

**Food Habits, Population Dynamics, and Bioenergetics of Four
Predatory Fish Species in Smith Mountain Lake, Virginia.**

by

Christopher Miles Moore

Dissertation submitted to the Faculty of the
Virginia Polytechnic Institute and State University
in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

in

Fisheries and Wildlife Sciences

APPROVED:

Richard J. Neves, Chairman

John J. Ney

Larry A. Nielsen

Donald J. Orth

George M. Simmons, Jr.

October, 1988

Blacksburg, Virginia

**Food Habits, Population Dynamics, and Bioenergetics of Four
Predatory Fish Species in Smith Mountain Lake, Virginia.**

by

Christopher Miles Moore

Richard J. Neves, Chairman

Fisheries and Wildlife Sciences

(ABSTRACT)

The food habits, survival rates, and abundance of four predatory fish species (striped bass, walleye, largemouth bass, smallmouth bass) were determined and combined with information on energetics and growth to quantitatively assess predator-prey interactions in Smith Mountain Lake, a large hydroelectric reservoir in south-central Virginia. A total of 1871 stomachs of the four species was examined from fish collections between April 1983 and December 1984. Food habits of each predatory species were assessed and compared by season using Schoener's (1970) diet overlap index. Significant diet overlap occurred between the pelagic predators (striped bass and walleye) and between the littoral black basses (largemouth bass and smallmouth bass) in all seasons and locations where sufficient stomach samples were collected.

Survival and abundance estimates for the four predators were derived from several data sets. First-year survival of striped bass fingerlings averaged 20.8% for an 11-year period (1973 to 1983) and ranged from 3.9% to 54.3%. Average survival of age-0 largemouth bass and smallmouth bass was 53% and 45%, respectively, for the period 1979 to 1983. Species-specific survival rates for predators age 2 and older ranged from 29% to

59%. Of the predators age 1 and older, largemouth bass were the most numerous at an estimated density of 61.2/ha, followed by striped bass at 16.3/ha. Age 1 and older smallmouth bass and walleye were less abundant, at densities of 8.2 and 2.0/ha, respectively.

A bioenergetics model was developed for striped bass and, with models developed for walleye and largemouth bass, used to estimate annual consumption of alewives and gizzard shad by the four piscivorous species. Annually, striped bass consumed the greatest amount of adult and young-of-year alewives, whereas largemouth bass ate nearly 70% of the total shad biomass consumed by all predators. A comparison of predator demand to clupeid supply substantiated diet overlap data; namely, that native and introduced predators were compatible in Smith Mountain Lake.

The striped bass bioenergetics model was used to make inferences about potential stocking strategies for striped bass based on availability of age-1 and older alewives. A stocking rate of 20-24 fingerlings/ha appears to maximize production of striped bass and minimize potential competitive interactions between striped bass and native black bass in Smith Mountain Lake.

TABLE OF CONTENTS

Acknowledgements.....iv
List of Figures.....viii
List of Tables.....xi
Introduction.....1
Study Area.....6
Chapter I.....9
 Introduction.....9
 Methods.....10
 Results.....13
 Stomach Collection.....13
 Predator Food Habits.....15
 Predator-Prey Length Relationships.....23
 Diet Overlap.....28
 Discussion.....33
 Predator Food Habits.....33
 Predator-Prey Length Relationships.....40
 Diet Overlap.....42
 Conclusion.....43
Chapter II.....45
 Introduction.....45
 Methods.....47
 Black Basses.....47
 Striped Bass.....50

Walleye.....	52
Results.....	54
Discussion.....	66
Chapter III.....	76
Introduction.....	76
The Bioenergetics Model.....	79
Consumption.....	83
Respiration.....	86
Specific Dynamic Action.....	93
Optimum and Maximum Temperatures.....	93
Excretion and Egestion.....	95
Energy Content of Predators and Prey.....	97
Water Temperature.....	108
Growth.....	109
Diet.....	123
Population Parameters.....	128
Bioenergetics Program.....	133
P-Values.....	134
Conversion Efficiencies.....	135
Predator Demand.....	140
Calculation of Demand.....	140
Demand Estimates.....	141
Overview of Demand.....	146
Predator Demand vs Clupeid Supply.....	150

Calculation of Clupeid Supply.....	150
Clupeid Biomass and Production Estimates.....	156
Overview of Demand vs Supply.....	161
Stocking Strategies.....	164
Calculation of Consumption Estimates.....	166
Simulation Output.....	168
Recommended Stocking Strategy.....	172
Sensitivity and Bias.....	176
Conclusion.....	180
Management Implications.....	183
Summary.....	187
Appendix.....	192
Literature Cited.....	200
Biographical Sketch.....	218

LIST OF FIGURES

Figure	Page
I.1. Smith Mountain Lake, Virginia. Hales Ford Bridge was designated as the landmark for separating the upper and lower lake.....	7
1.1. Relationship between sizes of alewives consumed and sizes of striped bass. The upper line (A) represents the estimated lengths of alewives a striped bass could consume based on the calculations of Jenkins and Morais (1978).....	24
1.2. Relationship between sizes of alewives consumed and sizes of walleye. The upper line (A) represents the estimated lengths of alewives a walleye could consume based on the calculations of Jenkins and Morais (1978).....	25
1.3. Mean lengths (+1 SD) of alewives in stomachs of all four predatory species from Smith Mountain Lake, April-December, 1983 and 1984.....	26
1.4. Relationship between sizes of gizzard shad consumed and sizes of striped bass. The upper line (A) represents the estimated lengths of gizzard shad a striped bass could consume based on the calculations of Jenkins and Morais (1978).....	27
1.5. Relationship between sizes of gizzard shad consumed and sizes of largemouth bass. The upper line (A) represents the estimated lengths of gizzard shad a largemouth bass could consume based on the calculations of Jenkins and Morais (1978).....	29
1.6. Relationship between sizes of gizzard shad consumed and sizes of walleye. The upper line (A) represents the estimated lengths of gizzard shad a walleye could consume based on the calculations of Jenkins and Morais (1978).....	30
2.1. The relationship between the number of stocked striped bass fingerlings surviving to age 1 and stocking density.....	64
2.2. The relationship between the number of stocked striped bass fingerlings and the marginal yield. Marginal yield is the number of survivors (age-1 fish) produced per additional stocking of fingerlings.....	65

3.1.	Model output for the energy budget of a 100 g striped bass, as a function of temperature.....	98
3.2.	Model output for striped bass at the optimum temperature for consumption, T_{oc} , as a function of body size.....	99
3.3.	Mean caloric content ± 2 SD of striped bass collected at four sampling dates in Smith Mountain Lake. Values are presented with the caloric content of age-1+ sauger as measured by Minton (1981) and used to model striped bass bioenergetics in this study.....	101
3.4.	Mean water temperatures taken at three locations and two depths, 1m and 10m, in Smith Mountain Lake. Data are from Hart (1978).....	110
3.5.	Seasonal growth (TL mm) of striped bass, ages 0 to 11. The line is derived from a modified von Bertalanffy growth function fit to monthly mean lengths of striped bass from Smith Mountain Lake, 1983-1984.....	114
3.6.	Seasonal growth (TL mm) of largemouth bass, ages 0 to 7. The line is derived from a modified von Bertalanffy growth function fit to monthly mean lengths of largemouth bass from Smith Mountain Lake, 1983-1984.....	115
3.7.	Seasonal growth (TL mm) of smallmouth bass, ages 0 to 7. The line is derived from a modified von Bertalanffy growth function fit to monthly mean lengths of smallmouth bass from Smith Mountain lake, 1983-1984.....	116
3.8.	Seasonal growth (TL mm) of walleye, ages 2 to 9. The line is derived from a modified von Bertalanffy growth function fit to monthly mean lengths of walleye from Smith Mountain Lake, 1983-1984.....	117
3.9.	Seasonal growth in weight (g) of striped bass, ages 0 to 11. Weights are derived from a modified von Bertalanffy growth equation and seasonal length-weight regressions. Derived weights are plotted with observed mean weight ± 1 SD.....	124
3.10.	Seasonal growth in weight (g) of largemouth bass, ages 0 to 7. Weights are derived from a modified von Bertalanffy growth equation and seasonal length-weight regressions. Derived weights are plotted with observed mean weight ± 1 SD.....	125

3.11.	Seasonal growth in weight (g) of walleye, ages 3 to 9. Weights are derived from a modified von Bertalanffy growth equation and seasonal length-weight regressions. Derived weights are plotted with observed mean weight ± 1 SD.....	126
3.12.	Seasonal growth in weight (g) of smallmouth bass, ages 0 to 7. Weights are derived from a modified von Bertalanffy growth equation and seasonal length-weight regressions. Derived weights are plotted with observed mean weight ± 1 SD.....	127
3.13.	Biomass levels (kg/ha) of gizzard shad collected by the Virginia Department of Game and Inland Fisheries in cove rotenone samples. Data are from Whitehurst (1985).....	165
3.14.	Biomass levels (kg/ha) of alewives collected by the Virginia Commission of Game and Inland Fisheries in cove rotenone samples. Data are from Whitehurst (1985).....	174
A.1.	Catch curve of striped bass collected in fall gill net samples by the Virginia Department of Game and Inland Fisheries, 1973-1983.....	197
A.2.	Catch curve of largemouth bass collected by electrofishing in Smith Mountain Lake, 1983-1984.....	198
A.3.	Catch curve of smallmouth bass collected by electrofishing in Smith Mountain Lake, 1983-1984.....	199

LIST OF TABLES

Table	Page
1.1. Total number of predator stomachs collected by location and season from Smith Mountain Lake, 1983-1984. Hales Ford Bridge was designated as the boundary between the upper and lower lake.....	14
1.2. Percent of total number of prey items (N) and percent of total food weight (W) contributed by different types of prey consumed by striped bass in Smith Mountain Lake, 1983-1984...	16
1.3. Percent of total number of prey items (N) and percent of total food weight (W) contributed by different types of prey consumed by largemouth bass in Smith Mountain Lake, 1983-1984.....	18
1.4. Percent of total number of prey items (N) and percent of total food weight (W) contributed by different types of prey consumed by walleye in Smith Mountain Lake, 1983-1984.....	20
1.5. Percent of total number of prey items (N) and percent of total food weight (W) contributed by different types of prey consumed by smallmouth bass in Smith Mountain Lake, 1983-1984. Smallmouth bass were collected only in the lower lake.....	22
1.6. The minimum number of predator stomachs necessary to adequately characterize diets as determined by cumulative prey species curves (Brodeur and Pearcy 1984).....	31
1.7. Diet overlap values for predators in Smith Mountain Lake, calculated by location and season (W=winter, S=spring, Su=summer, F=fall). Only seasonal samples that exceeded the minimum number of stomachs necessary to adequately characterize the predator diets (as determined by cumulative prey species curves) were used.....	32
2.1. Estimates of mean standing stocks (kg/ha) of largemouth bass and smallmouth bass in Smith Mountain Lake, 1979 to 1983, from cove rotenone sampling. Data are from Whitehurst (1985).....	48
2.2. Summary of annual survival estimates for age 0 and older predators in Smith Mountain Lake and the source used to derive the estimate.....	55

2.3.	Numbers of age 0 to 2 largemouth bass in Smith Mountain Lake, 1979-1983. Estimates were derived from cove rotenone sampling data obtained in August of each year.....	56
2.4.	Estimates of the number of major fish predators, by species and age, in Smith Mountain Lake during 1983.....	57
2.5.	Numbers of age 0 to 2 smallmouth bass in Smith Mountain Lake, 1979-1983. Estimates were derived from cove rotenone sampling data obtained in August of each year.....	58
2.6.	Annual survival rates (%) for age 1 striped bass, computed from gill net CPUE data collected by the Virginia Department of Game and Inland Fisheries.....	60
2.7.	Total number of fingerling striped bass stocked, CPUE of fish the following year, estimated number of age-1 striped bass, and the estimated annual survival (%) for stocked fingerlings in Smith Mountain Lake, 1973 to 1984.....	62
2.8.	Annual survival rates of largemouth bass from selected southeastern reservoirs.....	68
2.9.	Annual survival rates of smallmouth bass from selected water bodies in the United States.....	69
3.1.	Symbols and parameter values used to implement the bioenergetics model for walleye. Values are from Kitchell et al. (1977).....	80
3.2.	Symbols and parameter values used to implement the bioenergetics model for black basses. Values are from Rice et al. (1983).....	82
3.3.	Symbols and parameter values used to implement the bioenergetics model for striped bass.....	84
3.4.	Caloric content (cal/g wet weight) of ages 2 to 6 largemouth bass used in the bioenergetics model. Values were derived from unpublished data (S.M. Adams pers. comm.) and from data presented by Adams et al. (1982a).....	104
3.5.	Caloric content (cal/g wet weight) of walleye (ages 3-8) used in the bioenergetics simulation. Values are from Minton (1981).....	105

3.6.	Caloric content (cal/g wet weight) of prey items used in bioenergetics models for all four predatory species.....	107
3.7.	Parameters used to describe seasonal growth curves for all age groups of predators in Smith Mountain Lake, 1983-1984. Parameters correspond to the modified von Bertalanffy growth function.....	113
3.8.	Seasonal length-weight regression equations developed for striped bass age groupings. Equations were developed using nonparametric, Theil-Sen regression procedures. Y is ln weight in grams and X is ln total length in millimeters.....	119
3.9.	Seasonal length-weight regression equations developed for largemouth bass age groupings. Equations were developed using nonparametric, Theil-Sen regression procedures. Y is ln weight in grams and X is ln total length in millimeters.....	120
3.10.	Seasonal length-weight regression equations developed for smallmouth bass age groupings. Equations were developed using nonparametric, Theil-Sen regression procedures. Y is ln weight in grams and X is ln total length in millimeters.....	121
3.11.	Seasonal length-weight regression equations developed for walleye. Equations were developed using nonparametric, Theil-Sen regression procedures. Y is ln weight in grams and X is ln total length in millimeters.....	122
3.12.	Seasonal diet of striped bass as percent of total food weight for five prey categories. Values are given by age, date, and the corresponding day in the modeling simulation.....	129
3.13.	Seasonal diet of largemouth bass as percent of total food weight for six prey categories. Values are given by age, date, and the corresponding day in the modeling simulation..	130
3.14.	Seasonal diet of walleye as percent of total food weight for five prey categories. Values are given by age, date, and the corresponding day in the modeling simulation.....	131
3.15.	Seasonal diet of smallmouth bass as percent of total food weight for six prey categories. Values are given by age, date, and the corresponding day in the modeling simulation..	132
3.16.	Mean seasonal P-values, the proportion of maximum consumption, for predator populations in Smith Mountain Lake.....	136

- 3.17. Mean weight gain, ration and gross conversion efficiency for striped bass age groups in Smith Mountain Lake. The values represent the growing season, March 15 to December 15.....137
- 3.18. Mean weight gain, ration and gross conversion efficiency for striped bass age groups in Smith Mountain Lake. The values are for the summer period, June 1 to August 31.....139
- 3.19. Seasonal consumption (kg) of clupeids by predators in Smith Mountain Lake. Estimates are derived from bioenergetics simulations.....142
- 3.20. Biomass (kg) of clupeids consumed by ages 0 to 10 striped bass in Smith Mountain Lake, 1983-1984.....144
- 3.21. Biomass (kg) of clupeids consumed by ages 0 to 6 largemouth bass in Smith Mountain Lake, 1983-1984.....145
- 3.22. Biomass (kg) of clupeids consumed by ages 3 to 8 walleye in Smith Mountain Lake, 1983-1984.....147
- 3.23. Biomass (kg) of clupeids consumed by ages 0 to 6 smallmouth bass in Smith Mountain Lake, 1983-1984.....148
- 3.24. The mean number of alewife larvae (per 1000 m³), 5 to 10 mm TL, collected in meter net tows in Smith Mountain Lake, 1983 and 1984. Data are from Tisa (unpublished).....151
- 3.25. The mean number of gizzard shad larvae (per 1000 m³), 5 to 10 mm TL, collected in meter net tows in Smith Mountain Lake, 1983 and 1984. Data are from Tisa (unpublished).....152
- 3.26. Mean weight (W), instantaneous growth (G), biomass (B), corrected biomass (CB), mean corrected biomass (B), and production (P) of the 1983 and 1984 cohorts of alewives in Smith Mountain Lake.....157
- 3.27. Mean weight (W), instantaneous growth (G), biomass (B), corrected biomass (CB), mean corrected biomass (B), and production (P) of the 1983 and 1984 cohorts of gizzard shad in Smith Mountain Lake.....159
- 3.28. Estimates of cumulative consumption (kg) by predators in Smith Mountain Lake compared to production estimates (kg) for young-of-year alewives and gizzard shad by season. Production estimates represent estimates for the 1983 and 1984 cohorts of both clupeids.....160

3.29.	Estimated consumption (kg) of clupeids over time by a cohort of striped bass based on a single stocking of 100,000 fingerlings and a survival rate of 21% for fingerlings.....	169
3.30.	Estimated consumption (kg) of clupeids by a cohort of striped bass stocked at different densities. Survival rates (%) were derived from an equation relating survival to stocking density.....	170
A.1.	Mean percent by weight of food items in the stomach contents of striped bass collected in Smith Mountain Lake, 1983-1984.....	193
A.2.	Mean percent by weight of food items in the stomach contents of largemouth bass collected in Smith Mountain Lake, 1983-1984.....	194
A.3.	Mean percent by weight of food items in the stomach contents of walleye collected in Smith Mountain Lake, 1983-1984.....	195
A.4.	Mean percent by weight of food items in the stomach contents of smallmouth bass collected in Smith Mountain Lake, 1983-1984.....	196

INTRODUCTION

Smith Mountain Lake, a large hydroelectric reservoir in south-central Virginia, is like many reservoirs of the southeastern U.S. in that both introduced and indigenous game species comprise the predator assemblage. Resident sport fish include the black basses, largemouth bass (Micropterus salmoides) and smallmouth bass (M. dolomieu). Striped bass (Morone saxatilis), as well as walleye (Stizostedion vitreum vitreum), were initially stocked in Smith Mountain Lake in the early 1960s by the Virginia Department of Game and Inland Fisheries. The striped bass population did not reproduce but annual stockings, ranging as high as 55 fingerlings per hectare, established an exceptional trophy fishery characterized by high growth and harvest rates (Hart 1978).

However, in the late 1970s, harvest rates for striped bass and other predators decreased significantly with subsequent reductions in growth rates and condition factors (La Roche 1981). There was a concomitant decline in the sport fishery; angler trips decreased 43% between 1977 and 1980.

This precipitous decline in the Smith Mountain Lake fishery prompted the initiation of a research project to investigate the factors affecting the recreational fishery of Smith Mountain Lake. A total of four major factors were studied from 1982 to 1985, to include the effects of reduced nutrient inputs (Yurk unpublished), influence of added pumpback operation (Ney et al. 1988), and availability of forage fishes (Tisa unpublished)

A final, fourth factor, and the focus of this dissertation, involved an investigation of the trophic relationships between striped bass and the other major predators in Smith Mountain Lake.

Although food habit studies indicate striped bass may compete for food with other important game species in reservoirs, including walleye and black basses, trophic interactions between striped bass, other stocked predators, and resident predator populations are poorly understood. Saul (1981) reported that chironomid larvae were the principal food item in the diet of introduced young-of-year striped bass and native black bass populations in Cherokee Reservoir, Tennessee. The predominant food items in the diet of juvenile and adult striped bass in southern reservoirs are clupeids -- gizzard shad (Dorosoma cepedianum), threadfin shad (Dorosoma petenense), and alewife (Alosa pseudoharengus) (Stevens 1958, Ware 1970, Hart 1978, Morris and Follis 1978, Combs 1980, Kohler and Ney 1981, Matthews and Hill 1982). Because clupeids can also be a major component of the diet of walleye (Colby et al. 1979) and black bass in reservoirs (Jenkins 1975, Noble 1981), striped bass introductions could limit production of these predators through exploitative competition.

Estimation of competitive interaction between striped bass and other predators in reservoirs must consider the amount of the available food resource in relation to the size of predator populations and their demand for this food. In studies involving young-of-year striped bass and black bass, competitive interaction was considered minimal due to the excessive availability of large numbers of chironomid larvae (Saul 1981). Compet-

itive interactions could theoretically increase as striped bass and other predators increase in size and their diets become largely piscivorous. If introduced striped bass severely deplete the clupeid forage base, as they did in Santee-Cooper Reservoir, South Carolina (Stevens 1969), and Lake E.V. Spence, Texas (Morris and Follis 1978), a significant impact on other predator populations could occur.

Most investigations of trophic relationships of striped bass in reservoirs have been descriptive studies of diet composition (Bailey 1974). However, Jenkins and Morais (1978) developed an available prey/predator ratio (AP/P) as an instantaneous measure of the adequacy of a reservoir's forage base in August to sustain existing predator populations, including striped bass, through the remainder of the growing season. Although useful as a management tool, the AP/P ratio is based on estimates of what predators could physically consume (derived from the size of the predator's mouth and availability of prey) and not the specific composition of the predator's diet; i.e., selection of food items by the predator. Thus, this measurement is limited in its contribution to the ecological understanding of predator-prey interactions. Similarly, Ploskey and Jenkins (1982) used a biomass model to evaluate trophic relationships among fish species, including striped bass, in reservoirs, but the model estimated production and food requirements of different piscivorous predators as one functional trophic group.

Quantitative assessments of specific interactions between predators in reservoirs are lacking. The goal of this study was to quantitatively assess trophic interactions among indigenous and stocked game species by

determining predator demand for alewives and gizzard shad, the primary forage species in Smith Mountain Lake. Predator demand for these prey items was estimated using a bioenergetics modeling approach. Ancillary information required for these bioenergetic models include data on predator food habits, survival rates, and abundance. This dissertation incorporates these data in three chapters.

Chapter I details how available forage was utilized by piscivorous sizes of four major predators, striped bass, walleye, largemouth bass, and smallmouth bass, that coexist in Smith Mountain Lake. Specifically, I assessed and compared food habits of each predatory species by season in distinct habitats, the upper and lower reservoir, using Schoener's (1970) diet overlap index.

In Chapter II, I derived age-specific survival rates and population estimates for each of the four predatory species. Included in this chapter is an innovative technique for assessing survival of stocked striped bass fingerlings.

Finally, Chapter III utilizes information on diets and population parameters in conjunction with bioenergetics models to assess predator demand for alewife and gizzard shad, the principal prey species consumed by predators in Smith Mountain Lake. Specifically, I developed a bioenergetics model for striped bass based on a compilation of data from several studies on striped bass metabolism and growth. Bioenergetic models previously developed for largemouth bass and walleye were used to derive similar consumption estimates for the other three predators that

coexist in the reservoir. Annual estimates of predator demand for gizzard shad and alewife were then evaluated to answer two questions:

1. Are introduced and native predator populations compatible in Smith Mountain Lake?
2. Can estimates of predator demand be used to determine striped bass stocking strategies?

STUDY AREA

Smith Mountain Lake is a pumpback, hydroelectric reservoir located in south-central Virginia. The reservoir, an impoundment of the Blackwater and Roanoke Rivers, was formed by the Appalachian Power Company in the early 1960s. Smith Mountain Lake has a surface area of 8337 ha at a maximum pool elevation of 241.7 m, a mean depth of 16.8 m, and a 805 km shoreline that is highly dendritic. The mean annual fluctuation in water level is 1.5 m.

Smith Mountain Lake is eutrophic and riverine in the upper Roanoke River and Blackwater River arms and becomes progressively more mesotrophic and lacustrine downstream (Virginia State Water Control Board 1980). This study was limited to collections from the Roanoke River arm of the reservoir to the lower main portion of the lake below the confluence of the Blackwater and Roanoke Rivers. For purposes of this study, Smith Mountain Lake was considered to consist of two distinct habitats, the upper and lower reservoir, arbitrarily divided at the Hales Ford Bridge (Fig. 1).

Several investigations have been conducted in Smith Mountain Lake since its formation in 1963, including limnological and water quality studies (reviewed by Simmons 1976 and Virginia State Water Control Board 1980) and studies investigating the impacts of artificial reefs on fishing success (Brouha 1974, Prince 1975). In addition, the Virginia Department of Game and Inland Fisheries (VDGIF) has collected information on the

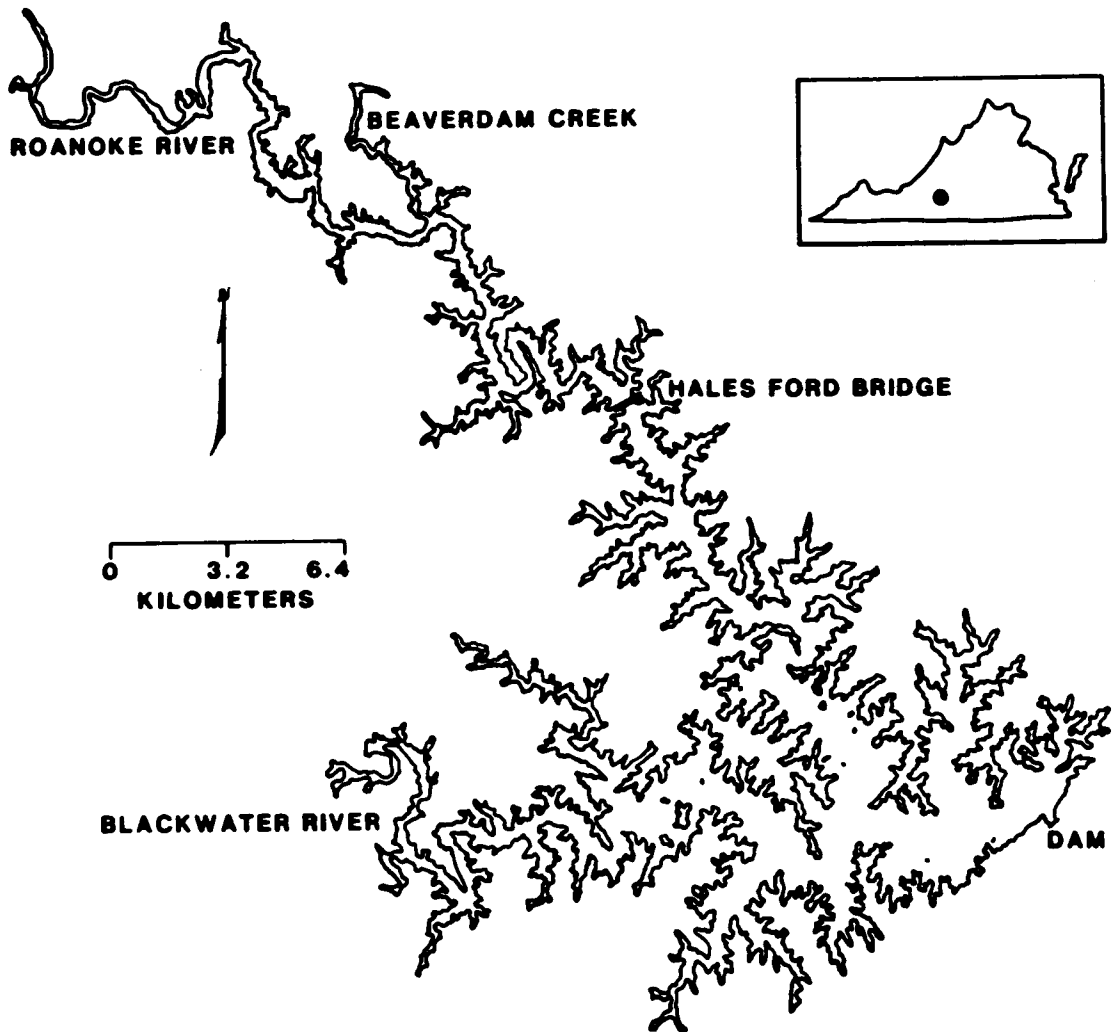


Figure 1. Smith Mountain Lake, Virginia. Hales Ford Bridge was designated as the landmark for separating the upper and lower lake.

sport fishery of the lake since 1973 (Hart 1978, La Roche 1981, Whitehurst 1985).

Numerous game and non-game fish species inhabit Smith Mountain Lake. A total of 44 species of native and stocked fish were listed by Hart (1978) as present in the lake during the 1960's and early 1970's. Largemouth bass and smallmouth bass were the primary game species after the initial formation of the reservoir. Stocking of striped bass and walleye began in the early 1960's. Although the VDGIF still stocks fingerling striped bass annually, no walleye have been stocked in Smith Mountain Lake since 1979. The principal forage fish are the clupeids, gizzard shad and alewife. Alewives were introduced in the lake in 1965 when the VDGIF stocked approximately 3,000 adult fish. Gizzard shad are native to the Roanoke River drainage basin. Other forage species include various minnows (Pimephales spp.), shiners (Notemigonus crysoleucas and Notropis spp.), and crayfish (Orconectes spp.).

CHAPTER I

Food Resource Partitioning Among Coexisting Predators in Smith Mountain Lake, Virginia

Introduction

Southern U.S. reservoirs are complex ecosystems characterized by fish assemblages of indigenous and introduced species. Pelagic piscivores, such as striped bass (Morone saxatilis) and walleye (Stizostedion vitreum vitreum), have been stocked widely with complementary, pelagic forage species such as alewife (Alosa pseudoharengus) or threadfin shad (Dorosoma petenense), to utilize the large, open water habitat that dominates these aquatic systems. Although introductions would tend to intensify interactions within the reservoir fish assemblage (Magnuson 1976, Li and Moyle 1981), quantitative measurements of trophic interactions between introduced and resident predator populations in southern reservoirs are generally lacking. Furthermore, although clupeids are predominant in the diet of predators in southern reservoirs (Jenkins and Morais 1978), and most of these systems contain more than one clupeid, no study has adequately assessed resource partitioning among predators in a reservoir containing codominant clupeids.

The purpose of this investigation was to determine if negative interactions between predators could explain the precipitous decline in harvest and growth rates documented for predators in Smith Mountain Lake in the late 1970s and early 1980s (La Roche 1981). Because a study of food habits represents one of several approaches for determining the compatibility of species in reservoirs (Aggus 1973, Kohler and Ney 1981), my objective was to determine how available forage was utilized by piscivorous sizes of four major predators, striped bass, largemouth bass (Micropterus salmoides), smallmouth bass (M. dolomieu), and walleye, that coexist in Smith Mountain Lake, Virginia, a reservoir where both alewives and gizzard shad (Dorosoma cepedianum) are abundant. Specific objectives were to describe and compare the food habits of the black basses, walleye and striped bass by season in distinct habitats, the upper and lower reservoir, using Schoener's (1970) diet overlap index.

Methods

Striped bass, walleye, and the black basses were collected from Smith Mountain Lake with gill nets and electroshocking equipment from April to December in both 1983 and 1984. Collections were limited to the Roanoke River arm and the main area of the reservoir below the confluence of the Blackwater and Roanoke River arms. Only piscivorous sizes of predators, those greater than approximately 100 mm TL, were collected. These samples of piscivores were supplemented with fish caught by anglers. Experimental gill nets, 61 m long and 2 m deep, consisting of panels with bar meshes of 38 to 76 mm, were fished overnight each week from April to September

of each year and once per month in October, November, and December, in both the upper and lower reservoir. Nets were set in both littoral and limnetic areas so as to adequately sample available habitat. Shore electrofishing at night was conducted periodically in April, May, August, and November 1983, and April to August, November, and December 1984.

Stomachs excised from all predators collected in the nets and contributed by anglers were preserved in 10% buffered formalin. Hollow plastic tubes of various diameters were used to remove stomach contents from electroshocked fish (Van Den Avyle and Roussel 1980). These fish were then released alive, and the stomach contents were preserved in 10% formalin.

In the laboratory, stomach contents were identified to the lowest possible taxa. Partly digested gizzard shad and alewives were identified on the basis of the presence (or absence) of a gizzard and the color of the peritoneum (Manooch 1973). Food items were blotted dry and weighed to the nearest 0.1 g. Stomach content data were tabulated by location and season -- winter (December), spring (March-May), summer (June-Aug.), and fall (Sept.-Nov.) -- and were expressed as percent of the total number of food items, percent of total food weight, and average of the weight percentages. Differential digestion rates of fish and crayfish were assumed inconsequential (Windell 1966).

Total, standard, and backbone lengths of identifiable fish in stomachs were measured to the nearest 1 mm. Standard (SL) and backbone lengths (BL) of clupeids consumed were converted to total lengths (TL)

using regression equations developed from specimens collected in the reservoir. These regression equations for alewife were:

$$TL = 1.256(SL) - 1.989, N=348, r^2 = 0.99$$

$$TL = 1.616(BL) - 2.994, N=348, r^2 = 0.98$$

Similar equations for gizzard shad were:

$$TL = 1.466(SL) + 1.25, N=341, r^2 = 0.97$$

$$TL = 1.482(BL) + 1.993, N=341, r^2 = 0.98$$

Alewives were divided into two distinct prey groups, young-of-year and adult, based on an observed or calculated TL. A total length of 86 mm, derived from scale analysis, was used to separate these fish. The relation between total lengths of consumed clupeids and the predators from which they were taken was compared by linear regression. In addition, a regression equation developed by Jenkins and Morais (1978) to describe the relationship between predator total length and maximum ingestible total length of clupeid prey was compared to measured or derived total lengths of clupeids consumed by predators in Smith Mountain Lake. Because the predictive equation was derived from a comparison of largemouth bass size and gizzard shad body depth (Lawrence 1958), a conversion factor of 1.25 was used to adjust for the smaller body depth -- total length ratio of alewives relative to gizzard shad (Nigro and Ney 1982).

Diet overlap was calculated among predator populations by season and locations using the average of the weight percentages and Schoener's (1970) overlap index:

$$\alpha = 1.0 - 0.5 \sum_{i=1}^n |Px_i - Py_i|$$

where α is the overlap index, Px_i is the proportion of food category i in the diet of species x , Py_i is the proportion of food category i in the diet of species y , and n is the number of food categories. Wallace (1981) determined that this index, used with volume (or weight) percentages, was the most appropriate method for calculating overlap when accurate data on prey abundance were unavailable. The index ranges from 0 (no overlap) to 1 (complete overlap). Values greater than 0.6 are considered significant (Zaret and Rand 1971). Only seasonal samples which adequately described the diet of each predator by location, as determined by cumulative prey species curves (Brodeur and Pearcy 1984), were used in diet comparisons. Cumulative prey species curves for each predator (by season and location) were obtained by plotting cumulative number of prey taxa found in a cumulative number of randomly ordered stomachs. The asymptote of the curve corresponded to the minimum number of stomachs needed to adequately describe the diet. If an asymptote was not reached, the sample was considered inadequate for subsequent comparisons.

Results

Stomach Collection

A total of 1871 stomachs of the four predatory species was examined from fish collected between April 1983 and December 1984 (Table 1.1).

Table 1.1. Total number of predator stomachs collected by location and season from Smith Mountain Lake, 1983-1984. Hales Ford Bridge was designated as the boundary between the upper and lower lake.

Species	Upper Lake			Lower Lake			Total		
	Winter	Spring	Summer	Fall	Winter	Spring		Summer	Fall
Striped bass	74	46	86	86	9	161	163	83	708
Largemouth Bass	71	127	135	58	0	88	24	15	518
Smallmouth bass	-	-	-	-	4	73	83	27	187
Walleye	11	30	26	21	5	240	113	12	458

Of the four predators, striped bass and largemouth bass were collected most frequently in the reservoir. Largemouth bass were the most abundant predator in the upper, more fertile portion of the reservoir over all seasons, whereas lack of littoral habitat appeared to limit the number of largemouth bass in the lower reservoir.

Habitat constraints, specifically high water temperatures, appeared to limit the coolwater species, walleye and smallmouth bass, and to a lesser extent, striped bass, from fully utilizing the upper reservoir from late spring to early fall (Ney et al. 1988). Collections of these species during this period were limited to areas immediately above the Hales Ford Bridge where thermal refugia were available. Of the 458 walleye stomachs collected, roughly 75% (370) came from the lower reservoir. Although walleye and striped bass were collected from the upper Roanoke River arm from late fall to early spring, no smallmouth bass were collected above the Hales Ford Bridge in any season.

Predator Food Habits

Alewives and gizzard shad were by far the dominant food items in striped bass stomachs (Table 1.2). Adult alewives comprised 30% of prey items found in stomachs and 31% of stomach contents by weight. The comparable values for young-of-year alewives were 21% and 8%, respectively, and 39% and 58% for gizzard shad. As judged by general clupeoid body shape, most of the unidentified fish were either alewives or gizzard shad. Crayfish (Orconectes spp.) occurred consistently in stomachs, but nearly always at frequencies of less than 10%. Food items which occurred rela-

Table 1.2. Percent of total number of prey items (N) and percent of total food weight (W) contributed by different types of prey consumed by striped bass in Smith Mountain Lake, 1983-1984.

Location and Season	Striped Bass Examined With Food (%)	Adult Alewife		Y-O-Y Alewife		Gizzard Shad		Crayfish		Lepomis		Unidentified Fish		Other	
		N	W	N	W	N	W	N	W	N	W	N	W	N	W
Upper Lake															
Winter	74	1	T	1	T	97	99	1	T	0	0	1	T	T	T
Spring	46	47	69	14	6	26	22	2	T	4	1	5	2	3	1
Summer	86	67	86	15	10	12	2	4	2	1	T	2	1	0	0
Fall	86	9	14	39	32	28	43	10	8	0	0	15	3	0	0
Total	292														
Lower Lake															
Winter	9	0													
Spring	161	54	71	29	20	1	2	1	1	1	1	11	5	2	T
Summer	163	44	60	26	14	15	18	8	6	T	T	4	2	1	T
Fall	83	12	35	61	28	9	28	6	7	0	0	10	2	2	T
Total	416														

^a T = <0.05%

tively infrequently included sunfish (Lepomis spp.) and miscellaneous food items; minnows (Notropis spp.), darters (Etheostoma sp.), and insects (Diptera, Ephemeroptera, Lepidoptera).

Food habits of striped bass, and the other three predators as well, were significantly different between habitats and among seasons (χ^2 , $p < 0.05$). In the upper lake, gizzard shad were 100 times more important (by weight) than alewives (adults and young-of-year combined) in the diet of striped bass in winter. However, alewives comprised more of the diet (by weight) in spring and summer by roughly 3:1 and 90:1, respectively, and the frequency of alewives to gizzard shad was nearly equal in the fall. In the lower lake, alewives were consumed more frequently than gizzard shad in spring, summer, and fall by roughly 80:1, 45:1, and 8:1, respectively.

Food items in largemouth bass stomachs consisted mainly of gizzard shad, crayfish (Orconectes spp.), and to a lesser extent, sunfish (Table 1.3). A total of 29% of prey items in largemouth bass stomachs was gizzard shad, which comprised 39% of stomach contents by weight. Comparable values were 26% and 26%, respectively, for crayfish, and 6% and 14% for sunfish. Infrequent food items included young-of-year and adult alewives, other fish (black crappie Pomoxis nigromaculatus, minnows Notropis spp., largemouth bass, catfish Ictalurus spp.), aquatic insects (Hemiptera, Diptera, Odonata), terrestrial insects (Arachnida, Hymenoptera) and terrestrial vertebrates (Cricetidae, Reptilia, Amphibia).

Table 1.3. Percent of total number of prey items (N) and percent of total food weight (W) contributed by different types of prey consumed by largemouth bass in Smith Mountain Lake, 1983-1984.

Location and Season	Largemouth Examined	With Food (%)	Adult Alewife		Y-O-Y Alewife		Gizzard Shad		Crayfish		Sunfish		Unidentified Fish		Other	
			N	W	N	W	N	W	N	W	N	W	N	W	N	W
Upper Lake																
Winter	71	59	0	0	0	0	51	66	30	26	0	0	19	8	0	0
Spring	127	35	5	8	0	0	0	0	35	32	12	44	30	9	18	7
Summer	135	67	5	9	1	2	36	44	15	14	6	22	14	4	24	5
Fall	58	45	0	0	0	0	39	58	24	15	12	3	18	7	6	16
Total	391															
Lower Lake																
Winter																
Spring	88	44	10	13	6	6	8	5	45	55	4	3	18	16	10	2
Summer	24	38	0	0	20	15	20	76	13	3	0	0	47	6	0	0
Fall	15	33	0	0	0	0	57	80	29	19	0	0	14	1	0	0
Total	127															

Gizzard shad dominated the diet of largemouth bass in the upper lake during winter, summer, and fall (66%, 44%, and 58% by weight, respectively) and during summer and fall (76% and 80% by weight, respectively) in the lower lake. Crayfish appeared consistently in stomachs of largemouth bass, and frequently occurred in spring in both the upper (35%) and lower (45%) lake. Crayfish occurred less frequently in bass stomachs from both locations during summer. Sunfish appeared frequently in stomachs of largemouth bass in the upper reservoir, comprising 44% of diet items in spring and 22% in summer, whereas they were absent or inconsequential in the diet of largemouth bass from the lower reservoir. Although alewives occurred infrequently in the diet, young-of-year alewives did comprise 20% by number and 15% by weight of the spring diet of largemouth bass from the lower reservoir. No largemouth bass were collected in the lower lake in winter.

Clupeids were the only identifiable piscine prey items in walleye stomachs from both locations in all seasons (Table 1.4). Adult alewives totaled 52% of the prey items and comprised 66% of stomach contents by weight; young-of-year alewives were 21% and 11%, respectively, and gizzard shad were 20% and 20%, respectively. Unidentified fish, mostly clupeids, comprised 8% of prey items and 2% of total food weight. Crayfish remains were found in one walleye stomach collected in the upper reservoir during summer.

Gizzard shad were the only identifiable prey items in walleye stomachs from the upper reservoir in winter. All five of the walleye stomachs collected during this period in the lower lake were empty. In

Table 1.4. Percent of total number of prey items (N) and percent of total food weight (W) contributed by different types of prey consumed by walleye in Smith Mountain Lake, 1983-1984.

Location and Season	Walleye Examined	Walleye With Food (%)	Adult Alewife		Y-O-Y Alewife		Gizzard Shad		Crayfish		Unidentified Fish	
			N	W	N	W	N	W	N	W	N	W
Upper Lake												
Winter	11	73	0	0	0	0	98	97	0	0	3	3
Spring	30	30	43	51	53	43	2	4	0	0	2	1
Summer	26	46	73	90	18	8	0	0	2	T ^a	8	2
Fall	21	14	0	0	0	0	100	100	0	0	0	0
Total	88											
Lower Lake												
Winter	5	0										
Spring	240	10	78	91	15	6	0	0	0	0	7	4
Summer	113	33	58	78	28	19	1	1	0	0	13	2
Fall	12	8	100	100	0	0	0	0	0	0	0	0
Total	370											

^a T = <0.05

spring, adult and underyearling alewives were almost equally prevalent in the diet (43% and 53%, respectively) of walleye collected in the upper lake. However, adult alewives appeared approximately five times more frequently than young-of-year alewives in stomachs of walleye from the lower reservoir during this period. In the fall, three walleye stomachs collected in the upper lake contained only gizzard shad, whereas the one stomach collected in the lower lake contained only alewives.

