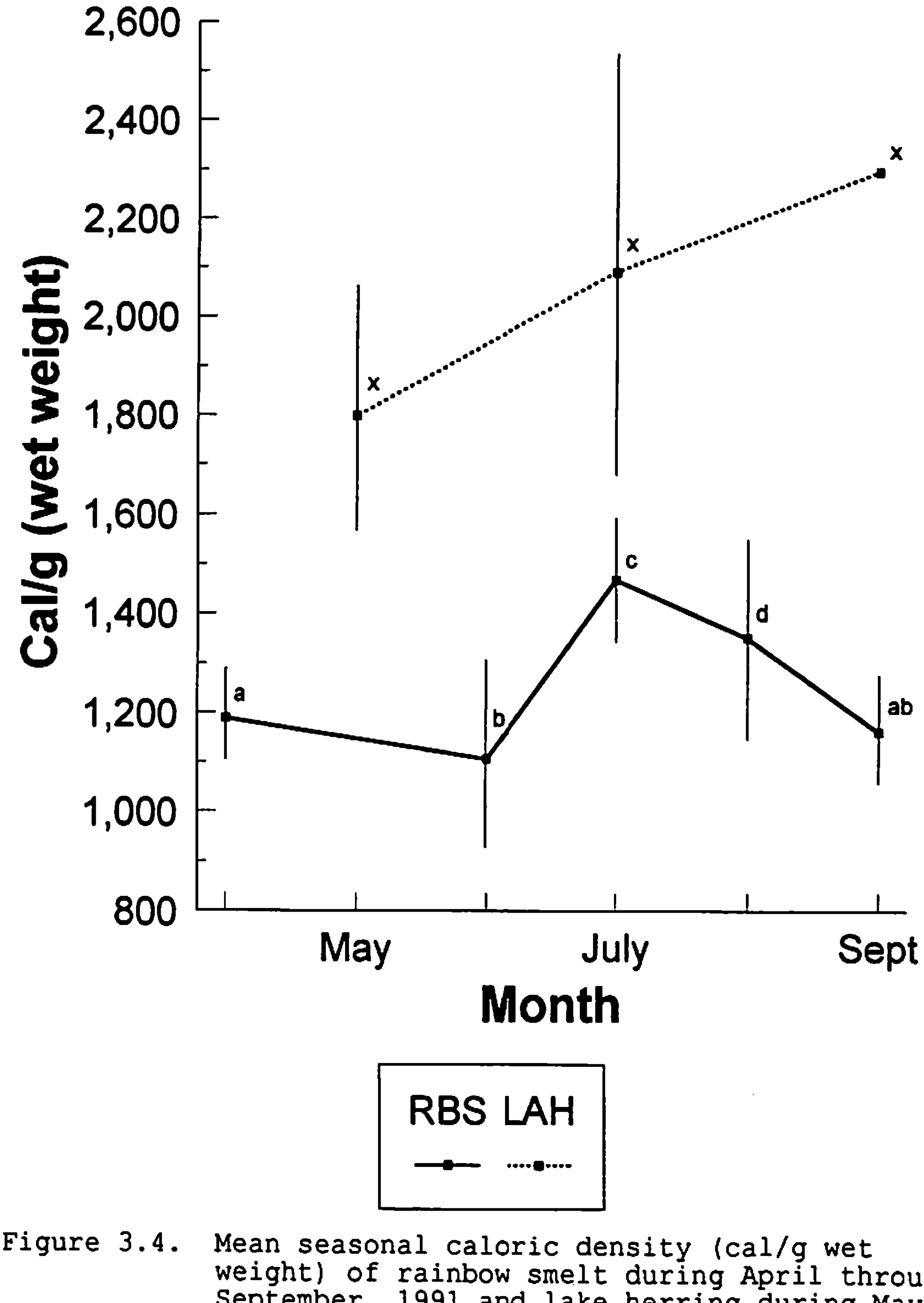


Figure 3.4. Mean seasonal caloric density (cal/g wet weight) of rainbow smelt during April through September, 1991 and lake herring during May through September, 1994 in Lake Oahe. Vertical lines represent one standard deviation. Mean caloric density for species with the same letters are not significantly different ($\alpha=0.05$).

perch and spottail shiners. Mean caloric density of yellow perch was greatest during July (Figure 3.5), however, no seasonal patterns were identifiable. All yellow perch analyzed were age-1 or older (97-204 mm). Spottail shiners increased in mean caloric density from May through September (Figure 3.5). However, among month differences in caloric density of spottail shiners ($P = 0.1309$, df = 2) was not significant. Mean caloric densities of white sucker *Catostomus commersoni*, common carp, common shiner *Luxilus cornutus*, emerald shiner, and fathead minnows *Pimephales promelas* were determined during the months in which they were captured (Table 3.1).

DISCUSSION

Caloric density of fishes varies among individuals, among seasons and age classes within populations, and geographically among populations. Published data on the variability of caloric density of fishes is scarce and limits generalizations. I found that mean caloric density of mature walleyes, chinook salmon, and rainbow trout increased during May through September. Greater caloric values during fall may be due to an increase in fat reserves in preparation for overwintering and spawning (Kelso 1973; MacKinnon 1972; Foltz and Norden 1977; Flath and Diana 1985). These fat reserves are subsequently used during winter metabolism and maturation of gonads (MacKinnon 1972).

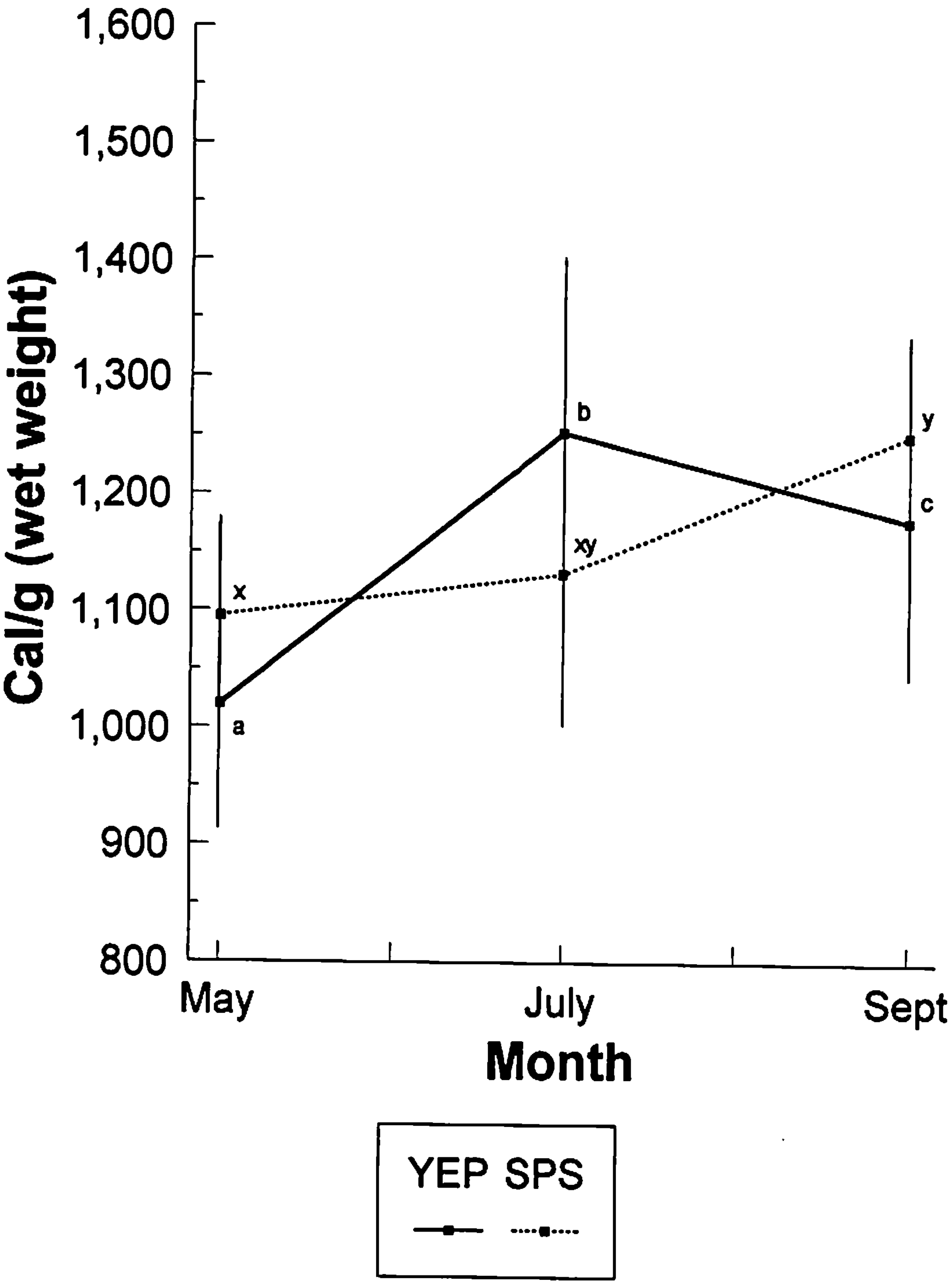


Figure 3.5. Mean seasonal caloric density (cal/g wet weight) of yellow perch and spottail shiners during May through September, 1994 in Lake Oahe. Vertical lines represent one standard deviation. Mean caloric density for species with the same letters are not significantly different ($\alpha=0.05$).

Table 3.1. Mean caloric density (cal/g wet weight) of common prey fishes captured in Lake Oahe during 1994. Standard deviations are in parentheses.

Species	Month collected	Number of fish[a]	Length range (mm)	Cal/g
White Sucker	May	3	107-119	883.49(32.25)
	Sept.	6(3)	79-94	856.98(37.69)
Common Carp	July	7(3)	49-67	857.29(65.81)
Common Shiner	July	8(1)	50-62	1193.61
Emerald Shiner	July	8(1)	49-88	1233.18
	Sept.	5(3)	73-81	1221.58(39.40)
Fathead Minnow	July	8(1)	48-65	1072.48
	Sept.	10(3)	49-63	934.12(33.56)
Goldeye	July	5	194-206	1449.42(73.32)

[a] Value in parentheses for this column indicates number of combustions if different from number of fish.

Mature fishes typically have higher caloric density values than immature fishes because of body size, composition, and the development of gonads (Meakins 1976; Craig 1977; Rottiers and Tucker 1982; Weatherley and Gill 1983). Mean seasonal caloric density of immature predators differed from adults in Lake Oahe. Immature walleyes did not use fat reserves for maturation of gonads and appeared to retain these fat reserves longer than mature fish. Consequently, immature walleyes had greater mean caloric density values during May than during July or September. Similarly, seasonal changes in the fat of Eurasian perch in Windermere were reflected in the same seasonal changes in caloric density (Craig 1977).

My data indicates that age-3 and older chinook salmon have a greater caloric density than the smaller, younger fish during the summer and fall. Because chinook salmon are semelparous, maturation of their gonads occurs over most of their lifespan. Landlocked female chinook salmon mature at age 4, while males mature as early as age 1 in Lake Sakakawea, North Dakota (Aadland 1987).

While mean caloric density of immature rainbow trout was less than in adults, both appeared to increase at the same rate between May and July. The low mean caloric density observed in immature rainbow trout may be due to feeding on zooplankton, while mature rainbow trout are feeding on larger invertebrates and fish.

Seasonally, the mean caloric density of rainbow smelt in Lake Oahe was greatest in July and decreased through September. This differed from the seasonal patterns from Lake Michigan (Foltz and Norden 1977) and Lake Ontario (Rand et al. 1994) in which caloric density of rainbow smelt increased from May through October. A decrease in caloric density between April and June was observed in Lake Ontario (Rand et al. 1994), similar to the decrease observed in Lake Oahe, and may be due to physiological stress incurred by spawning fishes. Declining overall zooplankton abundance through the late summer months (Karnitz 1992) may explain the decreasing mean caloric density of rainbow smelt during this time.

Rainbow smelt are the predominant prey fish for most predators in Lake Oahe. However, the energy density of rainbow smelt is substantially lower than that of lake herring. If the population size of rainbow smelt in Oahe Reservoir declines dramatically, lake herring may become better established (Wisconsin Department of Natural Resources 1988), and be a more important prey fish for walleyes, chinook salmon, and rainbow trout than rainbow smelt. The greater caloric density and larger size of the lake herring could result in faster growth rates of predatory fishes in Lake Oahe. Although I found that mean caloric density of yellow perch and spottail shiners in Lake Oahe varied little seasonally, yellow perch in West Blue

Lake, Manitoba exhibited a significant increase in caloric density from July to October (Kelso 1972).

Minor errors in caloric density values can easily be magnified when literature values are extrapolated to populations (Kelso 1973) and constant values should not be used for the energy incorporated as growth in studies of fish production and energetics (Meakins 1976). Seasonal changes in caloric density of fishes not only indicate seasonal changes in body condition, but also can be related to changes in community biomass, food density, or climatic changes. Sensitivity analysis of site-specific parameters associated with bioenergetics models shows that these seasonal changes in caloric density can affect both the consumption of prey and the seasonal growth of predators (Chapter 4).

Additional work is needed to determine mean seasonal caloric density of Lake Oahe fish species, especially during winter; however, the seasonal trends that I found in this study are an important step in understanding the energetics of walleye, chinook salmon, and rainbow trout in Oahe Reservoir.

Chapter 4.

Bioenergetics of Walleyes

Introduction

Increasing pressure to predict the possible consequences of their decisions has fisheries managers searching for quantitative tools to evaluate and understand the complex biological relationships in aquatic ecosystems (Brandt and Hartman 1993). The value of bioenergetics models in describing energy budgets and production dynamics of fishes has been widely recognized since Winberg (1956) published the "balanced energy equation" (Minton and McLean 1982). The model provides a theoretical framework for relating growth rates and feeding rates of an organism to environmental conditions and provides some insight into causal relationships between these variables (Adams and Breck 1990).

Bioenergetics models are based on the assumption that all food consumed by an organism is either expended as heat energy, incorporated into body tissue, or excreted as waste (Brandt and Hartman 1993). Each model must be parameterized for the balanced energy equation by selecting species-specific physiological estimates of consumption or growth, respiration, egestion, and excretion (Kitchell et al. 1977). The equation can be solved for any of these parameters when the others are known or estimated.

The bioenergetics approach has been applied to a wide variety of ecological problems involving fish growth and prey consumption. Most frequently, these models have been used to quantify predator trophic demand and the relationship of demand to prey supply (Ney 1990). Estimation of consumption or demand is an important application of bioenergetics models because of the need to regulate stocking and harvest of predator species (Hansen et al. 1993). Prey consumption by walleyes in Lake Erie (Hartman and Margraf 1992) and largemouth bass in Ohio reservoirs (Carline et al. 1984) have been estimated using bioenergetics models for the purpose of adjusting harvest rates. The impact of walleye predation on the prey assemblage has been assessed in a small Wisconsin lake through the use of energetics modeling (Lyons 1984). The effects of increased predation on rainbow smelt by lake trout following sea lamprey *Petromyzon marinus* control was estimated using a bioenergetics model (LaBar 1993). Optimal stocking densities for salmonids in the Great Lakes (Stewart et al. 1981), esocids in five Ohio reservoirs (Bevelhimer et al. 1985), and coolwater piscivores in Virginia (Moore 1988) have been determined through bioenergetics modeling.

