Analysis of the Impact of Flathead Catfish Predation on the Abundance of Four Centrarchid Species

by

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(ABSTRACT)

The top piscivore in Byllesby Reservoir, a 98.6 ha hydropower impoundment in southwestern Virginia, is the flathead catfish *Pylodictis olivaris*. The most numerically abundant fish in the reservoir are centrarchids, specifically bluegill *Lepomis macrochirus*, redbreast sunfish *L. auritus*, smallmouth bass *Micropterus dolomieu*, and spotted bass *M. punctulatus*. A bioenergetics model was used to estimate the number of age-1 and older centrarchids consumed annually by the flathead catfish population. These estimates were then compared to estimated abundances of each centrarchid species (age-1 and older) in the impoundment, resulting in an estimate of predation impact.

Smallmouth bass (2440 fish age-1 and older) were the most abundant centrarchid in Byllesby. Redbreast sunfish were the next most abundant species (2036) followed by spotted bass (1698) and bluegill (320). Although centrarchids are the most abundant fish in Byllesby, density estimates were considerably lower for all species other than smallmouth bass compared to a larger downstream New River reservoir.

Sunfish were the predominant prey item for Byllesby flathead catfish and no *Micropterus* spp. were present in flathead catfish stomachs. Because accurate site-specific abundances, annual mortalities, and growth rates of flathead catfish were not determined due to low numbers of catfish sampled, a range of values obtained from the literature were modeled. Annual consumption estimates ranged from 4.0 to 20.6 redbreast sunfish and 0.6 to 3.2 bluegill per ha, with the results of the probable Byllesby Reservoir population being 7.7 redbreast sunfish and 1.2 bluegill per ha. Probable annual mortality estimates due to predation by catfish for the *Lepomis* species (age-1 and older) were 37 %. Annual consumption estimates ranged from 2.1 to 10.5 smallmouth bass and 1.5 to 7.5 spotted bass per ha, with the results of the probable flathead catfish population being 4.0 smallmouth bass and 2.8 spotted bass per ha. Probable impact estimates for smallmouth and spotted bass were 16 %. Consumption estimate ranges resulted from modeling consumption of several flathead populations.

Results from this research suggest that flathead catfish populations of sufficient size may cause substantial declines in the abundance of their prey. For this reason, efficacy of flathead catfish as an auxiliary predator to largemouth bass *Micropterus salmoides* in ponds to control bluegill populations should be examined further.

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"I listened hard but could not see," is a lyric from the song "And You and I.." off of the 1972 Yes album, "Close to the Edge". This sentiment characterizes my research experience. I'd like to thank the "brain trust", Drs. Paul L. Angermeier, Donald J. Orth, and especially John J. Ney who taught me either to look instead of listen, or pay attention to those things I heard instead of saw. Special thanks are extended to Dr. John J. Ney for his guidance, criticism, humor, and help in the field. Just remember Dr. Ney, players hitting below the Mendoza line in the Major Leagues are either outstanding fielders, unhittable pitchers, or not long for the season.

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TABLE OF CONTENTS

LIST OF ILLUSTRATIONS

LIST OF TABLES

INTRODUCTION

The flathead catfish, *Pylodictis olivaris* (Rafinesque), is among the largest of the North American catfish (Family Ictaluridae) reaching weights over 56 kilograms (123 pounds). Native to the Mississippi River and Rio Grande drainages (Minckley and Deacon 1959; Glodek 1980; Lee and Terrell 1987), flathead catfish have been introduced into North and South Carolina, Georgia, Florida, Arizona, California, Idaho, Oregon, and Washington (Gholson 1970). Although native to the New River, Virginia (Jenkins and Burkhead in press), this species has been introduced into other Virginia drainages such as the Roanoke and James Rivers. Following introduction, populations of this piscivore often expand rapidly followed by declines in some of their prey species (Guier et al. 1980; Davis 1985).