Clupeids and, to a lesser extent, crayfish (Orconectes spp.) were the major, identifiable food items in smallmouth bass stomachs (Table 1.5). Gizzard shad comprised 13% of prey items and 22% of stomach contents by weight; comparable values for adult alewives were 10% and 26%, 20% and 8% for young-of-year alewives, and 11% and 9% for crayfish, respectively. Unidentified fish, mostly clupeids, comprised 30% of prey items and 26% of total food weight. Relatively infrequent diet items included sunfish (Lepomis spp.), minnows (Notropis spp.), catfish (Ictalurus spp.), darters (Etheostoma sp.) and insects (Chironomidae, Odonata, and Orthoptera).

Smallmouth bass consumed comparable numbers of adult alewives (18%) and gizzard shad (16%) in spring. Although young-of-year alewives appeared infrequently in the spring diet, they were the dominant, identifiable prey item by number (31%) in the summer diet of smallmouth bass. Crayfish were a consistent food item but were most important in fall, when they comprised 34% of stomach contents by weight. Sunfish were relatively unimportant in the diet over all seasons.

Table 1.5. Percent of total number of prey items (N) and percent of total food weight (W) contributed by different types of prey consumed by smallmouth bass in Smith Mountain Lake, 1983-1984. Smallmouth bass were collected only in the lower lake.

Location and Season	Smallmouth Examined	With Food (%)	Adult Alewife		Y-O-Y Alewife		Gizzard Shad		Crayfish		Sunfish		Unidentified Fish		Miscellaneous	
			N	W	N	W	N	W	N	W	N	W	N	W	N	W
Lower Lake																
Winter	4	0														
Spring	73	37	18	38	5	6	16	20	11	6	8	7	24	18	19	5
Summer	83	40	6	17	31	12	9	24	7	7	0	0	36	37	11	4
Fall	27	48	6	3	18	6	18	22	24	34	6	12	24	22	6	1
Total	187															

Predator-Prey Length Relationships

The relationship between size of predator and size of alewives consumed was poor for striped bass and nonexistent for walleye. Small striped bass (150-200 mm TL) ate alewives that were 45-110 mm TL, a size range also frequently consumed by large striped bass 700-800 mm TL (Fig. 1.1). Although striped bass less than 250 mm TL consumed alewives greater than the largest size suggested by Jenkins and Morais (1978), striped bass with lengths greater than 250 mm did not. Alewives between 60 and 150 mm TL were consumed by walleye (Fig. 1.2), with nearly all below the maximum size predicted by the modified equation of Jenkins and Morais (1978). Too few alewives in black bass stomachs; i.e., fewer than 35 for each species, precluded a comparison between consumed alewives and total lengths of black bass.

Predators in Smith Mountain Lake generally consumed alewives from April through December, 1983 and 1984. However, a decrease in the mean size (TL) of alewives in predator stomachs, collectively, was found from August to October as abundant young-of-year alewives reached sufficient size to be eaten (Fig. 1.3).

Predators consumed young-of-year gizzard shad almost exclusively; only four shad age 1 or older were found in striped bass and largemouth bass stomachs. As with alewives, there was a weak or no linear relationship between consumed shad TL and predator TL. Smaller striped bass (< 300 mm TL) generally consumed gizzard shad less than 50% of striped bass TL, whereas larger striped bass consumed shad that averaged 20% of body length (Fig. 1.4).

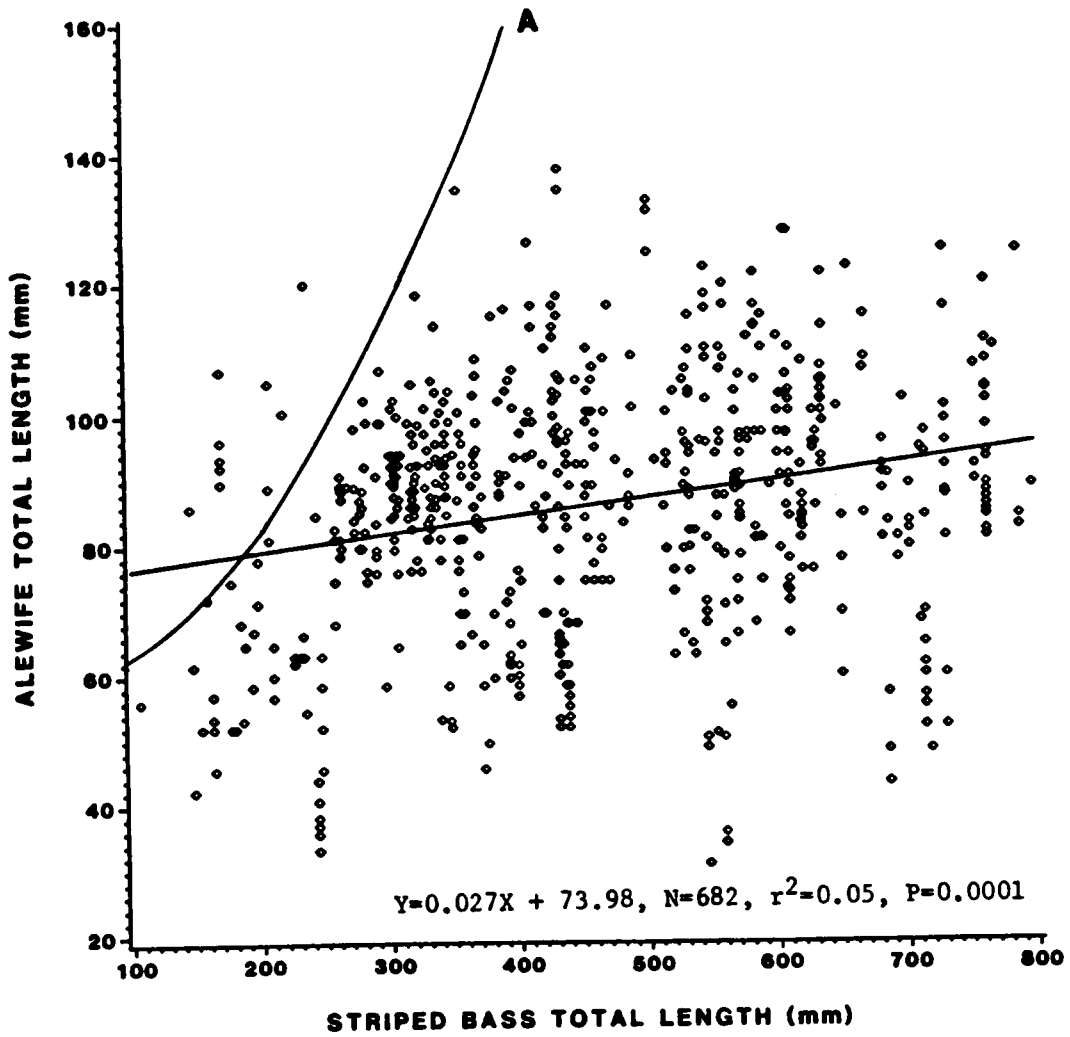


Figure 1.1. Relationship between sizes of alewives consumed and sizes of striped bass. The upper line (A) represents the estimated lengths of alewives a striped bass could consume based on the calculations of Jenkins and Morais (1978).

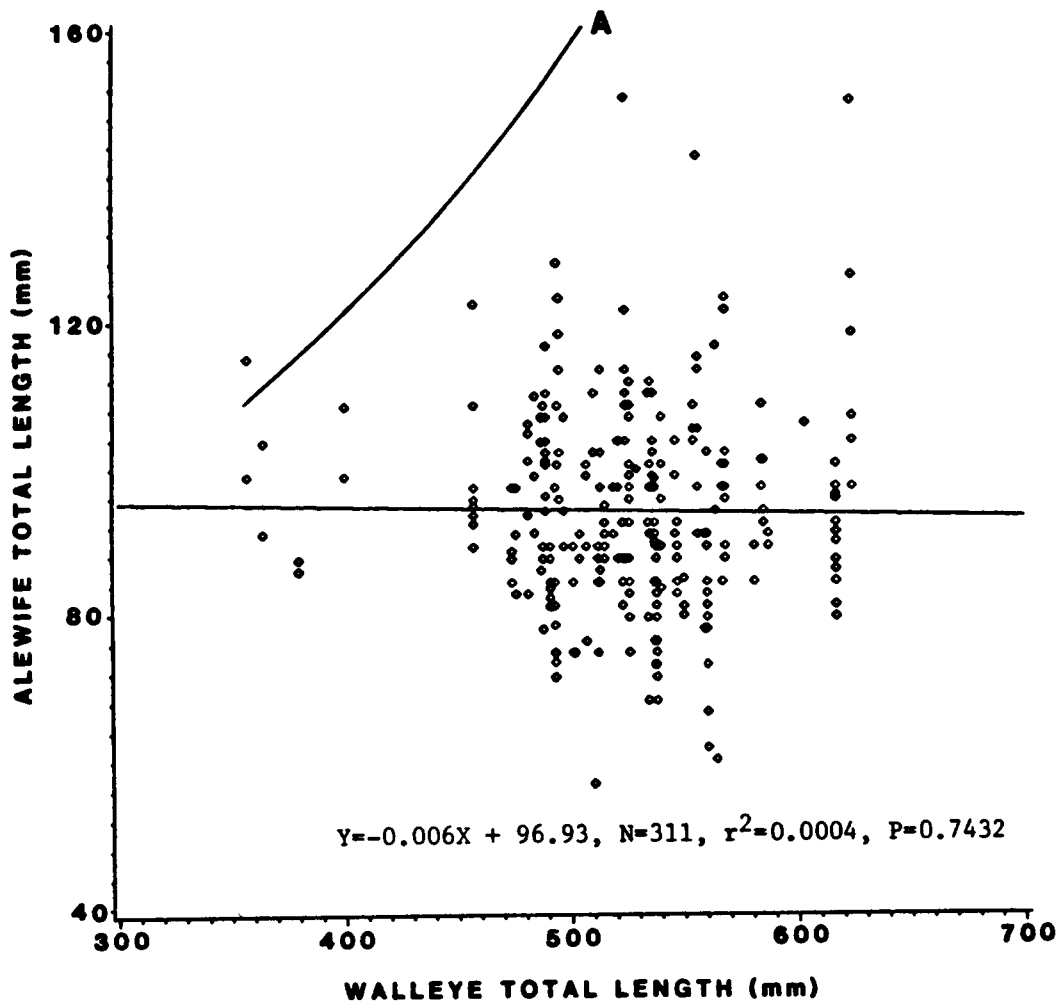


Figure 1.2 Relationship between sizes of alewives consumed and sizes of walleye. The upper line (A) represents the estimated lengths of alewives a walleye could consume based on the calculations of Jenkins and Morais (1978).

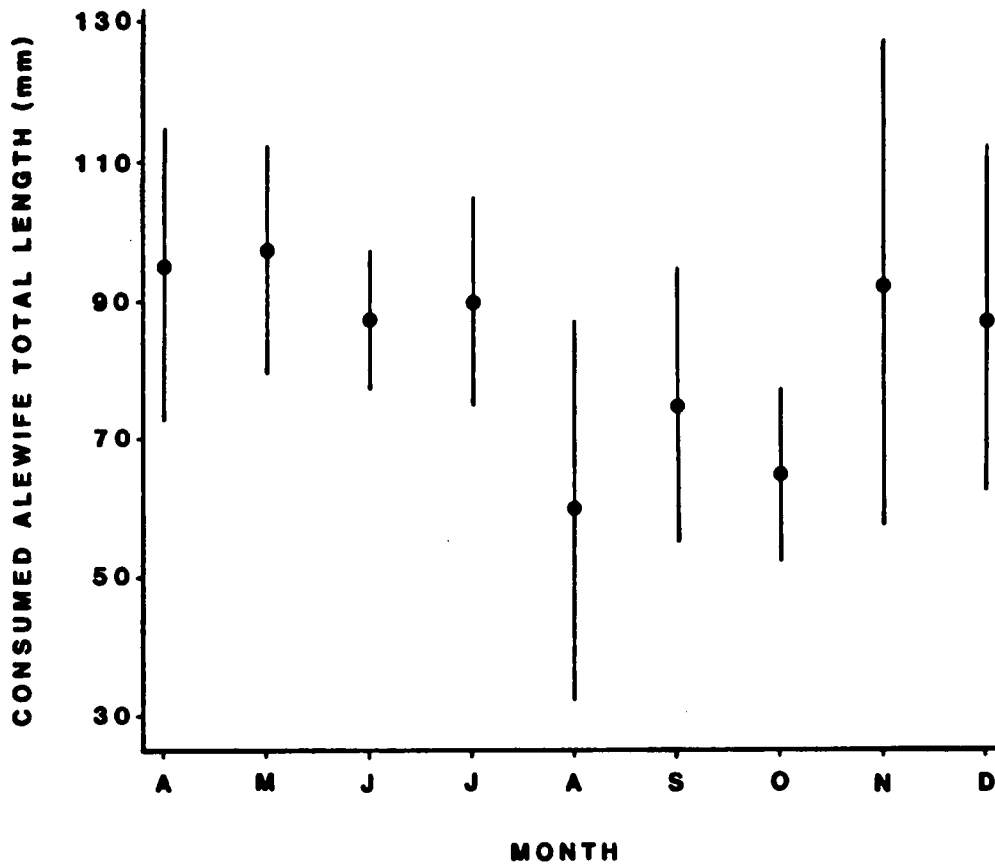


Figure 1.3. Mean lengths (± 1 SD) of alewives in stomachs of all four predatory species from Smith Mountain Lake, April-December, 1983 and 1984.

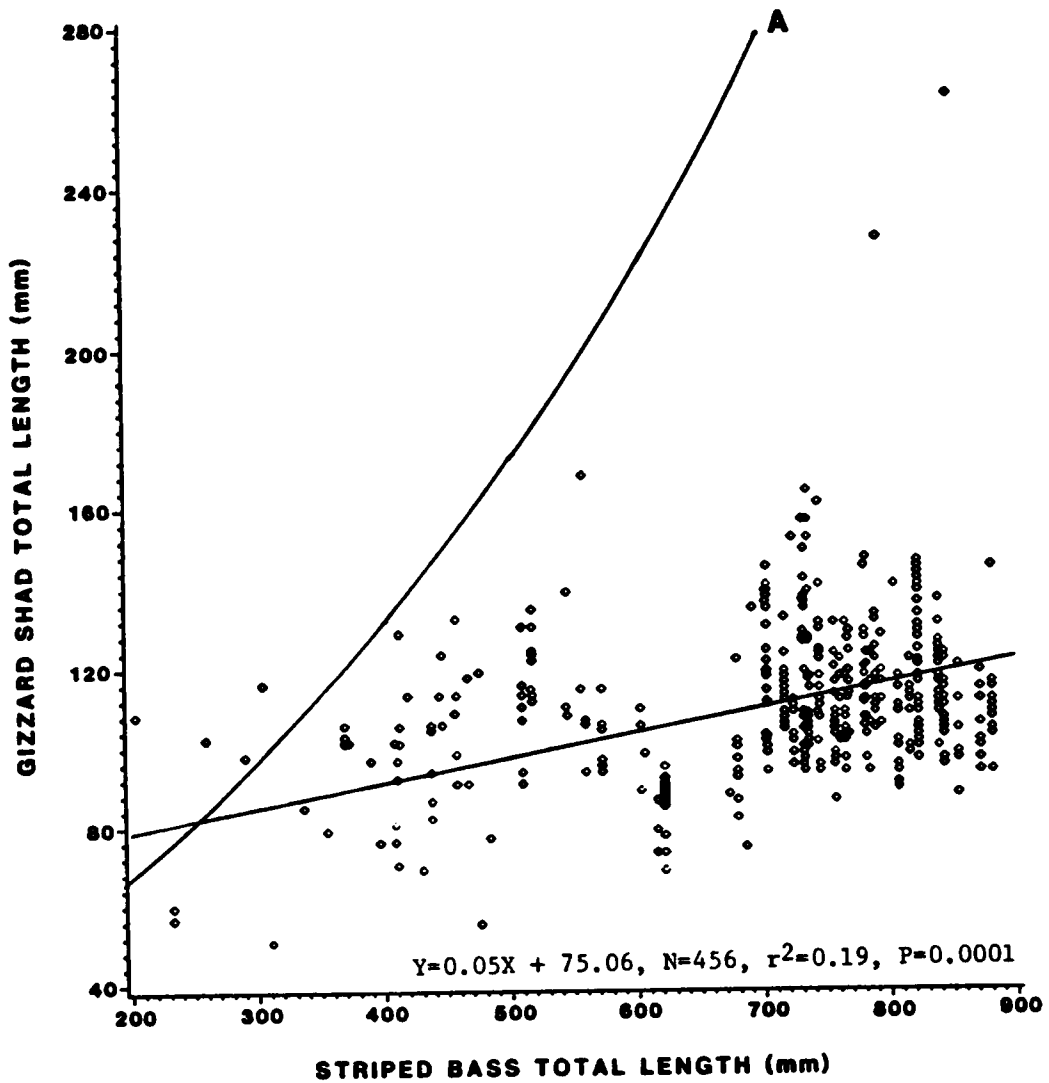


Figure 1.4. Relationship between sizes of gizzard shad consumed and sizes of striped bass. The upper line (A) represents the estimated lengths of gizzard shad a striped bass could consume based on the calculations of Jenkins and Morais (1978).

Striped bass smaller than approximately 300 mm TL consumed shad larger than predicted, and larger striped bass generally consumed shad much smaller than predicted by Jenkins and Morais (1978). Largemouth bass, 100 to 500 mm TL, ate gizzard shad principally between 50 and 150 mm TL (Fig. 1.5), whereas walleye consumed shad between 95 and 145 mm TL (Fig. 1.6). Although the maximum prey sizes suggested by Jenkins and Morais (1978) agreed well with empirical observations for largemouth bass, walleyes consumed some shad larger than predicted. The 14 gizzard shad in smallmouth bass stomachs were less than 50% of smallmouth bass TL.

Diet Overlap

Several seasonal samples contained less than the minimum number of stomachs necessary to adequately characterize the diet, thus precluding some calculations of diet overlap (Table 1.6). Diet overlap indices over 0.6, which may indicate interactions between predator populations (Zaret and Rand 1971), occurred between striped bass and walleye, as well as between the black basses in all seasons and locations where adequate stomach samples were available for comparison (Table 1.7). The largest diet overlap value, 0.98, occurred between striped bass and walleye, both of which consumed gizzard shad almost exclusively in the upper reservoir during winter. Diet overlap in winter between largemouth bass and the pelagic predators from the upper reservoir was insignificant due to consumption of crayfish by largemouth bass. The overlap value of 0.66, calculated for striped bass and smallmouth bass in the lower reservoir in spring, was considered spurious due to small sample size (Smith 1985).

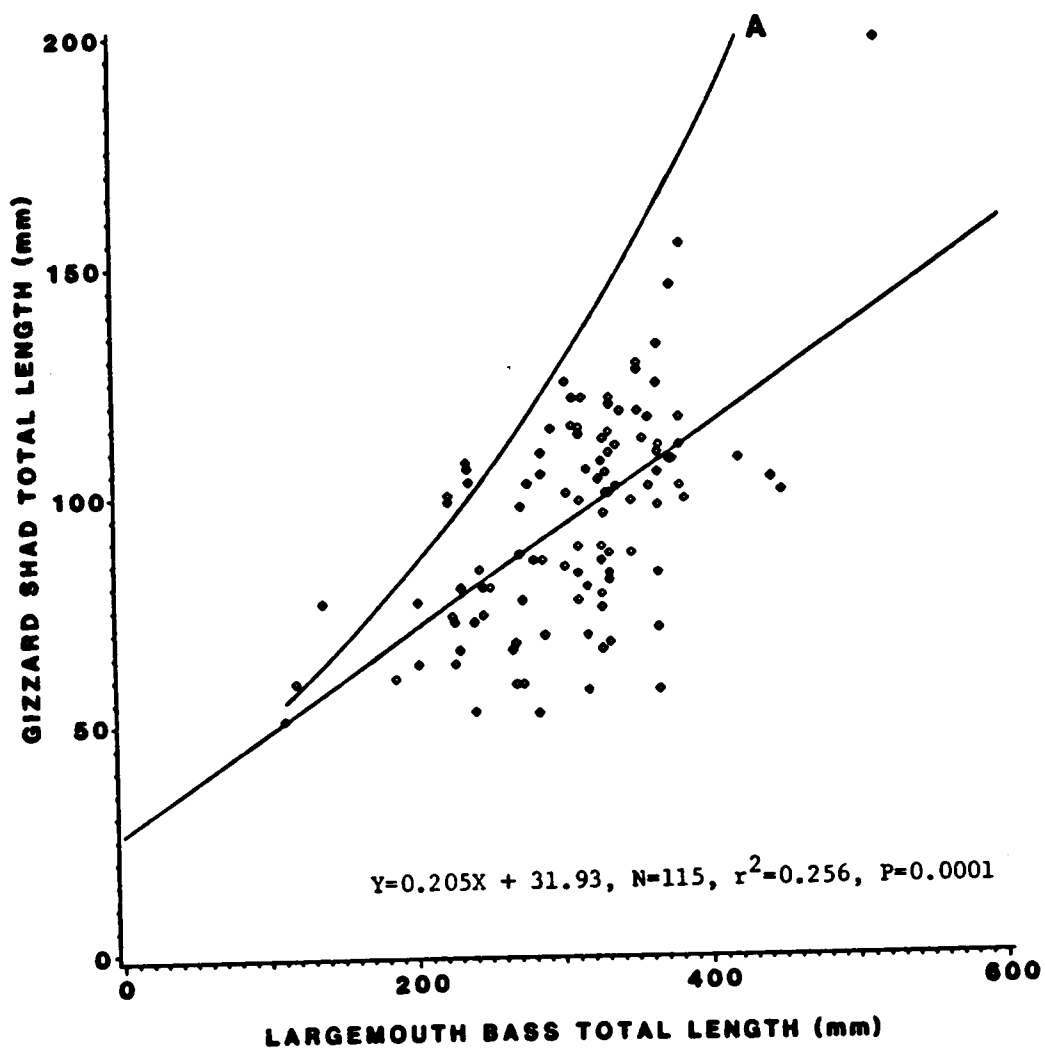


Figure 1.5. Relationship between sizes of gizzard shad consumed and sizes of largemouth bass. The upper line (A) represents the estimated lengths of gizzard shad a largemouth bass could consume based on the calculations of Jenkins and Morais (1978).

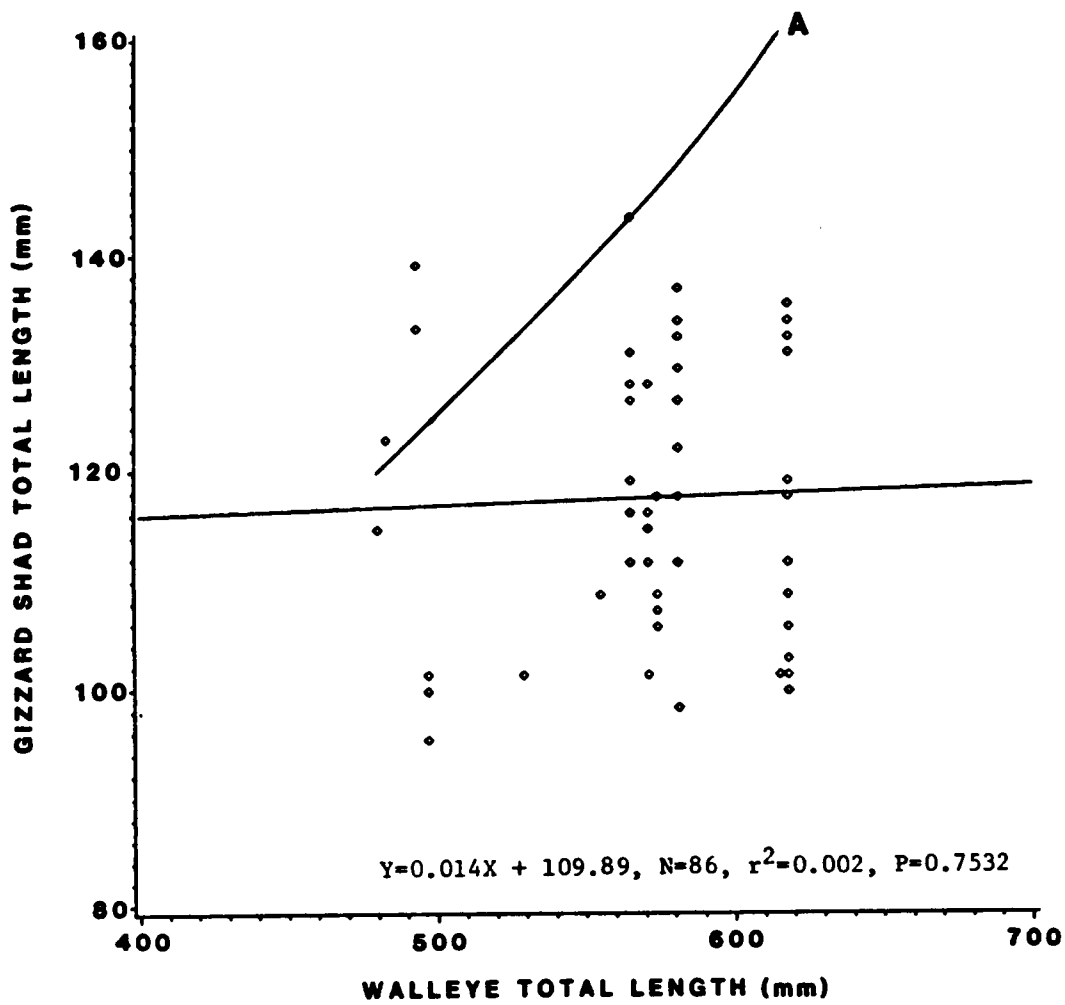


Figure 1.6. Relationship between sizes of gizzard shad consumed and sizes of walleye. The upper line (A) represents the estimated lengths of gizzard shad a walleye could consume based on the calculations of Jenkins and Morais (1978).

Table 1.6. The minimum number of predator stomachs necessary to adequately characterize diets as determined by cumulative prey species curves (Brodeur and Pearcy 1984).

Species	Upper Lake			Lower Lake				
	Winter	Spring	Summer	Fall	Winter	Spring	Summer	Fall
Striped bass	10	12	15	16	*	64	41	10
Largemouth bass	4	28	57	17	*	31	4	*
Smallmouth bass	*	*	*	*	*	13	16	8
Walleye	3	4	7	*	*	14	10	*

* Samples inadequate for determination of minimum sample size.

Table 1.7. Diet overlap values for predators in Smith Mountain Lake, calculated by location and season (W=winter, S=spring, Su=summer, F=fall). Only seasonal samples that exceeded the minimum number of stomachs necessary to adequately characterize the predator diets (as determined by cumulative prey species curves) were used.

Species	Upper Lake				Lower Lake			
	W	S	Su	F	W	S	Su	F
Striped bass x Largemouth bass	.50	.27	.25	.51	-	.42	.42	-
Striped bass x Walleye	.92	.79	.86	-	-	.73	.75	-
Striped bass x Smallmouth bass	-	-	-	-	-	.53	.51	.66
Largemouth bass x Smallmouth bass	-	-	-	-	-	.77	.79	-
Largemouth bass x Walleye	.56	.18	.15	-	-	.34	.26	-
Walleye x Smallmouth bass	-	-	-	-	-	.49	.36	-

Discussion

Predator Food Habits

In general, food habits of striped bass in Smith Mountain Lake agreed with diet data collected for striped bass in other impoundments. Gizzard shad, seasonally predominant in the diet of striped bass in Smith Mountain Lake, were consumed by striped bass in other reservoirs (Stevens 1958, Ware 1974, Morris and Follis 1978, Combs 1978, Matthews and Hill 1982, Lewis 1983, Filepek and Tommey 1984, Harper and Namminga 1986). Utilization of alewives (Kohler and Ney 1981) and infrequent consumption of crayfish by landlocked striped bass (Hepworth et al. 1977, Combs 1978) have also been previously reported.

The importance of gizzard shad as a forage item for largemouth bass has also been documented in other reservoirs (Aggus 1973, Lewis et al. 1974, Pasch 1975, Timmons et al. 1981, Adams et al. 1982a, Carline et al. 1984, Storck 1986). Seasonal patterns in the utilization of sunfish and crayfish by largemouth bass in Smith Mountain Lake substantiate Aggus (1973), who found that these prey items were not frequently utilized when shad were abundant.

Clupeids, the only identifiable piscine prey in walleye stomachs collected from Smith Mountain Lake, were eaten almost exclusively by walleye in other reservoirs (Dendy 1946, Jester 1971, Boaze and Lackey 1974, Momot et al. 1977, Fitz and Holbrook 1978, Kohler and Ney 1981). In addition, food habits of smallmouth bass in Smith Mountain Lake were

similar to those previously described for smallmouth bass in other impoundments (Dendy 1946, Applegate et al. 1966, Mullan and Applegate 1967, 1970, Aggus 1973, Hubert 1977).

Stomach content analysis did indicate some cannibalistic behavior in largemouth bass. A low incidence of cannibalism has been documented for this species when other potential prey items are abundant (Applegate et al. 1966, Mullan and Applegate 1970, Miller and Kramer 1971, Hubert 1977, Timmons et al. 1981). However, it appears that introduced predators did not directly influence native predators through predation in Smith Mountain Lake; i.e., no black bass were found in striped bass or walleye stomachs. Relatively low consumption of non-clupeid fish and gamefish has been previously reported for striped bass (Stevens 1958, Ware 1970, Combs 1978, Matthews and Hill 1982) and walleye (Colby et al. 1979) in other impoundments. Although there was no evidence to indicate that stocked fingerlings were eaten by black bass, it is possible that largemouth bass and smallmouth bass may eat striped bass fingerlings in Smith Mountain Lake. Kohler et al. (1986) determined that young pelagic predators were occasionally eaten by littoral predators in Claytor Lake, Virginia.

Alewives and gizzard shad were the predominant food items consumed by predators in Smith Mountain Lake. Distributional similarities between predators and their clupeid prey may explain the documented patterns of resource utilization by predators. Alewives are pelagic and tend to inhabit the broad, deeper waters characteristic of the lower reservoir (Ney et al. 1982), whereas gizzard shad tend to remain in the upper more

riverine portion of the lake (Rainwater and Houser 1982). A concurrent study in Smith Mountain Lake indicated a complete segregation of spawning areas for the two species; larval gizzard shad were found only in the upper lake and larval alewives only in the lower lake (Tisa et al. 1985). This spatial segregation of clupeids was also evident in the contents of predator stomachs. Stomachs collected in and above Beaverdam Creek in the upper portion of Smith Mountain Lake did not contain alewives, whereas those collected below the confluence of the Blackwater and Roanoke Rivers did not contain gizzard shad.

It's probable that the distribution of predators and the availability of prey in Smith Mountain Lake is influenced by temperature. Because striped bass prefer water temperatures between 18 - 25⁰C, they concentrate in the deeper portions of reservoirs during late spring and summer (Combs and Peltz 1982). Gizzard shad, especially young-of-year, are generally found in the warmest available water (Jester and Jensen 1972). In Smith Mountain Lake, water temperatures can exceed 30⁰C, with higher temperatures in surface waters and the shallower, upper portions of the reservoir (Virginia State Water Control Board 1980). Because temperatures exceeded the thermal preference of striped bass, it's possible that striped bass were thermally isolated from young-of-year shad (Coutant and Carroll 1980). This would explain the relatively low utilization of this prey item by striped bass during the late spring/summer period. Predator-prey interactions involving walleye may be similarly determined by thermal constraints. Momot et al. (1977) determined that gizzard shad in Hoover Reservoir, Ohio, were underutilized during summer because they

occurred at water temperatures far above 20 - 22⁰C, the preferred temperature of walleye. Because alewives tend to congregate in deep, coolwater areas, striped bass and walleye may simply have encountered this prey species most frequently. This temperature hypothesis would explain the dominance of alewives in the diet of striped bass and walleye in these seasons.

The pelagic nature of alewives probably accounts for their relatively low consumption by littoral-dwelling black bass. Range (1973) determined that black bass were not able to utilize abundant threadfin populations in Dale Hollow Reservoir, Tennessee, because of the pelagic nature of these shad. Infrequent consumption of alewives by largemouth bass has also been documented in other reservoirs (McGaig 1980, Kohler and Ney 1981, Lewis 1981, Daniel 1984). However, alewives were utilized more frequently by smallmouth bass than by largemouth bass in Smith Mountain Lake. Greater utilization of alewives by smallmouth bass, as compared to largemouth bass, probably occurs because of the mutual preference of smallmouth bass and alewives for the lower lake habitat.

Adult alewives appeared most frequently in stomachs of both largemouth bass and smallmouth bass collected in the spring. Kohler and Ney (1981) reported that alewives were of minor importance to black basses in Claytor Lake, but they were the major prey of these predators during spring. Inshore spawning habits of alewives during this season may account for this seasonal predation (Wagner 1972).

Gizzard shad were frequently consumed by predators in late summer and fall when young-of-year shad were at peak abundance. Declining water

temperatures in the fall, which eliminated upper temperature restrictions to striped bass movement, together with young-of-year shad abundance, may account for the greater consumption of gizzard shad by striped bass in autumn. Consumption of shad by walleye in the fall may occur in a similar manner. Stomachs of three walleye from the upper reservoir during this season contained only gizzard shad. Greater utilization of gizzard shad by largemouth bass, relative to smallmouth bass, is likely due to a mutual preference by gizzard shad and largemouth bass for the upper portion of the reservoir.

Gizzard shad dominated the winter diets of striped bass, walleye, and largemouth bass in the upper reservoir. Underyearling shad were observed to congregate in the upper Roanoke River arm of the reservoir during winter, where the majority of these predators were captured. The presence of abundant shad in this area may have triggered the seasonal, uplake movement of pelagic piscivores. It is also possible that mature striped bass (age 2 and older for males, age 4 and older for females) migrate uplake in preparation for spring spawning activity; co-occurrence of striped bass and shad may be coincidental. In fact, most of the striped bass collected in this area during winter were older than age 4; none were less than age 3.

In addition to patterns of distribution, seasonal changes in food habits of predators may also reflect differences in abundance and morphological availability of the two clupeids. Annually, alewives were consumed more frequently than gizzard shad by both striped bass and walleye. The greater frequency of alewives in the diet of these predators

may simply reflect greater numerical abundance of this clupeid. Although estimates of gizzard shad standing stocks in Smith Mountain Lake are available from cove rotenone samples, estimates of alewife biomass from rotenone samples are unreliable due to the pelagic nature of this clupeid. Hart (1978) and LaRoche (1981) assumed that the gizzard shad was the dominant forage species in the lake. Because of possible interspecific interactions, a reproductive failure of gizzard shad in 1978 (LaRoche 1981) may have allowed the alewife population to increase. When threadfin shad (D. petenense) were stocked in waters containing gizzard shad, they partly displaced them (Noble 1981). Alewives may have demonstrated similar displacement capabilities in Smith Mountain Lake.

Striped bass and walleye consumed adult alewives more frequently than young-of-year alewives in summer throughout the reservoir and in spring in the lower lake. The dominance of underyearling alewives in the diets of walleye in the upper reservoir during spring relates to the transitional size of these alewives; young-of-year are 11 months old. The greater consumption of adults or near adults is largely due to the absence of available young-of-year alewives during spring and summer. However, Wagner (1972) reported that larger walleyes in Lake Erie generally preferred larger prey. He found that although large numbers of young-of-year alewives were present in summer, they were not readily eaten because of their small size. The walleye population in Smith Mountain Lake consists principally of individuals greater than 400 mm TL. No walleye have been stocked since 1979, and only nominal natural reproduction has occurred (D. Whitehurst pers. comm.) Few alewives less than

60 mm TL were found in walleye stomachs; the greater proportion of consumed alewives were larger than 80 mm TL. Conversely, a large portion of alewives consumed by striped bass were less than 80 mm TL, and most size classes of alewives were consumed by a wide size range of striped bass.

Although predators consumed several age classes of alewives, older gizzard shad were insignificant in all predators' diets. Most of the larger predators, especially striped bass, were collected during periods of the year when young-of-year shad were abundant. It is possible that large predators may utilize older shad during periods when young-of-year shad are not available. However, Lewis (1983) found that although the distribution of adult gizzard shad and large striped bass (> 400 mm TL) overlapped, striped bass did not consume these larger shad in Lake Norman, North Carolina. The general absence of larger, older shad in the diet of striped bass in Smith Mountain Lake could reflect a preference for smaller, young-of-year shad, even by large predators morphologically capable of consuming larger shad.

Gizzard shad were eaten by piscivores, except walleye, in the spring before warming water temperatures accelerated shad growth beyond the point where they were morphologically available for smaller sizes of predators. If striped bass are capable of consuming prey equal to 60% of their body length (Manooch 1973), young-of-year striped bass (<180 mm TL) could consume gizzard shad up to 108 mm TL. Only 7% of the gizzard shad collected by electroshocking in early March 1985 were of this size or smaller. Similarly, based on this March collection and using the

calculations of Lawrence (1958), no gizzard shad would be available for smaller, young-of-year black basses. Knight et al. (1984) observed that young-of-year gizzard shad in Lake Erie outgrew vulnerability to most older walleyes by spring of the following year.

Winter mortality of young-of-year alewives and gizzard shad (Storck 1986), in conjunction with rapid spring growth of these species, may account for the greater variety of food items in striped bass, largemouth bass, and smallmouth bass stomachs during spring and early summer. An increase in the diversity of food items in predator stomachs in Smith Mountain Lake substantiates studies that indicate the diet breadth of predators typically increases as prey availability decreases (Ivlev 1961, Werner and Hall 1974).

Predator-Prey Length Relationships

In general, there was a better linear relationship between TL of consumed gizzard shad and striped bass TL than alewife and striped bass TL. This is indicative of the fact that gizzard shad can rapidly outgrow their vulnerability to smaller striped bass (and probably other predators as well), and furthermore relates to the greater morphological availability of alewives to all sizes of predators in Smith Mountain Lake. Regression slopes for clupeid-walleye relationships did not differ from zero ($p > 0.05$) largely due to the narrow size range of available walleye. The lack of smaller walleye in samples negated the possibility of observing any trends with increasing predator size.

The maximum sizes of shad available to largemouth bass, as determined by the equations of Jenkins and Morais (1978), agreed well with empirical observations for largemouth bass in Smith Mountain Lake, but not for striped bass or walleye. Striped bass less than 300 mm TL consumed shad significantly larger than predicted, as did some walleye. In addition, the values predicted by the equations of Jenkins and Morais (1978) did not agree well with maximum lengths of alewives consumed by smaller striped bass.

The equations relating maximum ingestible prey to predator size form the basis of available prey/predator (AP/P) ratios. The deviation of empirical data from predicted maximum lengths, especially for alewives, indicates that significant error may occur when AP/P ratios are used by fisheries managers to measure the adequacy of a reservoir's forage base to sustain predator populations. Alternatively, AP/P ratios could be based on a measure of relative prey size as determined from empirical data. Body length relationships between consumed clupeids and predators in Smith Mountain Lake were similar to those reported by Popova (1966), who found that young predators generally fed on piscine prey 40-50% of predator body length, whereas older adult predators consumed fish 10-25% of body length. Previous studies of striped bass (Manooch 1973), largemouth bass (Lawrence 1958, Wright 1970), walleye (Knight et al. 1984), and smallmouth bass (Probst et al. 1984) have found relative prey size relationships similar to those observed in Smith Mountain Lake.

Diet Overlap

Diet overlap analysis indicated competitive interactions could occur between striped bass and walleye as well as between largemouth bass and smallmouth bass in Smith Mountain Lake. Conversely, the introduced predators were less likely to compete for food with the native black bass. Greater use of non-clupeid fish and crayfish by black basses minimized diet overlap between walleye and black basses or striped bass and black basses in Smith Mountain Lake. Fedoruk (1966) and Johnson and Hale (1977) found no competitive interactions for food between walleye and smallmouth bass in northern lakes because of the preference of each predator for different prey items -- smallmouth bass for crayfish, walleye for fish. Similarly, Gilliland and Clady (1981) found no significant overlap in food habits between Morone hybrids and native largemouth bass in Sooner Lake, Oklahoma.

In addition, assuming predator collections are indicative of habitat preferences, it appears that predators are, in general, segregated by habitat in Smith Mountain Lake, limiting interactions between potentially competitive species (Larkin 1956, Schoener 1974). Thus, although diet overlap occurred between largemouth and smallmouth bass collected in the lower reservoir, potential negative interactions between these species were limited because of the differential distribution of each; largemouth bass resided in the upper reservoir, and smallmouth bass in the lower reservoir. Similarly, striped bass were more widely distributed in the reservoir, over a yearly period, whereas walleye were generally found in the lower reservoir in association with steep, rocky, shorelines.

Conclusion

Distributional similarities between predators and their clupeid prey, coupled with the seasonality of clupeid abundance and constraints of morphology, may explain the patterns of resource utilization documented for predators in Smith Mountain Lake. Based on Schoener's (1970) diet overlap index, these food resources were effectively partitioned between introduced and resident predators in Smith Mountain Lake in 1983-84. Although an assessment of competitive interactions requires a quantitative assessment of prey abundance and predator demand, it appears that interspecific competition for food would not occur between these groups of predators. However, the reliance of predators on the clupeid forage in Smith Mountain Lake indicates that a significant decrease in clupeid biomass, especially young-of-year, could have a significant impact on competitive interaction and ultimately on predator production. Swenson and Smith (1976) reported interspecific competition for food between walleye and sauger (Stizostedion canadense) during early summer when forage availability was low. Similarly, following a massive die-off of alewives (the only resident clupeid) in Claytor Lake, pelagic predators switched to an alternate diet of spiny-rayed fish and crayfish, the predominant food items of littoral, black basses (Kohler and Ney 1981). In Smith Mountain Lake, reduced food availability, following the reproductive failure of gizzard shad in 1978, may have resulted in intense competition among striped bass, walleye and black basses for the remaining available prey. In addition, although there was no evidence to indicate

that striped bass or walleye ate largemouth bass or smallmouth bass in Smith Mountain Lake, or that black bass fed on stocked fingerlings, a decline in the forage base may have intensified negative interactions between predators by increasing the incidence of interspecific predation.