Bioenergetics has also been used to predict the growth of fishes under a variety of potentially limiting factors. Factors examined have included the influence of temperature and prey availability (Kitchell et al. 1977; Rice et al.

1983; Hill and Magnuson 1990), the uptake of PCB's and mercury (Weininger 1978; Borgemann and Whittle 1992), and changes in energy flow and nutrient processing rates (Schindler et al. 1993; He et al. 1993). The influence of zebra mussels *Dreissenia polymorpha* on the growth of fishes in the Great Lakes (Schneider 1992) has also been modeled using bioenergetic concepts.

A rapid decline in the numbers and condition of rainbow smelt (population crash) in 1989 was cause for concern for reservoir biologists at Lake Oahe. The rainbow smelt population has since recovered, however preliminary observations indicate that several predators in Lake Oahe are now competing for rainbow smelt as a primary food source (SDGF&P, unpublished data). The cyclical nature of rainbow smelt population dynamics along with the current stocking practices of predators could cause the rainbow smelt population to collapse again. The effects a smelt population crash on the growth and condition of the predators that are utilizing rainbow smelt is not known. The purpose of this study was to determine the demand of rainbow smelt by walleyes in Lake Oahe. The bioenergetics model developed by Hewett and Johnson (1992) was modified using site-specific parameters to simulate the consumption and growth of walleyes in Lake Oahe. This model, along with estimates of rainbow smelt production, was used to determine the impact of walleye predation on the smelt population.

Model Parameters

Bioenergetics models - The bioenergetics modeling program developed by Hewett and Johnson (1992) was used to model walleye consumption and growth with site-specific data collected from Lake Oahe during 1993 and 1994. Bioenergetics modeling is probably the most cost effective and accurate method for estimating annual forage demand by a predator population (Stewart et al. 1983); therefore, the walleye bioenergetics model was used to derive estimates of total consumption of prey from observed growth of walleyes during the two years of the study.

The bioenergetics model essentially describes the energy intake and use by fish with an equation (Hewett and Johnson 1992):

$$C=(R+S)+(F+U)+(\Delta B)$$

where C = consumption, R = respiration, S = specific dynamic action, F = egestion, U = excretion, and ΔB = growth. All consumption and growth computations are based on grams of prey per gram of predator per day, wet weight (Hewett and Johnson 1987).

The species-specific variables used to model the energetics of walleyes in Lake Oahe (Table 4.1) are similar to those derived by Kitchell et al. (1977). A complete description of the model parameters is given by Hewett and Johnson (1992).

Site-specific inputs included observed growth rates (size at date), population and mortality estimates, dietary proportions throughout the year, seasonal caloric densities of walleyes and their prey, dates and age at spawning, percent of weight lost during spawning, and water temperatures where the fish were found throughout the year. In the case of population and mortality estimates, an adequate sample could not be obtained, so I relied on unpublished information gathered by the South Dakota Department of Game, Fish and Parks.

For modeling purposes, data were combined from all three regions of Oahe Reservoir (Figure I.1) because population estimates could not accurately be determined for each region separately. Modeling simulations were run for age 1 through age 6 walleyes on daily intervals for 365 days beginning on 16 May and ending on 15 May. Each age class of walleye was divided into three separate periods to better represent seasonal patterns of consumption and variability in prey abundance. These growth periods were: 16 May to 15 December (summer/fall), 16 December to 15 March (winter), and 16 March to 15 May (spring).

Growth Rates - Walleyes were collected from Lake Oahe with monofilament gill nets from January to September, 1993 and 1994, to determine seasonal growth rates. Collection procedures are detailed in Chapters 1 and 2. Upon capture, total lengths of all walleyes were measured to the nearest

Table 4.1. Symbols and parameter values used to implement the bioenergetics model for walleyes from Lake Oahe (described in Hewett and Johnson 1992).

Reference Equation	Symbol	Parameter Description	Parameter Value
		Consumption	
2	CA	Intercept for maximum consumption	0.250
	CB	Slope for maximum consumption	-0.270
	CQ	Slope for temperature dependence of consumption	2.300
	CTO	Optimum temperature for consumption	22.00
	CTM	Maximum temperature for consumption	28.00
		Respiration	
2	RA	Intercept for maximum standard respiration	0.011
	RB	Slope for maximum standard respiration	-0.200
	RQ	Slope for temperature dependence of standard respiration	2.100
	RTO	Optimum temperature for standard respiration	27.00
	RTM	Maximum temperature for standard respiration	32.00
	ACT	Activity parameter	1.00
	SDA	Specific dynamic action	0.172

Table 4.1. (continued)

		Egestion/Excretion	
2	FA	Intercept for proportion egested	0.158
	FB	Coefficient of egestion vs. temperature	-0.222
	FG	Coefficient of egestion vs. feeding level	0.631
	UA	Intercept for proportion excreted	0.025
	UB	Coefficient of excretion vs. temperature	0.580
	UG	Coefficient of excretion vs. feeding level	-0.299

millimeter. Scale samples were removed just above the lateral line below the anterior edge of the dorsal fin (Erickson 1983). Scales were prepared and aged using standard methodology (Jearld 1983; Smith 1954). DisBCal software was used to determine back-calculated lengths at age (Frie 1982).

I assumed that the majority of the annual growth of walleyes in Lake Oahe occurred between March 15 and December 15 since water temperatures were ≤ 6°C between December 15 and March 15. In a review of temperature requirements throughout their North American range, Hokanson (1977) reported that percids exhibited a zero net biomass gain at temperatures < 6°C. Later, Minton and McLean (1982) found no growth in length of sauger from Watts Bar Reservoir, Tennessee during winter. Winter growth rates of walleyes in Lake Oahe is probably also low, however, I was not able to test the validity of this assumption due to small sample size during winter.

Mean monthly lengths of walleyes were calculated from observed data for each age class. The von Bertalanffy growth function (von Bertalanffy 1938) was used to derive starting and final lengths for each age class of walleye based on mean monthly lengths:

$$L_t = L\infty(1-e^{(-K(t-t_0))})$$

where L_t = length (mm) at time t, and $L\infty$, K, and t_0 are species-specific parameters. Parameter estimates derived from observed monthly length of walleyes using FISHPARM software (Prager 1989) were:

$$L\infty = 102.50$$
$$K = 0.09777$$
$$t_0 = -1.475$$

Due to the small sample size of walleyes during the winter months, mean monthly lengths could not be accurately estimated with the von Bertalanffy growth function. Instead, back-calculated lengths were used as endpoints to seasonal growth (December 15).

Seasonal length-weight regression equations (Table 4.2) were developed for age 1 and older walleyes in Lake Oahe to determine starting and final weights for each cohort from calculated lengths (Table 4.3). The derived weights for walleyes were similar to the observed mean weights measured monthly, with a large portion of the derived weight curve within ± 1 SD of the measured means (Figure 4.1).

Population Size and Mortality Rates - The bioenergetics model developed by Hewett and Johnson (1992) is based on an average individual of the population. Population level energetics can be determined by multiplying average fish values by initial population size and mortality estimates. It is critical then, to be able to accurately estimate population size and mortality rate when modeling effects on the entire population.

Reliable population estimates in Lake Oahe are

Table 4.2. Seasonal length-weight regression equations developed for walleyes from Lake Oahe. Equations were derived from calculated mean seasonal lengths. Y is $\log_{10}$ weight (g) and X is $\log_{10}$ total length (mm).

Season	Equation	R^2
Summer/Fall	$Y = -5.583809 + 3.227709(X)$	0.988
Winter	$Y = -5.901098 + 3.347499(X)$	0.966
Spring	$Y = -5.425341 + 3.167039(X)$	0.902

Table 4.3. Starting and final weights (g) derived from length-weight regression equations and initial population estimates for each model cohort of walleyes from Lake Oahe.

Age class	Model Cohort	Simulation Days	Starting Weight	Final Weight	Initial Population
1	1	1-212	90.67	175.87	5.45×10^6
	2	213-302	175.87	191.33	3.52×10^6
	3	303-365	191.33	236.11	3.14×10^6
2	4	1-212	238.51	401.90	2.17×10^6
	5	213-302	401.90	418.18	1.40×10^6
	6	303-365	418.18	472.97	1.24×10^6
3	7	1-212	472.87	715.88	1.00×10^6
	8	213-302	715.88	722.06	6.44×10^5
	9	303-365	722.06	799.99	5.74×10^5
4	10	1-212	793.60	1119.80	7.62×10^5
	11	213-302	1119.80	1138.30	4.88×10^5
	12	303-365	1138.30	1210.80	4.35×10^5
5	13	1-212	1193.80	1563.60	2.89×10^5
	14	213-302	1563.60	1620.00	1.85×10^5
	15	303-365	1620.00	1694.50	1.65×10^5
6	16	1-212	1662.40	2041.10	1.40×10^5
	17	213-302	2041.10	2147.10	8.94×10^4
	18	303-365	2147.10	2238.00	7.97×10^4

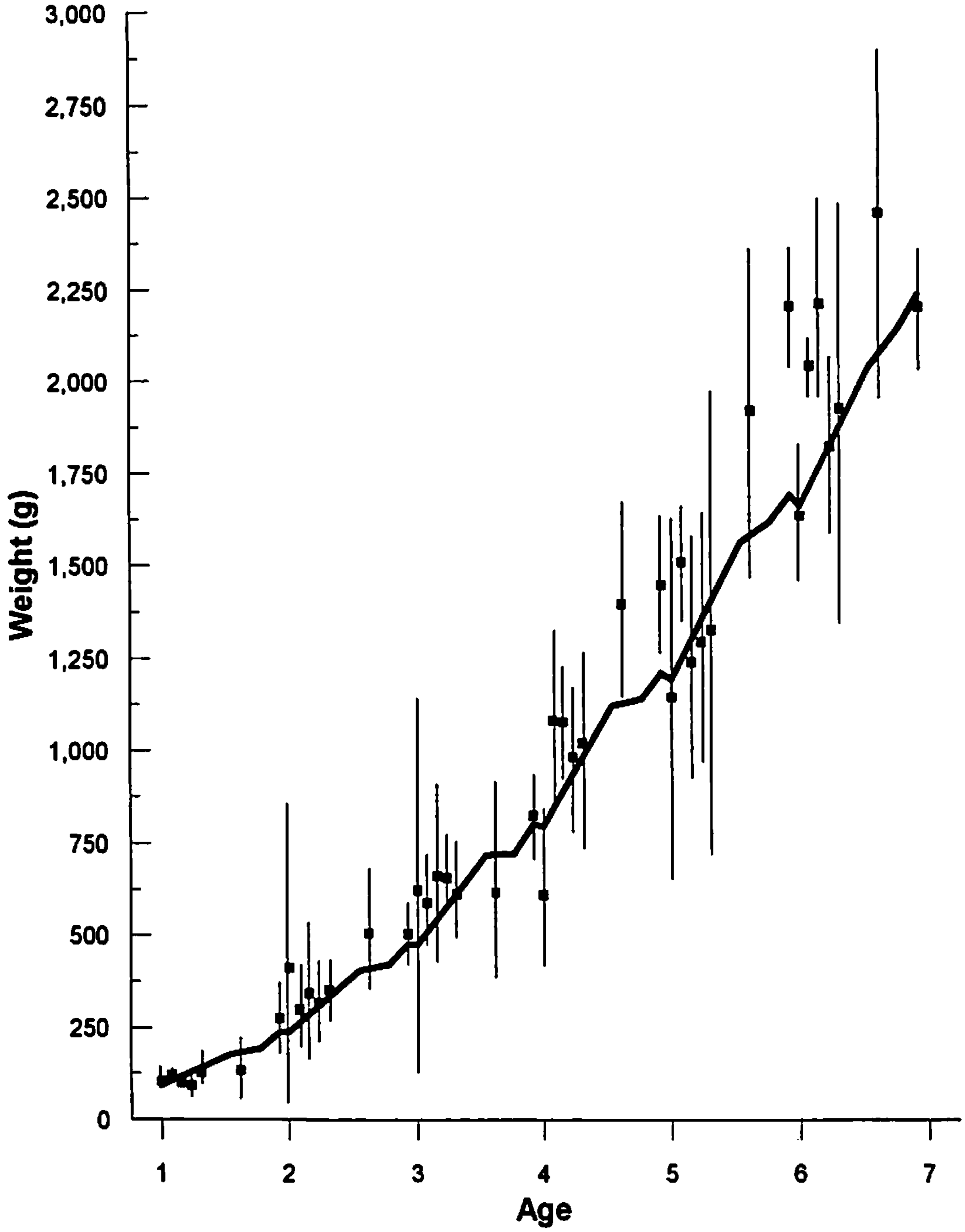


Figure 4.1. Seasonal growth in weight (g) of walleyes, ages 1 to 6, from Lake Oahe. Weights derived from a von Bertalanffy growth equation and seasonal length-weight regressions are plotted as a solid line. Square symbols are observed mean weights and verticle bars are ±1 standard deviation of the mean.

difficult due to the large size of the reservoir and the immigration of walleyes from Lake Sakakawea through Garrison Dam in North Dakota. However, for the purpose of population level modeling, it is necessary to be as accurate as possible when estimating population size. The Petersen single census mark recapture method was used to estimate the population of exploitable (age 2 and older) walleyes in Lake Oahe (Appendix A.2). Age frequency of walleyes captured during monthly sampling and fall sampling by the SDGF&P were combined and recorded as a percentage of the total sample in each age class. These percentages were then multiplied by the overall population estimate of exploitable fish to derive a population estimate for each age class (Table 4.3). A non-linear regression equation was developed for the populations of age 2 - 6 walleyes (R^2=0.989) and the regression line was extended back to determine the population of age 1 walleyes.

A catch curve (Ricker 1975) was used to determine total mortality of walleyes in Lake Oahe (Appendix A.3). Total mortality was assumed to be evenly spread over the year and was constant across age classes. Annual mortality was converted to daily instantaneous mortality and apportioned as natural and fishing mortality. Fishing mortality was derived from creel census data obtained from the SDGF&P (Table 4.4). Although improbable, it was assumed that no age 1 fish were harvested due to the increased acceptance of

Table 4.4. Natural and fishing mortality, number of walleyes dying naturally, and number of walleyes harvested from Lake Oahe as determined through bioenergetics modeling.

Age class	Total Mortality	Natural Mortality	Number Dying Naturally	Fishing Mortality	Number of Walleyes Harvested
1	0.5034	0.5034	2.72×10^6	0.0000	0
2	0.5034	0.4991	1.08×10^6	0.0043	9.34×10^3
3	0.5034	0.4146	4.20×10^5	0.0888	9.00×10^4
4	0.5034	0.3448	2.63×10^5	0.1586	1.21×10^5
5	0.5034	0.3588	1.04×10^5	0.1446	4.19×10^4
6	0.5034	0.3663	5.13×10^4	0.1371	1.92×10^4

catch-and-release ethics by anglers. In addition, a 14" minimum length limit is enforced during April through June. Natural mortality was calculated by subtracting fishing mortality from total mortality (Ricker 1975).