This ictalurid inhabits medium to large rivers and reservoirs. While young-of-the-year (YOY) flathead catfish are usually found in riffles, specimens greater than 400 mm tend to inhabit deep holes near large logs or other overhead cover (Minckley and Deacon 1959; Glodek 1980; Lee and Terrell 1987). In these lotic situations, flathead catfish are rarely found in areas with soft, silty bottoms or areas with little or no current (Lee and Terrell 1980). Specimens residing in reservoirs tend to associate with rocky substrates, especially rip-rap, which may be important for cover, spawning, and feeding (Lee and Terrell 1980).

Although the flathead catfish supported important commercial fisheries in the Mississippi River and its larger tributaries, its large size and strength when caught on hook and line have made it a prized recreational species. This popularity as a sport fish is the primary reason for introducing the flathead catfish across the United States.

Food habits of this catfish are fairly well documented. Small flathead catfish, those under 250 mm, feed primarily on aquatic insects, crayfish, debris, and occasionally small fishes (Minckley and Deacon 1959; Brown and Dendy 1961; Quinn 1987). At a length of about 250 mm, the diet of flathead catfish begins to shift from invertebrates to fishes (Minckley and Deacon 1959; Lee and Terrell 1987; Quinn 1987). Many of the fishes found in flathead catfish diets are soft-rayed species from the families Catostomidae (suckers), Clupeidae (herrings and shads), and Cyprinidae (minnows) (Minckley and Deacon 1959; Turner and Summerfelt 1970; Minckley 1982; Davis 1985; Ashley and Buff 1987; Quinn 1987; Roell 1989), although fishes of the families Centrarchidae (sunfishes and black basses), Ictaluridae, Moronidae (temperate basses), Percidae (perch and darters), and Sciaenidae (drums) also have been noted in various food habit accounts (Minckley and Deacon 1959; Brown and Dendy 1961; Swingle 1964; Hackney 1965; Turner and Summerfelt 1970; Edmundson 1974; Minckley 1982; Davis 1985; Ashley and Buff 1987; Quinn 1987; Roell 1989). Soft-rayed fishes seem to be preferred over spiny-rayed fishes by flathead catfish.

Several researchers have described declining populations of prey species following flathead catfish introductions, although a causal relationship has never been demonstrated. Within 15 years of stocking 11 flathead catfish into the Cape Fear River, North Carolina, this catfish expanded its range and became the top predator within the system (Guier et al. 1981). The increased abundance of flathead catfish coincided with reduced abundances of several ictalurid species and elimination of the brown bullhead *Ameiurus nebulosus* (Guier et al. 1980). Populations of common carp *Cyprinus carpio*, brown bullhead, black bullhead *Ameiurus melas*, and yellow bullhead *Ameiurus* *natalis* declined significantly within four years following adult flathead catfish introduction into a Minnesota lake (Davis 1985). It appears that through predation or competition, flathead catfish can impact abundances of other species.

Several attempts at using this piscivore to control bluegill *Lepomis macrochirus* populations have resulted in limited success. Swingle et al. (1965) stocked flathead catfish fingerlings (123 per ha) into an Alabama pond with an overcrowded, stunted bluegill population that was experiencing little reproductive success. The bluegill population was reduced to a size allowing the resumption of natural reproduction. Bamberg (1975) stocked flathead fingerlings (27 per ha) into a 259-ha reservoir in Texas with an established largemouth bass *Micropterus salmoides* population and noted no appreciable reduction in bluegill abundance. Adult flathead catfish (305-356 mm) stocked into a small Alabama pond at a rate of 123 per ha progressively reduced the number of intermediate-sized bluegill throughout a 320-day trial (Hackney 1965). Bluegill populations were not thinned to the levels expected by Swingle et al. (1965) and Bamberg (1975), prompting them to conclude that flathead catfish were not effective in controlling stunted sunfish populations. In these two instances, however, the ineffectiveness of flathead catfish in thinning sunfish was likely due to the small size of the catfish stocked and the short time spans of these projects.