Although sample sizes were too small to compare resource utilization within predator groups, scatter plots comparing lengths of clupeids consumed to predator lengths indicate several age classes ate similar-sized prey. This is particularly evident for striped bass. Because of increased stocking levels of fingerlings, a ten-fold increase from the early 1970's to the early 1980's, many large year-classes of striped bass may compete for clupeids during years of low clupeid abundance. Competitive interactions within the striped bass population therefore may partly explain the decline in growth rates and condition factors observed for these predators in Smith Mountain Lake since the mid-1970's.

CHAPTER II

Population Size and Survival of Predators in Smith Mountain Lake, Virginia

Introduction

An accurate population estimate of sport fish species is perhaps the greatest challenge for fisheries managers attempting to develop quantitative management plans. This problem is amplified in large, southern reservoirs where the recreational fisheries are typically complex and consist of resident game species as well as introduced sport fish. Population estimates and associated mortality rates for black basses, the dominant game species in southern reservoirs, have typically involved electrofishing, mark and recapture techniques, and/or creel surveys (Hanson 1962, Cole 1966, Bryant and Houser 1971, Aggus and Rainwater 1975, Hickman and Hevel 1975, Ager 1978, Yeager and Van Den Avyle 1978, Harris et al. 1979, Dewey and Moen 1981, Farman et al. 1982, Dent 1986). Black bass standing stocks have been estimated in a number of southern reservoirs (Jenkins and Morais 1978), but these data have generally not been used to determine population statistics.

Although striped bass fisheries have developed in a large number of southern reservoirs over the last decade, population dynamics of striped bass in freshwater impoundments are poorly defined (Axon and Whitehurst

1985). Van den Avyle and Higginbotham (1979) developed a relative annual mortality index to evaluate the effect of stocking density on survival of striped bass in Tennessee reservoirs. Similarly, Combs (1980) used the relative abundance of seined, striped bass fingerlings as an index of future year-class strength in Keystone Reservoir, Oklahoma. However, no study has adequately determined survival of stocked striped bass fingerlings or the contribution of these stocked cohorts to the future fishable population. In general, success of striped bass stocking has been defined in qualitative rather than quantitative terms (Bailey 1974, Hanson and Dillard 1976).

Population dynamics of walleye, another introduced predator in southeastern reservoirs, are also poorly understood. However, a number of studies have estimated mortality rates and population sizes for walleye in northern, temperate lakes and reservoirs (Colby et al. 1979).

Data on the population dynamics of predators in reservoirs, especially pelagic striped bass and walleye, have been limited due to the lack of funding and manpower necessary to obtain adequately a large, random sample of the population. However, reservoir biologists routinely collect data for purposes other than population estimation that, in the absence of directed studies, can be combined with other information to give some indication of predator population size and structure.

As part of a study investigating the trophic relationships of the major piscine predators in Smith Mountain Lake, Virginia, I determined the size and age structure of four predator populations; largemouth bass, smallmouth bass, striped bass, and walleye, that coexist in the lake.

Specifically, age-specific survival rates and population estimates were derived using a compilation of data collected by the Virginia Department of Game and Inland Fisheries (VDGIF), sampling statistics from this study, and population statistics obtained from the literature.

Methods

Black Basses

The VDGIF conducted yearly cove rotenone sampling in Smith Mountain Lake from 1979 to 1983. Four coves were sampled in August of each year using standard cove rotenone procedures (La Roche 1981, Whitehurst 1985). Because black bass are littoral, estimates of standing stock can be derived by cove rotenone technique (Table 2.1).

Yearly standing stock estimates were multiplied by 8337 ha (the surface area of Smith Mountain Lake) to derive whole-lake biomass estimates for each species. Numbers-at-age were then obtained from these total biomass estimates (TB) using the following formula:

$$N_x = \frac{F_x \times TB}{W_x \times 0.8 \times C} \quad (1)$$

where N_x = total number of black bass in each age group x , F_x = frequency (by % weight) of age group x in cove samples, and W_x = mean weight of age group x . The value of 0.8 represents a correction factor for non-recovery of tagged fish in cove rotenones and is the mean of values reported by Whitehurst (1985). The correction factor (C) to adjust for cove/open water ratios was assigned a value of 2.8 for age-0 fish, 1.3 for age-1

Table 2.1. Estimates of mean standing stocks (kg/ha) of largemouth bass and smallmouth bass in Smith Mountain Lake, 1979 to 1983, from cove rotenone sampling. Data are from Whitehurst (1985).

Year	Largemouth Bass	Smallmouth Bass
1979	9.7	0.7
1980	6.0	2.7
1981	5.7	1.4
1982	10.0	1.0
1983	10.2	1.2

fish, and 0.55 for age-2+ fish (Jenkins and Morais 1978, Hightower et al. 1982).

Length frequencies (by % weight) in rotenone samples were tabulated by size-class length (mm) increments. Lengths were assigned ages based on length-at-age data from VDGIF age and growth analysis of scales (La Roche 1981, Whitehurst 1985). Mean weights for age-0 black bass were obtained by dividing total weight of young-of-year individuals in cove samples by total number collected. Mean weights for age-1 and age-2 black bass were calculated using observed mean lengths in cove samples and length-weight relationships derived by the VDGIF (La Roche 1981, Whitehurst 1985)

Estimates of numbers-at-age were used to calculate annual survival (S) of age-0 and age-1 black bass using the following formulae:

$$z = -(\log_e N_{t+1} - \log_e N_t) \quad (2)$$

$$S = e^{-z} \quad (3)$$

where z =instantaneous rate of mortality and N_t =number of fish alive at time t . Specifically, mortality estimates were derived by following cohorts in successive years.

Cove rotenone data were not used to derive numbers of age 3 and older black bass because I felt these age classes were under-represented in August cove samples. Instead, survival estimates for age 2 and older black basses were calculated using age composition data obtained from spring and fall electrofishing samples. Although spring electrofishing samples may provide the most unbiased estimate of population age structure (Weithman et al. 1979), I included fall samples to increase sample size.

Dent (1986) concluded that age structure of largemouth bass collected in fall electrofishing samples was only slightly different than that of fish collected in the spring.

Shoreline electrofishing was conducted periodically in April, May, and November, 1983 and 1984, in both the upper and lower portions of the reservoir. A boom-type, boat-mounted electroshocker with pulsed D-C current was used for sampling. Bass were measured (TL to the nearest mm) and weighed (g), and scale samples were collected for age determination.

Survival of black bass was derived by standard catch curve analysis of age composition data (Ricker 1975), from 1983 and 1984 electrofishing samples combined. Age 2 was considered the age at first full recruitment to the electrofishing gear. Although this age was the most abundant in both the largemouth bass and smallmouth bass samples, this assumption was necessary to derive survival rates for age-2 fish. Survival was also calculated using the method of Robson and Chapman (1961):

$$S = \frac{T}{\sum N + T - 1} \quad (4)$$

where $T = N_1 + 2N_2 + 3N_3 + \dots + kN_k$, $\sum N = N_0 + N_1 + N_2 + \dots + N_k$, and N_k = number of age k fish. Survival rates for age 2 and older black basses were applied to population estimates of age-2 black basses in cove samples from 1979 to 1983 to derive the numbers of age 3 and 4 bass alive in 1983.

Striped bass

Gill nets were set annually in October, November, and December from 1974 to 1984 by the VDGIF to assess success of predator stocking (Hart 1978, La Roche 1981, Whitehurst 1985). Experimental, tri-panel gill nets

(137 x 2.5 m) with bar mesh sizes of 38, 64, and 102 mm were used from 1974 to 1979. Beginning in 1980, single panel gill nets of 38, 64, and 102 mm mesh were used. Yearly netting was standardized; nets were set the first week of each month at the same locations in the upper and lower reservoir. Catch per unit effort (CPUE) was reported as number of fish captured per m² of net mesh per sampling period; i.e., October, November, and December combined. Ages of fish captured in nets were determined by scale analysis.

Because stocking rates varied from year to year, yearly CPUE data for each age class were combined for the 11-year period (Robson and Chapman 1961, Ricker 1975). Instantaneous total mortality (and associated survival) was computed from a catch curve of these age composition data. Age 2 was considered the first age fully recruited to the gear. Survival rates were derived using the method of Robson and Chapman (1961).

Survival rates for age-1 striped bass were calculated using the CPUE data for successive years (i.e., survival of age-1 striped bass in 1979 to age 2 in 1980) and equations 2 and 3 above. The mean of these derived values was used as an estimate for age-1 striped bass survival in Smith Mountain Lake. Ricker (1975) indicated this method would avoid the difficulties caused by variable recruitment.

A daytime, roving creel survey was also conducted by the VDGIF from June, 1973 to July, 1976 (Hart 1978). In addition, aerial surveys were flown twice monthly from April, 1973 to December, 1976 to obtain an independent estimate of fishing pressure. Beginning in July, 1976 and ending December, 1977, the survey was changed to a point access type, and

a night survey was also conducted. The creel survey was designed by the Institute of Statistics at North Carolina State University to determine total fishing effort, total harvest, and average harvest rates of sport fish. Harvest data were used with the derived survival rates to estimate the number of striped bass present in 1983. Because population estimates incorporated results from the above analysis, the methodology involving the use of harvest data is presented in Results.

Walleye

Gill net catch data from the VDGIF were inadequate to calculate total mortality for walleye because: 1) the 1976 year class was absent; and 2) gill net CPUE for walleye was recorded only since 1979. Walleye fingerlings had been stocked from 1970 to 1974 and were again stocked in 1977, 1978, and 1979. No walleye have been stocked in Smith Mountain Lake since 1979.

Population estimates for walleye were derived from a synthesis of data presented in two previous studies. Chance (1958) calculated an average exploitation rate (u) of 0.232 for walleye caught over an 18-year period in Norris Reservoir, Tennessee. Assuming a Type I fishery (Ricker 1975), the calculated instantaneous rate of fishing mortality (F) from this exploitation rate is 0.264 ($u = 1 - e^{-F}$). Kempinger and Carline (1977) determined an average annual mortality (A) and exploitation rate of 0.47 and 0.28, respectively, for walleye in Escanaba Lake, Wisconsin. These values were used to calculate an instantaneous rate of natural mortality

(M) of 0.257 for walleye in Smith Mountain Lake using the following equations

$$u = \frac{F \times A}{Z} \quad (5)$$

$$Z = F + M \quad (6)$$

The calculated fishing mortality (0.264) and natural mortality (0.257) were combined to approximate a total annual mortality rate for age 2 and older walleye.

For lack of empirical data, I assumed that the mean survival rate of striped bass fingerlings to age 2 was applicable to stocked walleye fingerlings. Two-year survival rates were applied to the number of walleye stocked each year to estimate the number of walleye in Smith Mountain Lake in 1983.

I collected walleye in Smith Mountain Lake from April to December 1984 with experimental gill nets, 61 m long and 2 m deep. Nets consisted of panels with bar meshes of 38 to 76 mm and were fished overnight each week, from April to September. The presence of younger walleye (age 1-4) in gill net samples indicated that some natural reproduction or immigration had occurred after 1979. The relative proportion of each age group of walleye age 4 and less to age-5 walleye in 1984 gill net samples was multiplied by the estimated number of age-5 walleye present in 1984 to derive numbers-at-age for younger age groups; i.e., ages 1-4. I used the derived survival rate to back-calculate numbers within these age groups in 1983.

Results

Table 2.2 summarizes the estimated survival rates and data sources used to derive annual survival estimates for age 0 and older predators in Smith Mountain Lake.

From the analyses of the August 1979-83 cove rotenone data, the estimated number of largemouth bass in Smith Mountain Lake ranged from 228,014 to 1,238,797 for age 0, 109,705 to 400,658 for age 1, and 40,754 to 155,195 for age-2 fish during the 5-year period (Table 2.3). Mean annual survival estimates derived from these data were 53% and 29% for age-0 and age-1 largemouth bass, respectively. The calculated annual survival rates for age 2 and older largemouth from catch curve analysis was 37% ($N=264$, $z=-1.007$, $r^2=0.98$). The survival estimate based on the Robson-Chapman method was 39%. Although the Robson-Chapman method is less sensitive to variation in recruitment than catch curve analysis, it becomes more biased when several year classes are used (Ricker 1975). Thus, the average of these values, 38%, was used as an estimate of annual survival for largemouth bass age 2 and older. The total number of age 1 to 6 largemouth bass present in 1983 was 509,840 or approximately 61.2 bass per ha (Table 2.4). Most of these bass (77%) were age 1.

Numbers of smallmouth bass in Smith Mountain Lake, estimated from August rotenone samples, ranged from 23,477 to 203,894 for age-0 fish, 15,508 to 75,970 for age-1 fish, and 10,172 to 124,695 for age-2 fish during the years 1979 to 1983 (Table 2.5). Mean survival estimates for age-0 and age-1 smallmouth bass were 45% and 38%, respectively. Estimated survival values over 100%, which occurred for age-0 and age-1 fish in 1979

Table 2.2. Summary of annual survival estimates for age 0 and older predators in Smith Mountain Lake and the source used to derive the estimate.

Predator	Age	S	Data source
Largemouth bass	0	.53	VDGIF cove rotenone
	1	.29	VDGIF cove rotenone
	2-6	.38	Electrofishing
Smallmouth bass	0	.45	VDGIF cove rotenone
	1	.38	VDGIF cove rotenone
	2-6	.29	Electrofishing
Striped bass	0	.21	VDGIF gill net/ creel survey
	1	.40	VDGIF gill net
	2-10	.40	VDGIF gill net
Walleye	0	.083	Two-year survival age-0 striped bass (this study)
	2-8	.59	Chance (1958) and Kempinger and Carline (1977)

Table 2.3. Numbers of age-0 to 2 largemouth bass in Smith Mountain Lake, 1979-1983. Estimates were derived from cove rotenone sampling data obtained in August of each year.

Age	1979	1980	1981	1982	1983
0	228,014	863,867	383,670	988,623	1,238,797
1	400,658	109,705	256,913	364,665	391,312
2	155,195	96,515	40,754	85,217	71,729

Table 2.4. Estimates of the number of major fish predators, by species and age, in Smith Mountain Lake during 1983.

Age	Largemouth Bass	Smallmouth Bass	Striped Bass	Walleye
1	391,312	40,122	81,482	88 ^a
2	71,729	15,635	36,491	175 ^a
3	32,382	6,695	11,024	794 ^a
4	5,885	2,697	5,283	7,886
5	5,296	3,041	545	4,847
6	3,236	72	883	2,494 ^a
7			332	175 ^a
8			106	401 ^a
9			39	
10			42	
Total	509,840	68,262	136,227	16,860

^a Calculated from 1984 population estimate of walleye.

Table 2.5. Numbers of age 0 to 2 smallmouth bass in Smith Mountain Lake, 1979-1983. Estimates were derived from cove rotenone sampling data obtained in August of each year.

Age	1979	1980	1981	1982	1983
0	23,477	203,894	83,106	48,074	61,784
1	40,160	75,970	69,137	15,508	40,122
2	10,172	124,695	32,064	23,087	15,635

and age-1 fish in 1982, were discarded and not used in the mean survival estimates. Annual survival for older fish, determined from catch curve analysis, was 26% ($N=58$, $z=-1.337$, $r^2=0.88$), and the derived survival rate from the Robson-Chapman method was 31%. An annual survival rate of 29% was applied therefore to age 2 and older smallmouth bass in Smith Mountain Lake. I estimated that there were 68,262 ages 1 to 6 smallmouth bass (8.2 per ha) in Smith Mountain Lake in 1983. Age-1 fish were most abundant, comprising 59% of this total (Table 2.5).

Annual survival rates for age 2 and older striped bass, derived from the combined age composition data, were 39% (catch curve, $N=808$, $z=-.941$, $r^2=.98$) and 40.2% (Robson-Chapman method). Survival rates for age-1 striped bass ranged from 10.8% to 76.3% and averaged 39.9% for the 10-year period, 1973-1983 (Table 2.6). A value of 40% was used therefore as the estimate of mean annual survival for age 1 and older striped bass in Smith Mountain Lake.

Examination of creel survey data indicated that a total of 18,577 striped bass were harvested by anglers in 1977. Although the survey was initiated in 1973, 1977 was the only full year in which data were collected from both day and night anglers. The survey indicated almost equal numbers of striped bass caught during night and day. Creel data indicated that 33% of the striped bass harvested from 1973 to 1975 were age 4, the largest single age group of striped bass harvested by fishermen. Assuming the age composition of harvested fish for 1977 was the same for fish caught from 1973 to 1975, an estimated 6,130 age-4 striped bass ($0.33 \times 18,577$) were caught by anglers in 1977.

Table 2.6. Annual survival rates (%) for age 1 striped bass, computed from gill net CPUE data collected by the Virginia Department of Game and Inland Fisheries.

Year Interval	Annual Survival
1974-1975	10.8
1975-1976	33.3
1976-1977	38.3
1977-1978	75.2
1978-1979	26.1
1979-1980	110.5 ^a
1980-1981	45.1
1981-1982	14.1
1982-1983	76.3

^a This value was excluded from the calculation of mean survival for age 1 fish.

Since natural mortality of age-4 striped bass was probably low, I assumed that the estimated total mortality rate of 60% equaled an exploitation rate. Thus, the total number of age-4 striped bass in 1977 would be 10,217 (6130/0.6). Using this cohort size, the 40% annual survival estimate for age 1 and older striped bass, and the actual number of fingerlings stocked in 1973 (293,295), the estimated annual survival rate for fingerlings stocked in 1973 was 54.3%.

To determine survival (S) of fingerlings stocked each year from 1974 to 1983, I used the following formulae:

$$N_x = C_x \times \frac{159,644}{0.296} \quad (7)$$

$$S = \frac{N_x}{(D_{x-1})} \quad (8)$$

where 159,644 is the calculated number of age-1 striped bass in 1974 (0.543 x 293,295), 0.296 is the CPUE of age-1 striped bass in 1974, C_x = the CPUE of age-1 striped bass in year x, N_x = the number of age-1 striped bass in year x, and D_{x-1} = the number of fingerlings stocked the previous year. As an example, 306,884 fingerlings were stocked in 1974. The reported CPUE for these fish in 1975 was 0.111. N in 1975 is equal to 59,866, and the derived survival estimate for fingerlings stocked in 1974 is 19.5% (59,866/306,884). Although fry were stocked by the VCGIF from 1963 to 1979, I assumed that survival of these fish was negligible (Bailey 1974). Annual survival rates of stocked striped bass fingerlings, after 1973, ranged from 3.9% to 30.5% and averaged 20.8% for the 11-year period, 1973-1983 (Table 2.7). There was a significant inverse correlation ($r=-0.7$, $N=11$, $P=0.0157$) between the number of stocked fingerlings (D)

Table 2.7. Total number of fingerling striped bass stocked, CPUE of fish the following year, estimated number of age-1 striped bass, and the estimated annual survival (%) for stocked fingerlings in Smith Mountain Lake, 1973-1984.

Year Interval	Number Stocked	CPUE	Number Age 1	Annual Survival
1973-1974	293,925	.296	159,601	54.3
1974-1975	306,884	.111	59,842	19.5
1975-1976	455,241	.120	64,644	14.2
1976-1977	618,020	.150	80,961	13.1
1977-1978	416,732	.160	86,264	20.7
1978-1979	546,354	.040	21,308	3.9
1979-1980	809,246	.153	82,543	10.2
1980-1981	593,978	.128	68,901	11.6
1981-1982	412,790	.169	91,227	22.1
1982-1983	267,153	.151	81,482	30.5
1983-1984	205,654	.111	59,845	29.1

and associated survival rates (S). The equation describing this relationship was:

$$\ln (S) = -0.0000027(D) + 4.043 \quad (9)$$

Based on the relationship between stocking density and survival, a stocking of approximately 430,000 fingerlings would produce the maximum number of survivors each year in Smith Mountain Lake (Fig. 2.1). However, the number of age-1 fish produced per an additional stocking of 10,000 fingerlings is minimal, i.e., an additional stocking of 10,000 fish produces only 45 survivors at this stocking level. In contrast, at a stocking rate of 200,000 (24/ha) fingerlings, an additional stocking of 10,000 fish produces slightly over 2000 survivors, a marginal yield of approximately 20% (Fig. 2.2).

Although the period of time between stocking fingerlings in June to gill net sampling of yearling striped bass the following fall (October, November, December) was 16-18 months, survival estimates approximate annual estimates for the following reasons. The 1977 creel harvest was an annual estimate and the striped bass fishery in Smith Mountain Lake is year-round. Since June is the middle of the year, I assumed the number of age-4 striped bass estimated from the 1977 creel harvest were present in June. Striped bass are stocked in June each year. Thus, survival would be based on June 1973 to June 1977 estimates and would approximate annual (12 month) survival.

Survival estimates applied to stocking rates indicated that 136,227 (16.3 per ha) age 1 and older striped bass were present in Smith Mountain Lake in 1983 (Table 2.4). Only 27% of this total was comprised of age-1

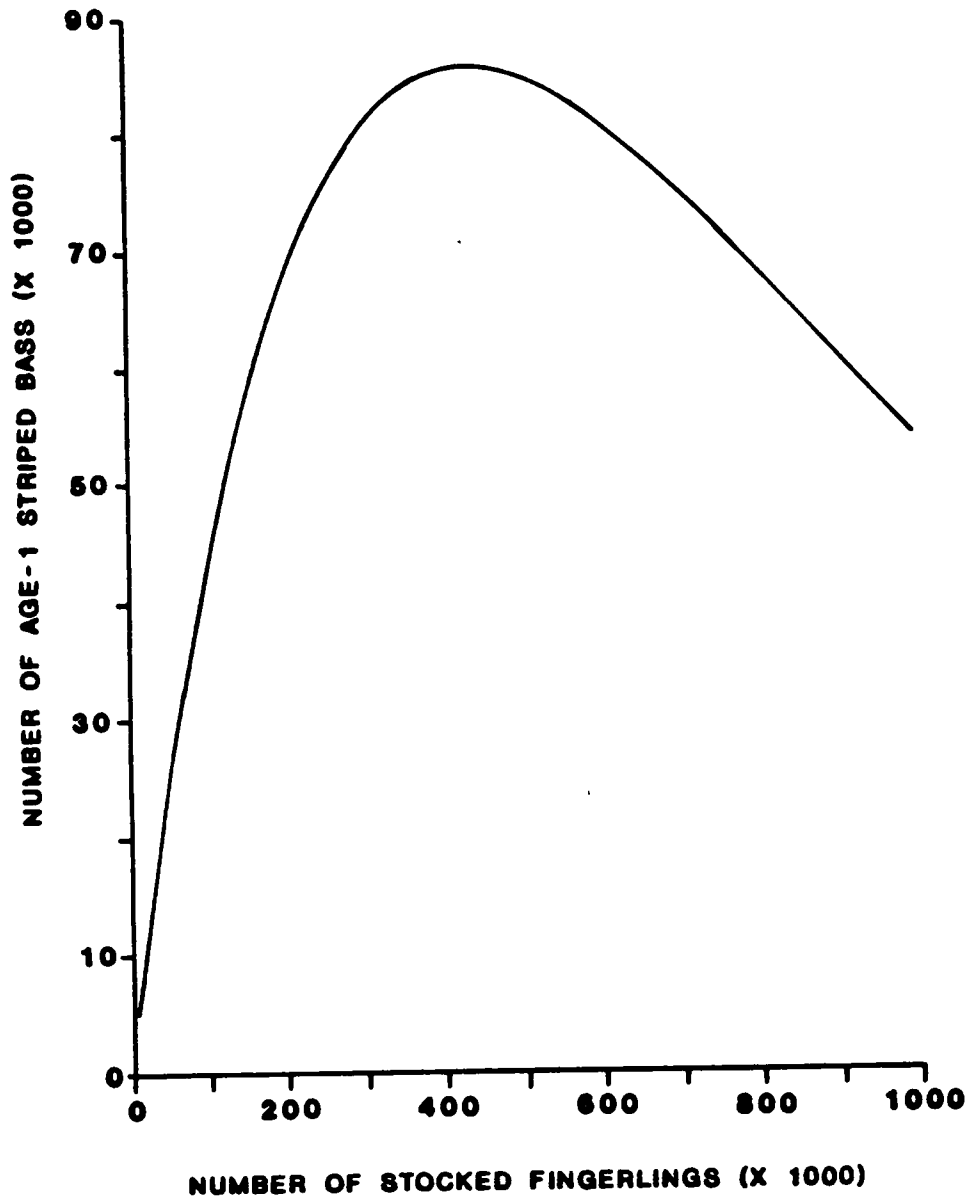


Figure 2.1. The relationship between the number of stocked striped bass fingerlings surviving to age 1 and stocking density.

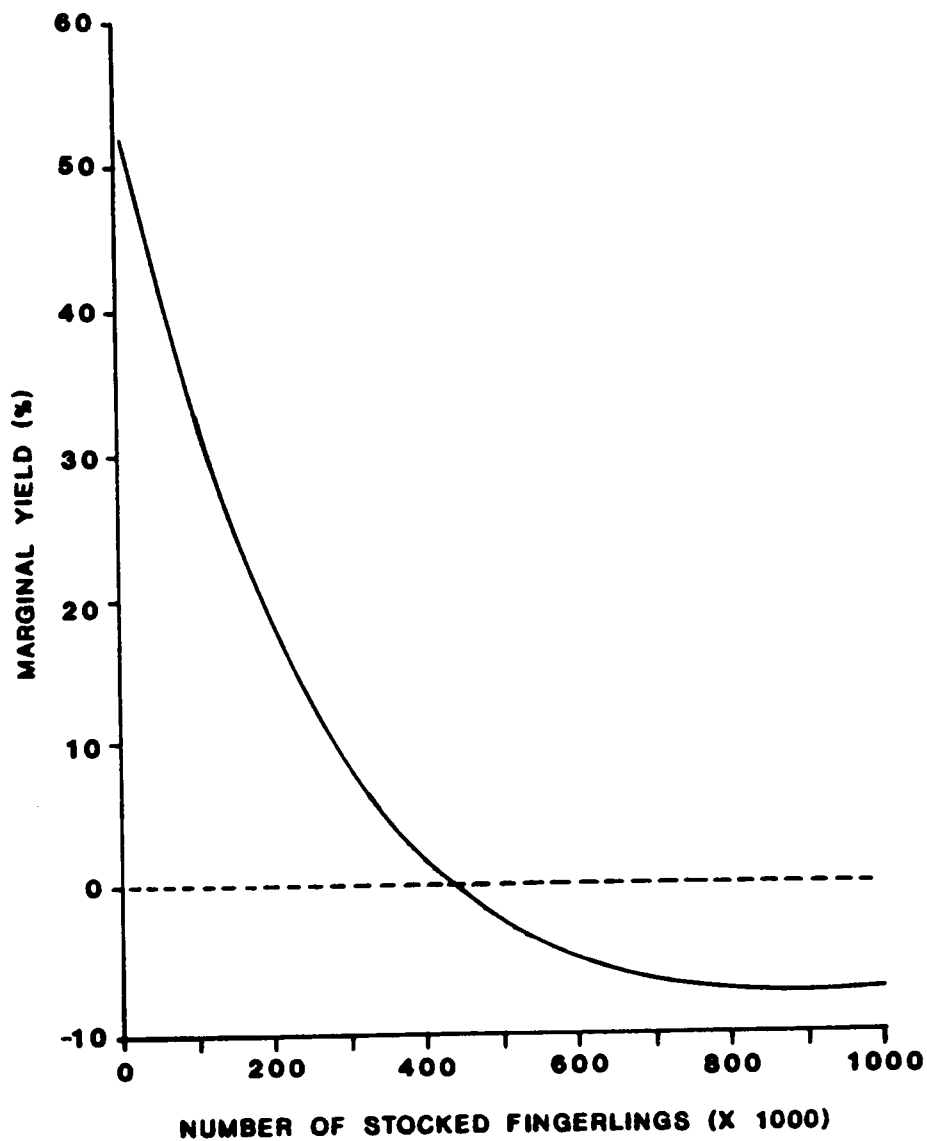


Figure 2.2. The relationship between the number of stocked striped bass fingerlings and the marginal yield. Marginal yield is the number of survivors (age-1 fish) produced per additional stocking of fingerlings.

fish. The harvestable portion of the population, those exceeding 508 mm TL (age 3 and older), comprised slightly more than 13% of the total.

Mean annual survival of stocked walleye fingerlings to age 2 was 8.3%. An annual survival value of 59% was calculated for walleye age 2 and older from previous studies (Chance 1958, Kempinger and Carline 1977). A total of 16,860 (2.02 per ha) walleye age 1 and older was estimated for 1983 from stocking records and these derived survival rates (Table 2.4). Age 4, the last cohort stocked in Smith Mountain Lake, was predominant, comprising 47% of this total.

Discussion

Cove rotenone data indicated that the number of young-of-year black bass fluctuated widely from year to year, with almost ten times more bass fingerlings present in some years than in others. Year-class fluctuations are common in reservoir fish populations and have been reported frequently for largemouth bass in large reservoirs (Summerfelt 1975). In addition, survival rates of age-0 largemouth and smallmouth bass in Smith Mountain Lake were similar to the 55% survival reported for age-0 largemouth bass in a Georgia reservoir (Hightower et al. 1982). The low number of age-0 black bass in 1979 may have resulted from a reproductive failure of gizzard shad in 1978 (La Roche 1981), affecting black bass survival and reproductive success in 1979 because of reduced food availability. Food habit studies indicated that gizzard shad are an important food item for black bass in Smith Mountain Lake, comprising as much as 57% of food items found in bass stomachs during different seasons (Chapter I). It is pos-

sible that due to a lack of food, smaller, sexually mature bass in 1978 may have had less energy available for sex products and spawning the following spring. Hanson (1962) noted evidence of poor condition in largemouth bass following a reproductive failure of gizzard shad in Bull Shoals Reservoir, Arkansas.

The annual survival estimate (29%) for age-1 largemouth bass was very similar to the 25.5% annual survival estimated for this species in an Oklahoma reservoir (Zweiacker and Brown 1971), and the 24% survival reported for Degray Lake, Arkansas (Dewey et al. 1981). Similarly, survival rates of older (>age 2) largemouth bass in Smith Mountain Lake are in agreement with rates reported for other southeastern reservoirs (Table 2.8). In addition, although population dynamics of smallmouth bass are poorly defined in southern reservoirs, survival estimates for age 2 and older smallmouth bass were similar to rates reported in other studies (Table 2.9).

The population estimate for largemouth bass, 61.2 per ha, is lower than the 86 to 163 age 1 and older largemouth bass per hectare estimated for Degray Lake, Arkansas (Dewey and Moen 1981). However, my estimate of 5.6 largemouth bass per ha, age 3 and older (those approximately greater than 305 mm in TL) in Smith Mountain Lake in 1983 is similar to values in previous studies. Aggus and Rainwater (1975) estimated that there were 4.9 largemouth per ha, greater than 300 mm TL, in Beaver Lake, Arkansas; Farman et al. (1982) estimated 6.7 bass/ha of this size in Back Bay, Virginia.

Table 2.8. Annual survival rates of largemouth bass from selected southeastern reservoirs.

Locality	Annual Survival	Source
Lake Carl Blackwell, OK	.40-.47	Zweiacker and Brown 1971
Beaver Lake, AR	.34-.74	Houser and Rainwater 1975
Bull Shoals Lake, AR	.31-.74	Houser and Rainwater 1975
Lake Tobesofkee, GA	.089	Ager 1978
Center Hill Reservoir, TN	.42	Yeager and Van Den Avyle 1978
Degray Lake, AR	.08-.69	Dewey and Moen 1981
Smith Mountain Lake, VA	.38	This study

Table 2.9. Annual survival rates of smallmouth bass from selected water bodies in the United States.

Locality	Annual Survival	Source
U. S. streams	.34-.49	Fajen 1975
Large natural lakes	.30-.76	Latta 1975
Center Hill Reservoir, TN	.35	Yeager and Van Den Avyle 1978
Brownlee Reservoir, ID	.27	Rohrer 1985
Merle Collins Reservoir, CA	.16	Pelzman et al. 1980
Smith Mountain Lake, VA	.29	This study

Survival estimates for young-of-year and older black bass may be biased. The value of 0.8, used to correct for non-recovery of tagged fish, may be too high for smaller, age-0 bass. Smaller fish would be less apparent to collectors and thus recovery of these fish would be reduced. A lesser value, such as 0.6 (Grinstead et al. 1976), would increase the estimate for young-of-year bass and decrease survival rates. Computed survival estimates of over 100% for some cohorts of age-0 smallmouth bass indicate that cove rotenone data do not consistently represent population size or structure of smallmouth bass in Smith Mountain Lake. Smallmouth bass are generally located in portions of the lower reservoir where deep, clear water coves with steep shorelines make rotenone sampling impractical.

Size selectivity of electrofishing gear also may have affected the accuracy of survival estimates for age 2 and older black basses (Reynolds 1983), and it is probable that sample size was insufficient to provide an unbiased estimate of stock structure (Dent 1986). Sampling bias would be exacerbated for smallmouth bass due to their habitat preference and the associated reduction in vulnerability to electrofishing gear.

Unlike largemouth bass, survival rates of striped bass have not been adequately determined in southern reservoirs, primarily because striped bass are pelagic and unavailable to traditional sampling techniques such as use of rotenone. However, my survival estimates agree well with annual rates determined for striped bass and other Morone spp. in freshwater systems. Annual survival of striped bass in the Sacramento-San Joaquin river system varied from 32% to 69% (Chadwick 1968, Miller 1974) and from

22% to 68% for striped bass from the Hudson River (Hoff et al., in press). Germann and Brunch (1983) calculated a survival rate of 30.9% to 39.9% for Morone hybrids in Clarks Hill Reservoir, Tennessee, and Moss and Lawson (1982) estimated annual survival of 30.9% for age-1 Morone hybrids in an Alabama Lake. Annual survival of white bass (Morone chrysops) averaged 40% in Beaver Reservoir, Arkansas (Yellayi and Kilambi 1975).

Use of these survival estimates (in conjunction with stocking rates, 1977 harvest data, and relative abundance of yearling striped bass from year to year) allowed me to estimate striped bass abundance. My use of harvest data in conjunction with mortality estimates is similar to virtual population or cohort analysis, used previously for a largemouth bass fishery in Lake Fort Smith, Arkansas (Cole 1966). Unlike cohort analysis, in which a minimum population size is estimated from mortality rates and sequential harvest estimates, I used striped bass harvest data to estimate survival of stocked fingerlings. Use of CPUE data from gill net sampling then allowed me to determine survival rates for stocked fish in successive years and incorporate yearling and adult survival estimates to determine population size.

My estimates indicate that survival of striped bass fingerlings was highest in 1973, dropped to a low in 1978, and then increased in the early 1980's. The reproductive failure of gizzard shad, and possibly alewives, in 1978, may explain the low survival rate of striped bass fingerlings observed that year since young-of-year clupeids are an important source of food for young striped bass in Smith Mountain Lake (Chapter I). Reduced fingerling survival in 1978, 1979, and 1980 would account for the

reduced harvest rates reported for striped bass in the early 1980's (La Roche 1981, Whitehurst 1985).

The negative correlation between the number of stocked fingerlings and associated survival rates appears to indicate a decreasing trend in survival with increasing number of fingerlings stocked, i.e., survival rate of fingerlings is density-dependent. Similarly, relative survival rates of striped bass fingerlings in Watts Bar Reservoir, Tennessee, were inversely related to stocking density (Van Den Avyle and Higginbotham 1979). This inverse relationship would be expected since prey resources are finite and density-independent mechanisms of mortality operate primarily on striped bass at life stages prior to fingerling size (Logan 1985).

The relationship between stocking density and survival indicated that approximately 430,000 fingerlings would produce the maximum number of age-1 striped bass. However, based on the marginal yield curve, the costs of stocking striped bass at this level would probably outweigh the benefit of the small number of additional survivors. Without a detailed analysis of the costs per fingerling stocked as well as the value of survivors, a level of stocking where the marginal yield was less than 20%, such as more than 24/ha, may be suboptimal.

Cove rotenone data can be used as an independent estimate of population size for comparison with my population estimate of striped bass. A total of 19 striped bass/ha were collected in 1983 rotenone samples by VDGIF biologists. Adjusting this number for non-recovery of tagged fish (80% recovery; Whitehurst 1985) and cove/open water ratios (0.5; Jenkins

and Morais 1978) results in a population estimate of 47.5 striped bass/ha. Although cove rotenone samples are biased against pelagic predators, this estimate compares favorably with my estimate of 41 striped bass per ha (stocked fingerlings plus age 1 and older striped bass.)

Striped bass population estimates rely on the accuracy of the 1977 harvest data and the use of gill net data as an index of relative abundance for yearling striped bass. Creel surveys can provide a reasonably accurate estimate of harvest (Malvestuto 1983), and standard gill net sampling schemes tend to be unbiased when tracking the relative abundance of a species over time (Powell et al. 1971). Although I could not determine selectivity curves, the use of several mesh sizes by the VDGIF probably reduced sampling bias (Hamley 1975). However, the survival value of over 100% calculated for age-1 striped bass in 1979 indicates some gear selectivity or bias due to fish behavior; e.g., schooling.

Smith Mountain Lake does not exhibit the temperature and dissolved oxygen conditions that limit survival of striped bass in other southern reservoirs (Coutant 1985); consequently, natural mortality of striped bass in Smith Mountain Lake is probably low. In the absence of empirical data, my assumption that all the mortality for age-4 fish in 1977 was due to fishing is reasonable. Accounting for natural mortality would decrease the exploitation rate and increase population estimates. Thus, derived population estimates may be slightly conservative.

Population estimates for walleye are less accurate than those calculated for other predators in Smith Mountain Lake, primarily because I was unable to derive population estimates from VDGIF or other sampling

statistics. The exploitation rate of walleye in Smith Mountain Lake is probably lower than the 23.2% observed in Norris Reservoir (Chance 1958), since stocking was discontinued because anglers were apparently not harvesting walleye. The natural mortality value for walleye, derived by Kempinger and Carline (1977), could be an underestimate for the walleye population in Smith Mountain Lake, as natural mortality may be higher in southern waters than in northern lakes (Hackney and Holbrook 1978). However, the computed annual survival rate (59%) is within the range of 45-60% reported as a common annual survival rate observed in exploited walleye populations (Colby et al. 1979) and agrees well with 44-58%, the mean survival rates for walleye ages 3 to 8 in three main-stem reservoirs on the Missouri River (Nelson and Walburg 1977). Unfortunately, I could not compare my population estimates of walleye in 1983 to cove rotenone data since no walleye were collected in cove samples that year.

Population estimates indicate that largemouth bass was the most abundant gamefish of those sampled. These estimates and those for smallmouth bass substantiate data that indicate the black bass population is recovering from the overfishing that occurred in the mid-1970's (Whitehurst 1985). In 1983, harvestable striped bass were second only to legal-sized largemouth bass in number of gamefish exceeding minimum size limits for harvest. An increase in survival rates of striped bass fingerlings stocked since 1978 indicates that the striped bass fishery may improve significantly in the late 1980's as the potential number of striped bass reaching harvestable size increases. Finally, population estimates indicate that the walleye population is declining, probably

because of the discontinued stocking and negligible natural reproduction. As the 1978 and 1979 year classes mature and succumb to natural and fishing mortality, walleye will comprise less of the predator biomass and angler harvest in future years.

In conclusion, this study illustrates how several different sampling techniques can be combined to estimate predator population size and structure in a reservoir. Although these techniques were developed with the best available data, they are not without bias. The methodology developed for striped bass will probably be the most useful to reservoir managers because the data bases used in this study exist for other reservoirs. Possible uses of this methodology include better estimates of pelagic predator biomass for AP/P ratios, more accurate estimates of stocking success, and greater predictive capabilities to quantify the impact of introduced, pelagic predators on native predators and the forage base.

CHAPTER III

Application of Bioenergetics Models to the Predator Assemblage in Smith Mountain Lake, Virginia

Introduction

Introduced to utilize abundant clupeid populations, striped bass have become an important component of the predator complex in many reservoirs across the United States. However, Axon and Whitehurst (1985), in a nationwide survey of fisheries agencies, reported that a lack of information on predator-prey relations was one of the major limitations to successful management of striped bass in freshwater impoundments. Introductions of striped bass have generally occurred without adequate consideration of either the amount of forage necessary to sustain healthy populations of striped bass or the potential impact of these introductions on other predators in the system. That striped bass can overcrop their food supply (Stevens 1969, Morris and Follis 1978, Keith 1986, Summerfelt 1986) indicates the need for a quantitative measurement of potential forage demand by stocked, striped bass cohorts.

A potential technique for assessing this forage demand is bioenergetics modeling. Bioenergetic models have been developed for a number of fish species to address both autecological and synecological questions (Kitchell 1983), and a number of reviews have been published

(Brett and Groves 1979, Elliot 1979, Cho et al. 1982, Brett 1983, Kitchell 1983, Brafield 1985, Soofiani and Hawkins 1985). Bioenergetics methodology has been used to quantify the impact of stocked salmonids on the forage base of Lake Michigan (Stewart et al. 1981), the potential demand of largemouth bass populations for gizzard shad in Ohio reservoirs (Carline et al. 1984), and the impact of walleye predation on the prey assemblage of a small Wisconsin lake (Lyons 1984). Recently, Bevelhimer et al. (1985) used a bioenergetic model to predict how three esocids, northern pike (Esox lucius), tiger musky, and muskellunge (E. masquinongy) would perform in Ohio reservoirs under different stocking regimes, which included fingerling size, time of stocking, and different thermal conditions.

Although a number of studies have been completed on the physiology of striped bass (reviewed by Westin and Rogers 1978, Setzler et al. 1980), no one has derived a complete energetics model for piscivorous sizes of this species. Eldridge et al. (1982) compiled an energy budget for striped bass embryos and larvae based on extensive laboratory research. Connolly and Tonelli (1985) developed a model to estimate the bioaccumulation of Kepone by striped bass in the James River estuary, Virginia. Although the latter model was adequate for their study, it would produce substantial error in other ecological applications primarily because of inadequate respiration data and a potentially inaccurate value for assimilation efficiency; i.e., Winberg's (1956) value of 0.8.