Diet - Walleyes captured with monofilament gill nets in 1993 and 1994 fed mainly on rainbow smelt in Lake Oahe (Chapter 2). Stomach samples were combined from the upper, middle, and lower regions of the reservoir to determine diet proportions of walleyes for the entire lake. Diet was categorized by age class and reported as a mean proportion of the total food (weight wet) in six separate food categories (Table 4.5).

Caloric density of walleyes and prey - Seasonal caloric densities of walleyes and their prey in Lake Oahe were determined using bomb calorimetrics (Chapter 3) and published literature. Caloric densities of walleyes were held constant during winter as fish maintained energy storage during that period for overwintering and spawning (Table 4.6).

Prey items consumed by walleyes in Lake Oahe included adult and juvenile rainbow smelt, yellow perch, spottail shiners, juvenile chinook salmon, insects, and zooplankton (Chapter 2). Rainbow smelt were considered to be adult at age 1 for calorimetric purposes, even though they do not spawn until age 2 (Scott and Crossman 1973). Caloric density values for prey were linearly interpolated when

Table 4.5. Seasonal diet of walleyes from Lake Oahe as a proportion of total food (wet weight) consumed for six prey categories. Values are given by age, date, and the corresponding simulation day.

Date	Simulation Day	Adult RBS[a]	Age 0 RBS	YEP & SPS[b]	FCS[c]	Insects[d]	Zoo[e]
Age 1							
May 16	1	0.9658	0.0000	0.0000	0.0000	0.0098	0.0244
Jun 20	34	0.9372	0.0000	0.0000	0.0000	0.0478	0.0150
Jul 20	64	0.6347	0.2613	0.0928	0.0000	0.0099	0.0013
Aug 20	95	0.8622	0.1270	0.0000	0.0000	0.0106	0.0002
Sep 20	126	0.3930	0.2526	0.3544	0.0000	0.0000	0.0000
Jan 20	248	0.8000	0.0000	0.0000	0.0000	0.0000	0.2000
Mar 20	297	1.0000	0.0000	0.0000	0.0000	0.0000	0.0000
May 15	365	0.8598	0.0000	0.0000	0.1311	0.0088	0.0002
Age 2							
May 16	1	0.8598	0.0000	0.0000	0.1311	0.0088	0.0002
Jun 20	34	0.9714	0.0000	0.0257	0.0000	0.0028	0.0001
Jul 20	64	0.9775	0.0095	0.0108	0.0000	0.0022	0.0000
Aug 20	95	0.6905	0.1606	0.1241	0.0000	0.0082	0.0166
Sep 20	126	0.9321	0.0675	0.0000	0.0000	0.0004	0.0000
Jan 20	248	1.0000	0.0000	0.0000	0.0000	0.0000	0.0000
May 15	365	0.8830	0.0000	0.0110	0.0932	0.0125	0.0003
Age 3							
May 16	1	0.8830	0.0000	0.0110	0.0932	0.0125	0.0003
Jun 20	34	0.9510	0.0000	0.0479	0.0000	0.0010	0.0001
Jul 20	64	0.9977	0.0023	0.0000	0.0000	0.0000	0.0000
Aug 20	95	0.9878	0.0090	0.0000	0.0000	0.0031	0.0001
Sep 20	126	0.9303	0.0341	0.0349	0.0000	0.0007	0.0000
Jan 20	248	1.0000	0.0000	0.0000	0.0000	0.0000	0.0000
May 15	365	0.9943	0.0000	0.0000	0.0000	0.0057	0.0000
Age 4							
May 16	1	0.9943	0.0000	0.0000	0.0000	0.0057	0.0000
Jun 20	34	1.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Jul 20	64	0.8683	0.0008	0.1303	0.0000	0.0006	0.0000
Aug 20	95	0.8784	0.0527	0.0676	0.0000	0.0012	0.0001
Sep 20	126	0.9093	0.0907	0.0000	0.0000	0.0000	0.0000
Jan 20	248	1.0000	0.0000	0.0000	0.0000	0.0000	0.0000
May 15	365	0.9329	0.0000	0.0652	0.0000	0.0019	0.0000

Table 4.5. (continued)

Date	Simulation Day	Adult RBS[a]	Age 0 RBS	YEP & SPS[b]	FCS[c]	Insects[d]	Zoo[e]
Age 5							
May 16	1	0.9329	0.0000	0.0652	0.0000	0.0019	0.0000
Jun 20	34	1.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Jul 20	64	0.9958	0.0000	0.0000	0.0000	0.0042	0.0000
Aug 20	95	1.0000	0.0000	0.0000	0.0000	0.0000	0.0000
May 1	348	1.0000	0.0000	0.0000	0.0000	0.0000	0.0000
May 15	365	0.8250	0.0000	0.0000	0.1732	0.0018	0.0000
Age 6							
May 16	1	0.8250	0.0000	0.0000	0.1732	0.0018	0.0000
Jun 20	34	1.0000	0.0000	0.0000	0.0000	0.0000	0.0000
Jul 20	64	0.9958	0.0000	0.0000	0.0000	0.0042	0.0000
Aug 20	95	1.0000	0.0000	0.0000	0.0000	0.0000	0.0000
May 1	348	1.0000	0.0000	0.0000	0.0000	0.0000	0.0000
May 15	365	0.5013	0.0000	0.0000	0.4983	0.0004	0.0000

[a] Rainbow smelt
[b] Yellow perch and spottail shiners
[c] Newly stocked fall chinook salmon
[d] Includes Ephemeroptera and Chironimidae
[e] Includes cladocera and copepoda

Table 4.6. Mean caloric density (cal/g wet weight) of walleyes ages 1-2 and ages 3-6 from Lake Oahe used in the bioenergetics simulation. Values were derived from calorimetric analysis (Chapter 3).

Date	Simulation Day	Caloric Density
Ages 1-2		
May 16	1	1413
July 20	64	1082
September 20	126	1182
November 18	185	1600
April 22	340	1600
May 15	365	1424
Ages 3-6		
May 16	1	1818
July 20	64	1826
September 20	126	1960
April 22	340	1960
May 15	365	1818

Table 4.7. Mean caloric density (cal/g wet weight) of prey consumed by walleyes from Lake Oahe.

Date	Simulation Day	Adult RBS[a]	Age 0 RBS[b]	YEP & SPS[a]	FCS[b]	Insects[c]	Zoo[d]
May 16	1	1148	797	1058	1181	972	475
Jun 20	34	1106	787	1148	1244	972	475
Jul 20	64	1470	804	1230	1301	972	475
Aug 20	95	1354	853	1206	1278	972	475
Sep 20	126	1165	956	1181	1255	972	475
Oct 20	156	1200	903	1181	1255	972	475
Nov 20	187	1200	847	1181	1255	972	475
Dec 20	217	1200	881	1181	1255	972	475
Jan 20	248	1200	915	1181	1255	972	475
Feb 20	279	1200	949	1181	1255	972	475
Mar 20	307	1200	879	1181	1255	972	475
Apr 20	338	1189	790	1181	1255	972	475
May 15	365	1148	797	1058	1181	972	475

[a] Mean value of adult rainbow smelt, yellow perch, spottail shiners, and fall chinook salmon from Chapter 3.
[b] Mean value of age 0 rainbow smelt from Lantry and Stewart (1993).
[c] Mean value for chironomids and ephemerids from Penczak (1985).
[d] Zooplankton mean caloric density from Cummins and Wuycheck (1971).

monthly values were missing (Table 4.7). Caloric density of age 0 rainbow smelt (< 60 mm) was determined by Lantry and Stewart (1993). Seasonal caloric density of yellow perch and spottail shiners were similar, so these prey were combined in the model. The mean energy density of Ephemeroptera and Chironomidae, 972 cal/g (Penczak 1985), was used as an annual caloric density for insects. The caloric density used for zooplankton (475 cal/g) was the mean reported for cladocerans and copepods by Cummins and Wuycheck (1971).

Spawning - The bioenergetics model computes losses due to spawning as a fixed proportion of weight on a specific day of the year (Hewett and Johnson 1992). Male walleyes typically mature at a younger age than do female walleyes (Scott and Crossman 1973), however, maturity tends to vary with water temperature and food availability within a given lake (Colby et al. 1979). In Lake Oahe, male walleyes mature as early as age 2 and females mature at age 3 or later. Because I did not differentiate between male and female walleyes in the model simulations, the first spawning cohort was designated as 7 (age 3) and the date of spawning was determined to be April 22, the peak of the spawning run. During April, 1993, 35 male and female walleyes were weighed prior to and after spawning. From these weights, I determined that the mean proportion of body weight lost during spawning was 9.28%.

Water temperatures - I recorded monthly water temperatures in each region of the reservoir (Figure I.1) at 1 m depth intervals using a Scout Model multi-probe water quality sensor (Hydrolab Inc., Austin, Texas). Depth and location at which each walleye was captured in gill nets (Chapter 1) was recorded and water temperatures were correlated with these measurements. Mean water temperatures at time of capture were then used in the bioenergetics model (Figure 4.2). Mean water temperatures concur with temperature data taken daily from the discharge at Oahe Dam by U.S. Army Corps of Engineers (unpublished data) during 1993 and 1994. Water temperatures taken at Oahe Dam were used during months in which sampling did not take place. Water temperatures in Lake Oahe did not exceed the maximum for consumption (28°C) or respiration (32°C) for walleyes (Hewett and Johnson 1992) during the period modeled.

Model Output

P-Values - After all species- and site-specific data files have been entered, the initial function of the program is to calculate the proportionality constant (P-value) for each cohort. The P-value represents the proportion of maximum consumption by an average fish in each cohort over the run interval. P-values are fit iteratively from starting and final weights. P-values for walleyes were most variable during spring with values ranging from 0.20 for age

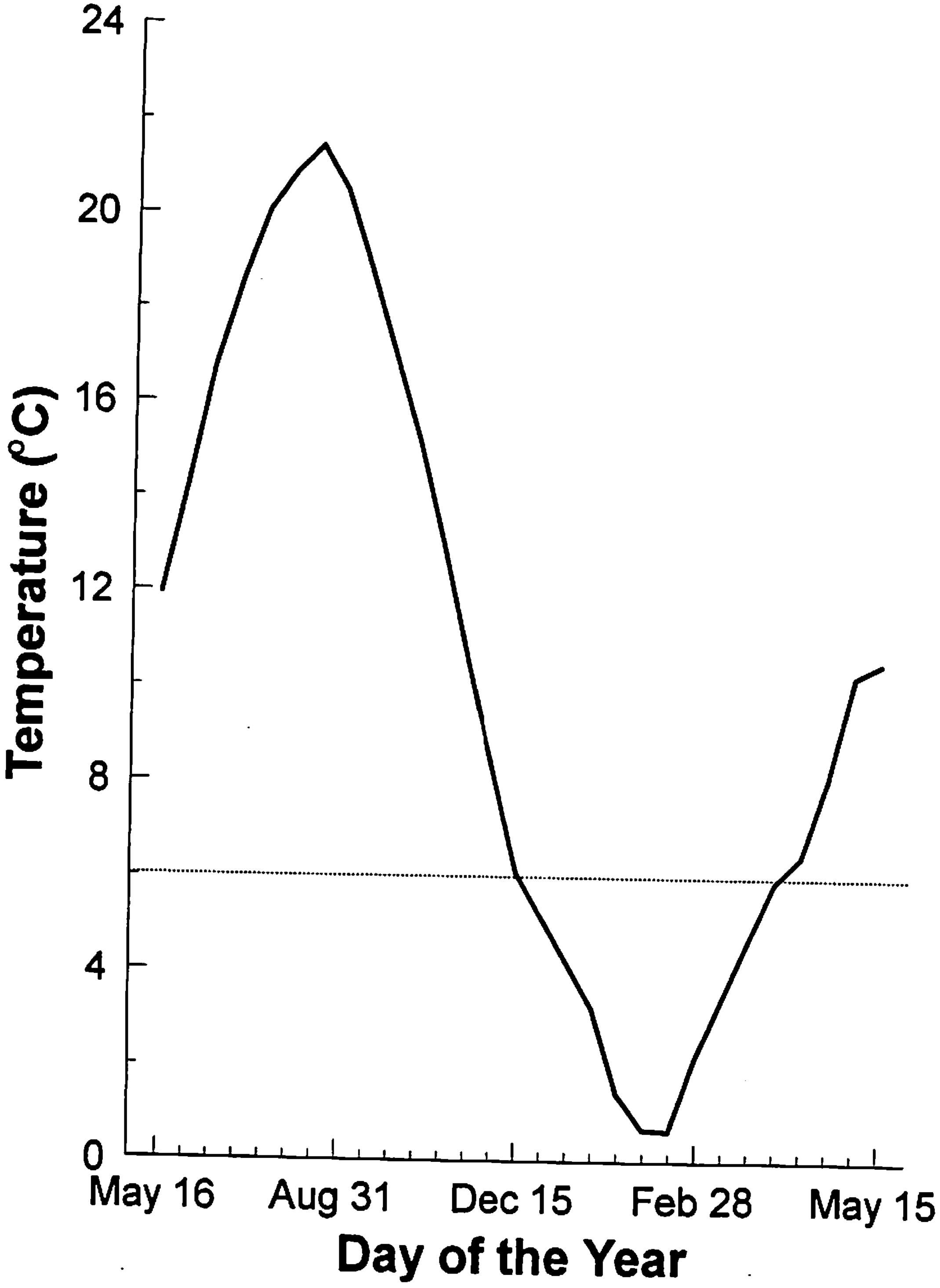


Figure 4.2. Mean water temperatures of Lake Oahe used in the bioenergetics model for walleyes. The dotted line at 6°C represents the temperature at which a zero net growth occurs in walleyes (Hokanson 1977).

Table 4.8. Seasonal P-values, the proportion of maximum consumption, and mean seasonal P-values for walleyes ages 1-6 from Lake Oahe.

Age class	Summer/Fall	Winter	Spring
1	0.3330	0.3867	0.3225
2	0.3355	0.3089	0.2022
3	0.3732	0.2596	0.5457
4	0.3812	0.2977	0.4695
5	0.3670	0.3818	0.4419
6	0.3544	0.4616	0.4499
Mean	0.3569	0.3494	0.4053

2 walleyes to 0.55 for age 3 walleyes (Table 4.8).

P-values are an index to predatory intensity as well as a reflection of prey availability (Rice et al. 1983). Mean seasonal P-values of walleyes were relatively constant throughout the year, which may indicate that availability and consumption of rainbow smelt were constant during all three seasons. Similarly, Moore (1988) observed constant P-values for walleyes throughout the growing season in Smith Mountain Lake, Virginia. The greatest mean seasonal P-value for walleyes was observed during spring, which may be explained by increasing temperatures and activity, intense feeding by walleyes soon after spawning, or vulnerability of spawning rainbow smelt during late March.