Although there is some evidence that flathead catfish may impact the abundance of its prey, little research has been attempted to quantify the impact of predation. In order to do this, annual consumption of prey items by a flathead catfish population must be estimated and compared to abundance estimates of the prey. Roell (1989) quantified flathead predation on a section of the New River in West Virginia. However, the flathead catfish in this section of the New River ate predominantly aquatic invertebrates (primarily crayfish). Thus, these annual consumption estimates are not transferable to a population of flathead catfish consuming predominantly fishes. Information regarding annual consumption by flathead catfish should shed light on future management of this species (feasibility for introduction and for use as a auxiliary predator with largemouth bass in ponds) and its prey.

Flathead catfish are native to Byllesby Reservoir, New River, Virginia (Jenkins and Burkhead in press) and are the dominant piscivore in this impoundment (Ney et al. 1990). Centrarchids, sunfish (*Lepomis*) and black bass (*Micropterus*) species, are the most abundant fish in Byllesby Reservoir. However, the abundance of centrarchids is lower in the reservoir than in contiguous sections of the New River, which support lower densities of flathead catfish (Ney et al. 1990). These reservoir versus river differences in catfish and centrarchid abundances suggest that predation by flathead catfish may be affecting and limiting bass and sunfish densities in Byllesby Reservoir. These circumstances presented an opportunity to study the impact of a population of flathead catfish on a group of sportfish species in a system where both are native.

The goal of this project was to estimate the impact of flathead catfish on abundances of four centrarchid species age-1 and older in Byllesby Reservoir, New River, Virginia. Specific objectives were to:

1) characterize diet composition of Byllesby Reservoir flathead catfish;
2) estimate annual consumption of centrarchids by the Byllesby Reservoir flathead catfish population:

    - a) estimate the number of each of four centrarchid species consumed annually by individual flathead catfish ages-4 through 15;
    - b) estimate age-specific abundances of flathead catfish in Byllesby Reservoir allowing extrapolation of annual consumption estimates from an individual to a population level; and

3) estimate the abundances of each of the four centrarchid species.
4) relate objectives 2) and 3) to derive annual mortality rates for each of the centrarchid species due to flathead catfish predation.

STUDY AREA

Byllesby Dam, constructed by Appalachian Power Company (APCO) for hydroelectric power generation in 1913, impounds approximately 98.6 hectares (ha) of the New River at full pool (Figure 1). Byllesby Dam is located 3.2 and 38.4 river kilometers upstream of the headwaters of Buck Reservoir (26.7 ha) and Claytor Lake (1,620 ha), respectively. Byllesby Reservoir lies within Carroll County just upstream (south) of Ivanhoe, Virginia at map coordinates 36° 47'N latitude and 80° 56'W longitude. Water was released from Byllesby on a run-of-the-river basis during 1991, although previous years' releases were peaked daily. Brush, Chestnut, and Crooked Creeks are second-order tributaries to the reservoir.

Byllesby Reservoir appears to be merely a slow, wide section of the river, measuring approximately 300 meters across at its widest point. Although mean depth is about 3 meters, some sections of the reservoir are over 15 meters deep at full pool. Mean annual discharge of the New River at Galax (the nearest gaging station, located 20.5 km upstream of Byllesby), is 1900 cubic feet per second (cfs). Mean annual discharges for the hydraulic years 1990 through 1992 (hydraulic year of 1992 begins in October of 1991 and ends September of 1992) were 2285, 2172, and 2074 cfs, respectively (U. S. Geological Survey 1991, 1992, 1993). Mean annual discharges, for the period of U. S. Geological Survey record, ranged from 1034 to 2807 cfs. Much of the substrate is silt and sand, but bedrock ledges, boulders, tree stumps, woody debris, and overhanging vegetation are available for cover (Ney et al. 1990). Both submerged and emergent macrophytes are present in some shallow areas of