I developed a bioenergetics model for striped bass based on a compilation of data collected in several studies on striped bass metabolism

and growth. Energetics information for several ecologically similar species was used to bridge various information gaps. My model is structurally similar to the model developed by Kitchell et al. (1974) and subsequently used and improved by Kitchell et al. (1977), Kitchell and Breck (1980), Rice et al. (1983), and Stewart et al. (1983).

Because bioenergetics modeling is probably the most cost effective and accurate method for estimating annual forage demand by a predator population (Stewart et al. 1983), the striped bass bioenergetics model was used to derive estimates of total annual consumption of prey from observed striped bass growth during 1983 and 1984 in Smith Mountain Lake, Virginia. Striped bass consumption estimates were compared to estimates derived for three other abundant predators that coexist in the reservoir; largemouth bass, smallmouth bass, and walleye. Consumption estimates for these predators were derived using bioenergetics models developed for largemouth bass (Rice et al. 1983) and walleye (Kitchell et al. 1977). Annual estimates of demand for gizzard shad and alewife, the principal prey species consumed by predators in Smith Mountain Lake, were then evaluated to address two questions:

1. Are introduced and native predator populations compatible in Smith Mountain Lake?
2. Can estimates of predator demand be used to determine striped bass stocking strategies?

The Bioenergetics Model

The equation used to describe the energetics of predators in Smith Mountain Lake is similar to that initially proposed by Ivlev (1939) and popularized by Winberg (1956). The mass balanced energy equation is of the general form:

$$C = G + R + F + U + SDA$$

where each component is a specific rate for consumption (C), growth (G), respiration (R), egestion (F), excretion (U), and specific dynamic action (SDA). All units for the equation are expressed in biomass equivalents; i.e., g/g day.

Recently, Hewett and Johnson (1987) developed a microcomputer program to implement the bioenergetics equation for any species based on appropriate species-specific and site-specific parameters. The program is derived from the FORTRAN model developed by Weininger (1978) and Stewart (1980). Species-specific data needed to implement the model include the various parameters used to derive the components of the energetics equation discussed above. Site-specific data include information on water temperature, diet, energy values of predators and prey, and predator growth (weight).

The species-specific variables used to model the energetics of walleye (Table 3.1) and largemouth bass (Table 3.2) are nearly identical to those derived by Kitchell et al. (1977) and Rice et al. (1983), with few minor exceptions. Smallmouth bass energetics were modeled using largemouth bass parameters with minor modifications (Table 3.2). The following discussion of model development will focus on the derivation

Table 3.1. Symbols and parameter values used to implement the bioenergetics model for walleye. Values are from Kitchell et al. (1977).

Reference Equation	Symbol	Parameter Description	Parameter Value
1	a_1	Intercept for maximum consumption	.25
	b_1	Slope for maximum consumption	-.27
	T_{oc}	Optimum temperature for consumption	22
	T_{mc}	Maximum temperature for consumption	27
	Q	Slope for temperature dependence of consumption	2.3
2	a_2	Intercept for maximum standard respiration	.035
	b_2	Slope for maximum standard respiration	-.2
	T_{or}	Optimum temperature for standard respiration	27
	T_{mr}	Maximum temperature for standard respiration	32
	Q	Slope for temperature dependence of standard respiration	2.1
	A	Active metabolism multiplier	1.0

Table 3.1. (Continued)

4	S	Specific dynamic action coefficient	0.172
5	FA	Intercept for proportion of consumed food egested	.158
	FB	Coefficient for egestion vs temperature	-.222
	FG	Coefficient for egestion vs feeding level	.631
6	UA	Intercept for proportion of consumed food excreted	.0292
	UB	Coefficient for excretion vs temperature	.58
	UG	Coefficient for excretion vs feeding level	-.299

Table 3.2. Symbols and parameter values used to implement the bioenergetics model for black basses. Values are from Rice et al. (1983).

Reference Equation	Symbol	Parameter Description	Parameter Value	
1	a_1	Intercept for maximum consumption	.33	
	b_1	Slope for maximum consumption	-.325	
	T_{oc}		Optimum temperature for consumption largemouth bass	27.5
			smallmouth bass	26
	T_{mc}		Maximum temperature for consumption largemouth bass	37
		smallmouth bass	35	
	Q	Slope for temperature dependence of consumption	2.3	
3	a_2	Intercept for maximum standard respiration	.008352	
	b_2	Slope for maximum standard respiration	-.355	
	m	Coefficient for temperature dependence of respiration	.0313	
	g	Coefficient for swimming speed dependence of respiration	.0196	
4	S	Specific dynamic action coefficient	.163	
7	f	Proportion of consumed food egested	.104	
8	u	Proportion of consumed food excreted	.079	

of striped bass parameters (Table 3.3), but will include discussion of the other predators for comparative purposes and review. Site-specific parameters are discussed in detail for all predators.

Consumption

The specific consumption rate for fish is a function of both weight and temperature and is a proportion of the physiological maximum consumption, C_{\max} , such that

$$C = C_{\max} \times P \times r_c \quad (1)$$

where C_{\max} = maximum consumption at the optimum temperature (T_{oc}). C_{\max} is equivalent to $a_1 B^{b_1}$, where a_1 and b_1 are allometric constants and B is wet weight in grams; P = proportionality constant of maximum ration that varies from 0 to 1; and r_c = a temperature dependent proportional scalar of consumption rate equivalent to $(V^X)(e^{X(1-V)})$ such that

$$V = \frac{T_{mc} - T}{T_{mc} - T_{oc}}$$

$$X = \frac{W^2(1 + (1 + 40/Y)^{0.5})^2}{400}$$

$$W = (\ln Q)(T_{mc} - T_{oc})$$

$$Y = (\ln Q)(T_{mc} - T_{oc} + 2)$$

The r_c function, developed by O'Neill et al. (1972), increases to a maximum value of 1.0 at the optimum temperature, T_{oc} , and declines to 0 at the maximum temperature for consumption, T_{mc} . As the value of r_c in-

Table 3.3. Symbols and parameter values used to implement the bioenergetics model for striped bass.

Reference Equation	Symbol	Parameter Description	Parameter Value
1	a_1	Intercept for maximum consumption	.33
	b_1	Slope for maximum consumption	-.30
	T_{oc}	Optimum temperature for consumption	25,22,20
	T_{mc}	Maximum temperature for consumption	30,27,25
	Q	Slope for temperature dependence of consumption	2.26
2	a_2	Intercept for maximum standard respiration	.02192
	b_2	Slope for maximum standard respiration	-.234
	T_{or}	Optimum temperature for standard respiration	30,27,25
	T_{mr}	Maximum temperature for standard respiration	35,32,30
	Q	Slope for temperature dependence of standard respiration	2.5
	A	Active metabolism multiplier	2.0
4	S	Specific dynamic action coefficient	.172
7	f	Proportion of consumed food egested	.104
8	u	Proportion of consumed food excreted	.068

creases with increasing temperature up to T_{OC} , the slope of the function, Q , approximates a Q_{10} for the rate. Q_{10} is a temperature coefficient used to describe a change in rate with an increase in temperature of $10^{\circ}C$.

No study has adequately assessed the body-size dependence of C_{max} for striped bass and as a result, a_1 and b_1 could not be derived from empirical data. I assumed a value of 0.33 for a_1 , the identical value derived by Rice et al. (1983) from the studies of Niimi and Beamish (1974). The intercept of the function relating maximum consumption to weight at the optimum temperature, a_1 , can be interpreted as the percent of maximum daily ration (i.e., 33%) consumed by a 1 g striped bass. This value is a reasonable approximation. Rogers and Westin (1978) observed newly feeding striped bass larvae to consume 25% of their body weight per day, on a dry weight basis, of live Artemia nauplii at $22^{\circ}C$. Assuming a similar relationship between dry and wet weight values as determined for larger juveniles in their study, this value would equate to approximately 40% on a wet weight basis. That these larvae weighed less than 1 g indicates this value would be less than 40% for a 1 g fish. My assumed value for a_1 is greater than the a_1 values of 0.25 and 0.26, assumed for walleye (Kitchell et al. 1977) and derived for lake trout (Stewart et al. 1983), respectively. However, it is reasonably close to 0.3, the value measured for lamprey (Petromyzon marinus) (Kitchell and Breck 1980), sockeye salmon (Oncorhynchus nerka) (Brett 1971), and assumed for skipjack tuna (Katsuwonus pelamis) (Kitchell et al. 1978).

The weight dependence exponent for maximum consumption, b_1 , was set equal to -0.3 for striped bass. This value falls between -0.27, the b_1

for walleye (Kitchell et al. 1977), and -0.325, the exponent used for largemouth bass (Rice et al. 1983). It is more than -0.327, the value derived for lake trout (Stewart et al. 1983), and is nearly twice -0.18, the exponent used by Bevelhimer et al (1983) to model esocid metabolism.

The value of Q , the slope of the r_c function, was derived from data measured by Cox and Coutant (1981) in laboratory experiments with juvenile striped bass. They measured consumption rates for 13 groups of 8 to 10 juvenile striped bass fed an unrestricted ration of fathead minnows at constant temperatures ranging from 16°C to 34°C. These data, presented as consumption per group on a gram per day basis, were regressed against temperatures up to 25°C, the optimum temperature for consumption (see below). The slope of the line ($N=6$, $r^2=0.857$, $p=0.0081$) was equal to 0.0814, which equates to a Q of 2.26 ($e^{0.0814 \times 10}$). This Q is very close to 2.3, the value used for bluegill (Kitchell et al. 1974), walleye and yellow perch (Kitchell et al. 1977), and lamprey (Kitchell and Breck 1980). The temperature dependence coefficient used by Rice et al. (1983) for largemouth bass equates to a Q of 2.65.

Respiration

Oxygen consumption is a function of size, water temperature, and activity. I used a model functionally similar to that developed by Kitchell et al. (1977) to derive the specific respiration rate (R) for striped bass:

$$R = R_{\max} A r_T + SDA \quad (2)$$

where R_{\max} = the specific standard respiration rate equivalent to the allometric relationship, $a_2 B^{b_2}$, where a_2 and b_2 are species-specific constants; A = a parameter (Winberg multiplier) to account for activity metabolism; and r_T = temperature dependent proportional adjustment of respiration rate ranging from 0 to 1. This value is derived in a manner analogous to that previously discussed for consumption.

The parameter a_2 is the intercept of the line relating maximum specific standard metabolism to weight at the optimum temperature, T_{OR} , for respiration (i.e., specific standard metabolism of a 1 g fish at T_{OR}). Standard metabolism is highly variable among species (Brafield 1985). Kitchell et al. (1977) used respiration data for yellow perch to derive an a_2 of 0.035 for walleye. Rice and Breck (unpublished manuscript) used multiple linear regression techniques to synthesize fish respiration data for striped bass from the laboratory work of Kruger and Brocksen (1978). Kruger and Brocksen (1978) determined the oxygen consumption of striped bass at three water velocities (1, 5, 10 cm/s) and at five water temperatures (8, 12, 16, 20, 24°C); sizes of striped bass ranged from 22.5 to 68.4 g. The derived equation from their data was as follows:

$$R = .0014B^{-0.234}e^{0.0917T}e^{0.0508SS}$$

where B =weight (grams), T =temperature (°C), and SS =swimming speed (cm/s). For a 1 g striped bass at 30°C, the optimum temperature for respiration, and 0 cm/s, a_2 , is equal to 0.02192.

This a_2 value compares favorably with the work of Klyashtorin and Yarzhombek (1975), who studied the respiration of striped bass (0.3 to

22 g) at different temperatures and oxygen concentrations. Their data indicated that a 1 g fish would consume 0.0132 to 0.0168 g O_2 /g day at 22°C (interpolated from Figs. 4 and 5 in Klyashtorin and Yarzhombek 1975). Using the equation derived from Kruger and Brocksen (1978), a 1 g striped bass at 22°C would consume 0.0105 g O_2 /g day. The close similarity between the results of these very different investigations indicates that my value for a_2 , 0.02192, is a realistic approximation.

The weight dependence coefficient (b_2) of -0.234 was derived from Kruger and Brocksen (1978) and used in my modeling simulations of striped bass metabolism. Although only a small range of weights was experimentally tested; i.e., 22.5 to 68.4 g, the value is very close to -0.2, the value postulated by Winberg (1956) to represent the weight dependence of metabolism for a representative fish species, and the value (-0.2) used by Kitchell et al. (1977) for walleye. The weight dependence coefficient also agrees well with other studies on striped bass metabolism. Converting the value of 0.72 (Eldridge et al. 1982) to a specific rate equates to a value of -0.28 for larval striped bass. Klyashtorin and Yarzhombek (1975) measured a b_2 value of -0.25 for juvenile striped bass. My coefficient is substantially greater than -0.355, the weight dependence exponent derived for largemouth bass by Rice et al. (1983) from the data of Beamish (1970), but within the range of values used to model salmonid metabolism, -0.295 to -0.217 (Stewart 1980).

The temperature dependence coefficient for striped bass metabolism, 0.0917, derived from Kruger and Brocksen (1978) data, equates to a Q_{10} of 2.5. This value approximates Q for the r_T function and is slightly

higher than 2.0, the Q equal to the temperature dependence derived by Klyashtorin and Yarzhombek (1975), as calculated for striped bass by Lewis et al. (1981). Comparable Q values used by other researchers include 2.1 for bluegill (Kitchell et al. 1974), walleye and yellow perch (Kitchell et al. 1977), and lamprey (Kitchell and Breck 1980) and 1.8 to 2.0 for salmonids (Stewart 1980). The temperature dependence coefficient derived for largemouth equates to a Q of 1.4 (Rice et al. 1983).

I compared the respiration values for striped bass derived by Kruger and Brocksen (1978) to those of Neumann et al. (1981). Connelly and Tonelli (1985) used data from this latter study to model striped bass respiration dynamics. Neumann et al. (1981) determined oxygen consumption rates for striped bass swimming at three speeds and two temperatures. Although measurements for individual fish were not available, I used the derived equations (a total of six for two temperatures at three swimming speeds) to compute oxygen consumption of striped bass within the range of weights tested by Neumann et al. (1981). I then used multiple linear regression to derive a single equation representing these data:

$$R = 0.02815B^{-0.454}e^{0.0322T}e^{0.0128SS}$$

For a 1 g fish at 30°C (T_{or}), the value for a_2 would be 0.074, more than twice the value used in my model. However, the b_2 value of -0.454 is far outside the range of -0.3 to -0.2 observed for most species, and the Q of 1.4, corresponding to the temperature coefficient 0.0322, is likely biased since only two temperatures were used. The derived equation differs from that used by Connelly and Tonelli (1985):

$$R = 0.0443B^{-0.3}e^{0.03T}e^{0.0176SS}$$

Although the authors do not discuss how this equation was derived from the data of Neumann et al. (1981), they do mention that the b_2 parameter was artificially restricted to -0.3. I recognize that the use of original data may have modified my equation, especially since r^2 values of the six equations range as low as 0.12. However, the bias involved in the data and analyses indicates that the parameters derived from the Kruger and Brocksen (1978) data, as outlined above, are probably more acceptable for modeling purposes.

Winberg's (1956) review of piscine metabolic research led him to conclude that a multiple of standard metabolism could be used to calculate the additional metabolic costs resulting from activity. He assumed a value of 2 (Winberg II multiplier) for the activity parameter. In the absence of complete information on the activity metabolism of striped bass, I assumed that the same value was applicable to striped bass respiratory costs.

Although there is no physiological reason to explain why activity metabolism is equal to a constant times standard metabolism (From and Rasmussen 1984), a number of studies have assumed such a relationship (Mann 1978). Penczak et al. (1984) used a value of twice standard metabolism to estimate the total metabolism of fish species in two Polish rivers. Similarly, Kitchell et al. (1978) cited research indicating that a value twice standard metabolism might be a reasonable estimate of activity metabolism for both yellowfin and skipjack tuna. An activity

multiplier of less than two has been used for less mobile fishes. Stewart (1980) used a swim speed model to estimate that activity multipliers for lake trout ranged from 1.4, at low temperature and small size, to 1.9, at high temperature and large size. Kitchell et al. (1977) assumed an A equal to 1 for walleye, based on field data that indicated little locomotor activity. Minton and McClean (1982) assumed a similar relationship for sauger in a Tennessee reservoir. Adams et al. (1982b) found that activity metabolism varied with time of year as well as sex, and ranged from 0.18 to 1.44 times standard metabolism for largemouth bass. Bevelhimer et al. (1985) incorporated measurements of swimming speed, number of daily feeding bouts, and the amount of burst and cruise swimming to determine that activity increased metabolic costs 13% over the standard metabolic rate for esocids. This estimate was not very different from Diana's (1983) assumption that activity costs of northern pike were negligible (i.e., $A=1$) based on telemetry observations.

My value of A (2.0) is probably a reasonable estimate for striped bass. Yarzhombek and Klyashtorin (1974) determined that metabolism at standard activity was 1.3 times the calculated resting metabolism for 1 to 3 g striped bass. However, activity measurements were made on fish maintained in small, glass flasks, with activity induced by mechanical and electrical methods. Thus, their multiple is probably not an accurate estimate of activity metabolism in the wild. Kruger and Brocksen (1978) determined that a value of five times the standard metabolic rate would equal the metabolic cost of a juvenile striped bass at the maximum swimming speed of 60 cm/s (as measured by Painter and Wixcom 1967). At more

reasonable swimming speeds, 10 to 20 cm/s, oxygen consumption would range from 1.6 to 2.8 times the standard metabolic rate, assuming oxygen consumption at activity varies directly with the specified weight and temperature dependence coefficients of standard respiration.

Activity metabolism of striped bass is likely a complex relationship of numerous factors. Activity includes a variety of behaviors dominated by swimming (Brett and Groves 1979, Soofiani and Hawkins 1985). Neumann et al. (1981) hypothesized, based on laboratory results indicating juvenile striped bass were weak swimmers and adults exhibited extensive coastal migrations, that swimming ability of striped bass with increasing age could best be described by a sigmoidal curve. Additional complexities include the confounding factors of aerobic vs anaerobic metabolism (Webb 1978, Priede 1985), and the fact that striped bass are facultative ram ventilators (Freadman 1979). Research consisting of swim speed measurements for striped bass at various sizes, temperatures and speeds, as well as optimal (or standard) swimming speeds and field measurements of activity, are necessary to adequately characterize the activity metabolism of striped bass.

Stewart (1980) developed a swim speed model to account for metabolism of lake trout, based on an extensive study that incorporated measurements of the above variables. Similarly, Rice et al. (1983) developed a simpler swim speed model for largemouth bass from the experimental work of Beamish (1970). The equation for largemouth bass was as follows:

$$R = 0.347B^{-0.355}e^{0.0313T}e^{0.0196SS} \quad (3)$$

The constant a_2 , 0.347, was converted to 0.008352 g/g day for implementation in my bioenergetic model.

Specific Dynamic Action

The metabolic costs of digestion, absorption, and assimilation of food plus specific dynamic action (SDA) are considered additional respiratory costs and defined as apparent SDA (Beamish 1974). Most of the energy of apparent SDA is associated with SDA, which in turn is primarily involved in deamination of proteins (Soofiani and Hawkins 1985). Many investigators have modeled SDA as a proportion of total consumption or ingested energy. However, error may result when the diet changes from invertebrates to fish or becomes heterogeneous (Stewart et al. 1983). Thus, I modeled SDA as a proportion (S) of the assimilated energy for all four predators such that

$$\text{SDA} = S(\text{Consumption} - \text{Egestion}) \quad (4)$$

I assumed that S was independent of both temperature and ration size (Stewart 1983). Beamish (1974) determined that SDA was 17.2% of metabolizable energy for fish on a piscivorous diet, and I used this value of S for striped bass and walleye. However, to account for the more heterogeneous diet of largemouth bass, I set the value at 16.3% (Rice 1981) and used this value for both largemouth and smallmouth bass.

Optimum and Maximum Temperatures

Values of T_{oc} , T_{mc} , T_{or} , and T_{mr} , the optimum and maximum temperatures for consumption and respiration, respectively, define the temper-

ature dependent proportional adjustments, r_c and r_r . Temperature values for striped bass were derived from research conducted by personnel of the Oak Ridge National Research Laboratory. Optima and maxima were derived in a manner analogous to that used for walleye and yellow perch (Kitchell et al. 1977).

Cox and Coutant (1981) found that 25°C was the optimum temperature for consumption and growth of juvenile striped bass. This value is in agreement with the work of Cech et al. (1984). Although there has been no adequate measure of upper incipient lethal temperature, juvenile striped bass died at temperatures above 35°C (Davies 1973). I considered 35°C as the upper incipient lethal temperature and the maximum temperature for respiration, T_{mr} . A temperature of 30°C , midpoint between 25°C and 35°C , was chosen to represent the maximum temperature for consumption (T_{mc}) and the optimum temperature for respiration (T_{or}). T_{mc} and T_{or} should correspond to the highest preferred temperature for striped bass. The 30°C value is midpoint between 29°C and 31°C , the highest preferred temperatures of juvenile striped bass acclimated at 24°C (Texas Instruments 1976).

There is a marked ontogenetic shift in thermal preferenda with age of striped bass. Temperature selection of subadult (age 2-4) striped bass ranged from $20 - 24^{\circ}\text{C}$ (Coutant and Carroll 1980) and $18 - 22^{\circ}\text{C}$ for adults (age 5-10) in freshwater impoundments (Schaich and Coutant 1980). Since thermal preferenda and optima are equivalent for most species (Beitinger and Fitzpatrick 1979), I used the midpoint of these ranges, 22°C and 20°C as T_{oc} for consumption by subadult and adult striped bass, respec-

tively. The values of T_{mc} , T_{or} , and T_{mr} for subadult and adult striped bass were scaled accordingly. The respective values ($^{\circ}C$) for juvenile, subadult, and adult striped bass were 25, 22, and 20 for T_{oc} , 30, 27, 25 for T_{mc} and T_{or} , and 35, 32, and 30 for T_{mr} .

Kitchell et al. (1977) used values of 22, 27, 27, and $32^{\circ}C$ for the T_{oc} , T_{mc} , T_{or} , and T_{mr} of walleye, respectively. Similarly, the T_{oc} and T_{mc} for largemouth bass are 27.5 and $37^{\circ}C$ (Rice et al. 1983). To reflect the differing thermal preferences of smallmouth bass, T_{oc} and T_{mc} were set equal to $26^{\circ}C$ and $35^{\circ}C$, respectively (Coutant 1975).

Excretion and Egestion

Elliott (1976) developed relatively complex relationships to explain egestion and excretion rates for brown trout, Salmo trutta. His equations related these rates to ration size, weight of the fish and temperature. These relationships, with slight modifications, were used by Kitchell et al. (1977) to model egestion (F) and excretion (U) rates for percids. These equations were of the form:

$$F = C0.158T^{-0.222}e^{0.631P} \quad (5)$$

$$U = C0.0292T^{0.58}e^{-0.299P} \quad (6)$$

where C is consumption, T is temperature, and P is the proportionality constant.

Research on egestion and excretion rates for striped bass is lacking. I therefore modeled egestion (F) for striped bass with a function identical to that used for largemouth bass by Rice et al. (1983), as derived from the work of Beamish (1972):

$$F = f C \quad (7)$$

where f =proportion of consumed energy (C) egested. I set the value of f equal to 0.104, the same value used for largemouth bass (Rice et al. 1983).

Cox and Coutant (1981) measured defecation rates for six schools of striped bass at different temperatures. Each school consisted of 8 to 10 fish fed an unrestricted ration of fathead minnows. Although the data were not sufficient to determine a proportionality constant, the trend in defecation rate with temperature closely parallels that of specific consumption rate with temperature (Figure 1 in Cox and Coutant 1981). Thus, the assumption that egestion is a constant proportion of total consumption is probably valid.

Like egestion, excretion varies as a function of size, temperature, and ration. Excretory products are chiefly ammonia and urea. I modeled excretion (U) as a proportion of utilizable energy:

$$U = u (C-E) \quad (8)$$

where u =proportion of utilizable energy (consumption - egestion) that is excreted. This proportion was set equal to 0.068, the value used by Rice (1981) for largemouth bass. This value differs from 0.079, the value used by Rice et al. (1983), because they modeled excretion as a proportion of total consumed energy. The combined effect of total waste loss, egestion + excretion, varies little with temperature since F and U respond in opposite ways to temperature change (Kitchell et al. 1977). Thus, assuming constant proportions of consumed or assimilated energy is probably reasonable.

For illustrative purposes, the bioenergetics model for striped bass was implemented for a 100 g fish at maximum ration (Fig. 3.1). As expected, maximum specific rates for all functions, except respiration, occur at 25⁰C, the optimal temperature for consumption. Specific respiration rates continue to rise to 30⁰C, then rapidly decline. Specific rates of all functions decrease with increasing weight of striped bass (Fig. 3.2).

Energy Content of Predators and Prey

A necessary prerequisite to implementing the bioenergetics model is knowledge of the energy content of both predators and prey. Energy content of a fish can vary as a function of body size, feeding rate, season, and activity level (Soofiani and Hawkins 1985) as well as sex (Meakins 1976, Adams et al. 1982b, Rottiers and Tucker 1982). Several investigators have modeled the energetics of predators by assuming a constant and equivalent energy value for both predator and prey (Kitchell et al. 1977, Rice et al. 1983, Bevelhimer et al. 1985). Although the mean caloric content of a predator may be equivalent to that of its major prey species (Rottiers and Tucker 1982), seasonal changes in both trophic groups can be pronounced (Soofiani and Hawkins 1985). In addition, energy content of a predator may double over its lifespan (Stewart 1980).

Caloric content of predators and prey in Smith Mountain Lake was derived from a series of investigations carried out in Tennessee reservoirs by personnel of the Oak Ridge National Research Laboratory (Minton 1981, Minton and McClean 1982, Adams et al. 1982a, 1982b). Data derived

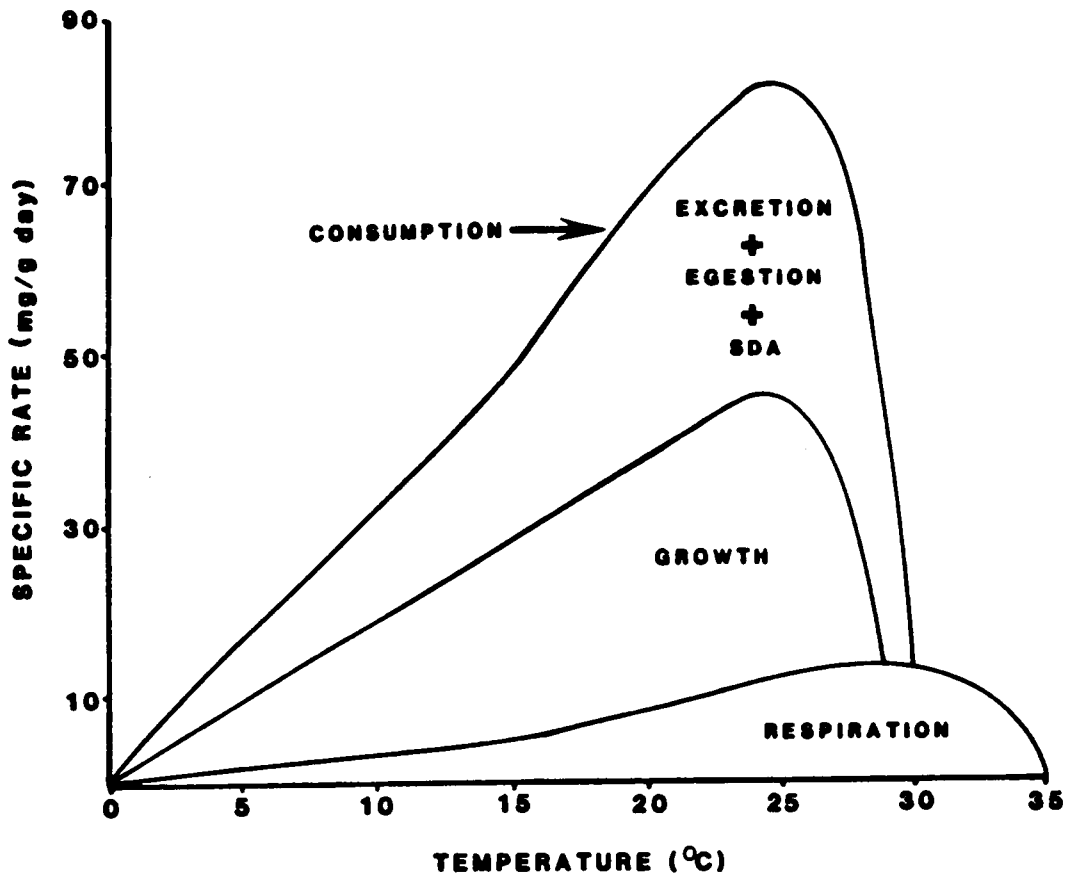


Figure 3.1. Model output for the energy budget of a 100 g striped bass, as a function of temperature.

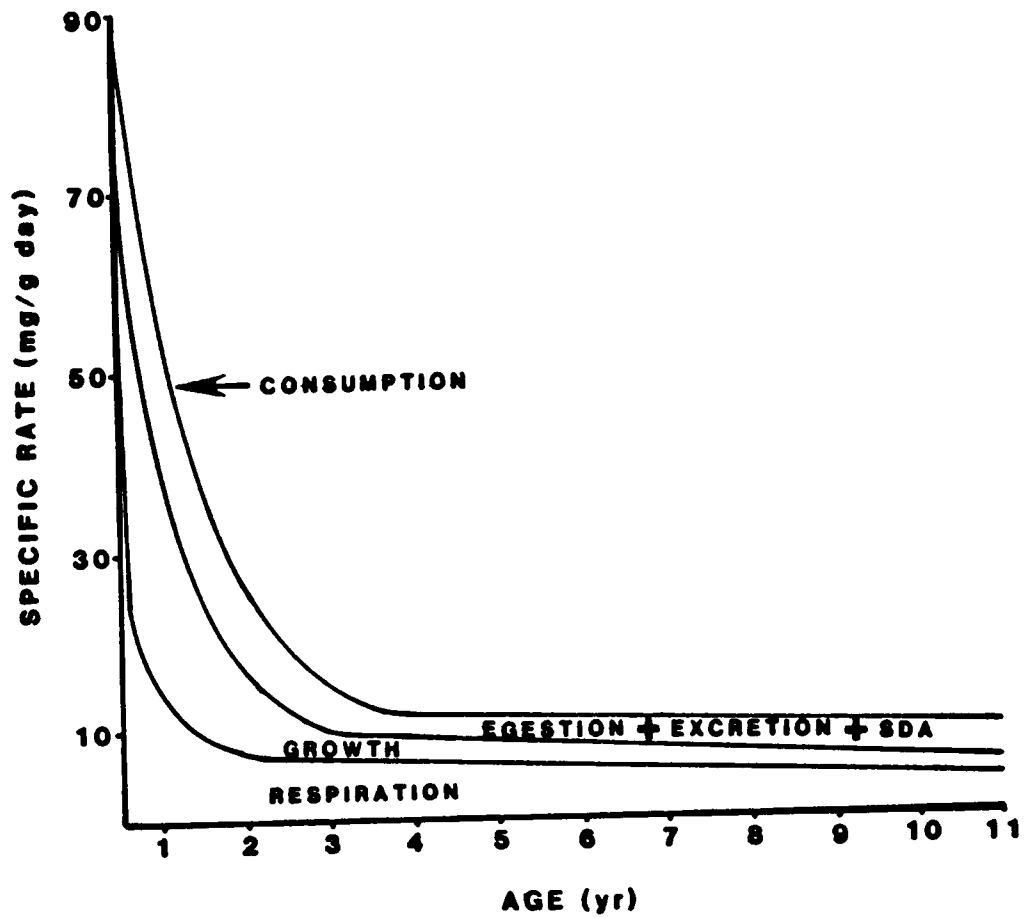


Figure 3.2. Model output for striped bass at the optimum temperature for consumption, T_{oc} , as a function of body size.

from these reservoirs should be more applicable to predatory fish in Virginia than data derived for predators in more northern lakes.

No study has adequately determined the proximate composition or caloric content of striped bass in freshwater. I assumed that caloric values calculated for age-1+ sauger (Minton 1981) were applicable to age 1 and older striped bass. Both species consume clupeids almost exclusively in freshwater impoundments (Minton and McClean 1982, Chapter I of this study). Because the "caloric content and proximate composition of forage are the major factors affecting the proximate composition of the predator" (Rottiers and Tucker 1982), sauger and striped bass should have similar caloric content. However, sauger are unlike striped bass in that they form larger deposits of fat (with associated high energy content) with increasing maturity (Minton 1981). Thus, although caloric content of older sauger was available, I felt the caloric values of the age-1+ sauger were probably more representative of all ages of striped bass.

I collected 16 striped bass between March and December, 1985 for caloric analysis to determine the validity of this assumption. The striped bass were between 341 and 647 mm TL (age 1 to 6). Whole fish were freeze-dried and then homogenized using a high-speed blender. Two subsamples were combusted from each sample using standard bomb calorimetry techniques (Paine 1971).

Considering the relatively small sample size ($N=4/\text{mo}$) and wide range of ages, the mean \pm 2 SD for each monthly sample agreed relatively well with the caloric values of age-1+ sauger as measured by Minton (1981) (Fig. 3.3). In addition, the caloric values derived for striped bass are

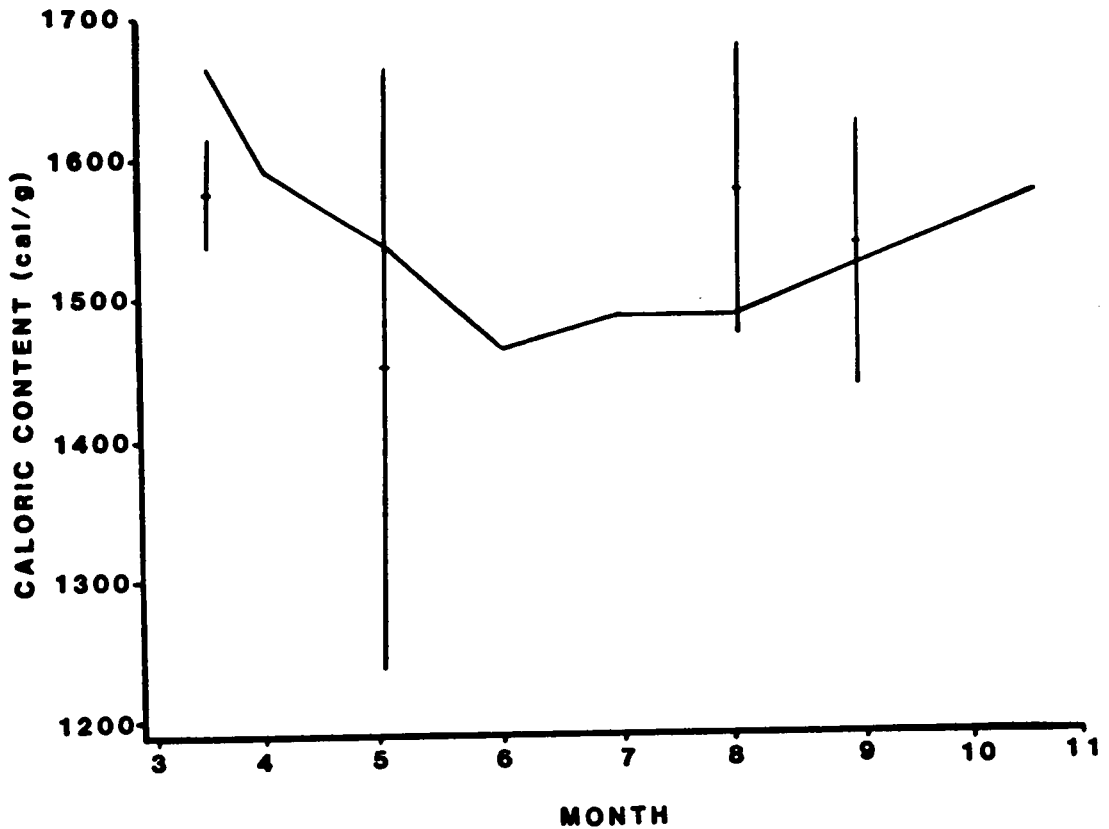


Figure 3.3. Mean caloric content (± 2 SD) of striped bass collected on four sampling dates in Smith Mountain Lake. Values are presented with the caloric content of age-1+ sauger as measured by Minton (1981) and used to model striped bass bioenergetics in this study.

within the monthly values derived for gizzard shad and alewives (see below), adding further credence to my assumption of similar caloric content. Caloric content of age-0 striped bass was assumed to equal the mean of the caloric content of gizzard shad and alewives, the major prey items consumed by this age class after they become piscivorous.

Although my caloric values appear reasonable, further research is needed to document cohort and seasonal changes in caloric content of striped bass in freshwater impoundments. Furthermore, like largemouth bass, caloric differences may occur between sexes. My sample size was too small to test statistically for this difference.

Marshall Adams (Oak Ridge National Laboratory, Oak Ridge, Tennessee, personal communication) supplied the original data on caloric values of largemouth bass in Watts Bar Reservoir, Tennessee. Unfortunately, the data were compiled for age 2 and 3 largemouth as whole carcass estimates in cal/g dry weight. To convert to whole fish estimates, I compared carcass values to wet weight estimates for largemouth bass carcasses reported by Adams et al. (1982b). The comparison indicated that a conversion factor of 0.261 and 0.257, when applied to dry weight values of age-2 and age-3 largemouth bass, respectively, would equate to the comparable wet weight values. The caloric values were increased 10% to account for the added caloric value of viscera and gonads (S. M. Adams, personal communication). Adams et al. (1982a) also measured a mean, annual value of 1430 cal/g wet weight for age 4 and older largemouth bass. Although samples were inadequate to derive monthly values for these cohorts, the value of 1430 cal/g represents a 4.4% increase in the mean caloric content

of age-3 largemouth bass. Thus, I assumed that a 4.4% increase in monthly caloric values of age-3 largemouth bass would adequately represent monthly caloric values for age 4 and older largemouth bass. I also assumed that an annual estimate of 1110 cal/g was applicable to age 0 and 1 largemouth bass (Adams et al. 1982b). The derived caloric values for largemouth are presented in Table 3.4. The mean of the monthly caloric values for ages 2 and 3 largemouth bass, 1279 cal/g and 1334 cal/g, agree closely with the means (1280 and 1370 cal/g, respectively) reported by Adams et al. (1982b) for whole fish of these age groups, males and females combined.

Caloric values used in modeling smallmouth bass energetics were set equal to those derived for largemouth bass. Monthly caloric content of ages 3 to 9 walleye in Smith Mountain Lake were assumed to be equivalent to values measured by Minton (1981) for age-2+ sauger in Watts Bar Reservoir, Tennessee (Table 3.5). Although caloric values are only presented for March through October, Minton (1981) indicated relatively little or no change in caloric content of sauger from October to January.

Prey items consumed by piscivorous predators in Smith Mountain Lake included gizzard shad, alewives, crayfish, insects, and other food items composed primarily of other fish and unidentified fish (Chapter I). Seasonal energy content of gizzard shad and alewives was calculated from data supplied by S. M. Adams (pers. comm.). Caloric values were calculated on a dry weight basis for gizzard shad and threadfin shad collected in Watts Bar Reservoir from December 1979 to December 1980. A correction factor of 0.2985, to convert dry weight to wet weight caloric values, was

Table 3.4. Caloric content (cal/g wet weight) of ages 2 to 6 largemouth bass used in the bioenergetics model. Values were derived from unpublished data (S.M. Adams pers. comm.) and from data presented by Adams et al. (1982a).

Month	Age Class		
	2	3	4-6
April	1173	1386	1446
May	1417	1397	1456
June	1357	1421	1483
July	1295	1352	1411
September	1278	1451	1514
October	1278	1451	1514
November	1238	1349	1408
December	1198	1247	1302

Table 3.5. Caloric content (cal/g wet weight) of walleye (ages 3-8) used in the bioenergetics simulation. Values are from Minton (1981).

Month	Caloric Content
March	1816
April	1791
May	1755
June	1756
July	1610
August	1728
September	1760
October	1788
November	1788

derived from proximate composition data for 247 gizzard shad collected in Watts Bar Reservoir from April to June 1983 (Adams et al. 1984).

I assumed that seasonal caloric values for threadfin shad from Tennessee would more closely approximate alewife caloric values from Smith Mountain Lake than those determined for alewives from Lake Michigan (Yeo 1978, Rottiers and Tucker 1982). Food habits of alewives and threadfin shad are relatively similar; both species are largely zooplanktivorous (Baker and Schmitz 1971, Ney et al. 1982), although threadfin shad will also consume quantities of phytoplankton (Miller 1967). I applied the identical correction factor derived for gizzard shad to caloric values for threadfin shad to derive monthly caloric values for alewives in cal/g wet weight. Identical values were used for both young-of-year and adult alewives even though there are possible ontogenetic shifts in caloric values with age (Yeo 1978). Monthly caloric values used for clupeids in Smith Mountain lake ranged from 1301 to 1493 cal/g for gizzard shad and 1361 to 1827 for alewives, respectively (Table 3.6).

The energy content value for gizzard shad may be a slight overestimate. Minton and McClean (1982) reported a mean energy value of 1169 cal/g for 66 gizzard shad collected in Watts Bar Reservoir, Tennessee. This value is 15% less than the mean (1372) of the derived monthly values (Table 3.6). Derived caloric values for alewives in Smith Mountain Lake are relatively similar to those determined by Yeo (1978). Accounting for temporal differences in reproduction due to different latitudes, the highest caloric content, 1827 cal/g (calculated from dry weight values

Table 3.6. Caloric content (cal/g wet weight) of prey items used in bioenergetics models for the four predatory species.

Month	Prey Items				
	Gizzard Shad	Alewives	Crayfish	Insects ^a	Other ^b
January	1463	1666	923	972	1110
February	1469	1725	923	972	1090
March	1493	1827	923	972	1090
April	1229	1588	923	972	1030
May	1337	1552	923	972	1080
June	1433	1504	923	972	1150
July	1301	1367	923	972	1000
August	1301	1394	923	972	1118
September	1349	1361	923	972	1090
October	1391	1421	923	972	1118
November	1409	1540	923	972	1160
December	1433	1606	923	972	1130

^a Mean value for aquatic and terrestrial insects from Penczak et al. (1984).