Growth - A majority of the simulated growth of walleyes in Lake Oahe occurred between the end of March, when temperatures warmed above 6°C, and the middle of December, when temperatures dropped below 6°C (Figure 4.3). Ages 1 and 2 walleyes lost weight between 30 September and 15 November, probably due to a switch in the diet which included more age 0 rainbow smelt and yellow perch, both of which have lower overall energy density than adult rainbow smelt. Older age classes increased in weight throughout the entire year, except during spawning. Growth during winter was much less pronounced than during other seasons. However, the fact that walleyes gained weight during winter coupled with high P-values, may indicate that adequate forage is

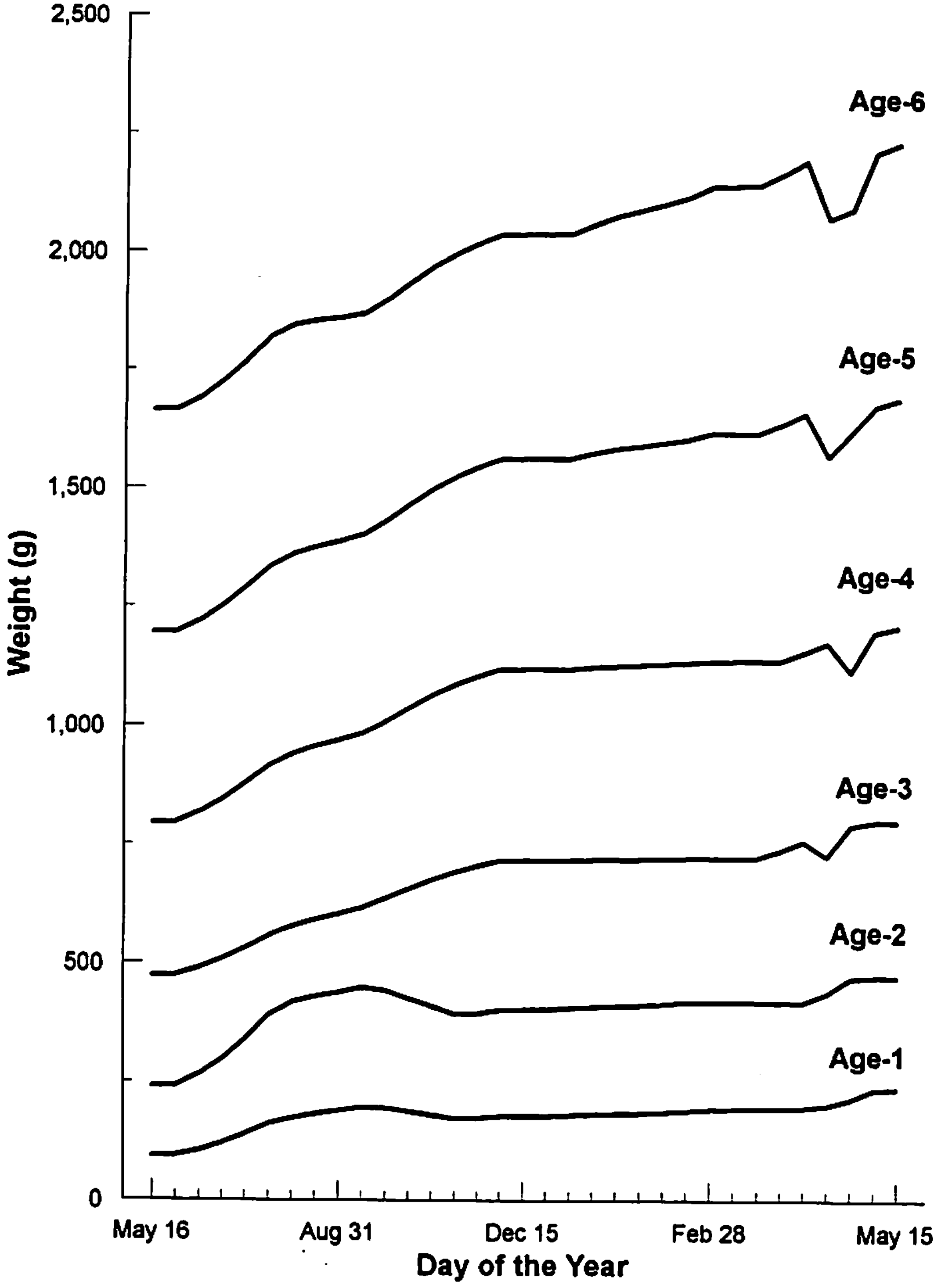


Figure 4.3. Estimated body weight (g) over a year of life for the average walleye, age 1 to 6, from Lake Oahe. Estimates are derived from bioenergetics simulations.

available in Lake Oahe year-round. During spawning, as much as 20% of the production of an age class was shed as gametes.

Conversion efficiency - Gross conversion efficiency is a measure of the ability of an organism to convert ingested food into new tissue (Lantry and Stewart 1993) and is dependent on the quantity and quality of food available and the environmental conditions of the habitat (Warren 1971). It is calculated by dividing the total weight gain of an individual walleye by total individual consumption. Conversion efficiency of walleyes decreased from 20.0% for age 1 fish to 12.0% for age 6 fish (Table 4.9). Growth efficiency typically declines with the increasing body size of fishes (Adams et al. 1982). The gross conversion efficiency averaged over all six age classes for walleyes in Lake Oahe was 15.4%.

Prey demand of walleyes - The bioenergetics program uses daily rates of metabolic processes, proportional diet data, and energy values to estimate daily consumption of prey by an average fish. Population size and mortality rates provide estimates of total consumption of prey by the entire population over a simulation period.

Total biomass consumed by an average individual walleye in Lake Oahe increased with each age class (Figure 4.4). Annually, an average age 6 walleye consumes about 6.6 times more biomass than does an average age 1 walleye.

Table 4.9. Mean weight gain, individual cumulative consumption, and gross conversion efficiency for walleye age classes from Lake Oahe based on bioenergetics simulations.

Age class	Weight Gain (g)	Individual Cum. Consumption (g)	Conversion Efficiency (%)
1	145.44	725.42	20.0
2	234.47	1272.72	18.4
3	327.12	2138.96	15.3
4	417.20	3019.24	13.8
5	500.70	3874.81	12.9
6	575.60	4789.67	12.0

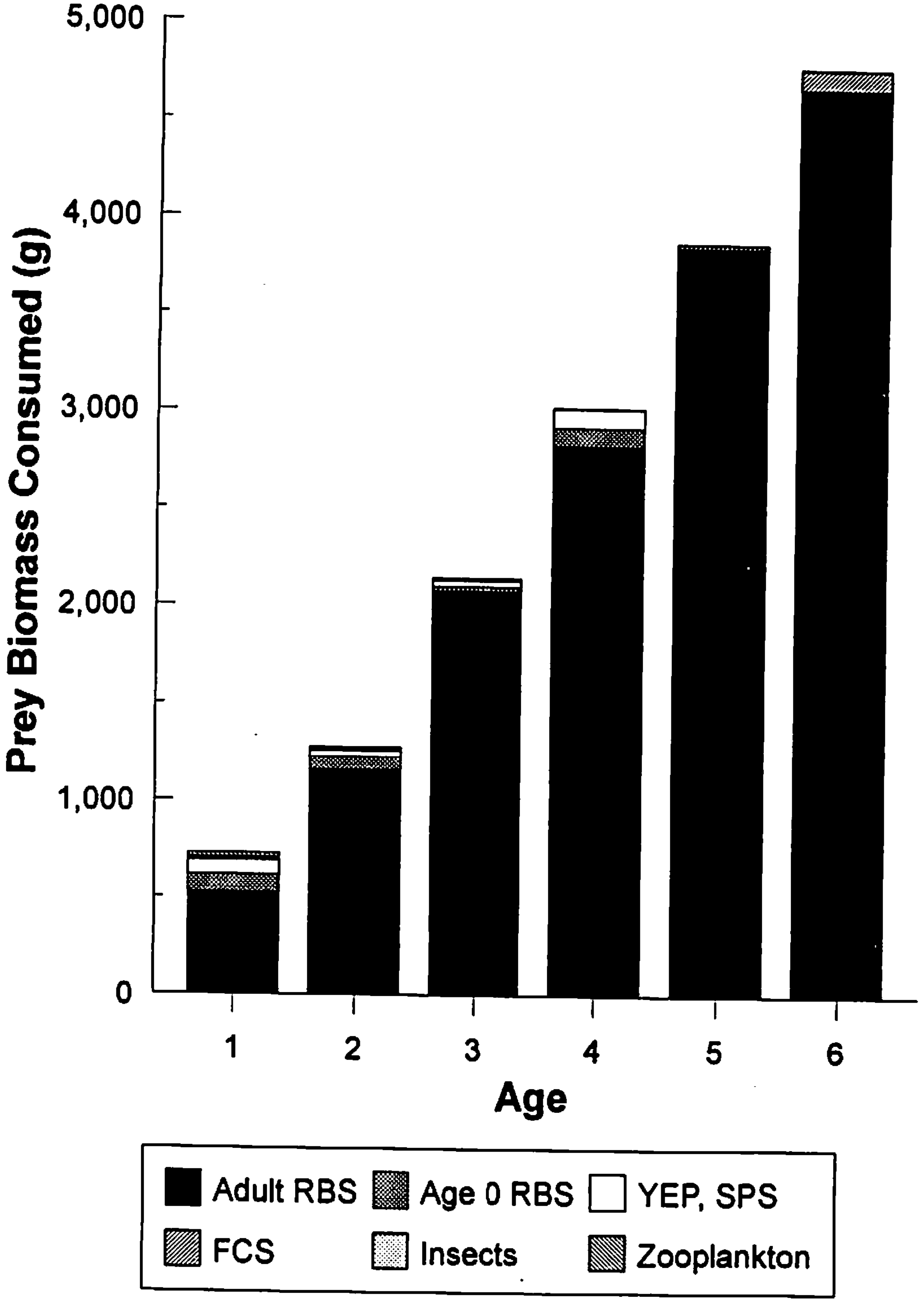


Figure 4.4. Model estimates of simulated yearly consumption (g) by an individual walleye from Lake Oahe. Values are cumulative biomass of prey consumed by each age class of walleye.

Adult rainbow smelt dominated the diet of walleyes with individual biomass consumption ranging from 522 g/year for an age 1 walleye to 4,684 g/year for an age 6 walleye. Age 0 rainbow smelt composed a small portion of the diet. Newly stocked chinook salmon smolts were consumed by several age classes of walleyes, however; they were only available for consumption in a small portion of the reservoir for a short period of time.

Total consumption of rainbow smelt decreased with the decreasing population size of walleyes in each age class (Figure 4.5). One exception to this observation was with age 4 walleyes, which consumed slightly more rainbow smelt than age 3 walleyes. Age 4 walleyes had a strong year-class and individual consumption of rainbow smelt was 27% higher for age 4 walleyes than age 3 walleyes. Ages 1 and 2 walleyes consumed 49.99% of the total rainbow smelt eaten by the walleye population.

Collectively, the six age classes of walleyes consumed an estimated 8.639×10^9 g (8,639 metric tons) of adult rainbow smelt over the course of one year (Table 4.10). Total consumption of age 0 rainbow smelt was 5.76×10^8 g over that same period. The six age classes of walleyes combined consumed most rainbow smelt, 7.651×10^9 g, during the summer/fall simulation. Consumption of rainbow smelt during winter and spring remained relatively constant.

Rainbow Smelt Supply - Because of the importance of

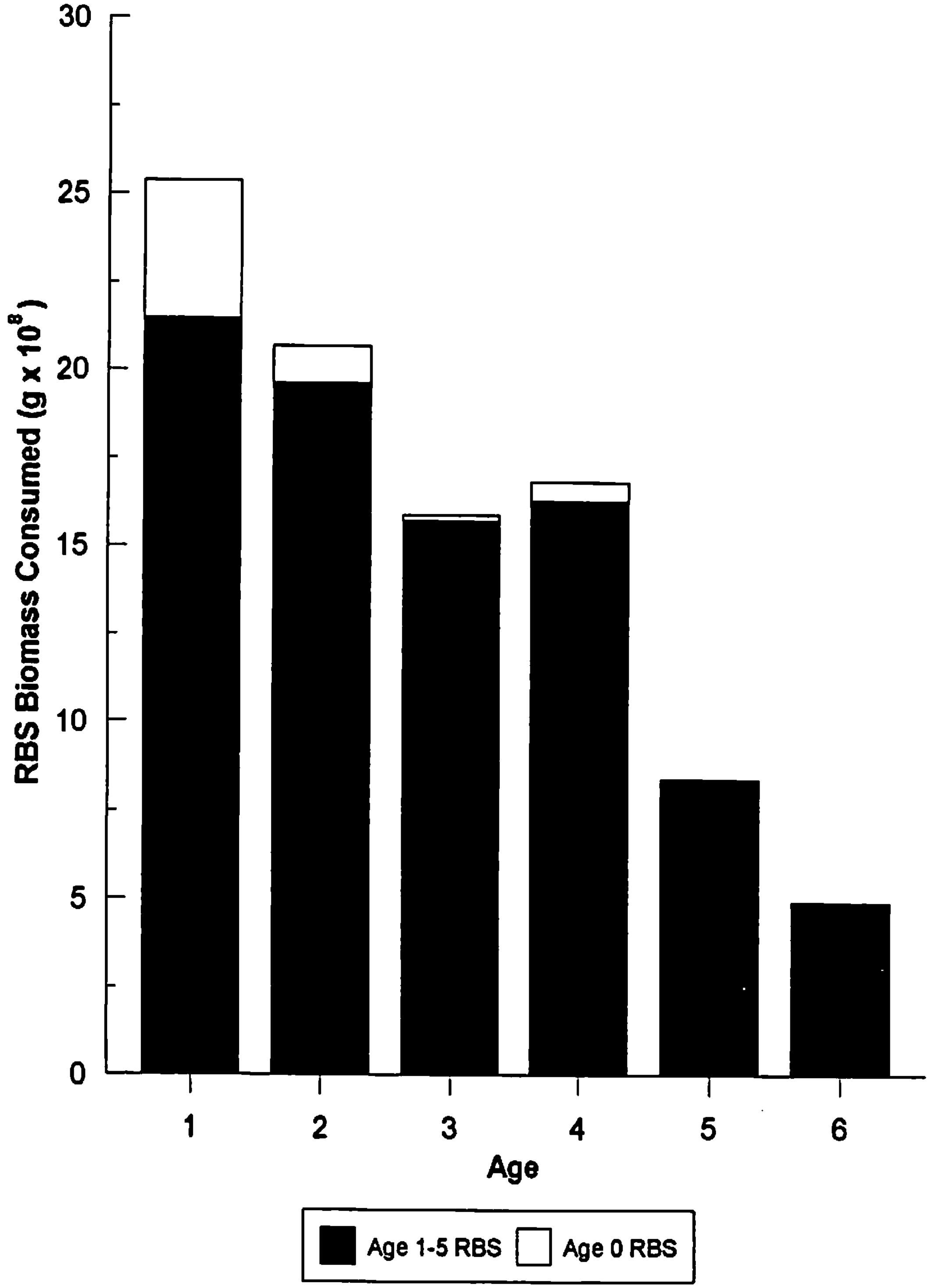


Figure 4.5. Model estimates of simulated total yearly consumption of adult and juvenile rainbow smelt by walleyes from Lake Oahe. Values are cumulative biomass of adult and juvenile rainbow smelt consumed by each age class of walleye.