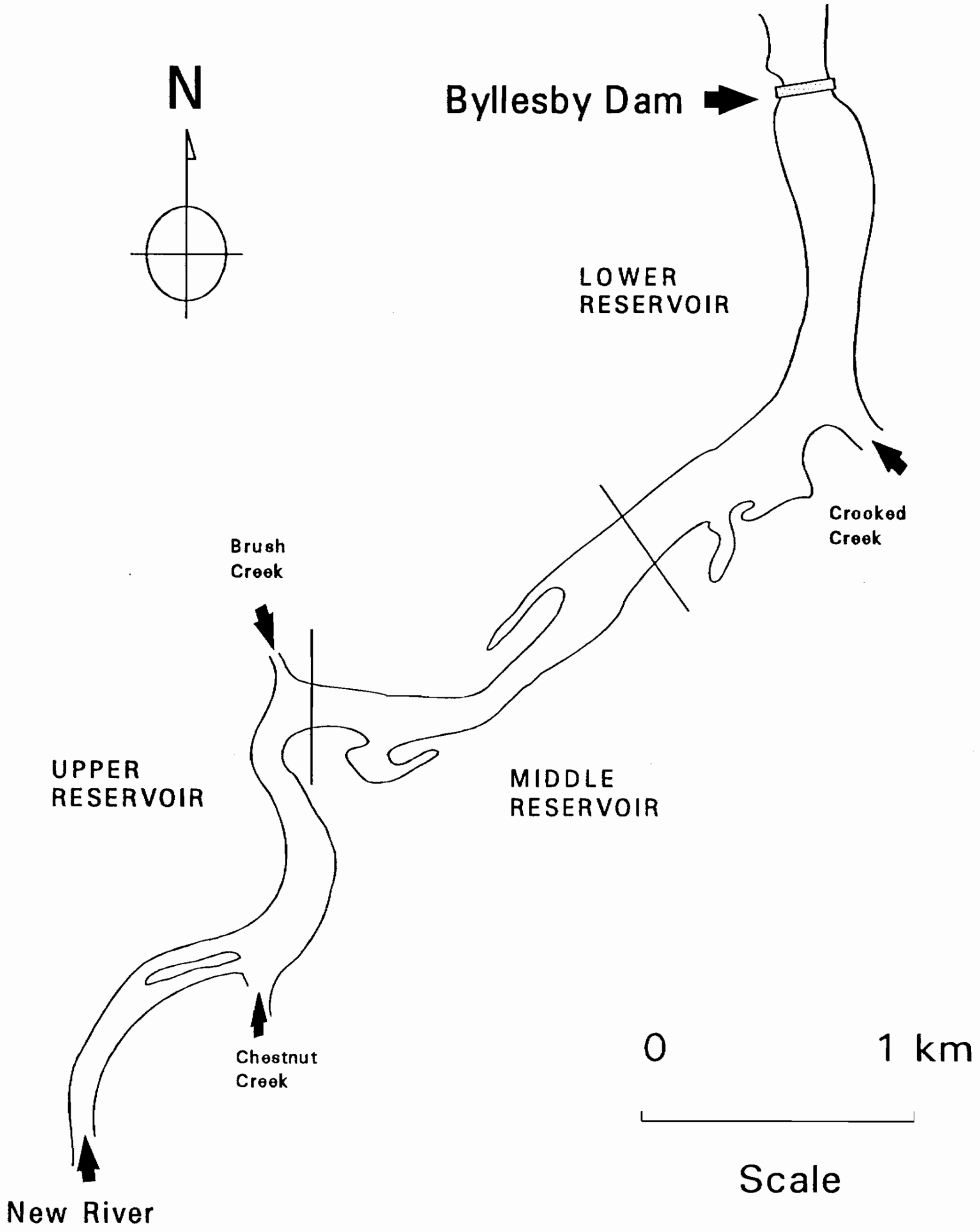

Figure 1. Map of Byllesby Reservoir, New River, Carroll County, Virginia. Suitable habitat for flathead catfish was most abundant in the upper and middle sections of the reservoir.

Byllesby Reservoir.