^b Includes non-clupeid fish, terrestrial vertebrates, and unidentified fish.

supplied by S. M. Adams), was observed for threadfin shad in March. This is less than the 2169 cal/g observed for alewives in November in Lake Michigan (Yeo 1978). The lowest value for threadfin shad, 1361 cal/g, was larger than the lowest monthly value of 1259 cal/g for alewives. Rottiers and Tucker (1982) determined a mean caloric content of 1636 cal/g for alewives collected from April to November in Lake Michigan. The mean caloric value derived for alewives in Smith Mountain Lake was 1525.5, a value 7% lower.

In the absence of seasonal data, I assumed a consistent caloric value of 923.4 cal/g for crayfish (Nielsen and Orth 1984). The mean of energy values measured by Penczak (1985) for Ephemeroptera, Diptera, and Chironomidae, 972 cal/g, was used as an annual caloric value for insects. These were the major insect groups found in stomachs of predators in Smith Mountain Lake. Caloric values for other food items were set equal to the mean, monthly caloric value used by Adams et al. (1982b) for sunfish, freshwater drum (Aplodinotus grunniens), and young-of-year bass (Table 3.6). Monthly caloric values were derived from dry weight estimates in a manner identical to that previously described, with a correction factor of 0.25.

Water Temperature

Accurate measurements of day to day temperatures experienced by a fish are only possible with intensive biotelemetry studies. Therefore, I assumed that predators occupied water temperatures nearest but not exceeding their preferred temperatures in Smith Mountain Lake. Water tem-

peratures were measured monthly at 1 m and 10 m depths from October 1973 to April 1976 at three locations in Smith Mountain Lake; the upper portion of the Roanoke River arm, the upper portion of the Blackwater River arm, and the main area of the lake below the confluence (Hart 1978). The means of these measurements for the three locations, at both 1 and 10 m depths (Fig. 3.4.), concur with temperature data taken quarterly by the Virginia State Water Control Board (unpublished data) during 1983 and 1984.

Oxygen measurements conducted during August, 1983 and 1984, the month when temperatures are highest and oxygen concentrations lowest, indicated that predators would not be oxygen limited at 10 m depths; i.e., values exceeded 4 ppm at least in the lower portions of the reservoir. There was no evidence of a "thermal-oxygen squeeze" (Coutant 1985), and predators apparently did not experience any temperatures above optimum for growth (as defined above), even during the hottest months of the year.

Growth

Striped bass, walleye, and the black basses were collected from Smith Mountain Lake with gill nets and electroshocking equipment from April to December, 1983 and 1984, to determine seasonal growth of all age groups. Collection areas and methodology are detailed in Chapter 1. Lengths and weights of all predators were measured to the nearest millimeter and gram, respectively. Scales were removed from the right side of all fish at a point just dorsal to the tip of the pectoral fin. Scales were prepared and aged using standard methodology (Jearld 1983). Annuli were counted,

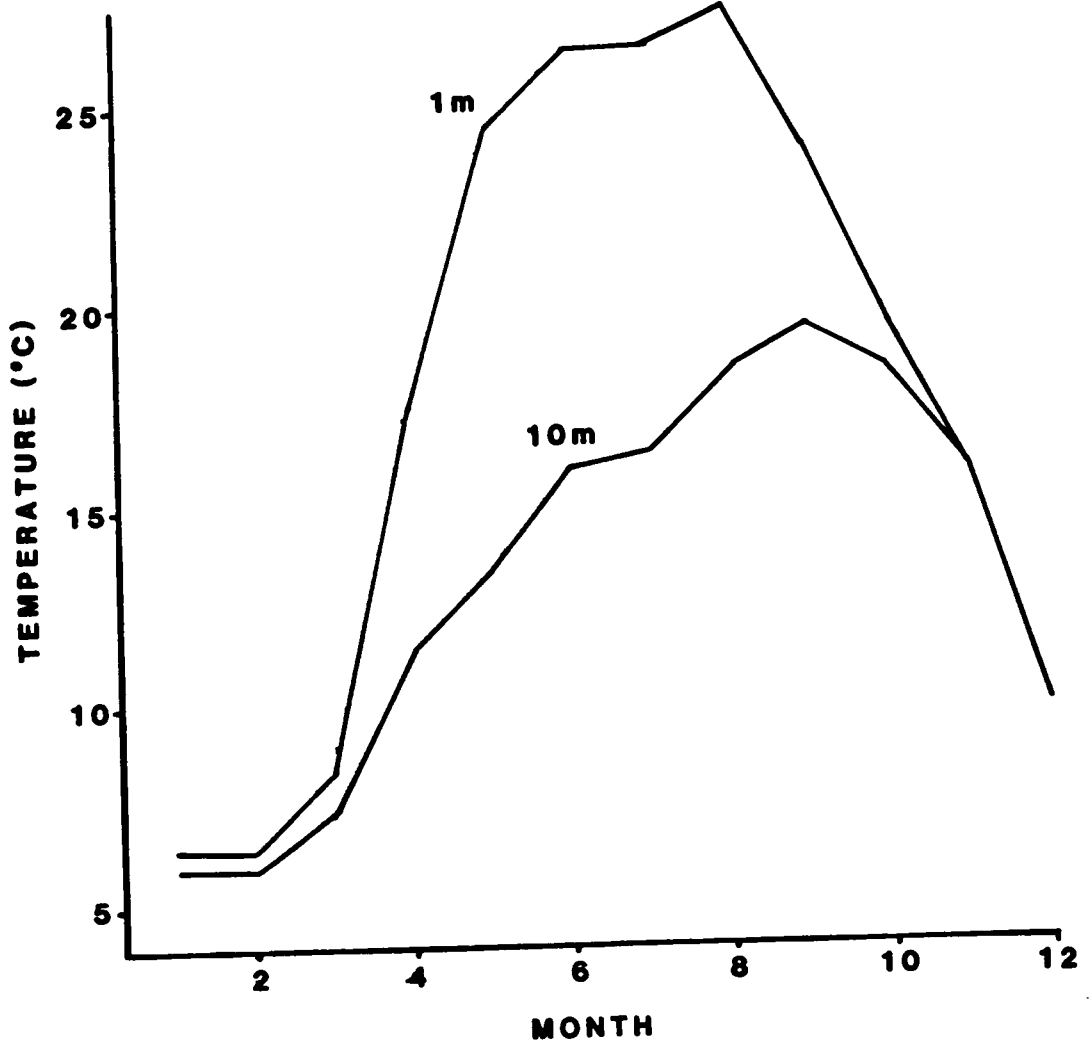


Figure 3.4. Mean water temperatures at three locations and two depths, 1 m and 10 m, in Smith Mountain Lake. Data are from Hart (1978).

and the distances from the focus to the annuli as well as to the scale radius were measured and recorded.

Based on water temperature data (temperatures below 10°C prior to approximately March 15 and after December 15), I assumed that annual growth for all predators occurred between March 15 and December 15 each year. Growth of largemouth bass does not occur below 10°C, and smallmouth bass may have a similar threshold (Coutant 1975). A Wilcoxon Rank Sum test between lengths of age 2 largemouth bass collected in the middle of December 1984 and mid-March 1985 in the same location with identical gear indicated no significant differences in lengths ($p=.299$). I was not able to test the validity of this assumption for the other predators. However, Minton and McClean (1981) found no growth in length of age-1 and age-2 sauger from Watts Bar Reservoir during winter. Seasonality of walleye growth is probably similar. Although juvenile striped bass were not tested below 18°C, the data of Cox and Coutant (1981) indicate that specific growth of striped bass would be negligible at temperatures below 10 - 12°C .

Mean monthly lengths of striped bass, largemouth bass, smallmouth bass, and walleye were calculated from empirical data for each age class. Observed values were assumed to represent lengths in the middle of the month, since sampling generally occurred throughout the entire monthly period. Although previous bioenergetic simulations have used measured weights in simulations (Adams et al. 1982, Minton and McClean 1982, Rice et al. 1983), not all age classes within each predator group in Smith Mountain Lake were adequately represented to use similar data.

Seasonal growth curves for all age groups of both striped bass and largemouth bass were derived using a modified version of the von Bertalanffy growth function fit to mean lengths measured monthly (Pauly and Gaschutz 1979 as cited in Moreau 1987):

$$L_t = L_{\infty}(1 - e^{(-K(t-t_0)A \times \sin(2\pi(t-t_s)))})$$

where L_t = length (mm) at time t , and L_{∞} , K , A , t_0 , and t_s , are species-specific constants. Coefficients in the revised model allow for more accurate estimates of intra-seasonal growth patterns. Curves were fit to observed data using a non-linear, least squares technique (Marquardt 1963 as cited in SAS Institute Inc. 1985).

Small sample sizes for a number of age groups precluded the use of monthly means to derive a growth curve for either the smallmouth bass or walleye populations. Instead, back-calculated lengths within age groups (i.e., only age-2 fish were used to determine a length at second annulus formation) were used as endpoints (December 15) for seasonal growth. Because I assumed no growth from December 15 to March 15, the modified von Bertalanffy growth function, as described above, was fitted to December 15 and March 15 values for both smallmouth bass and walleye. The values for parameters used in the modified von Bertalanffy equation to describe the seasonal growth of the four predators are presented in Table 3.7. These growth equations are graphically represented for striped bass (Fig. 3.5), largemouth bass (Fig. 3.6), smallmouth bass (Fig. 3.7), and walleye (Fig. 3.8).

Table 3.7. Parameters used to describe seasonal growth curves for all age groups of predators in Smith Mountain Lake, 1983-1984. Parameters correspond to the modified von Bertalanffy growth function.

Predator	Parameter				
	L_{∞}	K	t_0	A	t_S
Striped bass	883.383375	.280146	-.277699	.048502	-.200000
Largemouth bass	550.582187	.294079	-.414323	.059410	.900000
Smallmouth bass	533.430439	.330567	.219926	.050667	-.210155
Walleye	625.262039	.352818	-.700000	.056437	-.200000

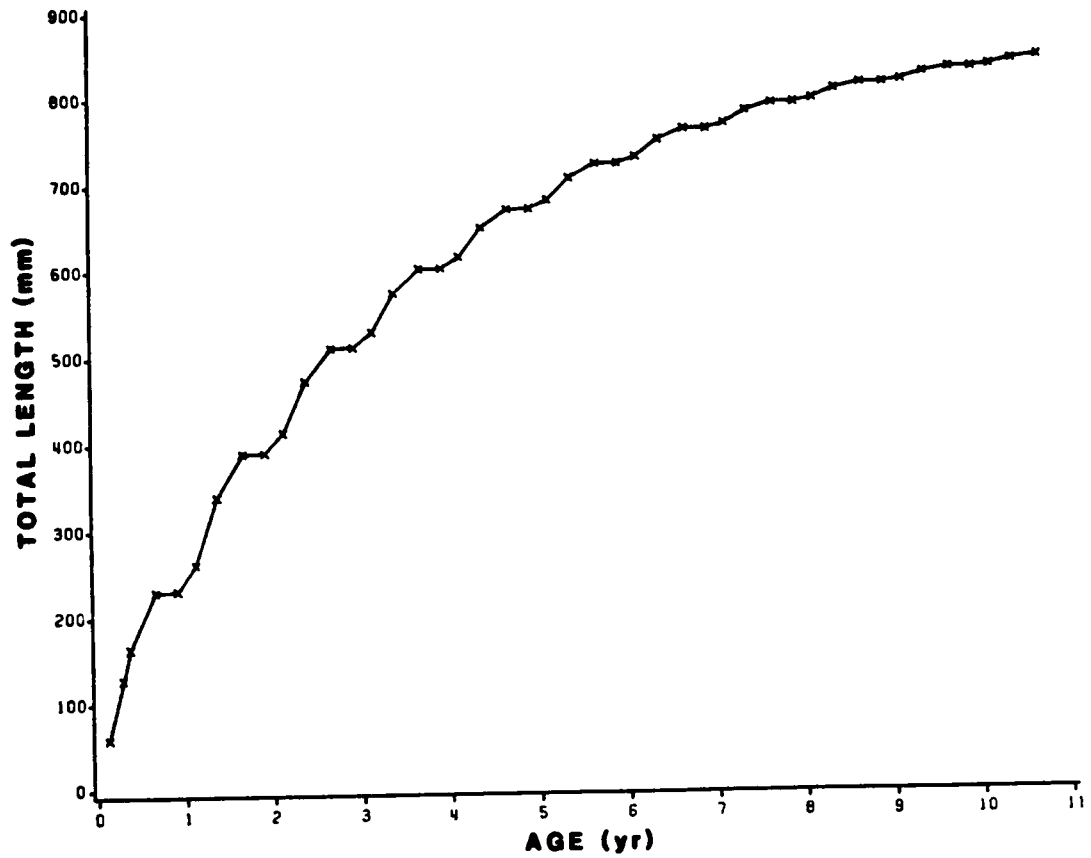


Figure 3.5. Seasonal growth (TL mm) of striped bass, ages 0 to 11. The line is derived from a modified von Bertalanffy growth function fit to monthly mean lengths of striped bass from Smith Mountain Lake, 1983-1984.

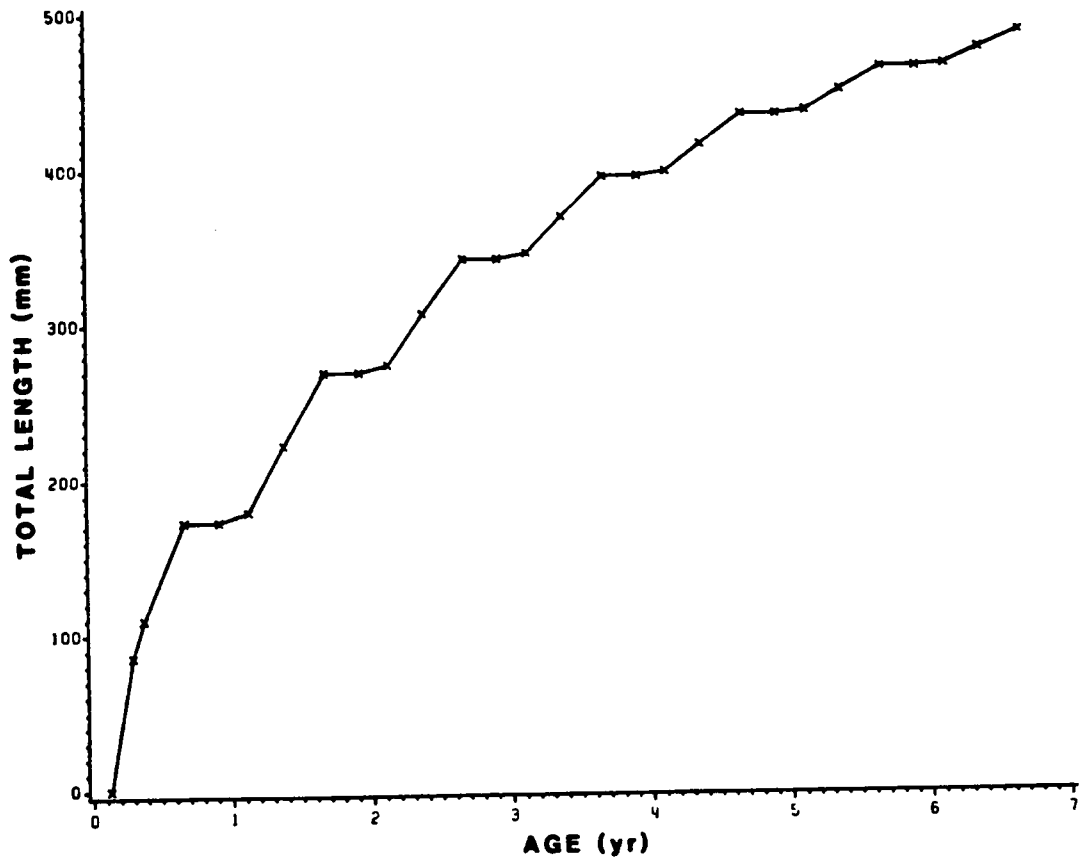


Figure 3.6. Seasonal growth (TL mm) of largemouth bass, ages 0 to 7. The line is derived from a modified von Bertalanffy growth function fit to monthly mean lengths of largemouth bass from Smith Mountain Lake, 1983-1984.

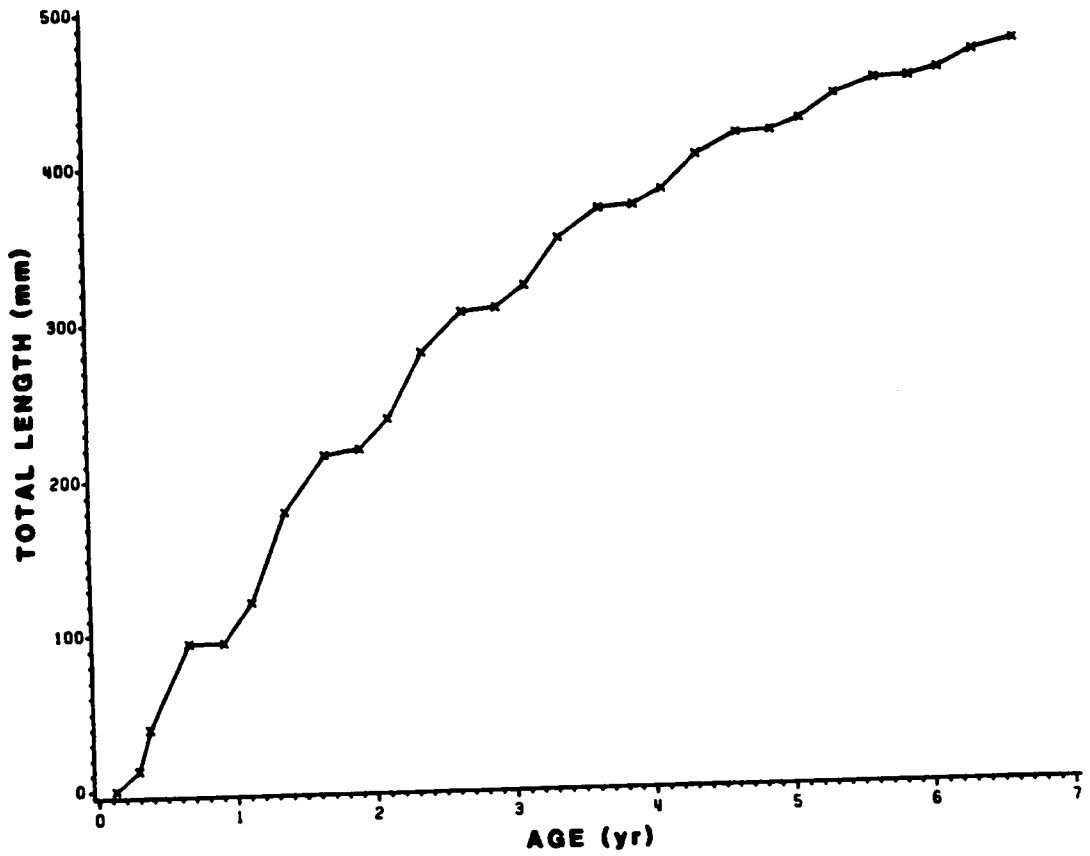


Figure 3.7. Seasonal growth (TL mm) of smallmouth bass, ages 0 to 7. The line is derived from modified von Bertalanffy growth function fit to monthly mean lengths of smallmouth bass from Smith Mountain Lake, 1983-1984.

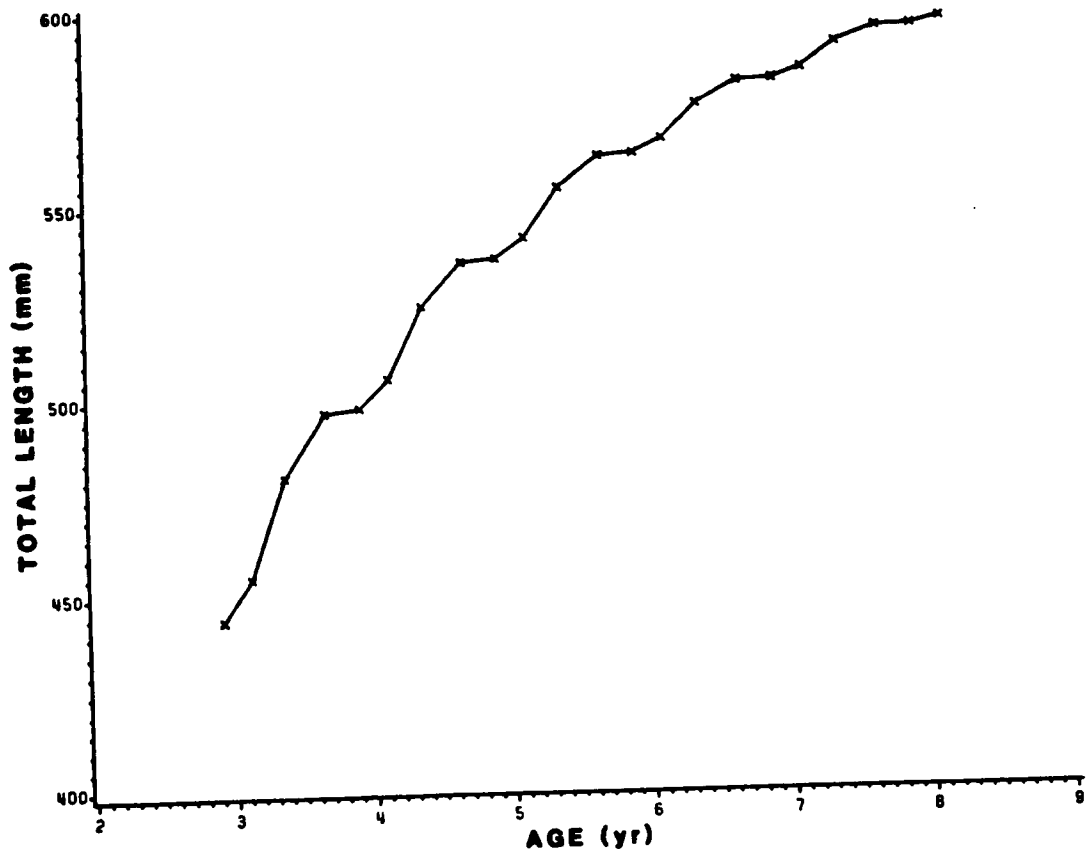


Figure 3.8. Seasonal growth (TL mm) of walleye, ages 2 to 9.
 The line is derived from a modified von Bertalanffy growth function
 fit to monthly mean lengths of walleye from Smith Mountain Lake,
 1983-1984.

Length-weight regression equations were developed for several age groupings of each of the four species to derive weights from calculated lengths. Ages were grouped to account for temporal changes in condition factor with size and season, although sample size precluded some groupings. Since some seasonal sample sizes were small, I used a nonparametric, Theil-Sen procedure (Hollander and Wolfe 1973) to derive regression equations. This technique is less sensitive to outliers in the data set and is more appropriate than parametric, least squares techniques when sample sizes are small. Striped bass sample sizes allowed the derivation of 13 separate regression equations for a total of four separate age groupings (Table 3.8). I derived eight regression equations for two separate age groups of largemouth bass (Table 3.9). Since sample sizes of smallmouth bass were prohibitively small, I calculated only four regression equations for this predator (Table 3.10). The walleye population in Smith Mountain Lake consists almost exclusively of adults (Chapter II). Thus, only four seasonal regression equations were calculated for walleye (Table 3.11).

Consumption estimates derived from annual endpoints of growth do not account for seasonal changes in prey abundance (Cochran and Rice 1981, Rice and Cochran 1984). Thus, I divided the yearly growth period into three separate intervals for each age class within each predator group. These periods were spring, March 15 to June 1; summer, June 1 to September 1; and fall, September 1 to December 15. Total lengths at each of the four separate dates (March 15, June 1, September 1 and December 15) were obtained from the species-specific growth equations. I assumed that age-0

Table 3.8. Seasonal length-weight regression equations developed for striped bass age groupings. Equations were developed using nonparametric, Theil-Sen regression procedures. Y is ln weight in grams and X is ln total length in millimeters.

Age	Season	Equation	N
0	Fall/ Winter	$Y = -11.50201 + 3.00741(X)$	54
1	Winter	$Y = -11.32310 + 2.99417(X)$	18
1	Spring	$Y = -13.90792 + 3.43806(X)$	45
1	Summer	$Y = -13.26736 + 3.33589(X)$	145
1	Fall	$Y = -11.30392 + 2.98828(X)$	85
2-4	Winter	$Y = -10.81254 + 2.90517(X)$	16
2-4	Spring	$Y = -9.71012 + 2.73575(X)$	103
2-4	Summer	$Y = -8.43289 + 2.53174(X)$	54
2-4	Fall	$Y = -10.21389 + 2.81003(X)$	30
5-10	Winter	$Y = -8.12095 + 2.50362(X)$	35
5-10	Spring	$Y = -10.38054 + 2.83499(X)$	36
5-10	Summer	$Y = -9.30696 + 2.66373(X)$	19
5-10	Fall	$Y = -10.20808 + 2.80916(X)$	32

Table 3.9. Seasonal length-weight regression equations developed for largemouth bass age groupings. Equations were developed using nonparametric, Theil-Sen regression procedures. Y is ln weight in grams and X is ln total length in millimeters.

Age	Season	Equation	N
0-1	Winter	$Y = -11.10916 + 2.99314(X)$	11
0-1	Spring	$Y = -12.52789 + 3.21424(X)$	15
0-1	Summer	$Y = -11.87437 + 3.1076(X)$	62
0-1	Fall	$Y = -14.61396 + 3.58826(X)$	26
2-6	Winter	$Y = -12.43533 + 3.23587(X)$	49
2-6	Spring	$Y = -12.93515 + 3.29841(X)$	118
2-6	Summer	$Y = -12.34697 + 3.20068(X)$	62
2-6	Fall	$Y = -13.40522 + 3.37883(X)$	30

Table 3.10. Seasonal length-weight regression equations developed for smallmouth bass age groupings. Equations were developed using nonparametric, Theil-Sen regression procedures. Y is ln weight in grams and X is ln total length in millimeters.

Age	Season	Equation	N
0-1	Annual	$Y = -8.68889 + 2.53532(X)$	26
2-6	Spring	$Y = -13.33335 + 3.35752(X)$	40
2-6	Summer	$Y = -12.13305 + 3.15648(X)$	56
2-6	Fall/ Winter	$Y = -11.45152 + 3.04619(X)$	14

Table 3.11. Seasonal length-weight regression equations developed for walleye. Equations were developed using nonparametric, Theil-Sen regression procedures. Y is ln weight in grams and X is ln total length in millimeters.

Season	Equation	N
Winter	$Y = -9.13052 + 2.64581(X)$	19
Spring	$Y = -10.77259 + 2.88907(X)$	219
Summer	$Y = -9.66791 + 2.72072(X)$	117
Fall	$Y = -9.75347 + 2.73928(X)$	31

fish were not primarily piscivorous until August 1. Thus, for age-0 striped bass, largemouth bass, and smallmouth bass, I only considered growth during two periods; summer (August 1 to September 1) and fall (September 1 to December 15). Derived lengths were used to compute weights from the appropriate periodic length-weight regression equations for input into the bioenergetics computer model.

The derived weights for striped bass agree closely with the observed mean weights measured monthly (Fig. 3.9). Agreement was best for the younger age groups due to larger sample sizes. Derived weights for largemouth bass were also similar to measured values (Fig. 3.10). The derived weights for walleye also concurred with the empirical weights, with a large portion of the derived weight curve within ± 1 SD of the measured means (Fig. 3.11). Similarly, where sample sizes were adequate, derived weight values for smallmouth bass agreed with empirical data (Fig. 3.12).

Diet

Collection of predators and treatment of stomach samples for food habit analysis are detailed in Chapter 1. I combined stomach samples from the upper and lower lake to determine food habits of each predatory species for the entire lake. Diet was classified as proportion of total food weight in six separate food categories for the black basses and five food categories for striped bass and walleye. If sample size was sufficient, the diet was categorized by age to account for any age-specific shifts in food habits.

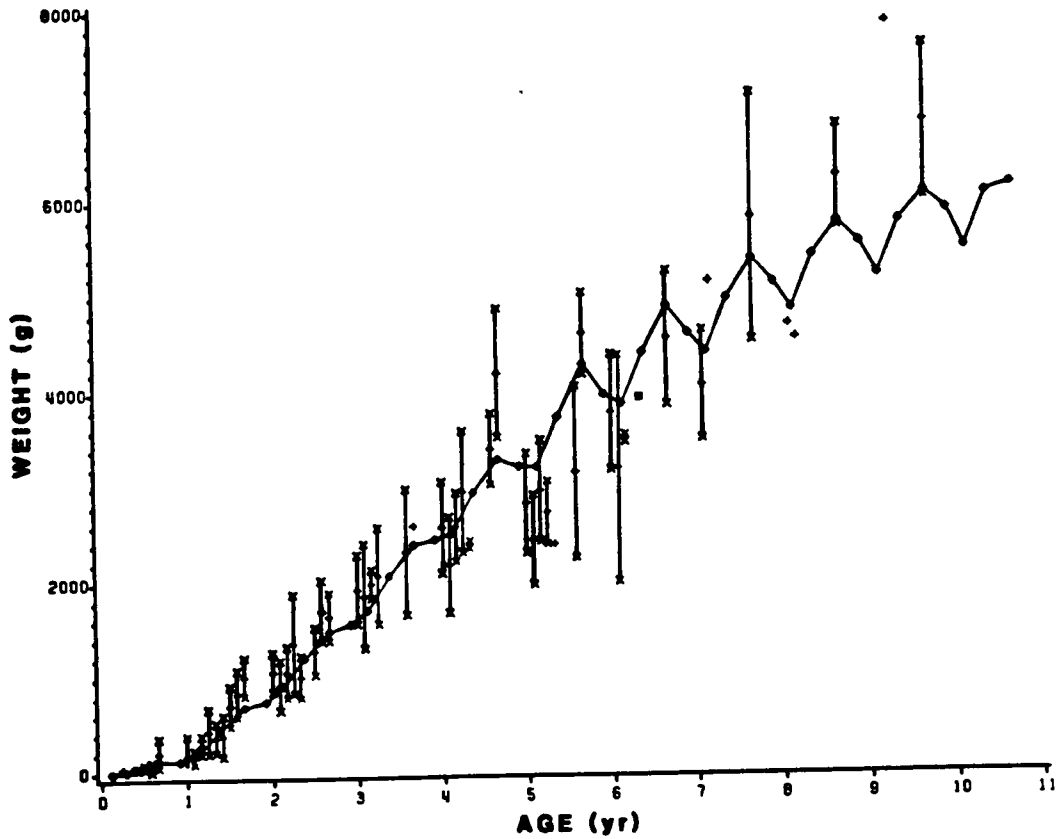


Figure 3.9. Seasonal growth in weight (g) of striped bass, ages 0 to 11. Weights are derived from a modified von Bertalanffy growth equation and seasonal length-weight regressions. Derived weights are plotted with observed mean weight \pm 1 SD.

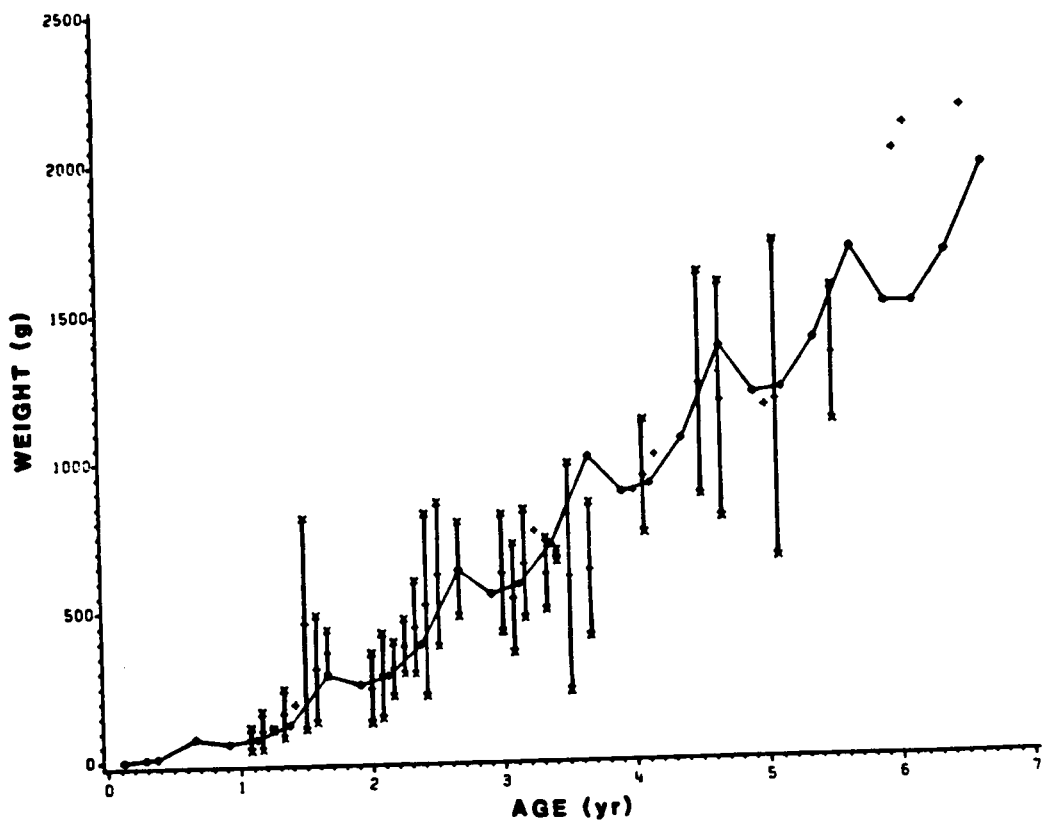


Figure 3.10. Seasonal growth in weight (g) of largemouth bass, ages 0 to 7. Weights are derived from a modified von Bertalanffy growth equation and seasonal length-weight regressions. Derived weights are plotted with observed mean weight \pm SD.

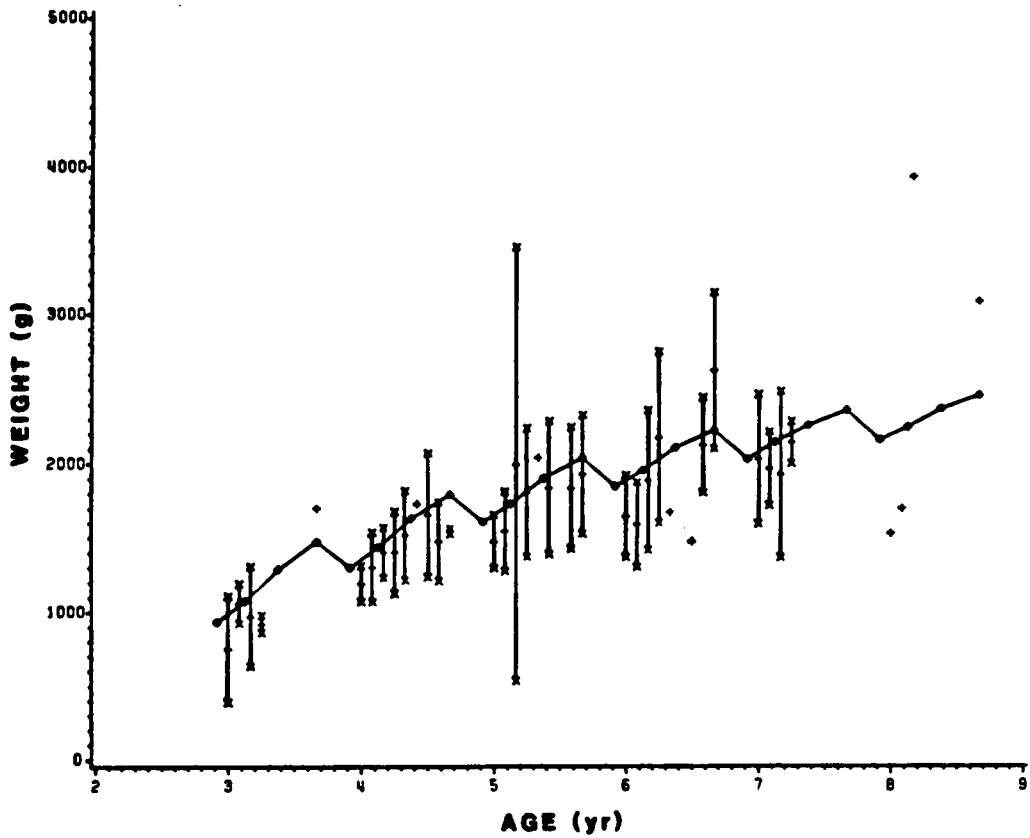


Figure 3.11. Seasonal growth in weight (g) of walleye, ages 3 to 9. Weights are derived from a modified von Bertalanffy growth equation and seasonal length-weight regressions. Derived weights are plotted with observed mean weight \pm SD.

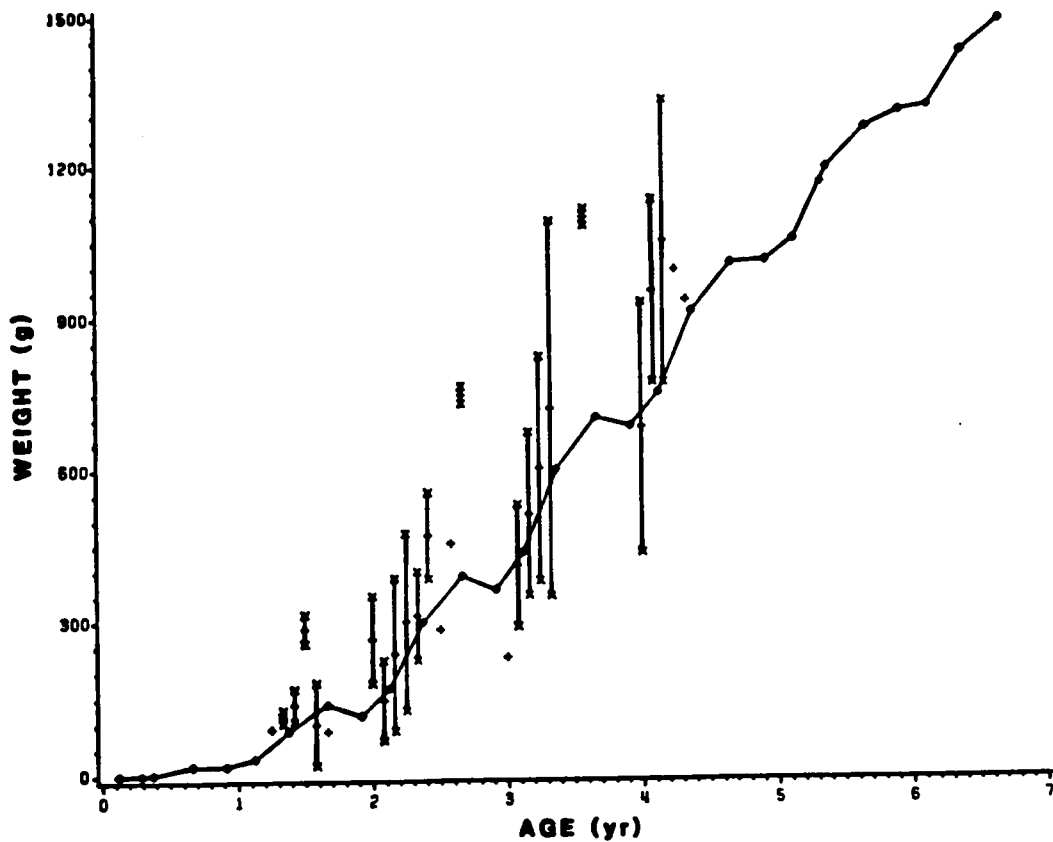


Figure 3.12. Seasonal growth in weight (g) of smallmouth bass, ages 0 to 7. Weights are derived from a modified von Bertalanffy growth equation and seasonal length-weight regressions. Derived weights are plotted with observed mean weight \pm SD.

I categorized the seasonal diet of striped bass by three age classifications: age 0, age 1, and ages 2 to 9 (Table 3.12). Similarly, sample sizes of largemouth bass were sufficient to categorize food habits by three age classifications: ages 0, 1, and ages 2 to 6 (Table 3.13). Limited sample size mandated a general representation of diet for all ages of walleye (Table 3.14) and smallmouth bass (Table 3.15). This is a reasonable assumption for the walleye population in Smith Mountain Lake since the population was composed largely of individuals age 3 and older. However, although the diet of age 1 and older smallmouth bass may be similar, diet of underyearling fish may be significantly different (Coble 1975). To account for this difference, I assumed that the diet of age-0 smallmouth was similar to that of age-0 largemouth bass, accounting for distributional differences between these species in the reservoir (Chapter I).

Population Parameters

The final site-specific variable needed to compute demand by a predator population is an estimate of survival. Survival estimates were derived for predators as described in Chapter II. Survival estimates were used to compute numbers-at-age for each predator at the beginning of the modeling simulation, March 15. Annual survival estimates were converted to daily rates for input into the bioenergetics model.

Table 3.12. Seasonal diet of striped bass as percent of total food weight for five prey categories. Values are given by age, date, and the corresponding day in the modeling simulation.

Date	Day for Modeling Simulation	Adult Alewife	^a Y-O-Y Alewife	Gizzard Shad	Crayfish	Other
Age 0						
August 1	123	.045	.387	.074	.226	.269
October 15	215	.081	.707	.136	0	.076
December 15	276	.289	.534	.11	0	.067
Age 1						
March 15	1	.593	.283	.072	0	.052
May 1	47	.754	.15	.052	0	.045
July 15	123	.821	.124	.024	.022	.01
October 15	215	.156	.382	.357	.074	.031
December 15	276	.049	.012	.78	.001	.158
Ages 2-10						
March 15	1	.486	.122	.36	.006	.027
May 1	47	.713	.178	.061	.009	.039
July 15	123	.541	.12	.242	.081	.016
October 15	215	.481	.077	.352	.08	.01
December 15	276	.052	.014	.929	.002	.003

^a Young-of-year

Table 3.13. Seasonal diet of largemouth bass as percent of total food weight for six prey categories. Values are given by age, date, and the corresponding day in the modeling simulation.