Table 4.10. Seasonal population consumption of adult and age 0 rainbow smelt by walleyes from Lake Oahe derived from bioenergetics simulations. All values are g x 10^8.

Age class	Summer/Fall	Winter	Spring	Total
	Adult Rainbow Smelt[a]			
1	16.84	2.35	2.27	21.46
2	16.98	1.59	1.04	19.61
3	12.71	0.93	2.08	15.72
4	13.47	1.12	1.69	16.28
5	6.91	0.70	0.78	8.39
6	3.99	0.50	0.44	4.93
Total	70.90	7.19	8.30	86.39
	Age 0 Rainbow Smelt[b]			
1	3.85	0.05	0.00	3.90
2	1.05	0.01	0.00	1.06
3	0.17	0.02	0.00	0.19
4	0.54	0.07	0.00	0.61
5	0.00	0.00	0.00	0.00
6	0.00	0.00	0.00	0.00
Total	5.61	0.15	0.00	5.76

[a] Rainbow smelt were considered adult at age 1 for calorimetric purposes, even though they do not spawn until age 2 (Scott and Crossman 1973).

[b] Age 0 rainbow smelt were considered to be age 1 during spring, so there was no consumption of age 0 rainbow smelt during spring.

rainbow smelt to walleyes in Lake Oahe, it is necessary to determine the amount of rainbow smelt biomass available for walleye consumption. Hydroacoustic surveys in the 1980's indicated that the rainbow smelt population size fluctuated between 6.0 x 10^7 fish in 1984 and 1.1 x 10^9 fish in 1988 (Freiburger 1992; Appendix A.4). A dramatic decrease in the rainbow smelt population size occurred between 1988 and 1989, which may be directly related to the massive influx of chinook salmon stocked into the reservoir in the years prior to this decline.

We used a bioenergetics model developed for rainbow smelt in Lake Oahe (Freiburger 1992) to determine the number and biomass of rainbow smelt needed to support the estimated walleye consumption. Model simulations were run with increasing population sizes until the biomass of adult rainbow smelt was equivalent to the consumption of walleyes ages 1-6, 8.639 x 10^9 g. Based on an estimated walleye population of 9.819 x 10^6 individuals, the population of adult rainbow smelt in Lake Oahe would need to be approximately 1.55 x 10^9 to support the feeding habits of walleyes in Oahe Reservoir.

Sensitivity Analysis - Comparisons of demand and supply are limited by the credibility of the data input and the assumptions used to compute these estimates (Moore 1988). Models are abstractions of reality and involve simplifications and assumptions (Levins 1966). Sensitivity analysis is used with bioenergetics models to measure the relative importance of input parameters for growth or consumption output (Kitchell et al. 1977). When determining consumption from a known growth curve, sensitivity analysis indicates that bioenergetics models may be used to make accurate estimations of reality (Kitchell et al. 1977; Stewart et al. 1981; Lyons 1984; Bartell et al. 1986). The overall conclusion of these studies was that the model was less sensitive to parameter errors when estimating consumption than when estimating growth (Carline 1987). The most important parameters affecting variability in consumption estimates include temperature-dependent maximum consumption and allometric relationships between weight and maximum consumption and between weight and respiration (Bartell et al 1986). There has also been heated debate as to the complexity of the activity parameter (Kerr 1982; Boisclair and Leggett 1989, 1991; Hewett et al. 1991; Boisclair and Sirois 1993), which can cause as much as a 10% error in consumption estimates (Kitchell and Breck 1980).

Because sensitivity analysis on metabolic parameters has been considered extensively by others (Kitchell et al. 1977; Lyons 1984; Bartell et al. 1986), I performed the analysis on site-specific parameters. Predator and prey caloric density, proportion of weight spawned, and temperature data were modified singularly by increments of ±10% (Kitchell et al. 1977) to evaluate the sensitivity of the model to predict individual cumulative consumption. I assumed that final weight would have a significant impact on consumption results (Freiburger 1992), so it was not tested in sensitivity analysis.

The model was most sensitive to changes in prey caloric density for each age class (Table 4.11). Sensitivity to prey caloric density did not appear to be affected by age. Changes in temperature also had an effect on consumption, but percent deviations were minor. Proportion of weight spawned had almost no effect on consumption estimates, however sensitivity increased with age.

Discussion

Predator production in reservoirs is highly dependent upon the availability and vulnerability of food, in particular, forage fishes (Lewis 1967). Walleyes in Lake Oahe are highly dependant on rainbow smelt as a food resource. Therefore, population size of rainbow smelt in the Oahe Reservoir can be a limiting factor to walleye growth and survival.

We used bioenergetic modeling to estimate the population size of rainbow smelt required to support simulated walleye consumption. Based on hydroacoustic surveys on Lake Oahe during the 1980's, the rainbow smelt population size during 1993 would have to have been at its greatest density for walleyes to maintain their present rate

Table 4.11. Sensitivity of individual cumulative consumption estimates for Lake Oahe walleyes age 1-6 to deviations in input site specific variables of ±10%.

	Percent deviation from consumption estimate	
Variable	+10%	-10%
	Age 1	
Prey caloric density	- 9.97	+ 11.52
Predator caloric density	+ 3.93	- 4.03
Proportion of weight spawned	N/A	N/A
Temperature	+ 5.68	- 6.20
	Age 2	
Prey caloric density	- 10.05	+ 11.38
Predator caloric density	+ 4.51	- 4.41
Proportion of weight spawned	N/A	N/A
Temperature	+ 5.20	- 5.64
	Age 3	
Prey caloric density	- 10.24	+ 11.42
Predator caloric density	+ 4.72	- 4.63
Proportion of weight spawned	+ 0.95	- 0.91
Temperature	+ 5.14	- 5.54
	Age 4	
Prey caloric density	- 10.19	+ 11.33
Predator caloric density	+ 4.41	- 4.36
Proportion of weight spawned	+ 1.00	- 1.02
Temperature	+ 5.37	- 5.82
	Age 5	
Prey caloric density	- 10.15	+ 11.36
Predator caloric density	+ 4.32	- 4.10
Proportion of weight spawned	+ 1.13	- 1.09
Temperature	+ 5.60	- 5.97
	Age 6	
Prey caloric density	- 10.20	+ 11.34
Predator caloric density	+ 4.16	- 3.94
Proportion of weight spawned	+ 1.22	- 1.18
Temperature	+ 5.75	- 6.12

of growth and consumption. This may not be unreasonable because the highest catch rates of rainbow smelt ever recorded in annual population surveys were observed in 1993 (Lott et al. 1994). Furthermore, the survey design used in the hydroacoustic surveys on Lake Oahe during the 1980's may have underestimated the rainbow smelt population size. Most sampling was conducted during night when rainbow smelt ascend into the water column, but some day sampling was conducted. Samples collected during the day could easily underestimate rainbow smelt density. The design also assumed that the thermocline restricted the vertical movement of rainbow smelt. Therefore, the upper epilimnion and shallow littoral areas (2-3 m) were excluded from surveys (Burczynski et al. 1987). However, I captured rainbow smelt throughout the water column and in shallow littoral areas (< 3 m) at night during both 1993 and 1994. I also observed rainbow smelt at the surface of the water using spotlights during both years. Differences in environmental conditions between 1993 and 1994 lead me to believe rainbow smelt in Lake Oahe routinely use shallow waters. In 1993, the water level of the reservoir was high, temperatures were cool, and no thermocline was established. In 1994, precipitation and temperatures were near normal and a thermocline was established. The result of these biases in hydroacoustic survey design may have been underestimated population sizes of rainbow smelt in the past.

Consumption estimates derived from bioenergetics simulations indicate that walleyes may be consuming a majority of the rainbow smelt production in Lake Oahe. Walleyes, however, are not the only predator utilizing rainbow smelt in the reservoir. Chinook salmon are currently stocked at a rate of 275,000 each year (Marrone and Stout 1993) and they are a very effective predator on rainbow smelt. Chinook salmon have been successfully used to eradicate rainbow smelt from small lakes in New Hampshire (Hoover 1936). In addition, high water in recent years in Lake Oahe has allowed the once abundant northern pike population to successfully spawn (Bruce Johnson, SDGF&P, personal communication), goldeye are one of the most abundant fishes in the reservoir (Lott et al. 1994), smallmouth bass are becoming a popular sport fish, and rainbow trout are being introduced at a rate of 75,000/year (Marrone and Stout 1993). All of these species feed on rainbow smelt, although not exclusively.

The cyclical nature of rainbow smelt population dynamics combined with the ever increasing number of predators in Lake Oahe may lead to an unavoidable crash of the rainbow smelt population. Excessive introductions of predators may result in high mortality or poor growth and it could devastate a major forage organism (Stewart et al. 1981). The question is, "How many predators are too many?" (Stewart et al. 1981). The size structure of the chinook salmon population in Lake Oahe declined after a dramatic decrease in the size of the rainbow smelt population in 1989. The rapid deterioration of the rainbow smelt population was attributed to the overstocking of chinook salmon and stocking rates were subsequently reduced by as much as 80% (Marrone and Stout 1993). Similarly, condition and growth of walleyes and chinook salmon in Lake Sakakawea, North Dakota decreased substantially following a rainbow smelt population crash in the early 1980's (Jeff Hendrickson, North Dakota Game and Fish Department, personal communication). Rainbow smelt biomass decreased by more than 90% from 1978 to 1981 in Lake Superior (MacCallum and Selgeby 1987; Hansen 1990) which occurred at the same time salmonid stocking was increasing and as a result, salmonid condition has declined (Conner et al. 1993).

The likelihood of a rainbow smelt population crash in Lake Oahe is cause for concern regarding the growth rates and condition of walleyes. Walleyes are traditionally versatile predators and are able to switch feeding habits according to prey availability (Colby et al. 1979). The high caloric density and year-round availability of rainbow smelt, however, allows for the fast growth rates of walleyes observed in Lake Oahe. Sensitivity analysis revealed that changes in prey caloric density can have profound effects on individual consumption. If walleyes are forced to switch to an alternative prey fish (i.e. yellow perch, spottail shiners, emerald shiners) because of a rainbow smelt population crash, condition and size structure of walleyes may decrease.

Lake herring have been stocked into Lake Oahe in recent years to provide an alternative prey should rainbow smelt decline in abundance (SDGF&P, unpublished report). Because lake herring frequently move from deep to shallow water, they are a common food for walleyes when the two species co-exist (Scott and Crossman 1973). The high caloric density of lake herring (Chapter 3) makes them an excellent alternative prey fish for walleyes. However, lake herring have not yet reached great enough densities to be considered an important prey species (SDGF&P, unpublished data). In Lake Superior, relative abundance of rainbow smelt and lake herring were inversely related (Wisconsin Department of Natural Resources 1988), indicating that lake herring may flourish if the rainbow smelt population crashes.

Confidence in the interpretations of walleye demand and prey supply in Lake Oahe is only limited by insufficient rainbow smelt biomass data and walleye population and mortality estimates. Regardless, bioenergetics modeling has provided the technology to address important questions about walleyes in this reservoir.

Simulations

The model that has been modified for walleyes in Lake

Oahe has several important applications to reservoir fisheries investigations. It allows the simulation of a walleyes response to such situations as water level changes which cause temperature fluctuations, changes in prey fish community structure, effects of increased stocking of additional predators, introductions of larger prey fish, or even effects of zebra mussel invasion. The bioenergetics model was used to estimate walleye consumption based on two scenarios involving changes in water temperatures and prey availability.

Drought Simulation

The first modeling situation assumed that summer air temperatures had increased, resulting in a moderate drought. Higher air temperatures caused water temperatures to increase by 5% during May and September and 10% during June, July, and August (Table 4.12). Warmer water temperatures set up a strong thermocline, resulting in hypolimnetic oxygen depletion. As a result, walleyes were forced to occupy warmer epilimnetic water. The drought conditions prompted the U.S. Army Corps of Engineers to increase discharge through the Oahe Dam during the summer to provide more water downstream. The climatological changes and increased discharge reduced available habitat for rainbow smelt resulting in a population crash. Walleye predation on rainbow smelt decreased substantially and they were forced

Table 4.12. Water temperatures (°C) of Lake Oahe used during the baseline simulation and the drought simulation. Water temperatures in the baseline simulation were based on field observations and U.S. Army Corps of Engineers discharge data.

Date	Simulation Day	Baseline Simulation	Drought Simulation
May 16	1	11.95	12.55
Jun 20	34	17.44	19.18
Jul 20	64	20.48	22.53
Aug 20	95	21.63	23.79
Sep 20	126	18.14	19.05
Oct 20	156	14.44	14.44
Nov 20	187	9.44	9.44
Dec 15	212	5.80	5.80
Dec 20	217	4.44	4.44
Jan 20	248	0.71	0.71
Feb 20	279	0.63	0.63
Mar 20	303	5.40	5.40
Apr 20	338	6.70	6.70
May 15	365	10.59	11.12

to feed more heavily on yellow perch and spottail shiners (Table 4.13). In addition P-values, decreased by 0.025 due to the lack of prey availability. All other model parameters were held constant.

Model results estimated that final weights of each age class would decrease dramatically, especially in older fish (Table 4.14). Final weight of an average age 6 walleye was only 1,119 g, a 50% decrease from baseline conditions. The decreasing body weight was due to warm water temperatures, reduced consumption rates (P-values), and the lower caloric density of yellow perch and spottail shiners during part of the year.

Conversion efficiency decreased steadily as walleyes became older and values in this simulation were substantially lower than baseline values for each age class (Figure 4.6). Total biomass consumed by individual walleyes increased with increasing age; however, overall consumption values were much lower than those of walleyes in the baseline simulation (Figure 4.7). Yellow perch, spottail shiners, and insects accounted for a majority of the food consumed, while the consumption of rainbow smelt decreased substantially.

Lake Herring Simulation

The second modeling situation assumed that increased stocking rates of chinook salmon and high predation by

Table 4.13. Seasonal diet of walleyes from Lake Oahe as a proportion of total food (wet weight) consumed for six prey categories used in the drought simulation. Values are given by age, date, and the corresponding simulation day.