Several species of centrarchid were among the most abundant fishes in Byllesby Reservoir and may serve as a prey base for the flathead catfish (Ney et al. 1990). These species include spotted bass *Micropterus punctulatus*, smallmouth bass *M. dolomieu*, redbreast sunfish *Lepomis auritus*, and bluegill. Other abundant fishes in the reservoir include white sucker *Catostomas commersoni*, northern hogsucker *Hypentelium nigricans*, common carp *Cyprinus carpio*, spotfin shiner *Cyprinella spiloptera*, rosyface shiner *Notropis rubellus*, and channel catfish *Ictalurus punctatus*. Although there are no clupeids in Byllesby Reservoir presently, gizzard shad *Dorosoma cepedianum* are present as far upstream in the New River as Buck dam, located 3.2 km downstream of Byllesby.

Much of the habitat suitable for flathead catfish (e.g. rock ledges, boulder piles, submerged logs, and undercut banks) were located in the upper and middle sections of Byllesby Reservoir (Figure 1). These sections of the reservoir were sampled for flathead catfish more heavily than the lower section.

METHODS

Impact (defined as finite annual mortality) on age-1 and older centrarchids due to flathead catfish predation on redbreast sunfish, bluegill, smallmouth bass, and spotted bass populations at Byllesby Reservoir was assessed by deriving estimates of the annual predation ascribed to flathead predation and comparing these to abundance estimates for each of the four centrarchid species:

$$\text{Annual Mortality (\% of population)} = \frac{\text{\# of prey consumed by flathead population}}{\text{\# of prey in Byllesby Reservoir.}} \qquad [1]$$

Estimates of the number of each centrarchid species consumed annually by a population of flathead catfish and their respective abundance were needed. Annual consumption by piscivorous flathead catfish at each age (ages-4 through 15 were modeled) was estimated using a bioenergetics simulation, referred to as the Wisconsin Bioenergetics Model, (Hewett and Johnson 1992). The model determines the amount of food a single catfish at each age consumes based on physiological parameters and site-specific information. Site-specific information necessary for the model includes diet composition, water temperature, and seasonal pattern of consumption. Abundance and annual mortality estimates of Byllesby Reservoir flathead catfish were necessary to expand individual consumption estimates to the population level. Abundances of age-1 and older centrarchids were estimated with mark-and-recapture experiments.

FIELD COLLECTIONS

Extreme rainfall in the New River drainage during late spring of 1992 created flood conditions and forced the removal of a section of the splash boards of the dam at Byllesby for approximately one month. Catch-per-effort data for flathead catfish and three of the four centrarchid species examined declined following the flood, suggesting that many fish may have emigrated downstream out of the reservoir during the flood period. Estimating flathead catfish abundance was compromised because of the reduced number of catfish sampled. In addition, abundance estimates of the four predominant centrarchids in the reservoir were believed to be atypical.

Flathead Catfish

Diet Composition

Flathead catfish were captured with horizontal, experimental gill nets (4 8.5-m panels, with 25, 50, 80, and 100 mm bar mesh) and hoop nets (bar meshes of 50 mm and 40 mm) during April through October of 1991 and September and October 1992 and with low frequency (between 15 and 20 hertz) electrofishing gear in 1992 (Quinn 1987; Gilliland 1987). This electrofishing device generates weak electric fields at low frequencies (between 15 and 20 hertz works best on flathead catfish) to which some ictalurids are susceptible (Peters and Bretshneider 1972; Peters and Buwalda 1972).

As many as three experimental gill nets were set in depths of 4 to 10 meters on flat bottoms on each netting date for the months of August through October 1991 and September and October 1992, totalling 14 net days of effort. Gill nets were generally angled downstream with the smallest mesh nearest the shore. Between ten and twelve hoop nets were also set on each sampling date, totalling 133 net days of effort. Hoop nets were set on flat bottoms in depths of 3 to 15 meters with the cod end upstream. Sampling effort was concentrated in the upper and middle sections of the reservoir (Figure 1), as these sections had the most suitable flathead habitat and consistently yielded more fish per net than the lower reservoir. Nets were set for 36 hours and were pulled and reset every 12 hours. When a net was pulled, all fish were removed from the net prior to resetting. Fishes other than flathead catfish were returned to the reservoir immediately.