Date	Day for Modeling Simulation	Adult Alewife	Y-0-Y Alewife	Gizzard Shad	Crayfish	Insects	Other
Age 0							
August 1	123	0	0	.614	.086	.228	.072
December 15	276	.074	0	.469	.203	0	.164
Age 1							
March 15	1	.117	0	.385	.272	.008	.218
May 1	47	.173	0	.33	.163	.012	.322
July 15	123	0	0	.748	.059	.002	.191
October 15	215	0	0	.848	.084	0	.068
December 15	276	.014	.009	.328	.628	0	.02
Age 2							
March 15	1	.142	.094	.127	.439	.001	.198
May 1	47	.209	.138	.021	.34	.002	.29
July 15	123	.118	.049	.411	.132	.001	.289
October 15	215	0	0	.725	.151	0	.124
December 15	276	.005	0	.647	.26	0	.088
Age 3-6							
March 15	1	.046	0	.223	.399	0	.339
May 1	47	.068	0	0	.473	0	.459
July 15	123	.082	0	.287	.196	0	.435
October 15	215	0	0	.395	.215	0	.39
December 15	276	.005	0	.753	.193	0	.049

Table 3.14. Seasonal diet of walleye as percent of total food weight by five prey categories. Values are given by age, date, and the corresponding day in the modeling simulation.

Date	Day for Modeling Simulation	Adult Alewife	Y-O-Y Alewife	Gizzard Shad	Crayfish	Other
Ages 4-8						
March 15	1	.706	.031	.173	0	.090
May 1	47	.834	.036	.028	0	.101
July 15	106	.876	.074	.025	.004	.021
October 15	215	.056	0	.907	0	.036
December 15	365	.706	.031	.173	0	.090

Table 3.15. Seasonal diet of smallmouth bass as percent of total food weight for six prey categories. Values are given by age, date, and the corresponding day in the modeling simulation.

Date	Day for Modeling Simulation	Adult Alewife	Y-O-Y Alewife	Gizzard Shad	Crayfish	Insects	Other
Age 0							
August 1 ^a	123	0	.250	.250	.250	.250	.0
December 15	276	.242	.144	.270	.172	.003	.169
Ages 1-6							
March 15	1	.382	.082	.282	.126	.004	.124
May 1	47	.485	.074	.258	.060	.003	.120
July 15	123	.285	.20	.405	.069	.007	.034
October 15	215	.05	.106	.384	.337	.007	.116
December 15	276	.185	.116	.343	.251	.006	.100

^a
The diet was assumed for this date.

Bioenergetics Program

The complete documentation and user's guide for the bioenergetics program used in this study are detailed in Hewett and Johnson (1987). An Apple IIe microcomputer (64K) with an eighty column card and two disk drives is needed to run the computer program. The program is versatile with several options for equations that can be used to calculate consumption, respiration, egestion and excretion rates. These equations are derived from the work of Kitchell et al. (1977), Stewart (1980), and Rice et al. (1983). A brief synopsis of the program operation and output is described below.

The program is capable of modeling the energetics of a particular fish species to derive estimated growth from field consumption estimates. However, the real utility of the program (and model) is in its ability to estimate consumption rates (daily, season, or year) from observed (or calculated) growth curves. A consumption estimate requires a set of data files that is of two main types. The first, cohort data files, include bioenergetics parameters, mortality values, and initial population sizes of each predator modeled. Seasonal/daily files, the second set, include caloric densities of predators and prey, water temperature and predator diet.

Seasonal or daily files can contain information for up to 36 separate days within a simulation period. Daily values between these intervals are estimated by linear interpolation. Caloric densities are entered as cal/g wet weight and temperature is entered in $^{\circ}C$. Diet is expressed as a proportion of as many as eight prey types. The sum of the proportions

must equal 1.0. The simulation can begin and end on any calendar date. Day 1 for the Smith Mountain Lake simulations was March 15, the beginning of the growing season.

P-Values

The first function of the program, after all initial data files have been entered, is to calculate the proportionality constant P (proportion of maximum daily ration consumed) by fitting the bioenergetics equations to initial and final weight values that are input for a particular cohort for a given time interval. Because a single P-value, fit to annual endpoints of growth, cannot adequately describe intra-seasonal growth dynamics (Rice et al. 1984), I divided the annual growing season into three separate intervals, spring, summer, and fall as previously described. These periods corresponded to seasonal changes in food availability, as well as temperature changes; i.e., increasing, stable, and decreasing. Three separate P-values were derived for each cohort, age 1 and older, of each of the four predator groups. I considered age-0 predators (striped bass, largemouth bass, and smallmouth bass) to be largely piscivorous after August 1. Thus, only two P-values were calculated for this age group. The program calculates the appropriate P-value through an iterative process after an initial, arbitrary P-value (e.g., 0.5) is entered.

P-values calculated for predators in Smith Mountain Lake ranged from 0.0734 for age-10 striped bass in spring to 0.6706 for age-0 largemouth bass in the fall. The mean P-values were calculated by season for pred-

ator populations in Smith Mountain Lake (Table 3.16). Striped bass, smallmouth bass, and walleye exhibited higher P-values during the summer period than in any other season, whereas largemouth bass exhibited the largest proportion of maximum consumption during fall.

P-values are a reflection of prey availability as well as an index of the intensity of predation (Cochran and Rice 1981, Rice et al. 1983). Adult alewives are the principal component in the diet of striped bass, smallmouth bass, and walleye during the summer months due to distributional similarities between these predators and this prey species (Chapter I). Availability, coupled with optimal temperatures for consumption, account for the higher summer P-values for these predators. In fact, P-values for walleye remain relatively constant throughout the growing period, perhaps reflecting the consumption of clupeids by this predator during all three seasons. Conversely, habitat preferences of largemouth bass in the upper lake limit access to abundant alewife schools during the summer. Highest P-values for this predator occur during fall when young-of-year shad are most abundant. Similarly, Rice and Cochran (1984) derived higher P-values for age-3 largemouth bass in Lake Rebecca, Minnesota during fall.

Conversion Efficiencies

Gross conversion efficiencies (growth/consumption) for the entire growing season were calculated for striped bass using the bioenergetics model and data for the striped bass population in 1983-1984 (Table 3.17).

Table 3.16. Mean seasonal P-values, the proportion of maximum consumption, for predator populations in Smith Mountain Lake.

Predator	^a		
	Spring	Summer	Fall
Striped bass	.1515	.4093	.3480
Largemouth bass	.3471	.2813	.4260
Smallmouth bass	.2931	.3085	.2673
Walleye	.3309	.3867	.3608

^a
 Because predators were not considered significantly piscivorous until August 1, no P-values were calculated for age-0 predators during this season.

Table 3.17. Mean weight gain, ration and gross conversion efficiency for striped bass age groups in Smith Mountain Lake. The values represent the growing season, March 15 to December 15.

Age	Weight Gain	Ration (C/Cmax)	% Gross Conversion Efficiency
0	109.2	.421	40.6
1	567.4	.363	34.4
2	753.3	.272	25.5
3	832.1	.283	16.5
4	836.0	.271	14.2
5	1072.0	.282	13.8
6	924.5	.279	10.7
7	775.0	.277	8.3
8	639.1	.275	6.4
9	522.7	.273	5.0
10	259.2	.270	2.0

Efficiencies decreased from 40.6% for age-0 striped bass to 2.0% for age-10 striped bass. It is typical for conversion efficiencies to decline with increasing body size (Adams et al. 1982a, Pauly 1986). The value for age-0 fish represents the efficiency for August 1 through December 15 only. Excluding age-0 fish, the mean conversion efficiency for the remaining 10 age groups was 13.7% for the entire growing season. Conversion efficiencies for striped bass during summer, when they would hypothetically experience optimum temperatures for consumption and growth, were higher and ranged from 34.5% to 18.4% for ages 0 to 10 (Table 3.18). Excluding age-0 fish, the mean conversion efficiencies were 21.9% for striped bass in summer. These results indicate that ecological growth efficiency values of 20% used in biomass models (Ploskey and Jenkins 1982) may result in considerable error when applied to striped bass during seasons other than summer. However, computed summer efficiencies substantiate the assumption of a 20% conversion efficiency to develop AP/P ratios for striped bass in August (Jenkins and Morais 1978).

These age-specific efficiencies can be used to derive striped bass consumption estimates, if the appropriate computer hardware is unavailable to use the bioenergetics model (Eck and Wells 1983). Efficiencies are applicable to a system where clupeids are the major food items, and striped bass do not experience any significant thermal stress. Although some bias is involved when annual estimates of conversion efficiency are used, the values should give a general indication of impact or demand of striped bass for a particular prey species. To determine this demand, age-specific gross conversion efficiencies can be applied to striped bass

Table 3.18. Mean weight gain, ration and gross conversion efficiency for striped bass age groups in Smith Mountain Lake. The values are for the summer period, June 1 to August 31.

Age	Weight Gain	Ration (C/Cmax)	% Gross Conversion Efficiency
0	27.8	.576	45.1
1	251.7	.474	35.7
2	287.2	.385	23.9
3	362.7	.380	21.6
4	425.4	.380	20.6
5	522.0	.390	21.0
6	540.3	.387	20.1
7	551.4	.385	19.5
8	558.1	.383	18.9
9	562.4	.382	18.7
10	565.0	.381	18.4

production estimates for each age to determine the amount of food required to produce the biomass of each striped bass cohort. Diet analysis can then be used to partition these annual food requirements into the various prey components.

Predator Demand

Calculation of Demand

The bioenergetics computer program was implemented using species specific parameters and derived P-values for all cohorts of the four predator species. The program calculated daily, specific rates of respiration, egestion, excretion, and SDA. Daily rates were used with proportional diet data and energy values to estimate daily consumption of a particular prey item by a cohort during the simulation period. Population size, coupled with daily survival values and consumption rates, provided estimates of total consumption of a prey item over a simulation period.

Diet analysis (Chapter I) indicated that clupeids, alewives and gizzard shad, were the principal prey items consumed by predators during 1983 and 1984 in Smith Mountain Lake. Although predators consumed young-of-year shad almost exclusively (i.e., few older shad were eaten), both young-of-year and adult alewives were important prey items. Thus, alewives were considered to represent two functionally separate prey groups. Since available food is typically the principal factor limiting predator production in reservoirs (Jenkins 1975, Rainwater and Houser 1975, Jenkins and Morais 1978), population sizes of these clupeids would

be the major determinant of predator growth and survival in Smith Mountain Lake. Thus, I implemented the bioenergetics program to estimate total consumption of these clupeids by individual cohorts of each predator during three periods within the annual growing season.

Demand Estimates

Collectively, the four predatory species consumed more adult and young-of-year alewives during summer, an estimated 125,530 kg and 39,453 kg, respectively, than in any other season (Table 3.19). The four species, particularly largemouth bass, consumed the largest amount of gizzard shad, 255,437 kg, during fall. Consumption values for largemouth bass were near 70% of the total shad biomass consumed by all predators during all three periods.

Analyses of the total annual consumption estimates by species indicated that striped bass ate more adult alewives, during all three seasons, than the other three species combined. Percentages of total consumed biomass ranged from 52.1% to 69.8% for the three seasons. Similarly, striped bass consumed the greatest proportion of young-of-year alewives relative to the other predators, with values of 47.9%, 63.1%, and 86.2% for spring, summer, and fall, respectively.

In general, smallmouth bass and walleye had relatively little impact on either the alewife or gizzard shad populations over the growing season. Low consumption estimates for these two predators resulted from their relatively low population levels. However, smallmouth bass did consume

Table 3.19. Seasonal consumption (kg) of clupeids by predators in Smith Mountain Lake. Estimates are derived from bioenergetics simulations.

Predator	Adult Alewife	Y-O-Y Alewife	Gizzard Shad
SPRING			
Striped bass	35,883	8,722	6,276
Largemouth bass	13,622	2,836	24,698
Smallmouth bass	4,863	5,966	3,608
Walleye	14,460	697	1,395
Total	68,828	18,221	35,977
SUMMER			
Striped bass	87,627	24,883	24,963
Largemouth bass	8,485	1,651	84,710
Smallmouth bass	6,044	3,677	8,205
Walleye	23,374	9,242	3,655
Total	125,530	39,453	121,533
FALL			
Striped bass	31,115	17,640	45,316
Largemouth bass	7,449	290	184,310
Smallmouth bass	1,884	2,099	6,062
Walleye	6,838	438	19,749
Total	47,286	20,467	255,437

nearly 33% of the total amount of young-of-year alewives eaten by the four predators during spring.

Comparison of the relative predatory impact of various age groups within each predator population indicated that ages 0-3, for all species except walleye, consumed the greatest biomass of clupeids annually. Based on 1983 population estimates and associated survival rates, ages 1 and 2 striped bass consumed over 70% of the total adult alewives eaten by the striped bass population (Table 3.20). Consumption of young-of-year alewives peaked with yearling striped bass, but consumption was also high for ages 0 and 2 striped bass. More gizzard shad were consumed by age-2 striped bass than any other striped bass cohort, with a value over twice that of age-3 fish.

Consumption of alewives by largemouth bass was relatively low compared to striped bass, but ages 1 and 2 largemouth consumed over 61% of the total adult alewives eaten by the largemouth bass population (Table 3.21). Although young-of-year alewives were relatively insignificant in the diet of largemouth bass, nearly all the age-0 alewives consumed by largemouth bass (4,770 kg) were eaten by age-2 largemouth bass. Age-1 largemouth bass consumed an estimated 147,280 kg of gizzard shad, more than any other predator cohort.

Estimates of clupeid consumption by smallmouth bass were the lowest of any predator population. Age-2 smallmouth bass consumed more adult alewives, 3,930 kg, than any other age group within this predator population, whereas more young-of-year alewives, 3,440 kg, were eaten by age-3

Table 3.20. Biomass (kg) of clupeids consumed by ages 0 to 10 striped bass in Smith Mountain Lake, 1983-84.

Age	Adult Alewife	Y-O-Y Alewife	Gizzard Shad
0	2,042	12,610	2,437
1	55,459	17,098	13,747
2	53,693	11,540	32,396
3	23,520	5,006	15,512
4	13,356	2,846	8,212
5	1,713	1,118	1,134
6	2,998	633	1,979
7	1,185	250	781
8	391	82	257
9	148	31	46
10	120	33	49
Total	154,625	51,247	76,550

Table 3.21. Biomass (kg) of clupeids consumed by ages 0 to 6 largemouth bass in Smith Mountain Lake, 1983-84.

Age	Adult Alewife	Y-O-Y Alewife	Gizzard Shad
0	6,588	-	81,380
1	9,516	15	148,280
2	8,531	4,762	38,189
3	2,989	-	16,535
4	701	-	3,564
5	734	-	3,512
6	495	-	2,265
Total	29,554	4,777	293,725

smallmouth bass (Table 3.22). Age-1 smallmouth bass consumed the greatest proportion of gizzard shad within the smallmouth bass population.

Age-4 walleye, the last cohort stocked in Smith Mountain Lake, were the principal consumers of alewives and shad relative to the other walleye age groups (Table 3.23). Age-5 walleye also consumed significant amounts of adult and young-of-year alewives.

Overview of Demand

The relative demand of each predator cohort, as well as each predator population, for alewives and gizzard shad can be explained by a number of factors related to both predators and prey. These factors, summarized below, are more fully detailed in Chapter I and to a lesser extent in Chapter II of this dissertation.

Striped bass and largemouth bass are the most abundant predators in the reservoir and thus consume the greatest proportion of available forage. In addition, ages 0, 1, and 2 fish are the most numerous individuals within each of these two predator populations. This predominance, as well as age-specific food habits, partly explain the greater amount of clupeids consumed by these age groups relative to the older predators. Similarly, age-4 walleye, the last cohort stocked in Smith Mountain Lake and thus the most abundant, consumed the greatest proportion of clupeids within the walleye population.

Young-of-year alewives and gizzard shad are consumed in greatest amounts as they reach a threshold size and thus become morphologically available to juvenile and adult predators in late summer and fall. Most

Table 3.22. Biomass (kg) of clupeids consumed by ages 3 to 8 walleye in Smith Mountain Lake, 1983-84.

Age	Adult Alewife	Y-O-Y Alewife	Gizzard Shad
3	1,770	117	1,018
4	20,423	8,780	11,433
5	13,517	890	7,454
6	7,248	477	3,963
7	512	33	279
8	1,202	79	652
Total	44,672	10,376	24,799

Table 3.23. Biomass (kg) of ciupeids consumed by ages 0 to 6 smallmouth bass in Smith Mountain Lake, 1983-84.

Age	Adult Alewife	Y-O-Y Alewife	Gizzard Shad
0	322	426	595
1	2,910	2,012	5,396
2	3,935	1,906	5,082
3	2,608	3,437	3,206
4	1,329	1,730	1,553
5	1,648	2,178	1,879
6	41	55	160
Total	12,793	11,744	17,871

of the young-of-year alewives and young-of-year shad are consumed by age-0 striped bass and largemouth bass during fall when ingestible sizes of these prey are most available. More young-of-year alewives and shad are consumed by age-1 striped bass and largemouth bass, respectively, than any other age groups, because these prey items are morphologically available to these larger predators for a longer period of time; i.e., fall to the following spring. Similarly, age-2 striped bass consumed more shad than any other striped bass age group because they are capable of consuming the fast-growing shad for a longer period of time. For example, shad comprised 36% of the food items consumed by age 2 and older striped bass in early spring (when shad are 7 to 10 months old) compared to roughly 7% for ages 0 and 1 striped bass.

Alewives are pelagic and tend to inhabit the broad, deep waters of the lower reservoir during most seasons. As a result, alewives are available to striped bass and walleye (and to a lesser extent smallmouth bass) which share a preference for this lower lake habitat, especially during the warmer months. Gizzard shad prefer the upper, more riverine sections of the reservoir and thus are more available to largemouth bass which are also found in greater abundance in this habitat. Conversely, the preference of shad for warmer, uplake waters may segregate this species from striped bass and walleye during spring and summer, when these predators are thermally restricted to the lower areas of the reservoir.

Predator Demand vs Clupeid Supply

Although demand for prey among predatory species is inherently interesting, greater utility of bioenergetics simulation is achieved through comparison with prey availability. However, unbiased estimates of clupeid supply are problematic. In the Great Lakes and some southern reservoirs, estimates of clupeid biomass have been based on mid-water and bottom trawl surveys and meter net tows. In reservoirs, estimates are relatively reliable if gear selectivity is accounted for or avoided (Houser and Netsch 1971) and sampling design is adequate, e.g. stratified random (Houser and Dunn 1967, Siler et al. 1986). However, in the Great Lakes, the correct conversion factor to transform the amount of alewife biomass in trawls to lakewide estimates of biomass is unknown (Hatch et al. 1981). Because of the importance of clupeids to predators in Smith Mountain Lake, I derived an estimate of clupeid supply from best available data.

Calculation of Clupeid Supply

Biomass and production estimates for alewives and gizzard shad in Smith Mountain Lake were derived from a concurrent study on larval distribution and abundance of alewife and gizzard shad (Tisa unpublished). This study provided data on the number of alewife and shad larvae, 5 to 10 mm TL, collected in meter nets, towed one night per week in both the upper and lower sections of the reservoir from May to August, 1983 and 1984 (Tables 3.24 and 3.25). This size range immediately follows hatching and is the most susceptible to meter net tows. Because of the absence

Table 3.24. The mean number of alewife larvae (per 1000 m³), 5 to 10 mm TL, collected in meter net tows in Smith Mountain Lake, 1983 and 1984. Data are from Tisa (unpublished).

1983		1984	
Date	Number	Date	Number
May 25	13	May 31	4.301
June 1	43	June 5	43.689
June 7	39	June 12	24.348
June 15	35	June 21	46.075
June 22	38	June 26	70.073
June 28	139	July 2	39.706
July 5	206	July 9	24.251
July 12	84	July 16	136.432
July 19	^a 59	July 25	57.722
July 25	34	July 30	25.237
August 1	55	August 6	91.483
August 8	^a 28	August 13	7.421
August 17	0		
August 23	3		
August 29	2		

^a Interpolated values.

Table 3.25. The mean number of gizzard shad larvae (per 1000 m³), 5 to 10 mm TL, collected in meter net tows in Smith Mountain Lake, 1983 and 1984. Data are from Tisa (unpublished).

1983		1984	
Date	Number	Date	Number
May 17	0	May 14	15.517
May 26	299	May 21	85.193
June 2	35	May 31	21.792
June 6	286	June 4	69.982
June 16	459	June 11	231.579
June 20	491	June 19	450.178
June 27	94	June 26	11.29
July 6	0	July 2	0.0
		July 9	3.063
		July 16	0.0
		July 25	3.130

of some weekly collections during 1983, I linearly interpolated between dates to obtain estimates for missing weeks.

Gizzard shad have a protracted spawning season that may extend from April to July, with highest larval densities reached 4-8 weeks after the spawning period begins (Netsch et al. 1971). Similarly, alewives spawn from early May through August in southeastern reservoirs (Nigro and Ney 1982). Although the spawning season is protracted, I assumed the larval counts in the 1 day/week tows represented a weekly average; i.e., the number entering the 5 to 10 mm size range during the 7-day period equaled the number dying or outgrowing this size range during this same period. Larval growth was measured at 0.84 mm/day for alewives and 1.33 mm/day for shad during the period, May 1 to August 31, 1983 and 1984. Growth slowed to 0.3 and 0.2 mm/day for alewife and shad, respectively, from September 1 to November 30. Daily growth rates indicated that alewife and shad larvae in a size range of 5 to 10 mm would exceed 10 mm in size within 7 days during the spawning season, May to August. Thus, each weekly sample is distinct; a larva would not be counted twice in successive weeks, and each weekly sample would represent a discrete cohort of larvae 5 to 10 mm in length.

Daily mortality estimates were also calculated for specific size ranges of larvae (Tisa unpublished). Mortality estimates were applied to each weekly cohort to derive an estimate of the number of age-0 larvae present June 1, August 1, September 1, and December 15, 1983 and 1984, and March 15, 1984 and 1985.

The number of larvae per 1000 m^3 (X) calculated for each date was converted to whole lake estimates (N) using the following formula:

$$N = X/1000m^3 \times 3m \times 4200ha \times 10,000m^2/ha$$

Tisa et al. (1985) indicated a complete segregation of spawning habitat for alewives and gizzard shad. However, the total area of spawning habitat and larval concentration were not measured, and I assumed 4200 ha, approximately half the surface area of Smith Mountain Lake, as an appropriate approximation for both species. The value of 3 m represents the depth of the water column in which most larvae were found (M. Tisa personal communication) .

Growth estimates were used to calculate lengths of larval fish over time. A length of 7.5 mm (mean of 5 and 10 mm) was considered the starting length for both species at week 1. Mean lengths for each date were calculated using derived length estimates for each weekly cohort. Lengths were weighted by cohort abundance before calculating the average length for a date. Weighted mean lengths were converted to weights using size specific length/weight regression equations for each species (Tisa unpublished). Population estimates for larval clupeids in Smith Mountain Lake were then multiplied by mean weights to obtain biomass estimates for each date.

A comparison of biomass estimates on August 1 to VDGIF cove rotenone data indicated that biomass for each species was probably underestimated by my method. Assuming cove rotenone estimates were more accurate indicators of biomass than the area/density method previously described,

correction factors were calculated by dividing the VDGIF values for age-0 alewife and gizzard shad biomass, from corrected cove rotenone data, by biomass estimates for August 1. These values were 18,520 kg and 10,163 kg for alewives in 1983 and 1984, respectively, and 273,620 kg and 41,975 kg for gizzard shad in these years. Correction factors were 10.25 and 29.49 for alewives in 1983 and 1984, respectively. Similarly, gizzard shad estimates were 10.1 and 2.27 times less than VDGIF values for August, 1983 and 1984.

The wide disagreement between biomass estimates based on meter-net tows and cove rotenone data is due principally to the assumption of area multipliers. One half the surface area of Smith Mountain Lake is probably an overestimate of the size of the spawning area, whereas 3 m may be an underestimate for the depth at which all larvae are found. In addition, some larvae may escape the net. However, estimates based on meter net tows are useful in that they serve as a relative index to extrapolate August cove rotenone estimates to seasonal biomass values.

Cove rotenone estimates are relatively unbiased for shad, whereas the pelagic nature of alewives makes estimates of biomass from rotenone data suspect. I examined gill net data from 1983 and 1984 collections to determine if alternative estimates of alewife biomass could be derived. Potentially, the proportion of alewives to shad in the gill nets could be applied to an estimate of shad biomass from cove rotenone data to derive estimates of alewife biomass. However, distributional differences and differences in seasonal availability confound the assumption that alewives and shad are equally vulnerable to nets at a given time. Gill

net catches may not reflect the relative proportion of each clupeid in the reservoir. Thus, estimates of alewife biomass using this methodology would also be biased.

Correction factors derived from cove rotenone data were applied to biomass estimates obtained for each of the dates; June 1, August 1, September 1, December 15. Corrected biomass values were used to calculate production (P) estimates seasonally using the following equation of Ricker (1975):

$$P = \bar{B}G$$

where \bar{B} =mean biomass for the period and G =instantaneous growth, $\ln (W_t/W_0)$.

Production estimates for age-1 and older alewives were not possible because of data limitations. Instead, I used a mean biomass value as an indicator of availability of adult alewives. Gill net data indicated that 20 g was a reasonable estimate of mean weight for age-2 and age-3 alewives collected in Smith Mountain Lake during 1983 and 1984. An annual mortality estimate of 80% (Tisa 1987) was used to derive an estimate of the number of age-2 and age-3 alewives in preceeding years from number of young-of-year alewives present in March of 1984 and 1985. This estimate was used with mean weight (20 g) to derive biomass estimates.

Clupeid Biomass and Production Estimates

Seasonal production estimates for age-0 alewives followed similar trends in both years, with highest production values during fall and lowest values during spring (Table 3.26).

Table 3.26. Mean weight (W), instantaneous growth (G), biomass (B), corrected biomass (CB), mean corrected biomass (B), and production (P) of the 1983 and 1984 cohorts of alewives in Smith Mountain Lake.

Date	W (g)	G (g)	B (kg)	CB (kg) ^a	B (kg)	P (kg)
1983 cohort						
6/01/83	0.00078		5	51		
		7.18			39,855	286,159
9/01/83	1.022		7,772	79,658		
		2.28			141,320	322,210
12/15/83	9.97		19,803	202,982		
		0.00			183,698	
3/15/84	9.97		16,040	164,414		
		0.10			124,836	12,484
6/01/84	11.0		8,318	85,258		
1984 cohort						
6/01/84	0.0006		3	101		
		7.35			80,756	593,557
9/01/84	0.93		5,473	161,411		
		2.16			301,778	651,840
12/15/84	8.1		14,993	442,144		
		0.00			400,136	
3/15/85	8.1		12,144	358,127		
		0.31			293,355	90,940
6/01/85	11.0		7,751	228,583		

^a Corrected biomass estimates were derived using cove rotenone data supplied by the VDGIF.

No production occurred during winter; mean weight remained constant and biomass declined. Seasonal production estimates for the 1983 cohort ranged from 12,484 to 321,210 kg; 1984 values ranged from 90,940 to 651,840 kg.

Production estimates for gizzard shad were higher than those derived for alewife (Table 3.27). Gizzard shad production was highest during summer, decreased in fall, and was lowest the following spring. Production estimates (kg) of the 1983 cohort ranged from 151,181 to 3,378,458; 1984 values ranged from 26,654 to 481,550.

Total demand by predators for young-of-year alewives in summer and fall was substantially less than both 1983 and 1984 estimates of alewife production. However, demand during spring fell between production estimates for the 1983 and 1984 alewife cohorts (Table 3.28).

The mean biomass values for adult alewives were 121,784 and 285,174 kg for the 1983 and 1984 cohorts, respectively. The demand estimate, 241,644 kg, approaches the maximum value derived for the 1984 cohort, and is more than double the value for the 1983 cohort.

Predator demand for young-of-year shad during spring was substantially less than the production estimate for the the 1983 gizzard shad cohort but exceeded the production estimate for the 1984 cohort (Table 3.28). Demand was nearly 30 times less than the amount of young-of-year shad produced during the summer of 1983 and approximately 25% of the 1984 production estimate for this season. Predator demand was substantially less than production estimate for fall, 1983, and predators consumed approximately 52,000 kg less shad than were produced during fall, 1984.

Table 3.27. Mean weight (W), instantaneous growth (G), biomass (B), corrected biomass (CB), mean corrected biomass (B), and production (P) of the 1983 and 1984 cohorts of gizzard shad in Smith Mountain Lake.

Date	W (g)	G	B (kg)	^a CB (kg)	B	P (kg)
1983 cohort						
6/01/83	0.0074		141	1,419		
		7.43			454,705	3,378,458
9/01/83	12.47		89,900	907,990		
		0.92			939,850	864,662
12/15/83	31.3		96,209	971,711		
		0.00			879,399	
3/15/84	31.3		77,929	787,086		
		0.24			629,920	151,181
6/01/84	40.0		46,807	472,754		
1984 cohort						
6/01/84	0.0026		30	68		
		7.05			68,305	481,550
9/01/84	2.999		60,150	136,541		
		2.37			129,916	307,900
12/15/84	31.99		54,313	123,291		
		0.00			111,564	
3/15/85	31.99		43,981	99,837		
		0.22			116,609	26,654
6/01/85	40.0		58,758	133,381		

^a Corrected biomass estimates were derived using cove rotenone data supplied by the VDGIF.

Table 3.28. Estimates of cumulative consumption (kg) by predators in Smith Mountain Lake compared to production estimates (kg) for young-of-year alewives and gizzard shad by season. Production estimates represent estimates for the 1983 and 1984 cohorts of both clupeids.

Season	Alewives		Gizzard Shad	
	Demand	Production	Demand	Production
Summer	1983	286,159		3,378,458
	1984	593,557	121,533	481,550
Fall	1983	322,210		864,662
	1984	651,840	255,437	307,900
Spring	1983	12,484		151,181
	1984	90,940	35,977	26,654

^a Summer is 6/1 to 8/31, fall is 9/1 to 12/15, and spring is 3/15 to 5/31.

Overview of Demand vs Supply

The above comparison indicates that predators may be capable of consuming all the available clupeid production during spring in Smith Mountain Lake. These results would tend to support diet information that indicated diet breadth of predators was greatest during this season (Chapter I). Increased breadth is often correlated with decreased abundance of preferred food items (Ivlev 1961, Werner and Hall 1974). Ploskey and Jenkins (1982) noted that May was a critical month in reservoirs because prey production was insignificant and the energy requirements of predators for respiration and reproduction were increasing. A similar situation appears to exist for the predator assemblage in Smith Mountain Lake.

Production estimates may be unreliable indicators of prey availability during spring due to reduced growth rates of clupeids; biomass may serve as a more reliable indicator of supply. A comparison of spring demand to spring biomass of young-of-year shad indicated a substantial underutilization of gizzard shad, with demand 10 to 20 times less than the calculated biomass (Table 3.27). This underutilization may result from reduced morphological availability of gizzard shad during spring. In fact, most age-0 predators in Smith Mountain Lake cannot consume young-of-year shad by March, following their first growing season (Chapter I).

The fact that consumption of prey in the summer is substantially less than clupeid supply may also be related to morphological availability;

clupeids have not yet reached a size where they are desirable and/or consumable by most predators. During fall, demand of young-of-year alewives may be mediated by the increased availability (morphological and distributional) of young-of-year shad, explaining demand for young-of-year alewives at levels far below calculated production estimates. Young-of-year shad are larger than young-of-year alewives at this time but they are still within the morphological size limits of even some age-0 predators. These large sizes may attract greater predator attention as explained by optimal foraging theory (Pyke et al. 1977, Townsend and Winfield 1985), i.e., predators receive more food per unit of expenditure.

Consumption of clupeids may occur during winter, but probably at substantially lower levels than those calculated for other periods of the year. I did not model the bioenergetics of predators during winter for two reasons. First, food habit data on predators during winter were incomplete. Second, bioenergetic models have been shown to be inaccurate during winter months because they do not accurately describe bioenergetic parameters (Minton and McClean 1982, Adams et al. 1982b). Adams et al. (1982b) found that largemouth bass had to consume some shad during winter to explain observed weights. This contradicts laboratory findings which indicated consumption by largemouth bass is negligible below 10°C (Lemons and Crawshaw 1985). Sauger consumed a large number of cold-stressed shad during winter in a Tennessee reservoir (Minton and McClean 1982), and walleye in Smith Mountain Lake may do the same. The fact that some bait fishermen catch striped bass during winter in Smith Mountain Lake indicates that striped bass probably feed during this season, although I could

find no study to substantiate this hypothesis. However, extrapolating the results of Cox and Coutant (1981) to lower temperatures indicates little or no prey consumption by juvenile striped bass below 10⁰C. If winter consumption of clupeids by predators does occur, this would increase my estimates of annual demand.

Perhaps the most important information derived from this study is that the two most abundant predatory species in Smith Mountain Lake are essentially dependent on separate clupeid populations, striped bass relying on alewives and largemouth bass on gizzard shad. These findings substantiate the work of Kohler et al. (1986), who determined that alewives served as a "buffer" between littoral residents and pelagic predators in Claytor Lake, Virginia. Estimates of predator demand exceeded production estimates of gizzard shad and young-of-year alewife in spring, implying that predators may have competed for a limited clupeid resource during this season. In addition, it is possible that predator demand could exceed adult alewife supply over a yearly period. However, because diets could change to reflect prey availability, and data on predator food habits collected in 1983 and 1984 were combined to estimate predator demand, this demand would have to exceed clupeid production and adult alewife biomass in both 1983 and 1984 to infer exploitative competition among predators in the reservoir during these years. In general, estimates of predator demand and clupeid supply in this study substantiate diet overlap data (Chapter I), which indicated native and introduced predators are compatible in Smith Mountain Lake.

The reliance of largemouth bass on gizzard shad for forage indicates reduction in population size of this prey item (Fig. 3.13), may explain the reduced growth rates and population levels observed for this predator in Smith Mountain Lake since 1978 (La Roche 1981, Whitehurst 1985). Carline et al. (1984) used bioenergetic simulations to demonstrate that a dense population of largemouth bass could consume all of the gizzard shad production in an Ohio impoundment. It appears that population levels of largemouth bass were severely affected by the reproductive failure of shad in Smith Mountain Lake in 1978, and in fact, both largemouth bass and shad have not returned to pre-1978 levels of abundance (LaRoche 1981, Whitehurst 1985).

Sustained availability of age 1 and older alewives may be the principal factor limiting striped bass production in the reservoir. Striped bass consume gizzard shad and young-of-year alewives principally during fall when young-of-year are abundant. However, during late spring and summer, the time of year when striped bass are facing increased metabolic costs due to rapidly rising temperatures, availability of these prey items is reduced. Consumption of adult alewives is highest during this period, at levels nearly four times that of either young-of-year alewives or gizzard shad. Adult alewives, in effect, serve to maintain the condition of striped bass cohorts between periods of young-of-year abundance.

Stocking Strategies

Successful stocking strategies for striped bass, or any other species, must consider three principal criteria when introducing the desired

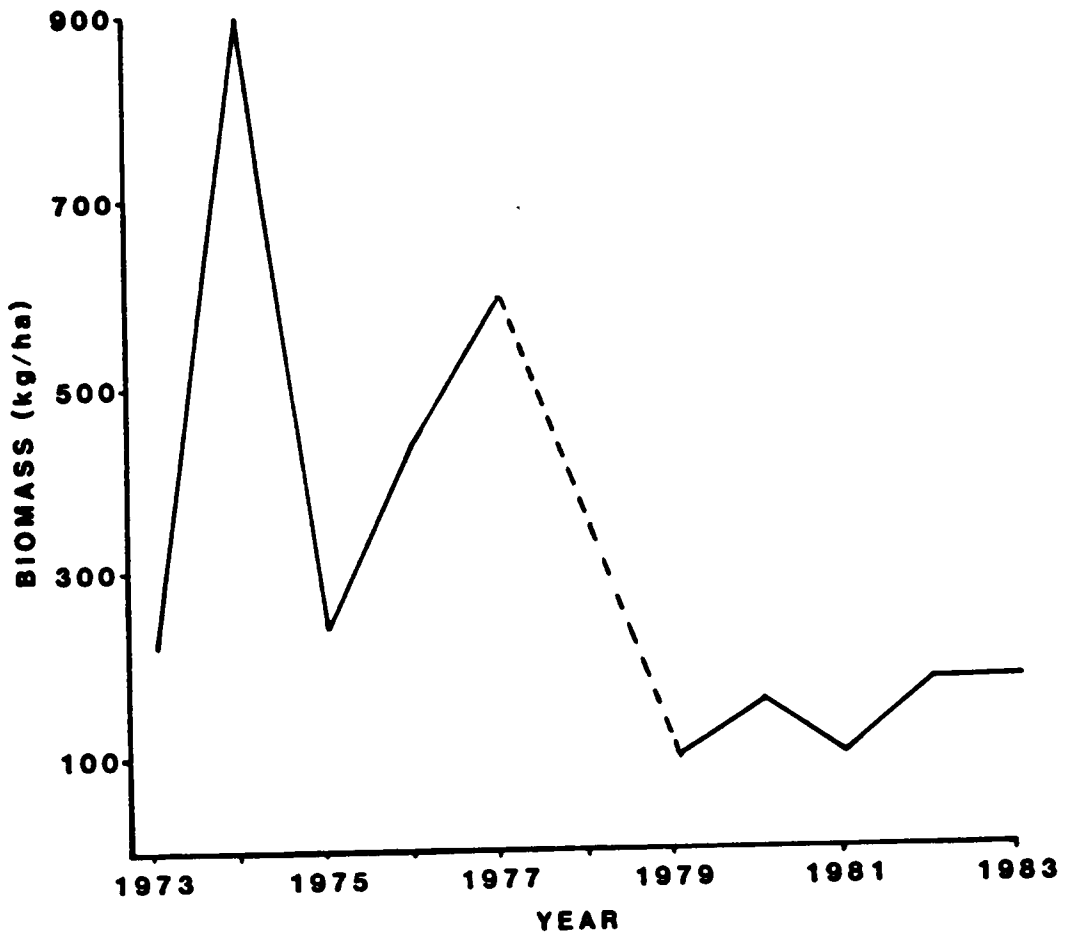


Figure 3.13. Biomass levels (kg/ha) of gizzard shad collected by the Virginia Department of Game and Inland Fisheries in cove rotenone samples. Data are from Whitehurst (1985).

species into an ecologically suitable system: time of stocking, size at stocking, and stocking densities (Keith 1986). VDGIF personnel stock striped bass in Smith Mountain Lake annually in early June, at sizes of 25 to 50 mm. Fingerling stocking in June ensures that striped bass are of sufficient size initially and will be large enough later to utilize abundant young-of-year clupeids when they become available. In addition, data from this study indicate that at least some stocked striped bass grow to sufficient sizes during their first summer to utilize adult alewives. Thus, stocking density is probably the most critical factor affecting successful stocking regimes in Smith Mountain Lake.

A determination of the relative impact of a stocked striped bass cohort on prey over time can produce useful information to guide managers in determining optimal stocking densities for striped bass. The optimal number of striped bass to stock would be the number which produces the highest concentration of harvestable striped bass and at the same time allows for minimal trophic interactions among striped bass and between striped bass and other predators.

Calculation of Consumption Estimates

I used the striped bass bioenergetics model to simulate the prey consumption over time by a one-time stocking of 100,000 stocked striped bass fingerlings. Survival of stocked fish was assigned a value of 21%, the mean survival rate observed for striped bass fingerlings from 1973-1983 (Chapter II). I also calculated consumption assuming a continuous yearly stocking regime of 100,000 (12/ha) to 400,000 (48/ha)

fingerlings (at intervals of 25,000 fingerlings). Survival rates of stocked fingerlings were derived from an equation relating survival to stocking density (Equation 9, Chapter II). For all simulations, survival of age 1 and older fish was 40%, and I assumed similar diet and growth patterns observed for striped bass in 1983-1984. Simulations were run for separate seasons and consumption was summed to derive cumulative consumption estimates for the three main prey items, young-of-year alewives, adult alewives, and gizzard shad, during the entire growing season.

Because availability of adult alewives may be the principal factor limiting striped bass production in the reservoir, consumption estimates were compared to supply of adult alewives to evaluate stocking strategies. A simplified version of the model developed by Eck and Brown (1985) offered a methodology to conduct this evaluation. The model is of the form:

$$Z\bar{B} = C_1 + C_2 + \dots C_n + U$$

where Z = the annual instantaneous mortality rate of adult alewives, \bar{B} = mean annual biomass of adult alewives, C_n = the annual biomass of adult alewives consumed by the i th predator population, U = annual biomass of adult alewives lost to other natural causes such as physiological stress and disease. Assuming predation is a substitute form of mortality, the amount of biomass defined by U gives an indication of the additional predator biomass that can be supported by the adult alewife population.

In addition, potential competitive interactions between striped bass and black bass for young-of-year shad must be considered when alternative

stocking rates for striped bass are examined. I used the above model with derived biomass levels for gizzard shad to assess combined predator demand for young-of-year shad, an important food item for striped bass and largemouth bass in Smith Mountain Lake (Chapter I).

Simulation Output

The simulation indicated that consumption of young-of-year alewives by striped bass was greatest at age 0, with more young-of-year alewives consumed by underyearlings than all other ages (subsequent years) combined (Table 3.29). Consumption of adult alewives and gizzard shad peaked at age 2 and slowly declined with increasing age.

Stocking simulations indicated a stocking of 100,000 fingerlings per year would result in a striped bass population that would consume nearly half of the adult alewives consumed by striped bass in 1983-1984, approximately 69,000 kg (Table 3.30). Consumption estimates would increase at higher stocking densities; e.g., at a stocking density of 400,000 fingerlings, demand for adult alewives would exceed 128,000 kg. Similarly, demand for young-of-year alewives would increase from 27,000 kg at the lower stocking density, to over 73,000 kg at an annual stocking of 400,000 fingerlings. Demand for gizzard shad would almost double between these two stocking rates.

In 1983 and 1984, biomass levels of adult alewives were estimated at 121,784 kg and 285,174 kg, respectively. Tisa (unpublished) estimated an annual mortality rate for alewives of approximately 80% ($z=1.609$). Using the smaller biomass estimate for alewives (121,784 kg), $Z\bar{B}$ would

Table 3.29. Estimated consumption (kg) of clupeids over time by a cohort of striped bass based on a single stocking of 100,000 fingerlings and a survival rate of 21% for fingerlings.

Age	Adult Alewife	Y-O-Y Alewife	Gizzard Shad
0	2,058	11,536	2,236
1	5,064	1,461	952
2	13,139	2,824	7,938
3	7,621	1,622	5,027
4	3,613	770	2,221
5	1,798	380	1,191
6	776	164	512
7	327	69	216
8	136	29	89
9	55	12	36
10	22	5	14

Table 3.30. Estimated consumption (kg) of clupeids by a cohort of striped bass stocked at different densities. Survival rates (%) were derived from an equation relating survival to stocking density.