Date	Simulation Day	Adult RBS[a]	Age 0 RBS	YEP & SPS[b]	FCS[c]	Insects[d]	Zoo[e]
Age 1							
May 16	1	0.1158	0.0000	0.3000	0.0000	0.3098	0.2744
Jun 20	34	0.0872	0.0000	0.8500	0.0000	0.0478	0.0150
Jul 20	64	0.0276	0.0184	0.9428	0.0000	0.0099	0.0013
Aug 20	95	0.1188	0.0204	0.8500	0.0000	0.0106	0.0002
Sep 20	126	0.0000	0.0000	1.0000	0.0000	0.0000	0.0000
Jan 20	248	0.0000	0.0000	0.8000	0.0000	0.0000	0.2000
Mar 20	297	0.1500	0.0000	0.8500	0.0000	0.0000	0.0000
May 15	365	0.0098	0.0000	0.3000	0.1311	0.4088	0.1502
Age 2							
May 16	1	0.0098	0.0000	0.3000	0.1311	0.4088	0.1502
Jun 20	34	0.1214	0.0000	0.8757	0.0000	0.0028	0.0001
Jul 20	64	0.1275	0.0095	0.8608	0.0000	0.0022	0.0000
Aug 20	95	0.0008	0.0003	0.9741	0.0000	0.0082	0.0166
Sep 20	126	0.0821	0.0675	0.8500	0.0000	0.0004	0.0000
Jan 20	248	0.1500	0.0000	0.8500	0.0000	0.0000	0.0000
May 15	365	0.0330	0.0000	0.4110	0.0932	0.4125	0.0503
Age 3							
May 16	1	0.0330	0.0000	0.4110	0.0932	0.4125	0.0503
Jun 20	34	0.1010	0.0000	0.8979	0.0000	0.0010	0.0001
Jul 20	64	0.1477	0.0023	0.8500	0.0000	0.0000	0.0000
Aug 20	95	0.1378	0.0090	0.8500	0.0000	0.0031	0.0001
Sep 20	126	0.0903	0.0241	0.8849	0.0000	0.0007	0.0000
Jan 20	248	0.1500	0.0000	0.8500	0.0000	0.0000	0.0000
May 15	365	0.1443	0.0000	0.4300	0.0000	0.4057	0.0200
Age 4							
May 16	1	0.1443	0.0000	0.4300	0.0000	0.4057	0.0200
Jun 20	34	0.1500	0.0000	0.8500	0.0000	0.0000	0.0000
Jul 20	64	0.0183	0.0008	0.9803	0.0000	0.0006	0.0000
Aug 20	95	0.0484	0.0327	0.9176	0.0000	0.0012	0.0001
Sep 20	126	0.0893	0.0607	0.8500	0.0000	0.0000	0.0000
Jan 20	248	0.1500	0.0000	0.8500	0.0000	0.0000	0.0000
May 15	365	0.0829	0.0000	0.6652	0.0000	0.2519	0.0000

Table 4.13 (continued)

Date	Simulation Day	Adult RBS[a]	Age 0 RBS	YEP & SPS[b]	FCS[c]	Insects[d]	Zoo[e]
Age 5							
May 16	1	0.0829	0.0000	0.6652	0.0000	0.2519	0.0000
Jun 20	34	0.1500	0.0000	0.8500	0.0000	0.0000	0.0000
Jul 20	64	0.1458	0.0000	0.8500	0.0000	0.0042	0.0000
Aug 20	95	0.1500	0.0000	0.8500	0.0000	0.0000	0.0000
May 1	348	0.1500	0.0000	0.8500	0.0000	0.0000	0.0000
May 15	365	0.0250	0.0000	0.7000	0.1732	0.1018	0.0000
Age 6							
May 16	1	0.0250	0.0000	0.7000	0.1732	0.1018	0.0000
Jun 20	34	0.1500	0.0000	0.8500	0.0000	0.0000	0.0000
Jul 20	64	0.1458	0.0000	0.8500	0.0000	0.0042	0.0000
Aug 20	95	0.1500	0.0000	0.8500	0.0000	0.0000	0.0000
May 1	348	0.1500	0.0000	0.8500	0.0000	0.0000	0.0000
May 15	365	0.0213	0.0000	0.4800	0.4983	0.0004	0.0000

[a] Rainbow smelt
[b] Yellow perch and spottail shiners
[c] Newly stocked fall chinook salmon
[d] Includes Ephemeroptera and Chironimidae
[e] Includes cladocera and copepoda

Table 4.14. Final weights (g) of each age class of walleyes from Lake Oahe by cohort for the baseline simulation, drought simulation, and lake herring simulation.

Age class	Cohort	Baseline Simulation	Drought Simulation	Lake herring Simulation
1	1	175.87	141.97	171.90
	2	191.33	153.09	188.09
	3	236.11	182.95	227.45
2	4	401.90	256.42	361.52
	5	418.18	265.12	376.69
	6	472.97	293.38	420.34
3	7	715.88	397.10	636.02
	8	722.06	398.24	645.84
	9	799.99	441.92	720.47
4	10	1119.80	590.40	1059.17
	11	1138.30	598.34	1085.00
	12	1210.80	638.22	1167.95
5	13	1563.80	792.81	1560.85
	14	1620.00	822.68	1633.90
	15	1694.50	864.63	1727.39
6	16	2041.10	1007.97	2139.85
	17	2147.10	1066.08	2278.99
	18	2238.00	1117.95	2398.59

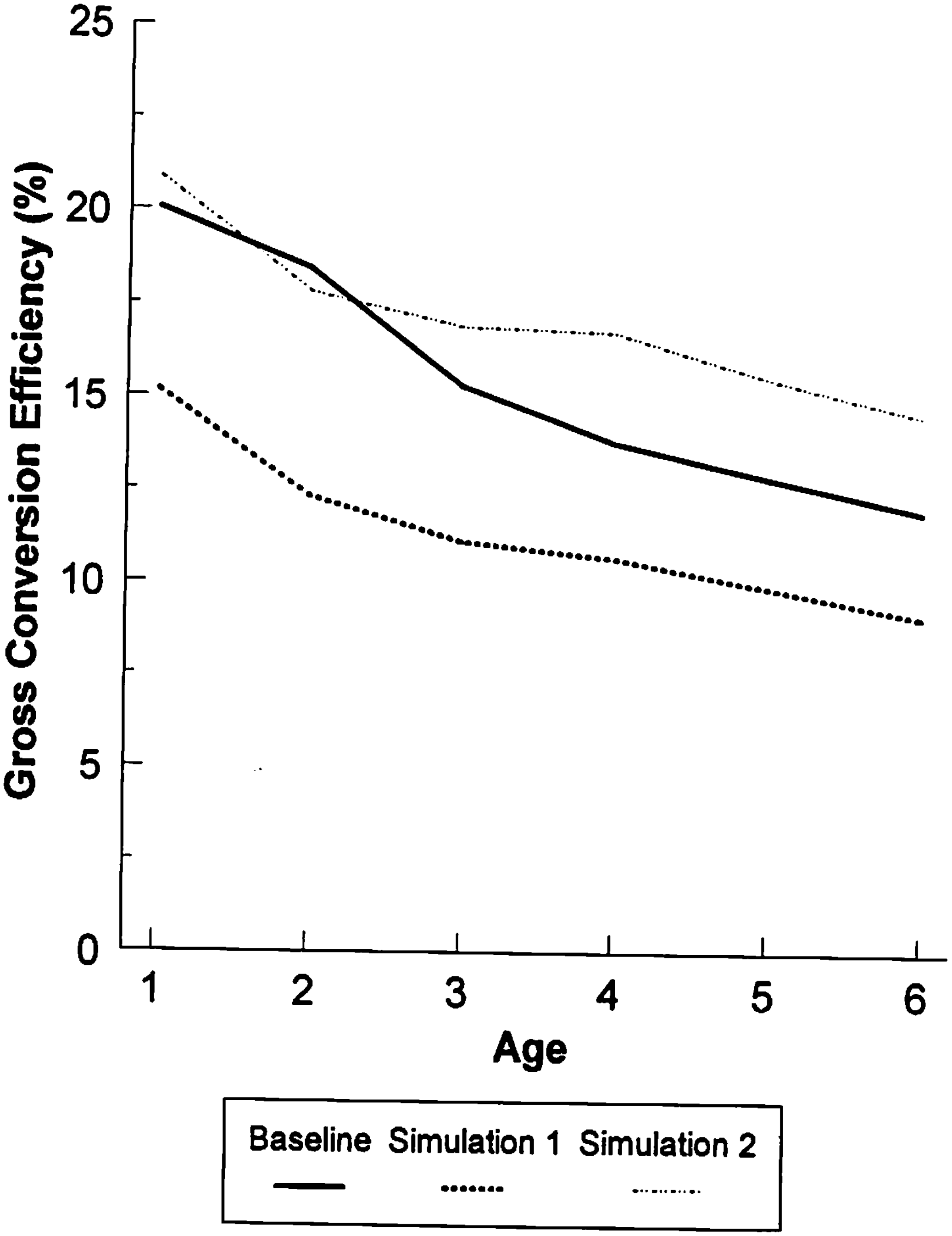


Figure 4.6. Estimates of the conversion efficiency (change in weight/total individual consumption) of walleyes, ages 1 to 6, in Lake Oahe. Estimates are derived from bioenergetics simulations of the current walleye population (baseline), after a drought (simulation 1), and after lake herring became established (simulation 2).

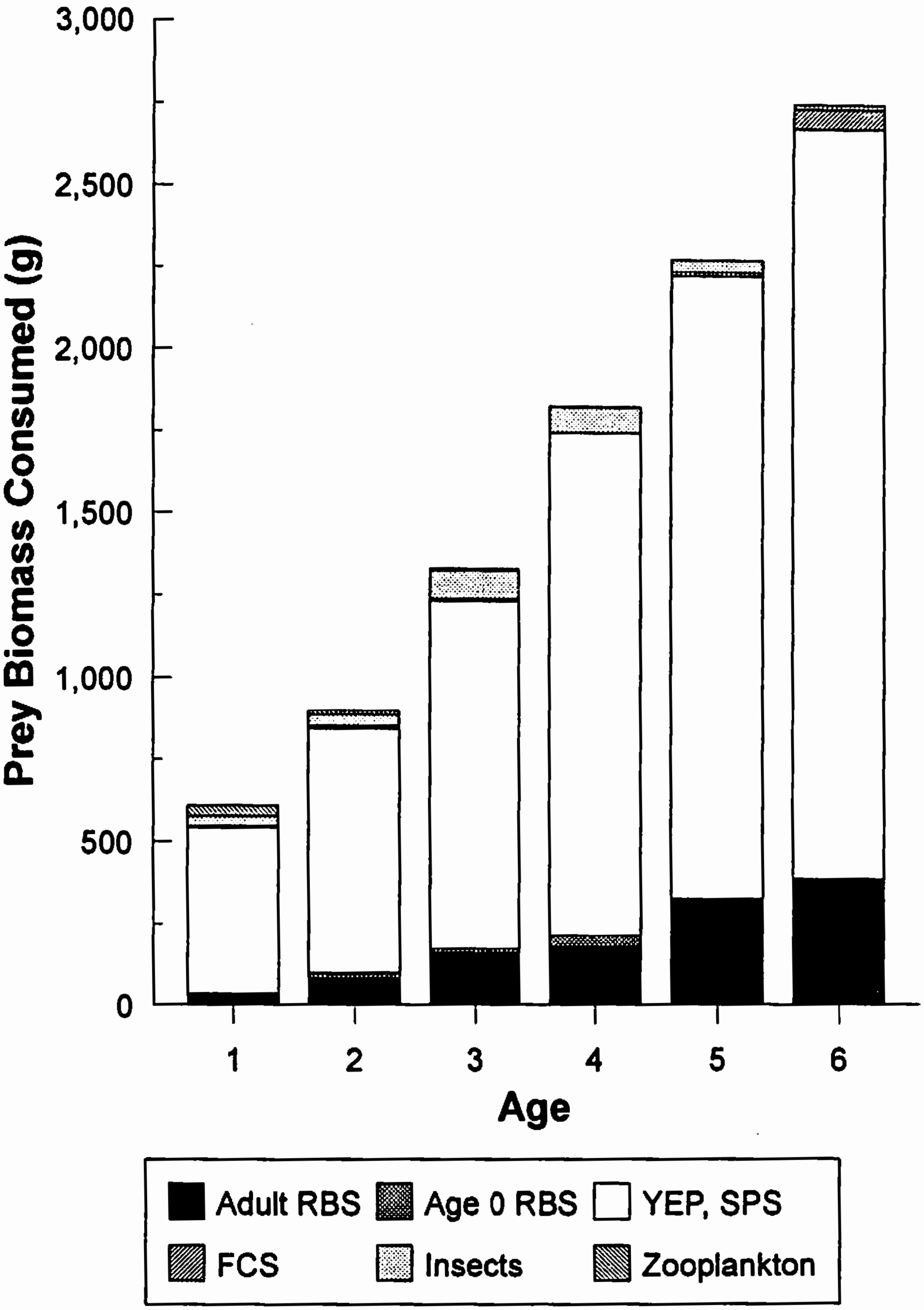


Figure 4.7. Model estimates of simulated yearly consumption (g) by an individual walleye from Lake Oahe after a drought causes a decrease in the rainbow smelt population. Values are cumulative biomass of prey consumed by each age class of walleyes.

northern pike, along with the cyclical nature of rainbow smelt, contributed to a dramatic decline in the smelt population. Population size of rainbow smelt decreased by 95%, from 1.55 x 10^9 to 7.75 x 10^7. With the declining number of rainbow smelt, lake herring were able to produce an exceptional year class. As a result, walleye predation on rainbow smelt decreased as they switched to feeding on lake herring and yellow perch (Table 4.15). However, because of the pelagic nature of lake herring and the low numbers of yellow perch available for consumption, the proportion of maximum consumption (P-value) decreased by 0.05.

Simulated final weights of ages 1-4 walleyes were lower than baseline values, however age 5 and 6 walleyes grew to a larger size than those that were feeding almost exclusively on smelt (Table 4.14). Gross conversion efficiency decreased with increasing age, but was higher than baseline values for all age classes except age 2 walleyes (Figure 4.6). Even though the proportion of maximum consumption (P-value) was 5% lower than baseline values, the high caloric density of lake herring (Table 4.16) and the improved conversion efficiency allowed older walleyes to gain 19.5% more weight than walleyes feeding on smelt.

Total biomass consumed by individual walleyes again increased with increasing age (Figure 4.8). Lake herring,

Table 4.15. Seasonal diet of walleyes from Lake Oahe as a proportion of total food (wet weight) consumed for six prey categories used in the lake herring simulation. Values are given by age, date, and the corresponding simulation day.