From May through August of 1992, the entire reservoir was sampled with low frequency electrofishing gear four days per month; no sampling was conducted in June because the reservoir was inaccessible due to flooding. Using one boat for electrofishing and having another as a chase boat was the most efficient method when using this gear. The electrofishing boat was motored to a location and left stationary over that spot. To aid in holding position, the boat was anchored on windy days. That location was electrofished for no longer than 10 minutes before moving to the next location. Any catfish that surfaced were retrieved by the chase boat. It generally took 1 to 2 minutes for catfish to surface, although surfacing took longer in depths greater than 10 meters. Flathead catfish affected by this gear came to the surface and swam erratically until they left the electric field, at which time they immediately descended. Locations greater than 5 meters deep near the shoreline with logjams, fallen timber, overhanging vegetation, submersed logs, boulders, or rock ledges were sampled most intensively. Once a location was thoroughly electrofished, another location, approximately 200 m away, was sampled in the same manner. There were 48 locations in the reservoir.

Once captured, flathead catfish were placed in a livewell until the net was reset or the location was electrofished for 10 minutes. Every flathead catfish collected during both field seasons was released alive. All catfish from one net or electrofishing location were worked up and released prior to retrieving the next net or sampling the next electrofishing location. Each catfish was anesthetized with tricaine methanesulfonate (MS-222) in a separate container to reduce handling stress. Total length of each catfish was measured to the nearest millimeter. Weight of each fish was determined to the nearest gram for fish less than 1 kg on a platform scale and to the nearest 10 grams for fish greater than 1 kg on a spring scale.

Stomach contents were collected from flathead catfish from June through October in 1991 and May through November in 1992. An acrylic tube of the appropriate diameter was inserted through the esophagus and into the stomach of each anesthetized catfish (Van den Avyle and Roussel 1980). A small amount of water was forced into the stomach, through the tube, to aid in the removal of stomach contents by inverting the fish slightly and removing the tube. A clawed retriever was inserted through the tube to remove items lodged in the stomach (Dimond 1985). Once removed from the fish, stomach contents were preserved in 10 % buffered formalin. Following the removal of stomach contents, catfish were allowed to recover from the anesthetic in clean water and released.

Abundance and Mortality

Estimates of flathead catfish abundance were attempted during the summers of 1991 and 1992 through mark-and-recapture efforts. All flathead catfish collected were marked with an individually-numbered metal strap tag placed in the dorsal edge of the opercle. During 1992, a single punch through the adipose fin was used as a second mark on all flathead catfish sampled. Numbers of fish caught, marked and released, and recaptured each sampling period (generally three days duration) were recorded to be used in a modified Schnabel abundance estimator. However, insufficient data were collected in either year, due to inefficient technique in 1991 and flooding-induced population decimation in 1992, to allow for accurate abundance estimation. Just 73 flathead catfish were marked and three recaptured during the two years of this study. Flathead density values from other southeastern rivers and reservoirs were used to estimate the probable, normal catfish density in Byllesby Reservoir.

Similarly, sufficient data to calculate accurate annual mortality estimates were not available; therefore, a range of annual mortality estimates from similar systems (ie. southeastern rivers and reservoirs) was taken from the literature. In calculating age-specific abundances of flathead catfish in Byllesby Reservoir, the age distribution was treated as stable. Annual mortality rates were assumed to be constant for all age groups. Thus, the number of age-5 flathead catfish was assumed to be the number of age-4 catfish minus the number of age-4 fish predicted to die in one year, based on the annual mortality rate.