Number Stocked	Survival Rate (%)	Adult Alewife	Y-0-Y Alewife	Gizzard Shad
100,000	43.5	69,485	26,732	39,928
125,000	40.6	81,237	32,149	46,769
150,000	38.0	91,440	37,216	52,743
175,000	35.5	99,898	41,890	57,743
200,000	33.2	107,039	46,268	62,006
225,000	31.1	112,921	50,361	65,565
250,000	29.0	117,523	54,167	68,410
275,000	27.1	121,177	57,758	70,723
300,000	25.4	124,055	61,175	72,604
325,000	23.7	126,081	64,399	74,007
350,000	22.2	127,370	67,458	75,000
375,000	20.7	128,040	70,377	75,645
400,000	19.4	128,206	73,182	76,009

equal 195,950 kg. Annual consumption of adult alewives by largemouth bass, smallmouth bass, and walleye in Smith Mountain Lake was approximately 78,000 kg/yr. Thus, slightly over 118,000 kg of additional biomass of adult alewives would be available to support the striped bass population. At a stocking rate of 250,000 (30/ha) fingerlings, estimated annual consumption of adult alewives by striped bass would be approximately 117,000 kg, a value almost equal to this surplus biomass. However, variable survival of fingerlings would change consumption estimates. For example, if 250,000 fingerlings were stocked each year and first-year survival was 50% (instead of the derived 29%), consumption of adult alewives would exceed 200,000 kg. This value is nearly double that estimated for the same stocking density but at a lower survival rate.

An optimal stocking regime should be based not only on the estimated survival of fingerlings but also on the estimated biomass of adult alewives. At 1984 levels of adult alewives, a surplus of 380,845 kg ((285,174 x 1.609) - 78,000) would exist. An annual stocking of 400,000 fingerlings would result in an annual consumption estimate of 128,000 kg for adult alewives (Table 3.30). Thus, supply of adult alewives could support a stocking rate of approximately twice this amount, or 800,000 fingerlings.

An annual mortality for young-of-year shad is approximately 99% ($Z=2.69$). Assuming that biomass levels in September represent the mean biomass of young-of-year shad morphologically available to predators throughout the year, and using the lower estimate for the years 1983 and 1984, then $Z\bar{B}$ would equal 367,295 kg. Demand estimates for shad by black

bass were over 311,000 kg/yr in 1983 and 1984. Predator demand compared to supply indicates a surplus of over 56,000 kg. This surplus would support an annual stocking of nearly 175,000 fingerlings, based on a consumption estimate of over 57,000 kg for this stocking rate (Table 3.30).

Recommended Stocking Strategy

The temporal pattern of clupeid consumption by striped bass in Smith Mountain Lake has important ramifications. Ideally, the reservoir should be stocked with striped bass at favorable predator/prey ratios to crop abundant young-of-year alewives in the fall (and possibly winter), taking into consideration that overconsumption (or excessive winter mortality of young-of-year alewives) by young-of-year striped bass may result in insufficient numbers of adult alewives in the system to support subsequent demand by age-1 and older striped bass. Striped bass of all ages consume alewives of similar size ranges (Chapter I). Coupled with the fact that striped bass are probably depensatory mortality agents, consuming alewives more in relation to their density than to alewife density, indicates that overstocking of striped bass may result in competition for the reduced alewife biomass such that survival of stocked fish and condition of adult fish are reduced. This large increase in forage demand with increasing survival rates of striped bass emphasizes the importance of continued fall gill netting in Smith Mountain Lake to determine survival of stocked striped bass and to potentially adjust future stocking densities. Furthermore, environmental variability, as it relates to re-

productive success of clupeids, must also be considered. It is likely that the striped bass fishery of Smith Mountain Lake was severely affected when fingerlings stocked in 1977 had a high survival rate (Chapter II) followed by a reproductive failure of clupeids the following year (La Roche 1981).

A conservative approach for stocking striped bass in Smith Mountain Lake would be to base stocking levels on a long-term mean or even a minimum estimate of annual clupeid biomass. The alewife population in Smith Mountain Lake is probably similar to Lake Michigan's population in that abundance oscillates around some average equilibrium level from year to year (Stewart et al. 1983, Eck and Brown 1985). Data from the VDGIF annual cove rotenone sampling, although somewhat biased, tend to support this hypothesis (Fig. 3.14). An accurate determination of this mean level would allow a reservoir manager to develop more accurate stocking strategies for striped bass based on consumption estimates.

In addition, the simulation indicated that the biomass of gizzard shad in 1984 would support a relatively low stocking rate of striped bass each year. However, abundance of gizzard shad would have to remain constant at this level from year to year to support this biomass of striped bass. If survival and/or stocking rates of striped bass fingerlings increased or young-of-year shad biomass decreased, potential demand for shad could exceed supply and competitive interactions between predators would likely intensify.

The above simulations are somewhat simplistic. Survival of fingerlings, clupeid supply, and predator demand are variable and not

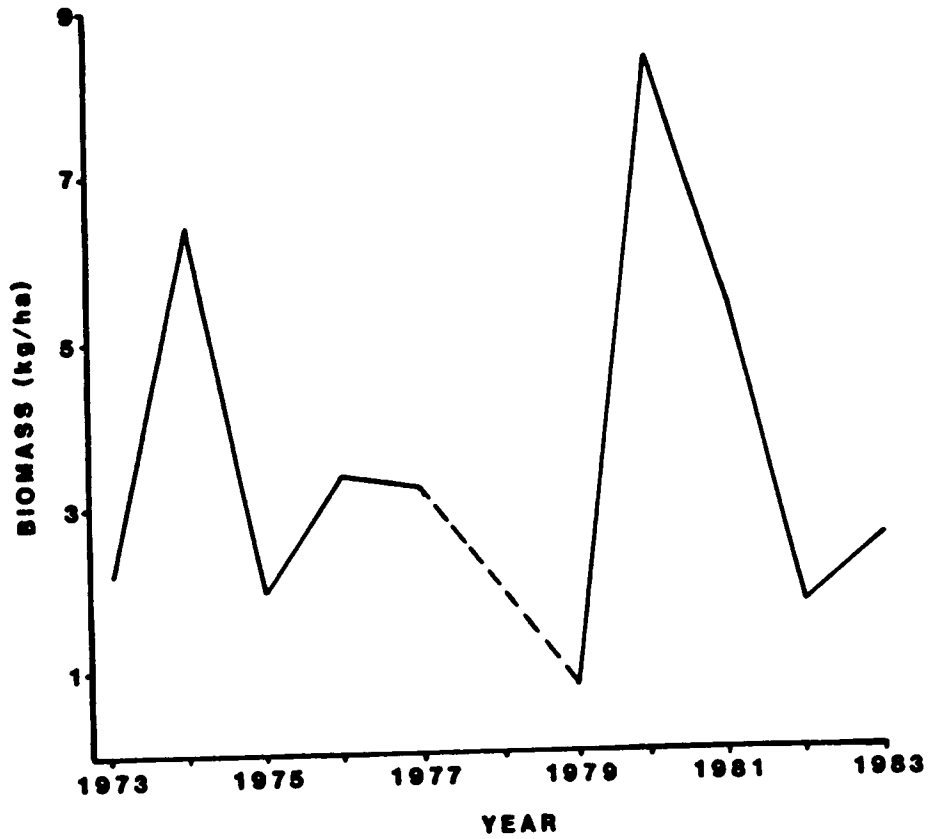


Figure 3.14. Biomass levels (kg/ha) of alewives collected by the Virginia Department of Game and Inland Fisheries in cove rotenone samples. Data are from Whitehurst (1985).

fixed from year to year. In addition, other piscivores in the system, such as channel catfish (Ictalurus punctatus), certainly eat clupeids but were not accounted for in the Eck and Brown (1985) model. Nevertheless, the above information indicates that a stocking rate of 20-24 fingerlings/ha appears optimal for Smith Mountain Lake. At this rate, and based on the derived biomass levels for the clupeids, striped bass would not overcrop their food supply, and potential interactions among striped bass and between striped bass and other predators would be minimal. In addition, data from Chapter II of this dissertation indicated a decrease in fingerling survival with increased stocking levels. At stocking rates greater than 24 fingerlings/ha, the marginal yield (number of survivors per additional 10,000 fingerlings stocked) decreased to less than 20% (Chapter II). Economically, a higher survival rate at a lower stocking level equates to a better benefit cost ratio assuming the cost of hatching, raising, and stocking a fingerling remain constant at any stocking density. Also, reduced stocking rates allow for a reduction in intraspecific competition for prey or, at least, a greater concentration of food per stocked fingerling. More food equates to faster growth such that striped bass reach a larger size more quickly and are more able to utilize larger prey items at an earlier date increasing condition factor and potentially avoiding starvation. Thus, stocking levels greater than 24/ha may be costly both ecologically and financially.

Predator inertia, the time from stocking to when maximum predation impact occurs, is two years for striped bass relative to both adult alewives and young-of-year gizzard shad. A three-year stocking cycle,

where striped bass are stocked at a constant level for two years followed by a year when stocking levels are reduced, might be appropriate. Assuming a reduction in demand for adult and young-of-year alewives the third year, this strategy might allow for an increase in adult alewives the following years such that peak demand of age-2 striped bass would be supported. However, consumption may increase with increase in prey density (Swenson and Smith 1976), and thus stocking levels would have to be adjusted to account for this compensatory consumption; i.e., smaller population size consuming the same amount of prey with concomitant increase in growth (Weatherly 1972).

The marked decrease in conversion efficiency of striped bass with age indicates a degree of inefficiency in a system managed solely to support numbers of large striped bass to maintain a trophy fishery. Consideration should be given to liberal harvest regulations that allow harvest of smaller striped bass when abundant. If prey is limited, reductions in biomass of these smaller striped bass will have the additional benefit of allowing increased availability of prey for larger individuals.

Sensitivity and Bias

The major limitation of this comparison of demand and supply is the credibility of the inputs and assumptions used to compute these estimates. Sensitivity and error analysis of bioenergetic models identical to those used for largemouth bass, smallmouth bass, and walleye in this study, and similar to my striped bass model, indicate that the models are robust when

estimating consumption from a known growth curve (Kitchell et al. 1977, Stewart et al. 1981, 1983, Rice et al. 1983, Kitchell 1983, Lyons 1984, Bartell et al. 1986). These studies indicate that the most important parameters affecting the amount of variability in specific consumption estimates of a particular prey item include b_2 , the weight dependence exponent for respiration, initial and final weights of a cohort for a simulation period, and diet composition. In addition, Kitchell and Breck (1980) found that variation in the activity parameter, A , can cause an approximate 10% error in consumption estimates.

I believe my estimate of b_2 for striped bass is reasonably accurate, based on a comparison of studies on striped bass metabolism. Bioenergetic parameters, including b_2 , for largemouth bass and walleye have been defended in earlier studies (Kitchell et al. 1977, Rice et al. 1983). It is fortuitous that estimates for consumption, egestion and excretion parameters, and measurements of the relative energy content of predators and prey, have low sensitivities; a large change in these variables has relatively little effect on consumption estimates. Both sets of these variables have the largest measure of uncertainty, especially for striped bass.

The growth curves derived from observed data realistically reflect growth of an average individual in each cohort. The fitted curves agreed with empirical data for most age groups, reflecting monthly and seasonal growth trends, but differed somewhat from measured values when sample sizes were small. Ideally, one needs to have large enough sample sizes such that empirical mean weights can be used in model simulations.

The P-values of age 3 and older striped bass are responsible for the low mean P-value calculated for striped bass in the spring. Values for these age groups are less than 0.2 and less than 0.1 for ages 8 to 10. These values may reflect low prey availability or an underestimate of A, the activity parameter, for sexually mature striped bass. If all other parameters are held constant, increases in the value of A result in higher P-values. Cheek (1982) measured movements of adult striped bass in Cherokee Reservoir, Tennessee. Straight line values between telemetry interceptions indicated a swimming speed of approximately 12 cm/s for individuals tracked during spring, the season when traveled distances were most extreme. Increased swimming speed was correlated with spawning migrations in the reservoir. Using the equations of Kruger and Brocksen (1978), the 12 cm/s swimming speed would equate to a metabolic increment 1.8 times standard metabolism. However, the actual distance traveled would be greater since fish do not travel linearly; swimming speed would undoubtedly be higher.

The mean P-value for striped bass is higher than the value derived for the other predators in Smith Mountain Lake during summer. This may be indicative of a slight overestimate of A. Subadult and adult striped bass restrict movements during the hottest months to thermal refugia in Cherokee Reservoir (Cheek et al. 1985). Striped bass movements in Smith Mountain Lake may also be constrained in summer since these fish are found chiefly in the lower reservoir during this season. It's likely that P-values for striped bass reflect both availability of prey and changes in activity levels. However, without prior knowledge of striped bass ac-

tivity levels or direct measures of activity metabolism, any alteration in the activity parameter would be based on conjecture.

Linear interpolation between days in the modeling simulation may result in some inaccuracies in diet description due to abrupt changes in prey availability (Rice and Cochran 1984). Similarly, age-specific changes in diet may not have been accurately reflected in my diet measurements due to small sample size and grouping of some predator age classes, especially smallmouth bass. In addition, bias may result from combining predators from 1983 and 1984 for diet analysis. Predators may "prey switch" from year to year, reflecting relative changes in the abundance of clupeids. Some error may also result from spatial heterogeneity of predator food habits in the reservoir and associated sampling bias (Chapter I).

The potential biases involved in specific consumption estimates for an average individual in an age group are minor compared to the biases inherent in population estimates when consumption is extrapolated to an entire predator population. Population estimates for predatory species in Smith Mountain Lake may be significantly biased, especially for the less abundant predators, smallmouth bass and walleye (Chapter II). Furthermore, other predators, such as channel catfish and muskellunge, occur in the lake as well and undoubtedly consume some of the available clupeid biomass.

It is likely that actual population levels of clupeids are different from those estimates derived in this study, especially for alewives. Although cove rotenone data are relatively accurate for gizzard shad, the

pelagic nature of alewives makes the use of cove rotenone data unreliable for this species. Finally, although I assumed that all alewives and young-of-year gizzard shad were vulnerable to predation, availability of prey involves a number of factors including morphology, behavior, and distributional similarities between predators and prey (Chapter I). These factors must be considered when determining the amount of prey "available" for consumption by a predator.

Conclusion

Estimates of annual consumption by Smith Mountain Lake predators indicate that indigenous and introduced predators are compatible in Smith Mountain Lake largely due to the presence of the two clupeids, gizzard shad and alewife. The two most abundant predators in Smith Mountain Lake are essentially dependent on separate clupeid populations, striped bass relying on alewives and largemouth bass on shad. Relative to the other predators, striped bass consumed 64% of the adult alewives, annually, and largemouth bass consumed 72% of the gizzard shad. However, results from this study indicate predator populations in Smith Mountain Lake are capable of consuming all the available clupeid production on a seasonal basis. This possibility emphasizes that overstocking of pelagic predators and/or decline in the clupeid biomass could allow predators to over-crop their food supply, increasing negative interactions between predatory species.

The importance of clupeids to the well-being of the predator populations indicates that further stocking of pelagic predators must con-

sider present and future prey abundance to maximize predator production and the eventual harvest of gamefish by anglers. Consumption estimates for striped bass and other predators can be used, in conjunction with estimates of clupeid supply and survival estimates for striped bass fingerlings, to determine optimal stocking strategies. Results from my simulations indicate a stocking rate of 20-24 fingerlings/ha may be optimal for Smith Mountain Lake.

Confidence in interpretations of predator demand and prey supply, and precise recommendations for quantitative stocking plans for striped bass, are hindered only by insufficient data, especially accurate estimates of alewife biomass. The importance of the alewife population to striped bass survival and growth stresses the importance of determining a correction factor or simple method, based on trawl (Siler et al. 1986) or hydroacoustic estimates (Johannesson and Mitson 1983), that could be applied to standard sampling schemes currently used such as electroshocking or cove rotenone.

The striped bass bioenergetics model can be further refined to more accurately reflect the physiology of this species, especially activity metabolism. However, this refinement can only occur with additional laboratory and field research. As is, the model I developed can have several important applications to reservoir fisheries investigations, particularly where striped bass are a species of concern. Rice and Cochran (1984), in an independent evaluation of the largemouth bass bioenergetics model, found an 8.5% difference in model predictions versus extrapolations from field estimated data. The close similarity

in functional design between the largemouth bass model and other bioenergetics models used in this study, including striped bass, indicate that the bioenergetics model is a valid tool for evaluating predator-prey relationships in reservoirs.

MANAGEMENT IMPLICATIONS

Fisheries managers must consider food resource partitioning among predators when formulating management strategies that involve manipulation of predator/prey ratios in reservoirs. Results of this study indicate that introduction of alewives into Smith Mountain Lake has benefited striped bass and walleye, and perhaps native black bass as well. Alewives have increased forage availability for pelagic predators, relative to gizzard shad, because of their slower growth and spatial distribution. They are especially important as forage for young-of-year striped bass, which can only consume young-of-year shad for a brief period during late summer and fall. Although black bass consumed alewives relatively infrequently in Smith Mountain Lake, introduction of alewives may have increased forage availability for these predators by decreasing demand for young-of-year shad, an important food item for black bass. Diet overlap data and comparisons of predator demand to clupeid supply indicate that alewife introduction has created a dual forage base in Smith Mountain Lake such that the two most abundant predators are essentially dependent on separate clupeid populations, striped bass relying on alewives and largemouth bass on gizzard shad.

Food habit data indicated that striped bass and walleye consumed similar species of clupeids during all seasons of the year where adequate stomach samples were available for comparison. Significant diet overlap between these species and finite clupeid forage base indicates that if

stocking of walleye is reinstated in Smith Mountain Lake, stocking rates of striped bass will have to be proportionately reduced. Stocking of walleye without this reduction could intensify competitive interactions between these predators, ultimately reducing survival and production for both predator populations.

My study emphasizes the importance of fishery independent surveys to monitor the balance between predators and prey in the reservoir. Fall gill net surveys should continue each year and CPUE of yearling striped bass should be used as an index of striped bass stocking success. Survival rates of stocked fingerlings and probable future densities of harvestable striped bass can be estimated using the method presented in Chapter II. Cove rotenone sampling in August should continue, and these data used to monitor reproductive success of black bass and availability of young-of-year gizzard shad. The importance of alewives to the well-being of the striped bass population necessitates additional study to more accurately determine the abundance of this clupeid in the reservoir. Such a study should stress the importance of determining a conversion factor or a simple, inexpensive methodology to be applied to standard sampling schemes. Monitoring clupeid populations will ensure that the catastrophic effects of clupeid reproductive failure will not be exacerbated by the stocking of excess predators as apparently occurred in Smith Mountain Lake in 1978 and 1979.

Investigation of stocking strategies indicate that fingerling density is probably the most critical factor affecting successful stocking regimes in Smith Mountain Lake. Information from this study indicates

an optimal stocking density, the number which maximizes striped bass harvest and minimizes trophic interactions among striped bass and other predators, of 20-24 fingerlings per ha. This density approximates the number of fingerlings stocked in 1983 and 1984 by the Virginia Department of Game and Inland Fisheries. In the event that a surplus number of striped bass fingerlings are stocked or fall gill netting indicates increased survival (significantly above the average determined in this study), then that year's stocking should be followed by one or two years of reduced stocking levels. The degree of reduction would depend on the extent of surplus survivors.

Predator inertia is two years for striped bass relative to adult alewives and young-of-year gizzard shad in Smith Mountain Lake. A three-year stocking cycle, where striped bass are stocked at a constant level for two years followed by a year when stocking levels are reduced, might be appropriate. Assuming a reduction in demand for adult and young-of-year alewives the third year, this policy may result in an increase in adult alewives the following years such that peak demand of age-2 striped bass would be supported. Alternatively, consideration could be given to stocking Morone hybrids. Faster growth and shorter life span of hybrids equates to a reduction in predator inertia that would allow for more flexible stocking rates based on yearly fluctuations in the clupeid forage base.

Finally, the Virginia Department of Game and Inland Fisheries should reassess their management regulations for striped bass in Smith Mountain Lake that restrict harvest to two fish per day with a minimum size limit

of 508 mm. These regulations were instituted primarily to maintain a trophy fishery for striped bass. A system managed to maintain a standing stock of larger, older fish is inefficient; conversion efficiencies indicate that older predators consume a disproportionate amount of forage per unit gain in weight. Considerations should be given to liberal harvest regulations that allow harvest of smaller striped bass when abundant. Scatter plots comparing lengths of clupeids consumed to striped bass lengths indicate a wide size range (TL) of striped bass ate similar-sized prey. Reductions in biomass of smaller striped bass will therefore have the additional benefit of increasing availability of prey for larger individuals.

SUMMARY

1. The food habits, survival rates, and population size of four predatory fish species were determined and combined with information on energetics and growth to quantitatively assess predator-prey interactions in Smith Mountain Lake, a large hydroelectric reservoir in south-central Virginia.

2. A total of 1871 stomachs of the four species was examined from fish collections between April 1983 and December 1984. Alewives and gizzard shad, and to a lesser extent crayfishes and sunfishes, were the predominant food items consumed by predators in this lake. Food habits of each predatory species were significantly different between habitats (upper and lower reservoir) and among seasons.

3. The relative proportion of alewives and gizzard shad consumed by predators was related to several factors: the differential distribution of predators and prey in the reservoir, the relative abundance of alewives and gizzard shad, and the seasonal and morphological availability of clupeids.

4. Schoener's (1970) diet overlap index indicated that food resources were effectively partitioned among introduced and resident predators in Smith Mountain Lake in 1983 and 1984. Greater use of non-clupeid fish

and crayfish by littoral black basses minimized diet overlap between these predators and pelagic predators (striped bass and walleye). Significant diet overlap (greater than 0.6) occurred between the pelagic predators and between the littoral black basses in all seasons and locations where adequate stomach samples were available for comparison. Habitat partitioning probably minimized potential competitive interactions among these predators.

5. Survival estimates for the four predatory species were derived from cove rotenone data, gill net statistics, and creel survey estimates supplied by the Virginia Department of Game and Inland Fisheries. Sampling statistics from an electrofishing survey and mortality estimates obtained from the literature supplemented the analysis. Survival of striped bass fingerlings averaged 20.8% for an 11-year period (1973 to 1983) and ranged from 3.9% to 54.3%. There was a significant inverse correlation ($r=-0.7$, $N=11$, $P=0.0157$) between the number of stocked fingerlings and associated survival rates. Average survival of age-0 largemouth bass and smallmouth bass was 53% and 45%, respectively, for the period 1979 to 1983. Species-specific survival rates for predators, age 1 and older, ranged from 29% to 59%. Of the predators age 1 and older, largemouth bass were the most numerous at an estimated density of 61.2/ha, followed by striped bass at 16.3/ha. Age 1 and older smallmouth bass and walleye were less abundant at 8.2 and 2.02 per ha, respectively.

6. The importance of clupeids to the well-being of the predator population was also evident in survival and population estimates of the four predatory fish species. The reproductive failure of these prey species in 1978 appeared to severely affect subsequent spawning success of native predators as well as the survival of stocked striped bass. Analysis of cove rotenone data for the period 1979 to 1983 indicated that numbers of age-0 bass were lowest in 1979. The lowest estimated survival of fingerling striped bass stocked in the 11-year period, 1973-1983, was 3.9% for fingerlings stocked in 1978.

7. A bioenergetics model for striped bass was developed from a compilation of data collected in several studies on striped bass metabolism and growth. Gross conversion efficiencies for striped bass were derived using this model. Efficiencies decreased from 40.6% to 2% for increasing ages of striped bass, age 0 to 10. Efficiencies for age 1 and older fish averaged 13.7% for the entire growing season, and 21% during summer.

8. The striped bass bioenergetics model and models developed for walleye and largemouth bass were used to derive estimates of total annual consumption of alewives and gizzard shad by predators. Consumption of these clupeids was estimated for the cohorts of each predator during three seasons (spring, summer, and fall) within the annual growing period. The four predators consumed more adult and young-of-year alewives during summer, an estimated 125,530 kg and 39,453 kg, respectively, than in any other season. Striped bass ate the greatest amount of adult and young-

of-year alewives during all seasons. Predators, particularly largemouth bass, consumed the greatest amount of gizzard shad (255,437 kg) during fall. Largemouth bass consumed nearly 70% of the total shad biomass eaten by all predators during all three seasons. Smallmouth bass and walleye had relatively little impact on either the alewife or shad population. Comparison of the relative predatory impact of various age groups within each predator population indicated that ages 0 to 3 for all species, except walleye, consumed the greatest amount of clupeids annually. Age-4 walleye, the last cohort stocked in Smith Mountain Lake, were the principal consumers of alewives and shad relative to the other walleye age groups.

9. Estimates of clupeid biomass and production for 1983 and 1984 were derived from a concurrent study on larval distribution and abundance, and cove rotenone data from the Virginia Department of Game and Inland Fisheries. Production estimates for age-0 alewives followed similar trends in both years, with highest production values in fall and lowest values in spring. Gizzard shad production was highest in summer, decreased in fall, and was lowest the following spring.

10. Predator populations in Smith Mountain Lake may be capable of consuming all the available clupeid production in spring. Predator demand exceeded spring production estimates for the 1983 cohort of young-of-year alewives and 1984 cohort of gizzard shad. However, demand estimates were less than similar production estimates derived for alewives in 1984 and

gizzard shad in 1983. The fact that clupeids have not yet reached a size where they are desirable and/or consumable by most predator size classes may explain why predator demand during summer was substantially less than production estimates derived for young-of-year alewives and shad in 1983 and 1984. Demand for young-of-year alewives during fall was over 15 to 30 times less than production estimates for the 1983 and 1984 alewife cohorts. Predator demand exceeded shad production estimates during fall of both 1983 and 1984. Greater consumption of gizzard shad in fall, relative to alewives, may be explained by distributional shifts of predators and optimal foraging theory.

11. The two most abundant predator groups in Smith Mountain Lake are essentially dependent on separate clupeid populations, striped bass relying on alewives and largemouth bass on gizzard shad. Estimates of predator demand and clupeid supply substantiate diet overlap data which indicated that native and introduced predators were compatible in Smith Mountain Lake.

12. Sustained availability of age 1 and older alewives may be the principal factor limiting striped bass production in Smith Mountain Lake. The bioenergetics model was used to make inferences about potential stocking strategies based on availability of these alewives. A stocking rate of 20-24 fingerlings per ha appears to maximize production of striped bass and minimize potential competitive interactions between striped bass and native predators.

APPENDIX

Table A.1. Mean percent that each food category contributed to the total weight of stomach contents of striped bass collected in Smith Mountain Lake, 1983-1984.

Location and Season	Striped Bass Examined	With Food (%)	Adult Alewife		Y-O-Y Alewife	Gizzard Shad	Crayfish	Lepomis	Unidentified Fish		
									Fish	Miscellaneous	
Upper											
Winter	74	57	2.4	1.9	87.2	1.4	0.0	4.8	2.4		
Spring	46	33	20.0	39.8	20.0	1.8	3.6	8.0	6.8		
Summer	86	40	71.7	9.5	5.9	5.7	2.9	4.3	0.0		
Fall	86	40	8.2	35.9	27.0	10.6	0.0	18.2	0.0		
Total	292	43									
Lower											
Winter	9	0									
Spring	161	59	49.1	23.6	2.2	3.3	0.0	17.9	3.5		
Summer	163	55	42.9	22.0	12.0	11.6	1.1	7.9	2.3		
Fall	83	54	11.6	40.3	17.1	7.8	0.0	19.7	3.5		
Total	416	55									

Table A.2. Mean percent that each food category contributed to the total weight of stomach contents of largemouth bass collected in Smith Mountain Lake, 1983-1984.

Location and Season	Largemouth Bass Examined	With Food (%)	Adult Alewife	Y-O-Y Alewife	Gizzard Shad	Crayfish	Lepomis	Unidentified Fish	Other
Upper									
Winter	71	59	0.0	0.0	43.6	41.1	0.0	15.3	0.0
Spring	127	35	6.7	0.0	0.0	40.3	13.3	23.5	14.1
Summer	135	67	5.0	1.4	35.4	20.4	8.6	16.8	13.3
Fall	58	45	0.0	0.0	33.8	30.8	15.4	13.3	6.8
Total	391	52							
Lower									
Winter	0	0							
Spring	88	44	11.2	4.2	10.2	41.6	4.0	18.5	10.3
Summer	24	39	0.0	11.1	11.1	22.2	0.0	55.6	0.0
Fall	15	33	0.0	0.0	79.4	20.0	0.0	0.6	0.0
Total	127	42							

Table A.3. Mean percent that each food category contributed to the total weight of stomach contents of walleye collected in Smith Mountain Lake, 1983-1984.

Location and Season	Walleye Examined	With Food (%)	Adult Alewife	Y-O-Y Alewife	Gizzard Shad	Crayfish	Lepomis	Unidentified Fish	Other
Upper									
Winter	11	73	0.0	0.0	87.5	0.0	0.0	12.5	0.0
Spring	30	30	37.8	40.2	11.1	0.0	0.0	11.1	0.0
Summer	26	46	71.7	19.2	0.0	0.7	0.0	8.3	0.0
Fall	21	14	0.0	0.0	100.0	0.0	0.0	0.0	0.0
Total	88	36							
Lower									
Winter	5	0							
Spring	240	10	69.6	5.5	0.0	0.0	0.0	25.0	0.0
Summer	113	33	63.2	21.4	2.7	0.0	0.0	12.7	0.0
Fall	12	8	100.0	0.0	0.0	0.0	0.0	0.0	0.0
Total	370	18							

Table A.4. Mean percent that each food category contributed to the total weight of stomach contents of smallmouth bass collected in Smith Mountain Lake, 1983-1984.

Location and Season	Smallmouth Bass Examined With Food (%)						Unidentified Fish				
	Adult Alewife	Y-O-Y Alewife	Gizzard Shad	Crayfish	Lepomis	Other	Fish				
Lower ^a											
Winter	4	0									
Spring	73	37	22.2	4.9	9.7	8.6	7.4	31.9	15.4		
Summer	83	40	4.8	15.5	11.6	9.2	0.0	47.6	11.3		
Fall	27	48	7.7	10.2	18.8	27.4	7.7	20.5	7.7		
Total	187	39									

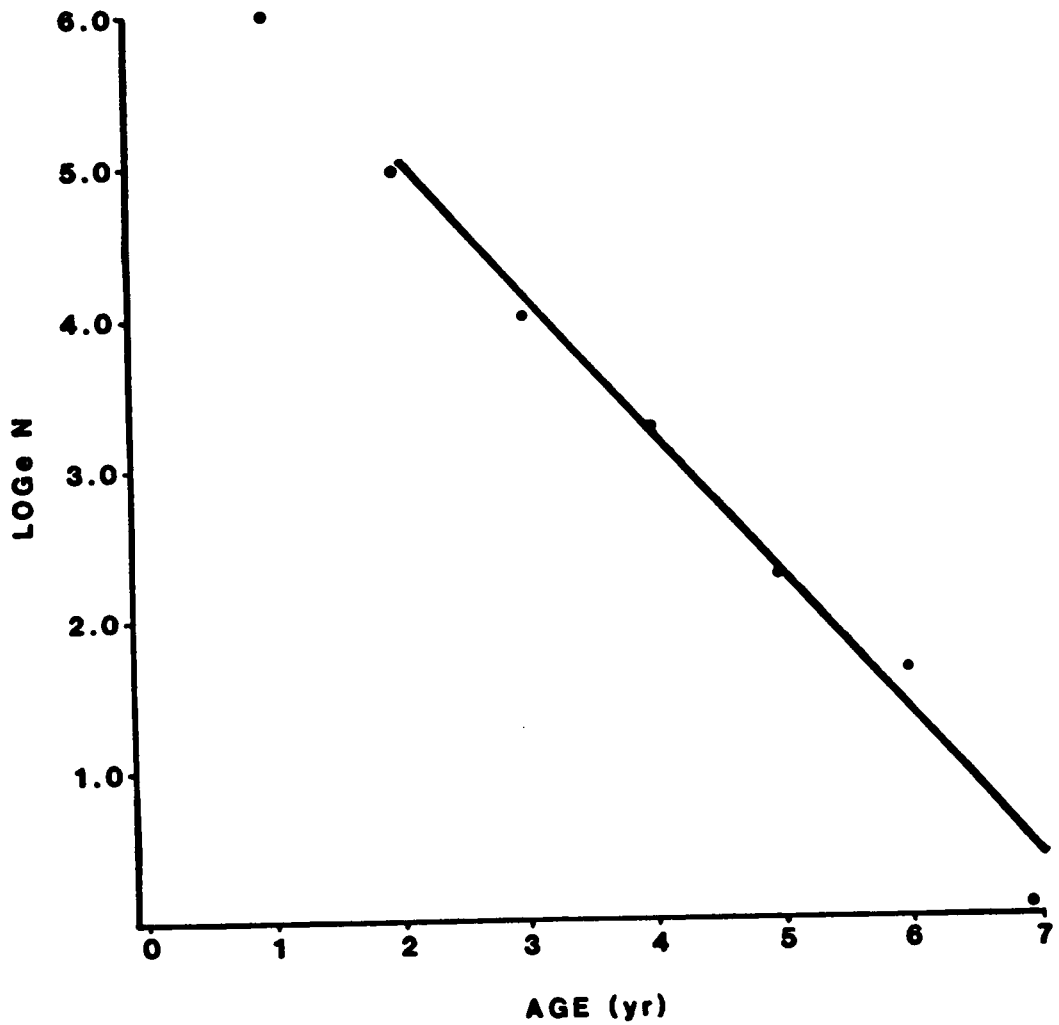


Figure A.1. Catch curve of striped bass collected in fall gill net samples by the Virginia Department of Game and Inland Fisheries, 1973-1983.

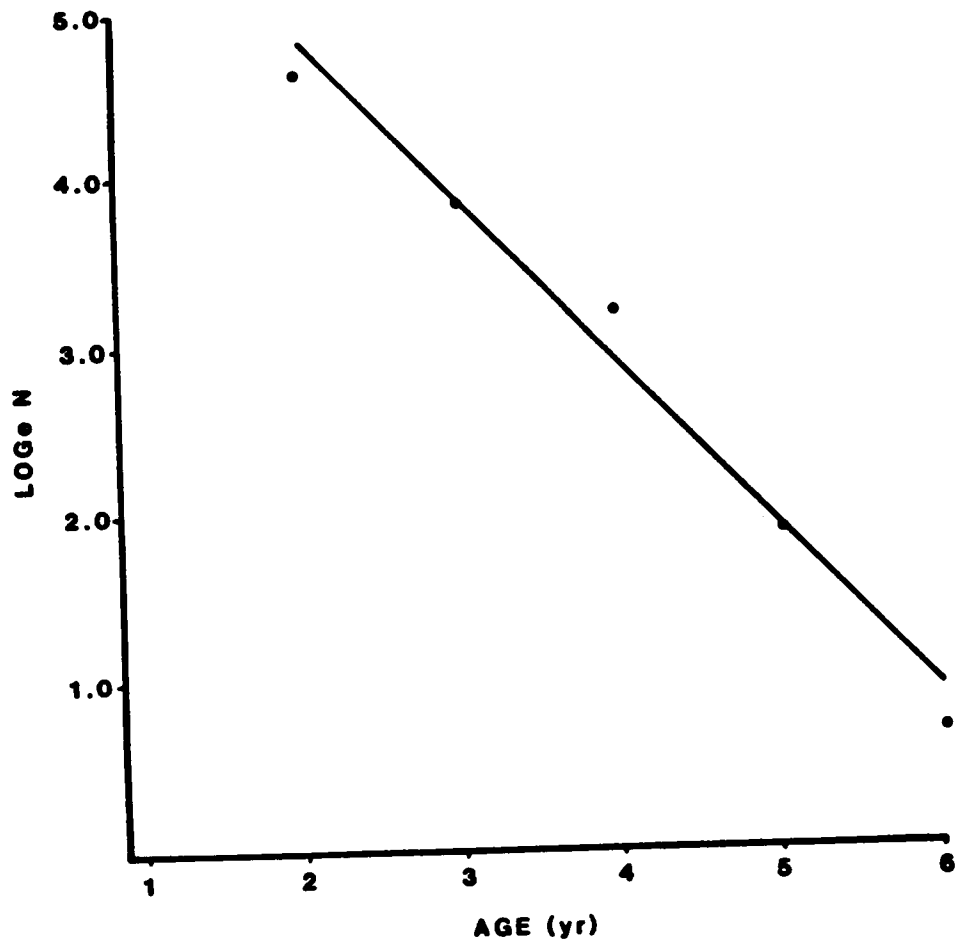


Figure A.2. Catch curve of largemouth bass collected by electrofishing in Smith Mountain Lake, 1983-1984.

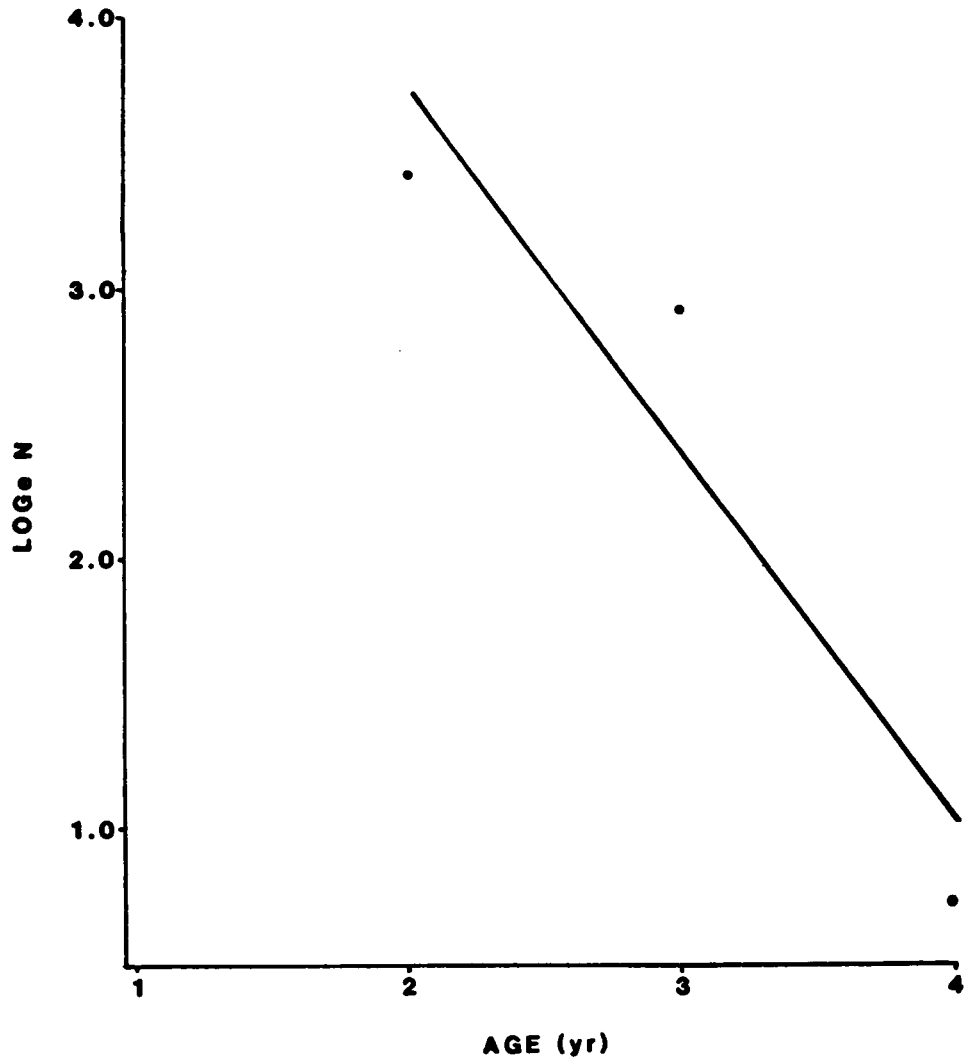


Figure A.3. Catch curve of smallmouth bass collected by electrofishing in Smith Mountain Lake, 1983-1984.

LITERATURE CITED

- Adams, S.M., R.B. McLean, and M.M. Huffman. 1982a. Structuring of a predator population through temperature mediated effects on prey availability. *Can. J. Fish. Aquat. Sci.* 39: 1175-1184.
- Adams, S.M., R.B. McLean, and J.A. Parrotta. 1982b. Energy partitioning in largemouth bass under conditions of seasonally fluctuating prey availability. *Trans. Am. Fish. Soc.* 111: 549-558.
- Adams, S.M., J.E. Breck, and R.B. McLean. 1984. Cumulative stress-induced mortality of gizzard shad in a southeastern U.S. reservoir. *Env. Biol. Fishes* 13: 103-112.
- Ager, L.M. 1978. Exploitation and mortality of largemouth bass in Lake Tobesofkee, Georgia. *Proc. Annu. Conf. Southeast. Assoc. Fish Wildl. Agencies* 32: 429-436.
- Aggus, L.R. 1973. Food of angler harvested largemouth, spotted and smallmouth bass in Bull Shoals Reservoir. *Proc. Annu. Conf. Southeast. Assoc. Game Fish Comm.* 26: 519-529.
- Aggus, L.R. and W.C. Rainwater. 1975. Estimating largemouth bass populations in reservoirs from catches in angling tournaments. *Proc. Annu. Conf. Southeast. Assoc. Fish Wildl. Agencies* 29: 106-114.
- Applegate, R.L., J.W. Mullan, and D.I. Morais. 1966. Food and growth of six centrarchids from shoreline areas of Bull Shoals Reservoir. *Proc. Annu. Conf. Southeast. Assoc. Game Fish Comm.* 20: 469-482.
- Axon, J.R. and D.K. Whitehurst. 1985. Striped bass management in lakes with emphasis on management problems. *Trans. Am. Fish. Soc.* 114: 8-11.
- Bailey, W. M. 1974. An evaluation of striped bass introductions in the southeastern U.S. *Proc. Annu. Conf. Southeast. Assoc. Game Fish Comm.* 28: 54-68.
- Baker, C.D. and E.H. Schmitz. 1971. Food habits of Adult gizzard and threadfin shad in two Ozark reservoirs. *Am. Fish. Soc. Spec. Pub.* 8: 3-11.
- Bartell, S.M., and three other authors. 1986. Individual parameter perturbation and error analysis of fish bioenergetic models. *Can J. Fish. Aquat. Sci.* 43: 160-168.