Date	Simulation Day	Adult RBS[a]	LAH[b]	YEP[c]	FCS[d]	Insects[e]	Zoo[f]
Age 1							
May 16	1	0.1158	0.1000	0.2000	0.0000	0.3098	0.2744
Jun 20	34	0.0872	0.1000	0.7500	0.0000	0.0478	0.0150
Jul 20	64	0.0276	0.1000	0.8612	0.0000	0.0099	0.0013
Aug 20	95	0.1188	0.1000	0.7704	0.0000	0.0106	0.0002
Sep 20	126	0.0000	0.1000	0.9000	0.0000	0.0000	0.0000
Jan 20	248	0.0000	0.1000	0.7000	0.0000	0.0000	0.2000
Mar 20	297	0.1500	0.1000	0.7500	0.0000	0.0000	0.0000
May 15	365	0.0098	0.1000	0.2000	0.1311	0.4088	0.1502
Age 2							
May 16	1	0.0098	0.1000	0.2000	0.1311	0.4088	0.1502
Jun 20	34	0.1214	0.1000	0.7757	0.0000	0.0028	0.0001
Jul 20	64	0.1275	0.1000	0.7703	0.0000	0.0022	0.0000
Aug 20	95	0.0008	0.1000	0.8744	0.0000	0.0082	0.0166
Sep 20	126	0.0825	0.1000	0.8175	0.0000	0.0004	0.0000
Jan 20	248	0.1500	0.1000	0.7500	0.0000	0.0000	0.0000
May 15	365	0.0330	0.1000	0.3110	0.0932	0.4125	0.0503
Age 3							
May 16	1	0.0330	0.1000	0.3110	0.0932	0.4125	0.0503
Jun 20	34	0.1010	0.1000	0.7979	0.0000	0.0010	0.0001
Jul 20	64	0.1477	0.2000	0.6523	0.0000	0.0000	0.0000
Aug 20	95	0.1378	0.2000	0.6590	0.0000	0.0031	0.0001
Sep 20	126	0.0903	0.2000	0.7090	0.0000	0.0007	0.0000
Jan 20	248	0.1500	0.2000	0.6500	0.0000	0.0000	0.0000
May 15	365	0.1443	0.1000	0.3300	0.0000	0.4057	0.0200
Age 4							
May 16	1	0.1443	0.1000	0.3300	0.0000	0.4057	0.0200
Jun 20	34	0.1500	0.2000	0.6500	0.0000	0.0000	0.0000
Jul 20	64	0.0183	0.2000	0.7811	0.0000	0.0006	0.0000
Aug 20	95	0.0484	0.2000	0.7503	0.0000	0.0012	0.0001
Sep 20	126	0.0893	0.2000	0.7107	0.0000	0.0000	0.0000
Jan 20	248	0.1500	0.2000	0.6500	0.0000	0.0000	0.0000
May 15	365	0.0829	0.2000	0.4652	0.0000	0.2519	0.0000

Table 4.15. (continued)

Date	Simulation Day	Adult RBS[a]	LAH[b]	YEP	FCS[d]	Insects[e]	Zoo[f]
Age 5							
May 16	1	0.0829	0.2000	0.4652	0.0000	0.2519	0.0000
Jun 20	34	0.1500	0.2000	0.6500	0.0000	0.0000	0.0000
Jul 20	64	0.1458	0.2000	0.6500	0.0000	0.0042	0.0000
Aug 20	95	0.1500	0.2000	0.6500	0.0000	0.0000	0.0000
May 1	348	0.1500	0.2000	0.6500	0.0000	0.0000	0.0000
May 15	365	0.0250	0.2000	0.5000	0.1732	0.1018	0.0000
Age 6							
May 16	1	0.0250	0.2000	0.5000	0.1732	0.1018	0.0000
Jun 20	34	0.1500	0.2000	0.6500	0.0000	0.0000	0.0000
Jul 20	64	0.1458	0.2000	0.6500	0.0000	0.0042	0.0000
Aug 20	95	0.1500	0.2000	0.6500	0.0000	0.0000	0.0000
May 1	348	0.1500	0.2000	0.6500	0.0000	0.0000	0.0000
May 15	365	0.0213	0.2000	0.2800	0.4983	0.0004	0.0000

[a] Rainbow smelt
[b] Lake herring
[c] Yellow perch and spottail shiners
[d] Newly stocked fall chinook salmon
[e] Includes Ephemeroptera and Chironimidae
[f] Includes cladocera and copepoda

Table 4.16. Mean caloric density (cal/g wet weight) of prey consumed by walleyes from Lake Oahe used in the lake herring simulation.

Date	Simulation Day	Adult RBS[a]	LAH[a]	YEP, SPS[a]	FCS[a]	Insects[b]	Zoo[c]
May 16	1	1148	1741	1058	1181	972	475
Jun 20	34	1106	1839	1148	1244	972	475
Jul 20	64	1470	1937	1230	1301	972	475
Aug 20	95	1354	2120	1206	1278	972	475
Sep 20	126	1165	2304	1181	1255	972	475
Oct 20	156	1200	2304	1181	1255	972	475
Nov 20	187	1200	2304	1181	1255	972	475
Dec 20	217	1200	2304	1181	1255	972	475
Jan 20	248	1200	2304	1181	1255	972	475
Feb 20	279	1200	2304	1181	1255	972	475
Mar 20	307	1200	2304	1181	1255	972	475
Apr 20	338	1189	2304	1181	1255	972	475
May 15	365	1148	1741	1058	1181	972	475

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[a] Mean values of adult rainbow smelt, lake herring, yellow perch, spottail shiners, and fall chinook salmon from Chapter 3.

[b] Mean value for chironomids and ephemerids from Penczak (1985).

[c] Zooplankton mean caloric density from Cummins and Wuycheck (1971).

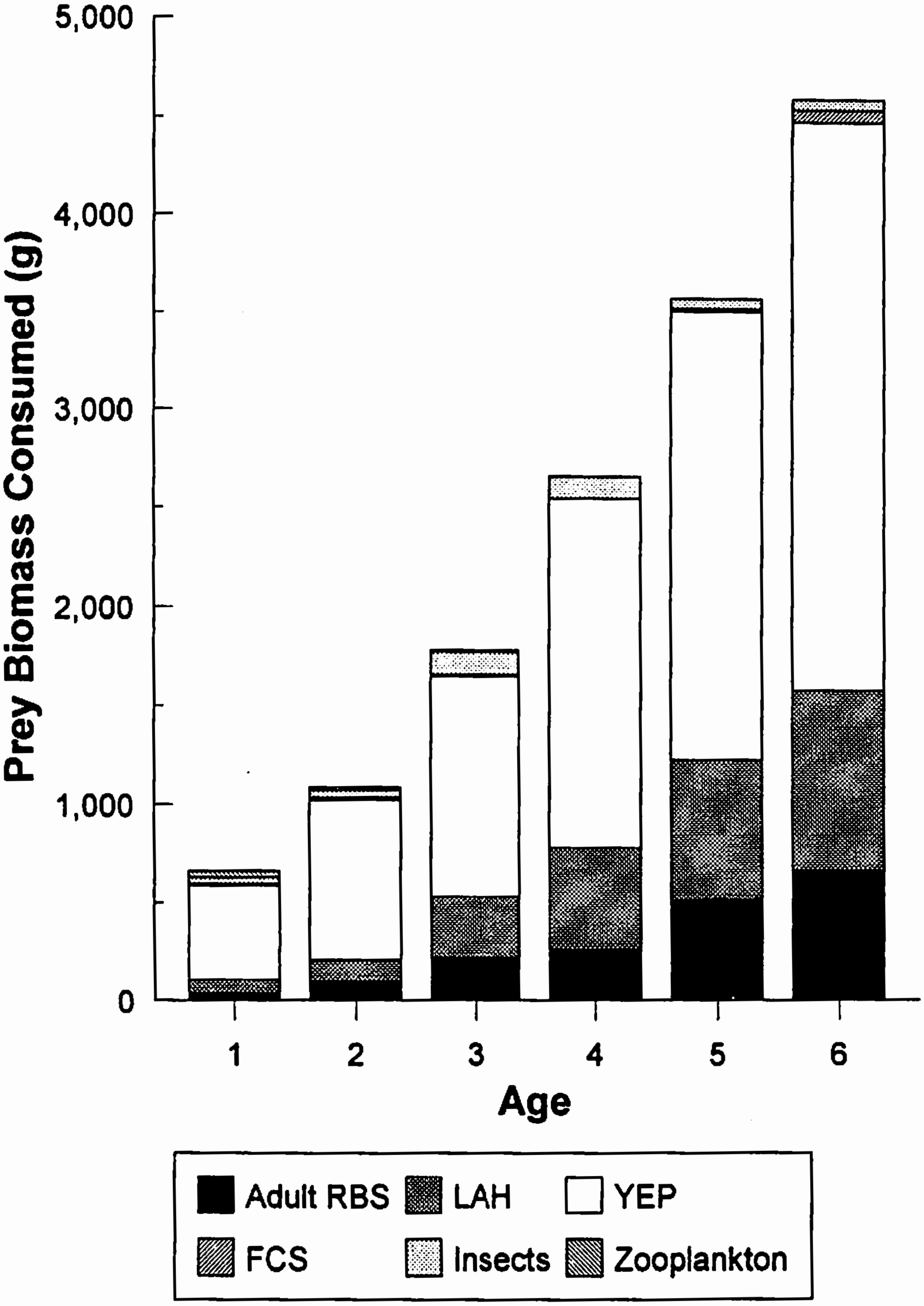

Figure 4.8. Model estimates of simulated yearly consumption (g) by an individual walleye from Lake Oahe after lake herring became established. Values are cumulative biomass of prey consumed by each age class of walleye.

yellow perch, and spottail shiners, made up most of the food biomass consumed, while rainbow smelt accounted for only a small portion of the total biomass consumed. At the population level, walleyes would consume 1.237 x 10^9 g of lake herring and 6.120 x 10^9 g of yellow perch (Figure 4.9). Age 4 walleyes consumed the greatest amount of lake herring. Ages 1 and 2 walleyes accounted for approximately 56% of the total yellow perch and spottail shiner biomass consumed.

Conclusions

These model simulations help demonstrate the delicate predator-prey balance in Lake Oahe. Any changes to this balance have the potential of impacting the trophic interactions in the reservoir. Variations in rainbow smelt population abundance appear to be continuous and sometimes extreme, and no method for predicting these variations have been found (Rupp 1968).

A drought situation in South Dakota was modeled in the first simulation. As a result of the drought, the rainbow smelt population crashed and walleyes were forced to alter their feeding habits. If all other conditions remained the same, switching to yellow perch or spottail shiners may not have a severe effect on the growth of walleyes because caloric density of the prey are similar. The possibility, however, of a rainbow smelt crash occurring without any other factors involved is remote. The results of this first

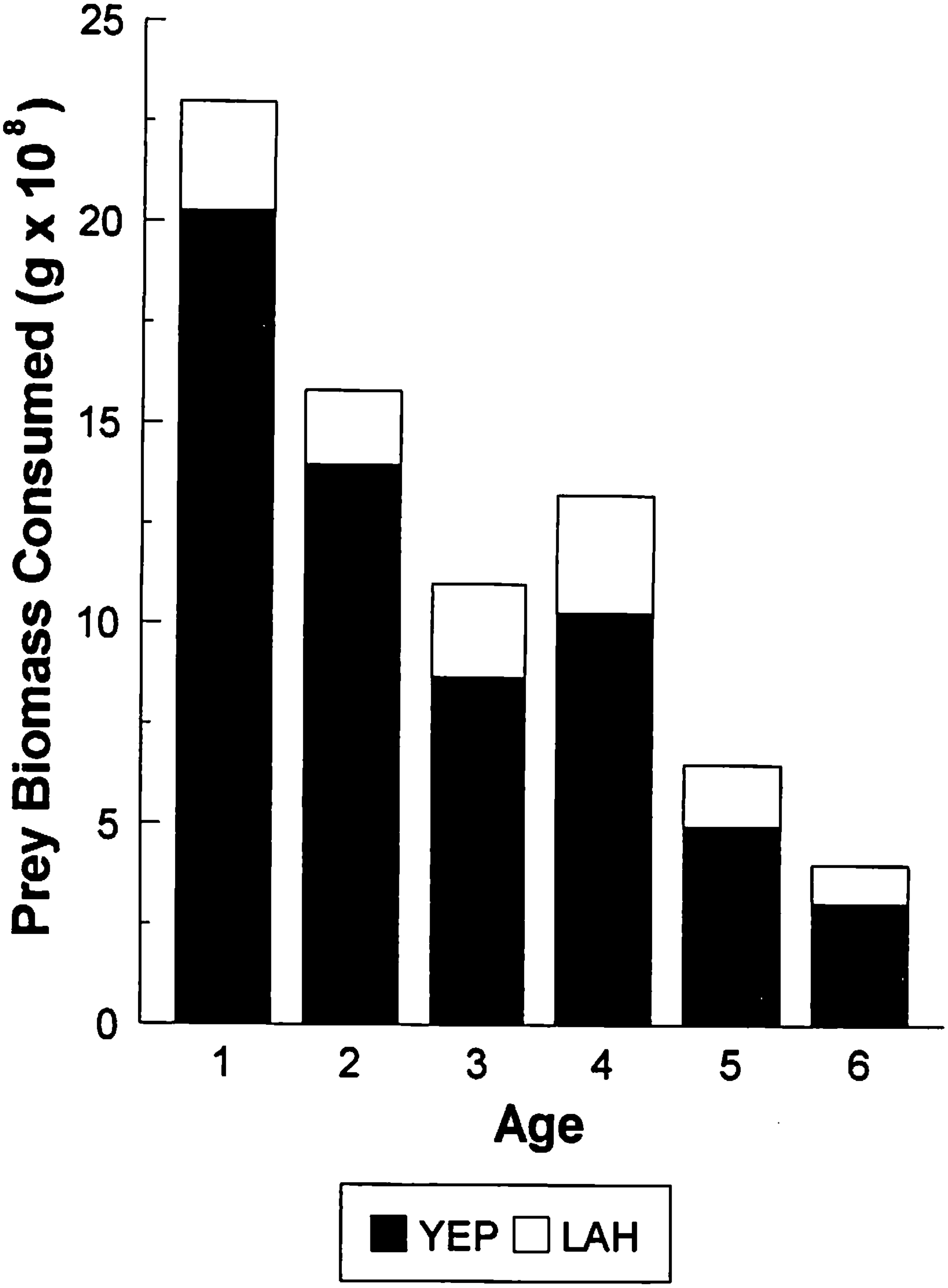

Figure 4.9. Model estimates of simulated total yearly consumption of lake herring and yellow perch by walleyes from Lake Oahe. Values are cumulative biomass of adult and juvenile rainbow smelt consumed by each age class of walleye.

simulation demonstrate the importance of rainbow smelt as a prey fish for walleyes in Lake Oahe. It also shows that environmental conditions and water level management can have significant effects on the rainbow smelt population as well as the consumption and growth of the walleyes in Lake Oahe.

The second simulation modeled a much more favorable situation for walleyes that may be just as likely to occur. A crash of the rainbow smelt population is almost certain to occur at some time in the future due to the cyclic nature of their population dynamics and predator stocking practices. If lake herring are able to establish themselves as a dominant prey fish in the reservoir, walleyes may actually benefit because of the high caloric density of the lake herring. However, because lake herring are pelagic, walleyes would need to make a radical change in their feeding habits to effectively utilize the lake herring.

Both of these simulations model extreme, but likely events in Oahe Reservoir. The rainbow smelt population will eventually crash. The severity and magnitude of the crash, however, may be partially under the control of biologists. Water levels and temperatures not only affect the spawning success of rainbow smelt during spring, but they also affect survival during summer months when coldwater habitat may be scarce. To manage the water level in Lake Oahe, cooperation with the U.S. Army Corps of Engineers is essential. In addition, continued stocking of all piscivorous fishes in

Lake Oahe without regard to the status of the rainbow smelt population is irresponsible, and coupled with the increasing northern pike population, will only increase the possibility of a rainbow smelt crash.

Management Implications and Future Needs

The question inevitably remains, "How many predators are too many?" (Stewart et al. 1981). The reason for the cyclical nature of rainbow smelt populations is not known. It could be due to a variety of environmental conditions or the explanation could lie in the biology of the species. Until this question is answered, the best solution may be to avoid a disaster for the Lake Oahe fishery by disturbing the predator-prey balance as little as possible.