Centrarchids

Abundance

The adjusted Petersen abundance estimator (Ricker 1975) was used to estimate the abundances of the predominant centrarchid species of Byllesby Reservoir. These species included redbreast sunfish, bluegill, smallmouth bass, and spotted bass. Ricker (1975) suggested the use of the adjusted Petersen population estimator when sampling closed, or essentially closed, populations. Although recruitment, natural and fishing mortality, emigration, and immigration occur in a reservoir, these sources of error were assumed negligible over the five days separating the mark and recapture periods of this experiment. The population size (N^*) at the time of the mark period can be estimated by setting up proportions based on the number of fish marked during the mark period (M), the number of fish sampled in the recapture period (C), and the number of marked fish recaptured during the recapture period (R), by the following formula :

$$N^* = \frac{(M + 1)(C + 1)}{(R + 1)}. \qquad [2]$$

Two sampling phases were conducted during July and August of 1992 to estimate centrarchid populations in the reservoir. The first phase was the mark period in which the entire shoreline of Byllesby Reservoir, at depths of one to two meters, was electrofished after dusk using a boat electrofishing unit. During this phase, centrarchids sampled were put in a livewell until approximately 200 m of shoreline were sampled. Redbreast sunfish and bluegill greater than 70 mm and smallmouth bass and spotted bass greater than 100 mm (sizes corresponding roughly to age-1 for all four species and the smallest sizes that could be marked without harming the fish) were lightly anesthetized with MS-222, measured to the nearest millimeter, and fin clipped in the soft dorsal fin. Following the work-up procedure, each fish was allowed to recover from the anesthetic prior to being released within 100 m of its point of capture. The mark phase was completed in five nights of shocking over an eight-day period.

During the second phase, or recapture period, the entire Byllesby shoreline was electrofished again, beginning five days after the completion of the mark period. The same boat electrofishing unit was used for this period, and 200 m sections in depths of one to two meters were sampled following dusk. Once captured, centrarchids were examined for evidence of fin-clipping and noted as a recapture (fin-clipped) or not. Each centrarchid was anesthetized, and the total length was measured to the nearest millimeter; weight was measured to the nearest gram on a platform scale. Several scales were removed from approximately 50 individuals of each sunfish species (redbreast and bluegill). The scales were stored in individually labelled coin envelopes for age assignment (see below). Scales for age-assignment of black bass were collected during a concurrent study (M. C. Scott, VPI & SU, unpublished). Fish were allowed to recover from the anesthetic prior to being released back into the reservoir.

Because flood conditions precipitated extreme habitat and flow fluctuations in the reservoir, due to work that was done to the dam, there is reason to believe that centrarchid abundances were atypically low in 1992. Thus, each 1992 abundance estimate was corrected by comparing catch-per-unit-effort (CPUE, measured as number of fish sampled per shocking minute) data from 1992 to boat-electrofishing CPUE data from a survey conducted in 1990 for each species and size group (Ney et al. 1990). Because three discrete transects were sampled monthly during the 1990 survey of Ney et al. (1990), only CPUE data from similar habitat stretches collected in 1992 were used to create an adjustment factor. This adjustment factor, the ratio of 1992 to 1990 CPUE, multiplied by the modified-Petersen point estimate of abundance, produced the adjusted, or pre-flood, abundance estimate for each sunfish and black bass species.

LABORATORY ANALYSIS

Diet Composition

In the laboratory, gut contents of each flathead catfish were separated into four categories: aquatic insects; crayfish; non-centrarchid fishes; and centrarchid fishes. Prey items in the categories non-centrarchid and centrarchid fishes were identified to the lowest possible taxon. Prey items were blotted dry and weighed to the nearest 0.01 gram. The proportion of each prey type, by wet weight, in the diet was determined for both years for two size classes. Small flathead catfish measured 300 to 499 mm total length (TL) and represented age classes 5 to 9 while large catfish were ≥ 500 mm TL and represented age classes 10 to 15. Total length of freshly consumed specimens was measured directly to establish predator-prey size relationships.