- Beamish, F.W.H. 1970. Oxygen consumption of largemouth bass, Micropterus salmoides, in relation to swimming speed and temperature. *Can. J. Zool.* 48: 1221-1228.
- Beamish, F.W.H. 1972. Ration size and digestion in largemouth bass, Micropterus salmoides Lacepede. *Can. J. Zool.* 50: 153-164.
- Beamish, F.W.H. 1974. Apparent specific dynamic action of largemouth bass, Micropterus salmoides. *J. Fish. Res. Board Can.* 31: 1763-1769.
- Beitinger, T.L. and C.C. Fitzpatrick. 1979. Physiological and ecological correlates of preferred temperature: preferenda versus optima. *Am. Zool.* 19: 319-329.
- Bevelhimer, M.S. 1983. Assessing significance of physiological differences among three esocids with a bioenergetics model. M. S. Thesis, The Ohio State Univ., Columbus, Oh.
- Bevelhimer, M.S., R.A. Stein, and R.F. Carline. 1985. Assessing significance of physiological differences among three esocids with a bioenergetics model. *Can. J. Fish. Aquat. Sci.* 42: 57-69.
- Boaze, J.L., and R.T. Lackey. 1974. Age, growth, and utilization of landlocked alewives in Clayton Lake, Virginia. *Prog. Fish-Cult.* 36: 163-164.
- Brafield, A.E. 1985. Laboratory studies of energy budgets. Pages 257-281 in P. Tytler and P. Calow (eds.), *Fish energetics: New perspectives*. John Hopkins Univ. Press, Baltimore, Md.
- Brett, J.R. 1971. Satiation time, appetite, and maximum food intake of sockeye salmon, Onchorhynchus nerka. *J. Fish. Res. Board Can.* 28: 409-415.
- Brett, J.R. 1983. Life energetics of sockeye salmon, Oncorhynchus nerka. Pages 29-63 in W.P. Aspey and S.I. Lustwick (eds.), *Energetics: Vertebrate costs of survival*. Ohio State Univ. Press, Columbus, Oh.
- Brett, J.R., and T.D.D. Groves. 1979. Physiological energetics. Pages 279-352. in W.S. Hoar, D.J. Randall, and J.R. Brett (eds.), *Fish physiology*, Vol. VIII: Bioenergetics and growth. Academic Press, New York, N. Y.
- Brodeur, R.D. and W.G. Pearcy. 1984. Food habits and dietary overlap of some shelf rockfishes (Genus Sebastes) from the Northeastern Pacific coast. *Fish. Bull.* 82: 269-293.
- Brouha, P. 1974. Evaluation of two reef materials and point or cove locations for construction of artificial reefs in Smith Mountain Lake,

Virginia. M.S. Thesis, Virginia Polytech. Inst. and State Univ., Blacksburg, Va.

- Bryant, H.E., and A. Houser. 1971. Population estimate and growth of largemouth bass in Beaver and Bull Shoals Reservoirs. *Am. Fish. Soc. Spec. Pub.* 8: 349-357.
- Carline, R.F., B.L. Johnson, and T.J. Hall. 1984. Estimation and interpretation of proportional stock density for fish populations in Ohio impoundments. *N. Am. J. Fish. Manage.* 4: 139-154.
- Cech, J.J., Jr., S.J. Mitchell, and T.E. Wragg. 1984. Comparative growth of juvenile white sturgeon and striped bass: effects of temperature and hypoxia. *Estuaries* 7: 12-18.
- Chadwick, H.K. 1968. Mortality rates in the California striped bass populations. *Calif. Fish Game* 54: 228-246.
- Chance, C.J. 1958. History of fish and fishing in Norris - A TVA tributary reservoir. *Proc. Annu. Conf. Southeast. Assoc. Game Fish Comm.* 11: 116-127.
- Cheek, T.E. 1982. Distribution and habitat selection of adult striped bass, Morone saxatilis (Walbaum), in Watts Bar Reservoir, Tennessee. M.S. Thesis, Tennessee Tech. Univ., Cookeville, Tenn.
- Cheek, T.E., M.J. Van Den Avyle, and C.C. Coutant. 1985. Influences of water quality on distribution of striped bass in a Tennessee River impoundment. *Trans. Am. Fish. Soc.* 114: 67-76.
- Cho, C.Y., S.J. Slinger, and H.S. Bayley. 1982. Bioenergetics of salmonid fishes: Energy intake, expenditure and productivity. *Comp. Biochem. Physio.* 73 B: 25-41.
- Coble, D.W. 1975 Smallmouth bass. Pages 21-33 in R.H. Stroud and H. Clepper (eds.), *Black bass biology and management*. Sport Fish. Inst., Washington, D.C.
- Cochran, P.A., and J.A. Rice. 1981. A comparison of bioenergetics and direct field estimates of cumulative seasonal food consumption by largemouth bass (Micropterus salmoides). Pages 88-96 in G.M. Cailliet and C.A. Simenstad (eds.), *Fish food habit studies*. Washington Sea Grant, Univ. of Washington, Seattle, Wash.
- Colby, P.J., R.E. McNicol, and R.A. Ryder. 1979. Synopsis of biological data on the walleye (Stizostedion vitreum vitreum) Mitchell 1818). *FAO Synopsis* 119.
- Cole, C.F. 1966. Virtual population estimations of largemouth bass in Lake Fort Smith, Arkansas, 1957-1960. *Trans. Am. Fish. Soc.* 95: 52-55.

- Combs, D.L. 1978. Food habits of striped bass in Keystone Reservoir and its tailwaters. Proc. Annu. Conf. Southeast. Assoc. Fish Wildl. Agencies 32: 571-575.
- Combs, D.L. 1980. Fish population changes in Keystone Reservoir fourteen years after striped bass introductions. Proc. Annu. Conf. Southeast. Assoc. Fish Wildl. Agencies 34: 167-174.
- Combs, D.L., and L.R. Peltz. 1982. Seasonal distribution of striped bass in Keystone Reservoir, Oklahoma. N. Am. J. Fish. Manage. 2: 66-73.
- Connolly, J.P. and R. Tonelli. 1985. Modelling Kepone in the striped bass food chain of the James River Estuary. Estuar. Coast. Shelf Sci. 20: 349-366.
- Coutant, C.C. 1975. Responses of bass to natural and artificial temperature regimes. Pages 272-285 in R.H. Stroud and H. Clepper (eds.), Black bass biology and management. Sport Fish. Inst., Washington, D.C.
- Coutant, C.C. 1985. Striped bass, temperature, and dissolved oxygen: a speculative hypothesis for environmental risk. Trans. Am. Fish. Soc. 114: 31-61.
- Coutant, C.C. and D.S. Carroll. 1980. Temperatures occupied by ten ultrasonic-tagged striped bass in freshwater lakes. Trans. Am. Fish. Soc. 109: 195-202.
- Cox, D.K. and C.C. Coutant. 1981. Growth dynamics of striped bass as functions of temperature and ration. Trans. Am. Fish. Soc. 110: 226-238.
- Daniel, K.L. 1984. Food habits, age and growth, and forage value of the alewife in Watauga Reservoir, Tennessee. Tenn. Wildl. Resour. Agency Tech. Rep. 84-2.
- Davies, W.D. 1973. Rates of temperature acclimation for hatchery reared striped bass fry and fingerlings. Prog. Fish-Cult. 35: 214-217.
- Dendy, J.S. 1946. Food of several species of fish, Norris Reservoir, Tennessee. J. Tenn. Acad. Sci. 21: 105-127.
- Dent Jr., R.J. 1986. Methods and parameters used in evaluating bass length limits on Pomme de Terre Lake, Missouri. Pages 65-72 in G.E. Hall and M.J. Van Den Avyle (eds.), Reservoir fisheries management: strategies for the 80's. Reservoir Comm., South. Div. Am. Fish. Soc., Bethesda, Md.
- Dewey, M.R., and T.E. Moen. 1981. Population dynamics of largemouth bass in DeGray Lake, Arkansas, 1975-1979. Proc. Annu. Conf. Southeast. Assoc. Fish Wildl. Agencies 35: 430-437.

- Dewey, M.R., T.E. Moen, and H.E. Bryant. 1981. Seasonal biomass of selected centrarchids in DeGray Lake, 1977-1979. Proc. Annu. Conf. Southeast. Assoc. Fish Wildl. Agencies 35:438-442.
- Diana, J.S. 1983. An energy budget for northern pike. Can. J. Zool. 61: 1968-1975.
- Eck, G.W., and E.H. Brown, Jr. 1985. Lake Michigan's capacity to support lake trout (Salvelinus namaycush) and other Salmonines: An estimate based on the status of prey populations in the 1970s. Can. J. Fish. Aquat. Sci. 42: 449-454.
- Eck, G.W. and L. Wells. 1983. Biology, population structure, and estimated forage requirements of lake trout in Lake Michigan. U.S. Fish Wildl. Serv. Tech. Pap. 111.
- Eldridge, M.B., Whipple, J.A., and Bowers M.J. 1982. Bioenergetics and growth of striped bass, Morone saxatilis, embryos and larvae. Fish. Bull. 80: 461-474.
- Elliott, J.M. 1976. Energy losses in the waste products of brown trout (Salmo trutta L.). J. Animal Ecol. 45: 561-580.
- Elliott, J.M. 1979. Energetics of freshwater teleosts. Pages 29-61 in P.J. Miller (ed.), Fish phenology: Anabolic adaptiveness in teleosts. Symp. Zool. Soc. Lond. 44.
- Fajen, O. 1975. Population dynamics of bass in rivers and streams. Pages 195-203 in R.H. Stroud and H. Clepper (eds.), Black bass biology and management. Sport Fish. Inst., Washington, D.C.
- Farman, R.S., L.A. Nielsen, and M.D. Norman. 1982. Estimating largemouth bass abundance using creel census and tournament data in the fishing-success method. N. Am. J. Fish. Manage. 2: 249-256.
- Fedoruk, A.N. 1966. Feeding relationship of walleye and smallmouth bass. J. Fish. Res. Board Can. 23: 941-943.
- Filipek, S.P., and W.H. Tommey. 1984. The food habits of adult striped bass from Lake Hamilton, Arkansas, before and during an extreme drawdown. Proc. Annu. Conf. Southeast. Assoc. Fish Wildl. Agencies 38: 327-334.
- Fitz, R.B., and J.A. Holbrook II. 1978. Sauger and walleye in Norris Reservoir, Tennessee. Pages 11-82 in R.L. Kendall (ed.), Selected coolwater fishes of North America. Am. Fish. Soc. Spec. Pub. 11.
- Freadman, M.A. 1979. Swimming energetics of striped bass (Morone saxatilis) and bluefish (Pomatomus saltatrix): gill ventilation and swimming metabolism. J. Exp. Biol. 83: 217-230.

- From, J. and G. Rasmussen. 1984. A growth model, gastric evacuation, and body composition in rainbow trout, Salmo gairdneri Richardson, 1836. Dana 3:61-139.
- Germann, J.F. and Brunch, Z.E. 1983. Age, growth, and survival of Morone hybrids in Clarks Hill Reservoir, Georgia. Proc. Annu. Conf. Southeast. Assoc. Fish Wildl. Agencies 37: 267-275.
- Gilliland, E.R. and M.D. Clady. 1981. Diet overlap of striped bass x white bass hybrids and largemouth bass in Sooner Lake, Oklahoma. Proc. Annu. Conf. Southeast. Assoc. Fish Wildl. Agencies 35: 317-330.
- Grinstead, B.G. and 4 other authors. 1976. Estimations of standing crop of fishes in the predator stocking evaluation reservoirs. Proc. Annu. Conf. Southeast. Assoc. Fish Wildl. Agencies 30: 120-130.
- Hackney, P.A. and J.A. Holbrook II. 1978. Sauger, walleye, and yellow perch in the southeastern United States. Pages 74-81 in R.L. Kendall (ed.), Selected coolwater fishes of North America. Am. Fish. Soc. Spec. Pub. 11, Washington, D.C.
- Hamley, J.M. 1975. Review of gillnet selectivity. J. Fish. Res. Board Can. 32: 1943-1969.
- Hanson, W.D. 1962. Dynamics of the largemouth bass population in Bull Shoals Reservoir, Missouri. Proc. Annu. Conf. Southeast. Assoc. Game Fish Comm. 16: 398-404.
- Hanson, W.D., and J.G. Dillard. 1976. Contribution of striped bass to the fishery of Lake of the Ozarks, Missouri. Proc. Annu. Conf. Southeast. Assoc. Game Fish Comm. 29: 162-167.
- Harper, J.L., and H.E. Namminga. 1986. Fish population trends in Texoma Reservoir following establishment of striped bass. Pages 156-165 in G.E. Hall and M.J. Van Den Avyle (eds.), Reservoir fisheries management: strategies for the 80's. Reservoir Comm., South. Div. Am. Fish. Soc., Bethesda, Md.
- Harris, F.A., L.M. Ager, E. Hayes. 1979. Comparison of various mark-recapture techniques for estimating abundance of largemouth bass in Barkley Lake, Kentucky. Proc. Annu. Conf. Southeast. Assoc. Fish Wildl. Agencies 33: 703-709.
- Hart, L.G. 1978. Project completion report, Smith Mountain Lake reservoir research study. Va. Comm. Game Inland Fish. D.J. Proj. F-30-R.
- Hatch, R.W., P.M. Haack, and E.H. Brown, Jr. 1981. Estimation of alewife biomass in Lake Michigan, 1967-1978. Trans. Am. Fish. Soc. 110: 573-582.

- Hepworth, D.K., A.W. Gustaveson, and F.M. Stowell. 1977. Lake Powell post-impoundment investigations. Utah State Div. Wildl. Res. D.J. Proj. F-28-R-5.
- Hewett, S.W., and B.L. Johnson. 1987. A generalized bioenergetics model of fish growth for microcomputers. Univ. of Wisconsin (Madison) Sea Grant Inst. Pub. WIS-SG-87-245.
- Hickman, G.D. and K.W. Hevel. 1975. Comparison of population estimates of largemouth bass in Forrest Lake, Missouri, utilizing a bass tournament and an electroshocker for collection of recaptures. Proc. Annu. Conf. Southeast. Assoc. Game Fish Comm. 29: 102-114.
- Hightower, J.E., R.J. Gilbert, and T.B. Hess. 1982. Shoreline and cove sampling to estimate survival of young largemouth bass in Lake Oconee, Georgia. N. Am. J. Fish. Manage. 2: 257-261.
- Hoff, T.B., J.B. McCaren, and J.C. Cooper. 1988. Stock characteristics of Hudson River striped bass. Am. Fish. Soc. Spec. Pub. In press.
- Hollander, M., and D.A. Wolfe. 1973. Nonparametric statistical methods. Wiley and Sons, New York, N.Y.
- Houser, A., and N.F. Netsch. 1971. Estimates of young-of-year shad production in Beaver Reservoir. Am. Fish. Soc. Spec. Pub. 8: 359-370.
- Houser, A., and J.E. Dunn. 1967. Estimating the size of the threadfin shad population in Bull Shoals Reservoir from midwater trawl catches. Trans. Am. Fish. Soc. 96: 176-184.
- Houser, A., and W.C. Rainwater. 1975. Production of largemouth bass in Beaver and Bull Shoals Lakes. Pages 310-316 in R.H. Stroud and H. Clepper (eds.), Black bass biology and management. Sport Fish. Inst., Washington, D.C.
- Hubert, W.A. 1977. Comparative food habits of smallmouth bass and largemouth bass in Pickwick Reservoir. J. Ala. Acad. Sci. 48: 167-178.
- Ivlev, I. 1939. Energy balance in the carp. Zool. Zn. 18: 303-318.
- Ivlev, V.S. 1961. Experimental ecology of the feeding of fishes. (Translated from Russian by D. Scott). Yale Univ. Press, New Haven, Conn.
- Jearld, A., Jr. 1983. Age determination. Pages 301-324 in L.A. Nielsen and D.L. Johnson (eds.), Fisheries techniques, Am. Fish. Soc., Bethesda, Md.

- Jenkins, R.M. 1975. Black bass crops and species associations in reservoirs. Pages 114-124 in R.H. Stroud and H. Clepper (ed.), Black bass biology and management. Sport Fish. Inst., Washington, D.C.
- Jenkins, R.M., and D.I. Morais. 1978. Prey-predator relations in the predator-stocking-evaluation reservoirs. Proc. Annu. Conf. Southeast. Assoc. Fish Wildl. Agencies 30: 141-157.
- Jenkins, R.M., C.A. Schultz, and W.M. Seawell. 1980. Prey-predator relations in Crooked Creek Bay, Barkley Lake, Kentucky. Proc. Annu. Conf. Southeast. Assoc. Fish Wildl. Agencies 33: 692-702.
- Jester, D.B. 1971. Effects of commercial fishing, species introductions, and drawdown control on fish populations in Elephant Butte Reservoir, New Mexico. Am. Fish. Soc. Spec. Pub. 8: 265-286.
- Jester, D.B., and B.L. Jensen. 1972. Life history and ecology of the gizzard shad, Dorosoma cepedianum (Lesuer) with reference to Elephant Butte Lake, New Mexico. New Mexico State Univ. Agric. Exp. Sta. Res. Rep. 218.
- Johannesson, K.A. and R.B. Mitson. 1983. Fisheries acoustics. A practical manual for aquatic biomass estimation. FAO Fish. Tech. Pap. 240.
- Johnson, F.H., and J.G. Hale. 1977. Interrelations between walleye (Stizostedion vitreum vitreum) and smallmouth bass (Micropterus dolomieu) in four northeastern Minnesota Lakes, 1948-1969. J. Fish. Res. Board Can. 34: 1626-1632.
- Kempinger, J.J. and R.F. Carline. 1977. Dynamics of the walleye (Stizostedion vitreum vitreum) population in Escanaba Lake, Wisconsin, 1955-72. J. Fish. Res. Board Can. 34: 1800-1811.
- Keith, W.E. 1986. A review of introduction and maintenance stocking in reservoir fisheries management. Pages 144-148 in G.E. Hall and M.J. Van Den Avyle (eds.), Reservoir fisheries management: Strategies for the 80's. Reservoir Committee, South. Div. Am. Fish. Soc., Bethesda, Md.
- Kitchell, J.F. 1983. Energetics. Pages 312-338 in P.W. Webb and D. Weihs (eds.), Fish biomechanics. Praeger Publ., New York, N.Y.
- Kitchell, J.F., and J.E. Breck. 1980. Bioenergetics model and foraging hypothesis for sea lamprey (Petromyzon marinus). Can. J. Fish. Aquat. Sci. 37: 2169-2174.
- Kitchell, J.F., and three other authors. 1978. Bioenergetics spectra of skipjack and yellowfin tunas. Pages 357-368 in G.D. Sharp and A.E. Dizon (eds.), The physiological ecology of tunas. Academic Press, Inc., New York, N.Y.

- Kitchell, J.F., D.J. Stewart, and D. Weininger. 1977. Applications of a bioenergetics model to yellow perch (Perca flavescens) and walleye (Stizostedion vitreum vitreum). J. Fish. Res. Board Can. 34: 1922-1935.
- Kitchell, J.F., and 5 other authors. 1974. Model of fish biomass dynamics. Trans. Am. Fish. Soc. 103: 786-798.
- Klyashtorin, L.B., and A.A. Yarzhombek. 1975. Some aspects of the physiology of the striped bass, Morone saxatilis. J. Ichthy. 15: 985-989.
- Knight, R.L., F.J. Margraf, and R.F. Carline. 1984. Piscivory by walleyes and yellow perch in western Lake Erie. Trans. Am. Fish. Soc. 113: 677-693.
- Kohler, C.C., J.J. Ney, and W.E. Kelso. 1986. Filling the void: Establishment of a pelagic fishery and its consequences to littoral fishes in a Virginia mainstream reservoir. Pages 166-177 in G.E. Hall and M.J. Van Den Avyle (eds.), Reservoir fisheries management: Strategies for the 80's. Reservoir Committee, South. Div. Am. Fish. Soc., Bethesda, Md.
- Kohler, C.C., and J.J. Ney. 1981. Suitability of alewife as a forage fish for southeastern reservoirs. Proc. Annu. Conf. Southeast. Assoc. Fish Wildl. Agencies 34: 137-150.
- Kruger, R.L., and R.W. Brocksen. 1978. Respiratory metabolism of striped bass, Morone saxatilis (Walbaum), in relation to temperature. J. Exp. Mar. Biol. Ecol. 31: 55-66.
- Latta, W.C. 1975. Dynamics of bass in large natural lakes. Pages 175-182 in R.H. Stroud and H. Clepper (eds.), Black bass biology and management. Sport Fish. Inst., Washington, D.C.
- Larkin, P.A. 1956. Interspecific competition and population control in freshwater fish. J. Fish. Res. Board Can. 18: 327-342.
- La Roche, A.L. 1981. Region II reservoir investigations: Smith Mountain Lake. Va. Comm. Game Inland Fish. D.J. Proj. F-39.
- Lawrence, J.M. 1958. Estimated sizes of various forage fishes largemouth bass can swallow. Proc. Annu. Conf. Southeast. Assoc. Game Fish Comm. 11: 220-225.
- Lemmons, D.E., and L.I. Crawshaw. 1985. Behavioral and metabolic adjustments to low temperatures in the largemouth bass (Micropterus salmoides). Physiol. Zool. 58: 175-180.
- Lewis, G.E. 1981. Characteristics of alewives in a small West Virginia impoundment. Prog. Fish-Cult. 43: 224.

- Lewis, R.E. 1983. Temperature selection and vertical distribution of striped bass during lake stratification. Proc. Annu. Conf. Southeast. Assoc. Fish Wildl. Agencies 37: 276-286.
- Lewis, W.M., and four other authors. 1974. Food intake of the largemouth bass. Tran. Am. Fish. Soc. 103: 277-280.
- Lewis, W.M., R.C. Heidinger, and B.L. Tetzlaff. 1981. Tank culture of striped bass production manual. Illinois striped bass project. IDC F-26-R.
- Li, H.W., and P.B. Moyle. 1981. Ecological analysis of species introductions into aquatic systems. Trans. Am. Fish. Soc. 110: 772-782.
- Logan, D.T. 1985. Environmental variation and striped bass population dynamics: a size-dependent mortality model. Estuaries 8: 28-38.
- Lyons, J. 1984. Walleye predation, yellow perch abundance, and the population dynamics of an assemblage of littoral-zone fishes in Sparkling Lake, Wisconsin. Ph.D. dissertation, Univ. Wisconsin, Madison, Wis.
- Magnuson, J.J. 1976. Managing with exotics - a game of chance. Trans. Am. Fish. Soc. 105: 1-9.
- Malevestuto, S.P. 1983. Sampling the recreational fishery. Pages 397-419 in L.A. Nielsen and D.L. Johnson (eds.), Fisheries Techniques. Am. Fish. Soc., Bethesda, Md.
- Mann, K.H. 1978. Estimating the food consumption of fish in nature. Pages 250-273 in S.D. Gerking (ed.), Ecology of freshwater fish production. Blackwell Sci. Pub., Oxford, England.
- Manooch, C.S., III. 1973. Food habits of yearling and adult striped bass, Morone saxatilis (Walbaum), from Albermarle Sound, North Carolina. Chesapeake Sci. 14: 73-86.
- Marquardt, D.W. 1963. An algorithm for least-squares estimation of non-linear parameters. J. Soc. Indust. Appl. Math. 11: 431-441.
- Matthews, W.J., and L.G. Hill. 1982. Preliminary monitoring of interaction among striped bass, forage fish species, and zooplankton in Lake Texoma, Oklahoma-Texas. Final report: Proj. U.S. Fish Wildl. Serv. Mon-RA-81-106.
- Meakins, R.H. 1976. Variations in the energy content of freshwater fish. J. Fish. Biol. 8: 221-224.
- Miller, L.W. 1974. Mortality rates for California striped bass (Morone saxatilis) from 1965-1971. Calif. Fish Game 60: 157-171.

- Miller, R.V. 1967. Food of the threadfin shad, Dorosoma petenense, in Lake Chicot, Arkansas. Trans. Am. Fish. Soc. 96: 243-246.
- Miller, K.D. and R.H. Kramer. 1971. Spawning and early life history of largemouth bass (Micropterus salmoides) in Lake Powell. Am. Fish. Soc. Spec. Pub. 8: 73-83.
- Minton, J. 1981. Bioenergetics of sauger in Watts Bar Reservoir, Tennessee. M.S. Thesis, Univ. of Tenn., Knoxville, Tenn.
- Minton, J.W., and R.B. McLean. 1982. Measurements of growth and consumption of sauger (Stizostedion canadense): implication for fish energetics studies. Can. J. Fish. Aquat. Sci. 39: 1396-1403.
- Momot, W.T., J. Erickson, and F. Stevenson. 1977. Maintenance of a walleye (Stizostedion vitreum vitreum) fishery in a eutrophic reservoir. J. Fish. Res. Board Can. 34: 1725-1733.
- Moreau, J. 1987. Mathematical and biological expression of growth in fishes: recent trends and further developments. Pages 81-114 in R.C. Summerfelt and G.E. Hall (eds.), Age and growth of fish. Iowa State Univ. Press, Ames, Ia.
- Morris, D.J., and B.J. Follis. 1978. Effects of striped bass predation upon shad in Lake E.V. Spence, Texas. Proc. Annu. Conf. Southeast. Assoc. Fish Wildl. Agencies 32: 697-702.
- Moss, L.J., and C.S. Lawson. 1982. Evaluation of striped bass and hybrid striped bass stockings in eight Alabama public fishing lakes. Proc. Annu. Conf. Southeast. Assoc. Fish Wildl. Agencies 36: 33-41.
- Mullan, J.W. and R.L. Applegate. 1967. Centrarchid food habits in a new and old reservoir during and following bass spawning. Proc. Annu. Conf. Southeast. Assoc. Game Fish Comm. 21: 332-342.
- Mullan, J.W. and R.L. Applegate. 1970. Food habits of five centrarchids during filling of Beaver Reservoir 1965-1966. Bureau Sport Fish. Wildl. Tech. Pap. 50.
- Nelson, W.R., and C.H. Walburg. 1977. Population dynamics of yellow perch (Perca flavescens), sauger (Stizostedion canadense) and walleye (Stizostedion vitreum vitreum) in four main stem Missouri reservoirs. J. Fish. Res. Board Can. 34: 1748-1763.
- Netsch, N.F., and three other authors. 1971. Distribution of young gizzard and threadfin shad in Beaver Reservoir. Am. Fish. Soc. Pub. 8: 95-106.

- Neumann, D.A., J.M. O'Connor and J.A. Sheik, Jr. 1980. Oxygen consumption of white perch (Morone americana), striped bass (Morone saxatilis) and spot (Leiostomus xanthurus). *Comp. Biochem. Physiol.* 69A: 467-478.
- Ney, J.J., and four other authors. 1988. The Smith Mountain Lake Fishery: factors affecting major sport and forage fish populations. Final Rep., Virginia Polytech. Inst. State Univ., Blacksburg, Va.
- Ney, J.J., C.C. Kohler, and A.A. Nigro. 1982. Landlocked alewife in Claytor Lake, Virginia: Evaluation as a forage species for inland waters. Management Publication No. 4. Dept. Fish. Wildl. Sci., Virginia Polytech. Instit. State Univ., Blacksburg, Va.
- Nielsen, L.A. 1980. Effect of walleye (Stizostedion vitreum vitreum) predation on juvenile mortality and recruitment of yellow perch (Perca flavescens) in Oneida Lake, New York. *Can. J. Fish. Aquat. Sci.* 37: 11-19.
- Nielsen, L.A., and D.J. Orth. 1984. Investigation of commercial invertebrate bait harvest in the New River, West Virginia. *Ann. Rep., West Va. Dep. Nat. Res.* 3-380-R-1.
- Nigro, A.A., and J.J. Ney. 1982. Reproduction and early life accommodations of landlocked alewives to a southern range extension. *Trans. Am. Fish. Soc.* 111:559-569.
- Niimi, A.J., and Beamish, F.W.H. 1974. Bioenergetics and growth of largemouth bass (Micropterus salmoides) in relation to body weight and temperature. *Can. J. Zool.* 52: 447-456.
- Noble, R.L. 1981. Management of forage fishes in impoundments of the southeastern U.S. *Trans. Am. Fish. Soc.* 110: 738-750.
- O'Neill, R.V. and three other authors. 1972. Terrestrial ecosystem energy model. Eastern Deciduous Forest Biome Memo Rep. No. 72-19.
- Paine, R.T. 1971. The measurement and application of the calorie to ecological problems. *Annu. Rev. Ecol. Syst.* 2: 145-164.
- Painter, R.E., and L.H. Wixom. 1967. Striped bass fishway and swimming endurance tests. Pages 31-47 in *Delta fish and wildlife protection study*, Res. Agency Calif.
- Pasch, R.W. 1975. Some relationships between food habits and growth of largemouth bass in Lake Blackshear, Georgia. *Proc. Annu. Conf. Southeast. Assoc. Game Fish Comm.* 28: 307-321.
- Pauly, D. 1986. A simple method for estimating the food consumption of fish populations from growth data and food conversion experiments. *Fish. Bull.* 84: 827-839.

- Pauly, D., and G. Gaschutz. 1979. A simple method for fitting oscillating length growth data with a program for pocket calculators. Int. Council Expl. Sea Dem. Fish Comm. CM 1979/G/24.
- Pelzman, R.J., S.A. Rapp, and R.R. Rawstron. 1980. Mortality and survival of tagged smallmouth bass, *Micropterus dolomieu*, at Merle Collins Reservoir, California. Calif. Fish Game 66: 35-39.
- Penczak, T., and four other authors. 1984. Food consumption and energy transformations by fish populations in two small lowland rivers in Poland. Hydrobiologia 108: 135-144.
- Penczak, T. 1985. A method of estimating total food consumed by fish populations. Hydrobiologia 123: 241-244.
- Ploskey, G.R., and R.M. Jenkins. 1982. Biomass model of reservoir fish and fish-food interactions, with implications for management. N. Am. J. Fish. Manage. 2: 105-121.
- Popova, O.A. 1966. The predator-prey relationship among fish. Pages 359-376 in S.D. Gerking (ed.), The biological basis of freshwater fish production. John Wiley and Sons, Inc., New York, N.Y.
- Powell, T.G., D.C. Bowden, and H.K. Hagen. 1971. Evaluation of five types of fishing gear in Boyd Reservoir, Colorado. Am. Fish. Soc. Spec. Pub. 8: 313-320.
- Priede, I.G. 1985. Metabolic scope in fishes. Pages 22-64 in P. Tyler and P. Calow (eds.), Fish energetics: new perspectives. John Hopkins University Press, Baltimore, Md.
- Prince, E.D. 1975. The biological effects of artificial reefs in Smith Mountain Lake, Virginia. Ph.D. Dissertation, Virginia Polytech. Inst. State Univ., Blacksburg, Va.
- Pritchard, D.L., O.D. May, Jr., and L. Rider. 1978. Stocking of predators in the predator-stocking-evaluation reservoirs. Proc. Annu. Conf. Southeast. Assoc. Fish Wildl. Agencies 30: 108-113.
- Pyke, G.H., H.R. Pullman, and E.L. Charnov. 1977. Optimal foraging: a selective review of theory and tests. Quart. Rev. Biol. 52: 137-154.
- Rainwater, W.C., and A. Houser. 1975. Relation of physical and biological variables to black bass crops. Pages 306-309 in R.H. Stroud and H. Clepper (eds.), Black bass biology and management. Sport Fish. Inst., Washington, D.C.
- Rainwater, W.C., and A. Houser. 1982. Species composition and biomass of fish in selected coves in Beaver Lake, Arkansas, during the first 18 years of impoundment (1963-1980). N. Am. J. Fish. Manage. 4: 316-325.

- Range, J.D. 1973. Growth of five species of game fishes before and after introduction of the threadfin shad into Dale Hallow Reservoir. Proc. Annu. Conf. Southeast. Assoc. Game Fish Comm. 26: 510-518.
- Reynolds, J.B. 1983. Electrofishing. Pages 147-163 in L.A. Nielsen and D.L. Johnson (eds.), Fisheries techniques. Am. Fish. Soc. Bethesda, Md.
- Rice, J.A. 1981. Derivation and application of a bioenergetics model for largemouth bass (Micropterus salmoides). M.S. thesis, Univ. of Wisconsin, Madison, Wis.
- Rice, J.A., and P.A. Cochran. 1984. Independent evaluation of a bioenergetics model for largemouth bass. Ecology 65: 732-739.
- Rice, J.A., and three other authors. 1983. Evaluating the constraints of temperature, activity, and consumption on growth of largemouth bass. Env. Biol. Fishes 9: 263-275.
- Ricker, W.E. 1975. Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Board Can. 191, Ottawa, Canada.
- Robson, D.S. and D.G. Chapman. 1961. Catch curves and mortality rates. Trans. Am. Fish. Soc. 90: 181-189.
- Rogers, B.A., and D.T. Westin. 1978. A culture methodology for striped bass, Morone saxatilis. EPA Ecol. Res. Ser. 660/3-78-000.
- Rohrer, R.L. 1985. Smallmouth bass research on Brownlee Reservoir, Idaho. Abstract, Am. Fish. Soc. 115th Annu. Meet. 112.
- Rottiers, D.V., and R.M. Tucker. 1982. Proximate composition and caloric content of eight Lake Michigan fishes. U.S. Fish Wildl. Serv. Tech. Pap. 108.
- SAS Institute Inc. 1985. SAS user's guide: Statistics version 5 edition. Cary, N.C.
- Saul, B.M. 1981. Food habits and growth of young-of-the-year striped bass in Cherokee Reservoir, Tennessee. M.S. Thesis, Univ. of Tennessee, Knoxville, Tenn.
- Schaich, B.A., and C.C. Coutant. 1980. A biotelemetry study of spring and summer habitat selection by striped bass in Cherokee Reservoir, Tennessee, 1978. Oak Ridge National Lab., ORNL/TM-7127, Oak Ridge, Tenn.
- Schneidermeyer, F., and W.M. Lewis. 1956. Utilization of gizzard shad by largemouth bass. Prog. Fish-Cult. 18: 137-138.

- Schoener, T.W. 1970. Non-synchronous spatial overlap of lizards in patchy habitats. *Ecology* 51: 408-418.
- Schoener, T.W. 1974. Resource partitioning in ecological communities. *Science* 185: 27-39.
- Setzler, E.M., and eight other authors. 1980. Synopsis of biological data on striped bass, Morone saxatilis (Walbaum). NOAA Tech. Rep., NMFS Circ. 433.
- Siler, J.R., W.J. Foris, and M.C. McInerney. 1986. Spatial heterogeneity in fish parameters within a reservoir. Pages 122-136 in G.E. Hall and M.J. Van Den Avyle (eds.), *Reservoir fisheries management: Strategies for the 80's*. Res. Comm, Southern Div., Am. Fish. Soc., Bethesda, Md.
- Simmons, G.M. 1976. The Smith Mountain-Leesville Project: A case history. *Trans. Am. Fish. Soc.* 105: 173-180.
- Smith, E.P. 1985. Statistical comparison of weighted overlap measures. *Trans. Am. Fish. Soc.* 114: 250-257.
- Soofiani, N.M., and A.D. Hawkins. 1985. Field studies of energy budgets. Pages 283-307 in P. Tytler and P. Calow (eds.), *Fish energetics: new perspectives*. John Hopkins Univ. Press, Baltimore, Md.
- Stevens, R.E. 1958. The striped bass of the Santee-Cooper reservoir. *Proc. Annu. Conf. Southeast. Assoc. Game Fish Comm.* 11: 253-264.
- Stevens, R.E. 1969. Landlocked striped bass. *Proc. 25th Annu. Northeast. Fish. Wildl. Conf.* 253-264.
- Stewart, D.J. 1980. Salmonid predators and their forage base in Lake Michigan: a bioenergetics-modeling synthesis. Ph.D. Dissertation, Univ. of Wisconsin, Madison, Wis.
- Stewart, D.J., J.F. Kitchell, and L.C. Crowder. 1981. Forage fishes and their salmonid predators in Lake Michigan. *Trans. Am. Fish. Soc.* 110: 751-763.
- Stewart, D.J., and three other authors. 1983. An energetics model for lake trout, Salvelinus namaycush: application to the Lake Michigan population. *Can. J. Fish. Aquat. Sci.* 40: 681-698.
- Storck, T.W. 1986. Importance of gizzard shad in the diet of largemouth bass in Lake Shelbyville, Illinois. *Trans. Am. Fish. Soc.* 115: 21-27.
- Summerfelt, R.C. 1975. Relationship between weather and year-class strength of largemouth bass in R.H. Stroud and H. Clepper (eds.), *Black bass biology and management*. Sport Fish. Inst., Washington, D.C.

- Summerfelt, R.C. 1986. Summarization of the symposium. Pages 314-327 in G.E. Hall and M.J. Van Den Avyle (eds.), Reservoir fisheries management: strategies for the 80's. Reservoir Comm., South. Div. Am. Fish. Soc., Bethesda, Md.
- Swenson, W.A., and L.L. Smith, Jr. 1976. Influence of food competition, predation, and cannibalism on walleye (Stizostedion vitreum vitreum) and sauger (Stizostedion canadense) populations in Lake of the Woods, Minnesota. J. Fish. Res. Board Can. 33: 1946-1954.
- Texas Instruments. 1976. Hudson river ecological study in the area of Indian Point. Thermal effects report. Prepared for Consolidated Edison Co. of New York, New York, N. Y.
- Timmons, T.J., W.L. Shelton, and W.D. Davies. 1981. Food of the largemouth bass before and during the first three years after impoundment of West Point Reservoir, Alabama and Georgia. J. Tenn. Acad. Sci. 56: 23-27.
- Tisa, M.S., J.J. Ney, and D.K. Whitehurst. 1985. Spatial and temporal distribution of larval alewives and gizzard shad in a Virginia reservoir. Proc. Annu. Conf. Southeast. Assoc. Fish and Wildl. Agencies 39: 65-73.
- Townsend, C.R. and I.J. Winfield. 1985. The application of optimal foraging theory to feeding behaviour in fish. Pages 67-98 in P. Tyler and P. Calow (eds.), Fish energetics: new perspectives. John Hopkins University Press, Baltimore, Md.
- Van Den Avyle, M.J., and B.J. Higginbotham. 1979. Growth, survival and distribution of striped bass stocked into Watts Bar Reservoir, Tennessee. Proc. Annu. Conf. Southeast. Assoc. Fish Wildl. Agencies 33: 361-370.
- Van Den Avyle, M.J., and J.E. Roussel. 1980. Evaluation of a simple method for removing food items from live black bass. Prog Fish-Cult. 42: 222-223.
- Virginia State Water Control Board. 1980. The impact of non-point sources on the water quality of Smith Mountain Lake. Planning Bull. 326.
- Wagner, W.C. 1972. Utilization of alewives by inshore piscivorous fishes in Lake Michigan. Trans. Am. Fish. Soc. 101: 55-63.
- Wallace Jr., R.K. 1981. An assessment of diet-overlap indexes. Trans. Am. Fish. Soc. 110: 72-76.
- Ware, F.J. 1970. Some early life history of Florida's inland striped bass, Morone saxatilis. Proc. Annu. Conf. Southeast. Assoc. Game Fish Comm. 24: 439-447.

- Webb, P.W. 1978. Partitioning of energy into metabolism and growth. Pages 184-214 in S.D. Gerking (ed.), Ecology of freshwater fish production. John Wiley and Sons, New York, N.Y.
- Weininger, D. 1978. Accumulation of PCBs by lake trout in Lake Michigan. Ph.D. Dissertation, Univ. of Wisconsin, Madison, Wis.
- Weithman, A.S., J.B. Reynolds, and D.E. Simpson. 1979. Assessment of structure of largemouth bass stocks by sequential sampling. Proc. Annu. Conf. Southeast. Assoc. Fish Wildl. Agencies 33: 415-424.
- Werner, E.E. and D.J. Hall. 1974. Optimal foraging and size selection of prey by the bluegill sunfish (Lepomis macrochirus). Ecology 55: 1042-1052.
- Westin, D.T., and B.A. Rogers. 1978. Synopsis of biological data on the striped bass, Morone saxatilis (Walbaum) 1972. Univ. Rhode Island Mar. Tech. Rep. 67, Kingston, R. I.
- Whitehurst, D.K. 1985. Region II reservoir investigations, Smith Mountain Lake. Va. Comm. Game Inland Fish. D.J. Rep.
- Winberg, G.G. 1956. Rate of metabolism and food requirements of fishes. Fish. Res. Board Can. Transl. Ser. 194.
- Windell, J.T. 1966. Rates of digestion in fishes. Pages 151-173 in S.D. Gerking (ed.). The biological basis of freshwater fish production. John Wiley and Sons, New York, N.Y.
- Wright, L.D. 1970. Forage size preference of the largemouth bass. Prog. Fish-Cult. 32: 39-42.
- Yarzhombek, A.A., and L.B. Klyashiorin. 1974. The relationship between standard metabolism and resting metabolism in fishes. J. Ichthy. 14: 439-443.
- Yellayi, R.R., and R.V. Kilambi. 1975. Population dynamics of white bass in Beaver Reservoir, Arkansas. Proc. Annu. Conf. Southeast. Assoc. Game Fish Comm. 29: 172-184.
- Yeager, D.M., and M.J. Van Den Avyle. 1978. Rates of angler exploitation of largemouth, smallmouth, and spotted bass in Center Hill Reservoir Tennessee. Proc. Annu. Conf. Southeast. Assoc. Game Fish Comm. 31: 449-458.
- Yeo, S.E. 1978. Seasonal variation in food consumption and caloric content of the alewife, Alosa pseudoharengus (Wilson), in Lake Michigan. M.S. Thesis, Univ. of Wisconsin, Milwaukee, Wis.

- Zaret, T.M. and A.S. Rand. 1971. Competition in tropical stream fishes: Support of the competitive exclusion principle. *Ecology* 52: 336-342.
- Zweiacker, P.L., and B.E. Brown. 1971. Production of a minimal largemouth bass population in a 3,000 acre turbid Oklahoma reservoir. *Am. Fish. Soc. Spec. Publ.* 8: 481-493.
- Zweiacker, P.L. and R.C. Summerfelt. 1974. Seasonal variation in food and diel periodicity in feeding of northern largemouth bass Micropterus salmoides (Lacepede), in an Oklahoma reservoir. *Proc. Annu. Conf. Southeast. Assoc. Game Fish Comm.* 27: 579-591.

**The vita has been removed from
the scanned document**