The most important immediate need is to obtain accurate population and biomass estimates for rainbow smelt in the reservoir. This includes determining loss of fishes through Oahe Dam, immigration of smelt from Lake Sakakawea through Garrison Dam, mortality estimates, and an accurate estimate of natural reproduction in Oahe Reservoir. Population estimates need to be made each year until reliable trends in year class strength can be identified. These trends will help to determine the number of predators that the rainbow smelt population can support from year to year.

Bioenergetics models are currently being developed for chinook salmon and rainbow trout in Lake Oahe to determine predator demand and optimum stocking rates. Monitoring the population trends of rainbow smelt, along with correct use of the energetic models will ensure that a catastrophic crash does not occur because of excessive stocking of predators. In addition, the increasing northern pike population in Lake Oahe may present an additional problem for rainbow smelt. Food habits and diet overlap need to be determined for northern pike to assess their possible impact on the predator-prey interactions in the Oahe Reservoir.

The one factor that could preserve walleye growth and condition at its present level in the event of a rainbow smelt crash would be lake herring abundance. If lake herring could reach densities high enough to support the walleye feeding habits, as well as the other predators in Lake Oahe, growth rates may increase due to the high caloric density of lake herring. Closely monitoring lake herring reproduction and population dynamics in Lake Oahe then becomes very important for the future of the walleye fishery.

Bioenergetics modeling is a powerful tool that allows fishery biologists to evaluate the effects of management strategies without the possibility of unfavorable results. However, the trend to more elaborate models has not resulted in an equal progression in accuracy of output. Field estimates of growth, consumption, water temperature, diet composition, and energy densities are susceptible to a considerable degree of error (Ney 1993) and validation of models has seldom been undertaken. True validity tests of bioenergetics models have not been performed because the field data is sometimes difficult and costly to obtain (Hewett and Johnson 1992). South Dakota's Department of Game, Fish and Parks is already collecting valuable growth information which can be used to partially verify the accuracy of this model and the additional information needed to adequately field test the model would not be difficult to obtain (see Wahl and Stein 1991). The continued use of bioenergetics modeling in Lake Oahe will allow biologists to address problems and concerns that not only involve rainbow smelt but also a wide variety of environmental and ecological circumstances that may develop.

"A model is a lie that helps you see the truth" (R. H. MacArthur from Hansen et al. 1993). The complexity of nature is underrepresented by the simplification of models, as are field and laboratory studies that are based on samples and subsamples (Hansen et al. 1993). Currently, bioenergetics models are best suited for making relative rather than absolute predictions (Ney 1993). Despite this, many important decisions have been made through the use of bioenergetics models and continued use and perfection of these models will only improve our knowledge of the trophic interactions that we strive to understand.

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APPENDICES

Appendix A.1. Percent frequency of occurrence, biomass (g), and relative importance (RI) of prey consumed by walleyes collected in Lake Oahe in winter (January and February) and May through September, 1994.

				Rainbow Smelt			Other Prey Fish[a]			Unidentifiable Fish			Invertebrates[b]		
Month	Region	N	% MT[c]	% Freq.	Biomass	RI	% Freq.	Biomass	RI	% Freq.	Biomass	RI	% Freq.	Biomass	RI
WINTER	1	10	50.0	100.0	156.7	100	0.0	---	--	0.0	---	--	0.0	---	--
	2	2	50.0	0.0	---	--	0.0	---	--	100.0	1.4	100	0.0	---	--
	3	7	57.1	33.3	24.7	54	0.0	---	--	33.3	1.1	24	33.3	0.1	22
MAY	1	23	60.9	26.1	53.6	77	0.0	---	--	4.3	1.3	8	8.7	<0.1	15
	2	33	30.3	42.4	197.5	61	6.1	39.3	10	3.0	0.8	3	21.2	1.2	26
	3	26	15.4	65.4	408.5	64	7.7	18.8	6	15.4	5.1	8	23.1	3.2	22
JUN	1	36	33.3	41.7	297.4	77	0.0	---	--	22.2	8.8	17	5.6	0.1	6
	2	34	20.6	52.9	275.0	74	2.9	6.9	3	17.6	7.7	14	8.8	<0.1	9
	3	38	42.1	23.7	214.4	55	0.0	---	--	5.3	2.5	5	28.9	0.5	40
JUL	1	38	10.5	76.3	363.4	88	0.0	---	--	15.8	11.2	10	2.6	<0.1	2
	2	31	6.4	77.4	441.6	83	3.2	5.2	3	22.6	8.7	12	3.2	<0.1	2
	3	31	54.8	16.1	56.3	49	0.0	---	--	22.6	17.8	35	12.9	0.8	16
AUG	1	37	21.6	51.4	93.7	81	0.0	---	--	21.6	11.2	19	0.0	---	--
	2	22	31.8	36.4	63.1	71	0.0	---	--	27.3	8.2	21	13.7	0.3	8
	3	31	54.8	22.6	130.1	58	0.0	---	--	16.1	10.8	27	6.4	0.5	15
SEP	1	22	45.5	18.2	9.4	41	4.5	2.6	9	31.8	8.8	50	0.0	---	--
	2	32	50.0	34.4	49.3	85	0.0	---	--	12.5	5.0	13	3.1	0.1	2
	3	12	83.3	14.3	33.6	100	0.0	---	--	0.0	---	--	0.0	---	--

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[a] Other prey fish includes chinook salmon, yellow perch, spottail shiners, and emerald shiners.

[b] Invertebrates includes ephemeridae, chironomidae, and zooplankton.

[c] Percent of stomachs collected that were empty.

Appendix A.2.

Petersen mark/recapture population estimate

Although all of the assumptions of the Petersen mark/recapture method of population estimation were not met (Ricker 1975), I felt it would give the best estimation of the exploitable (age 2 and older) walleye population in Lake Oahe. During April, 1993, 904 spawning walleyes were marked with dangler tags and released at three different sites (Grand River, Moreau River, and Cheyenne River; Figure I.1.). Creel survey results were used as the recapture method and 54 of the 269,392 walleyes that returned to the creel had been tagged.

The Petersen method calculates population size as:

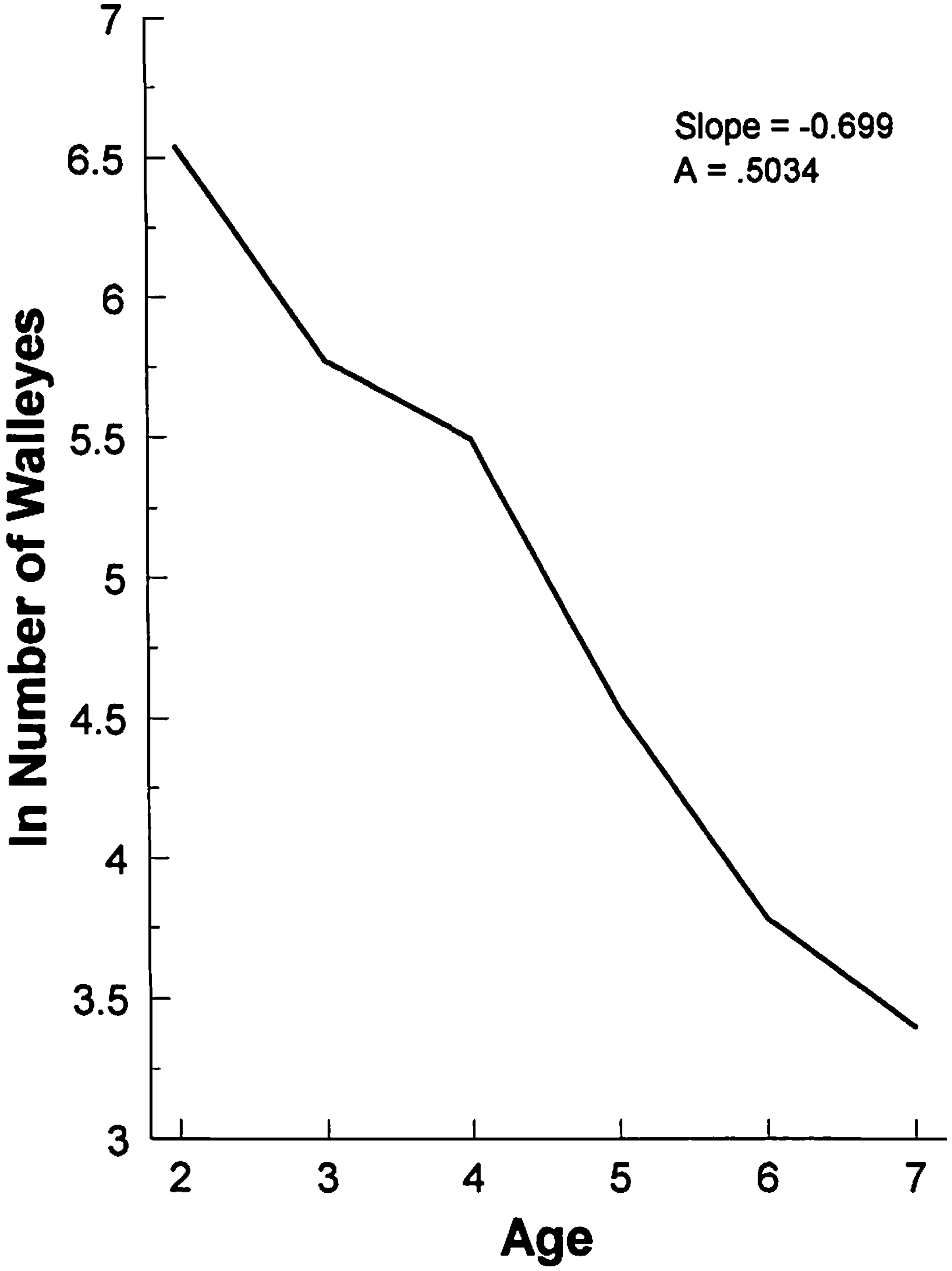
$$N=\frac{MC}{R}$$

where N is the population size at time of marking, M is the number of fish marked, C is the total number of fish in the second sample, and R is the number of recaptures in sample C. From this equation, I estimated that the exploitable population of walleyes in Lake Oahe is 4,509,821 (80% CI = ± 785,468).

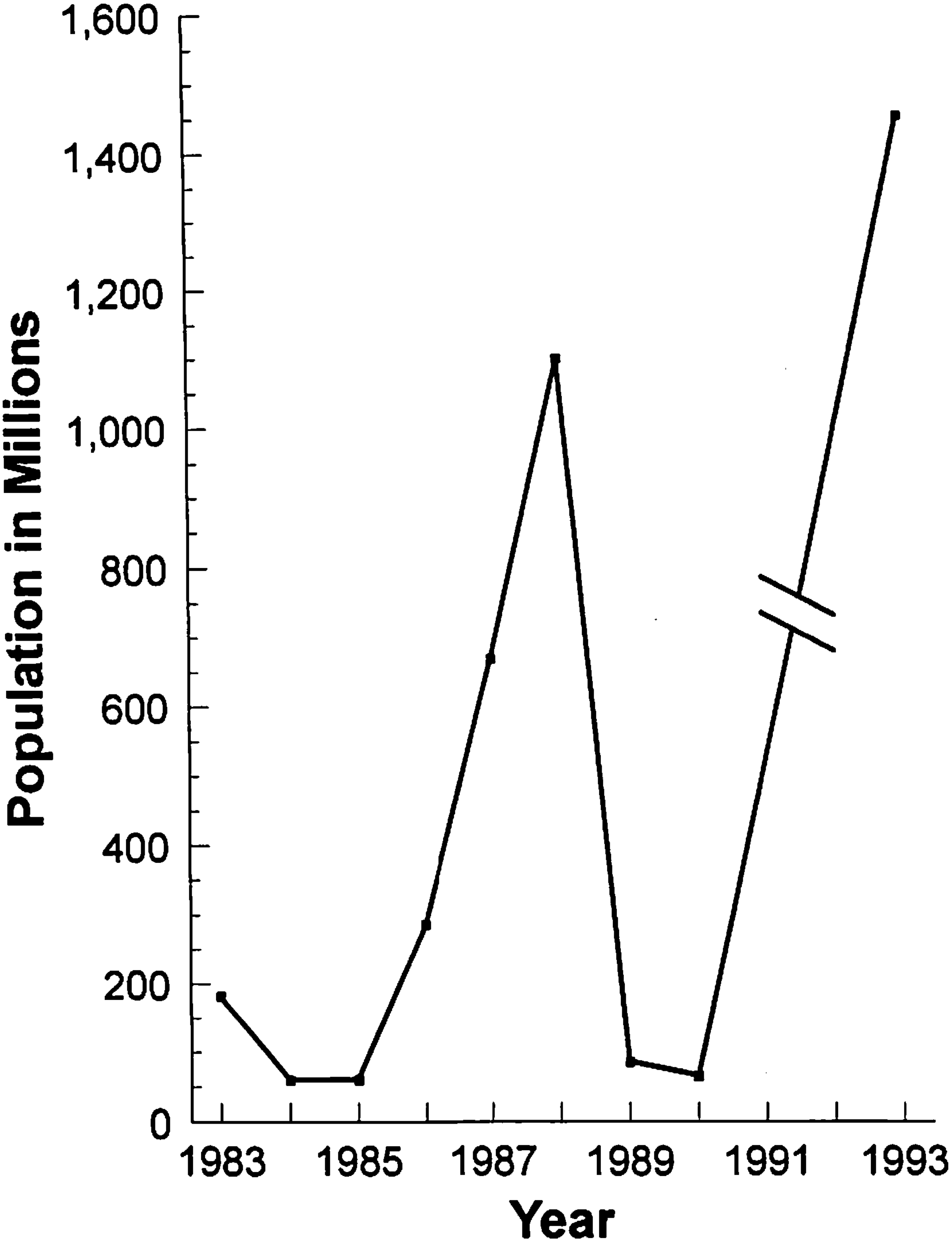
Age distribution was determined by combining the age frequencies of walleyes captured during my sampling and walleyes captured by the SDGF&P during the fall ($x = 1,442$), and multiplying the percent total of the sample of each year class by the total exploitable population.

Age class	Frequency	% of Total	Population
2	694	48.1	2.170×10^6
3	322	22.3	1.006×10^6
4	244	16.9	7.626×10^5
5	93	6.4	2.888×10^5
6	44	3.1	1.399×10^5
7	30	2.1	9.476×10^4
8+	15	1.1	4.961×10^4

Age 1 walleyes were not tagged and did not return to the creel, so the population of the age 1 year-class was determined through non-linear regression to be 5.451×10^6 ($R^2 = 0.9892$). Population estimation of age 0 walleyes is very difficult. About 1.5×10^6 fingerling walleyes are stocked into Oahe Reservoir each year by the SDGF&P (Fielder 1990). Because these stocked fish are not marked, the only way to tell the difference between hatchery and naturally reproduced fish is by size. An intensive investigation which addresses natural reproduction of walleyes in Lake Oahe is needed to determine the amount of reproduction occurring and factors that affect year-class strength.



Appendix A.3. Catch curve for estimating mortality rates from the age composition of exploitable walleyes from Lake Oahe (Robson and Chapman 1961).



Appendix A.4. Hydroacoustic estimates of the number of adult rainbow smelt inhabiting Lake Oahe 1983-1990 and the estimated population in 1993 using bioenergetics modeling.