Age and Growth

Flathead Catfish

Ages were estimated directly from pectoral spines of catfish. Left pectoral spines were removed from the flathead catfish via disarticulation in the field during the last two sampling periods. Catfish from the latest collections were used because increased mortality, from the stress of spine removal, of tagged flathead catfish could have caused abundance overestimation. Only two flathead catfish were sampled during September and October of 1992. The spines were thin-sectioned at the articulating process, as suggested by Turner (1977), with a low speed, diamond blade saw. Sections were then fixed to glass slides with mounting media. Age was assigned to each catfish based on the number of annuli identified from enlarged projections of the spine sections. Spine radius and distance to each annulus were measured for each spine to determine mean length at annulus using the corrected Lee method of back calculation:

$$L_n = a + (S_n/S_c) \cdot (L_c - a), \qquad [3]$$

where

L_n = total length of fish at time of annulus n formation;

a = intercept value of body-spine length regression;

S_n = scale measurement from focus to annulus n;

S_c = distance from focus to anterior spine margin; and

L_c = total length of fish at capture.

Growth data from Byllesby Reservoir flathead catfish were unreliable because only two fish were examined. Thus, growth data from Brooks Pool, New River, West Virginia (Roell 1989) were used after being corroborated with the extant Byllesby growth data. Mean length-at-annulus measurements for Brooks Pool flathead catfish were only available through age-9. Mean lengths-at-annulus were used in a length-weight regression, developed from $\log_{10}$ transformations of Byllesby Reservoir flathead catfish, to determine weight on the day of annulus formation for input to the catfish bioenergetics model.

Centrarchids

Ages were directly estimated from centrarchid scales for 56 redbreast sunfish, 50 bluegill, 45 smallmouth bass and 77 spotted bass. Scales from black bass were taken during a concurrent study of these species in Byllesby Reservoir (M. C. Scott, VPI & SU, unpublished). Scales were taken from five fish in each 10 mm size class (beginning with 70-79 mm for the sunfishes and 100-109 mm for the black basses) such that representatives from the entire size range of each centrarchid species were aged. Fewer than five representatives were available from most of the larger size classes for all four species. Impressions of all scales were made on acetate slides using a roller press. An age was assigned to each fish by examining a projected image of the scale impression for annuli.

Scale radius and annular measurements were made to determine length-at-annulus for each fish by back-calculation using the corrected Lee equation. These back-calculated lengths provided estimates of length-at-annulus. Mean length-at-annulus was determined for each species, ages-1 through 4.

Consumption estimates of the bioenergetic model are outputted as weight. Individual weights of the different age classes for each centrarchid species were necessary to convert the weight consumed by the flathead catfish population to numbers. Log_{10} transformations of length and weight were used to determine a length-weight equation for each species. The length of the average age-X centrarchid was assumed to be the midpoint between mean length-at-annulus X and mean length-at-annulus X+1. This midpoint length was then used in the appropriate length-weight equation to calculate a weight for this age-X fish. This procedure was used to determine average weights for ages-1, 2, and 3 individuals for each centrarchid species. The mean weights determined for age-1, 2, and 3 individuals of each species were assumed to be the same as the mean weight of individual centrarchids consumed by flathead catfish.

BIOENERGETIC SIMULATION OF ANNUAL CONSUMPTION

Bioenergetic simulations, via the Wisconsin bioenergetics model (Hewett and Johnson 1992), of flathead catfish were used to estimate cohort-specific annual consumption. The bioenergetics model is a mass-balance equation that can be solved to estimate consumption of individual fish based on energy expenditures for growth (G) and respiration (R) and energy lost in waste products (W):

$$C = G + R + W \qquad [4]$$

Five groups of information about flathead catfish were required for the bioenergetics model. The five groups are:

1) a mass balance equation with associated algorithms and parameter estimates representing flathead catfish energetics and physiology;
2) initial and final weight estimates flathead catfish, corresponding to the beginning and end of each time interval;
3) energy density estimates for flathead catfish and their prey;
4) diet composition by prey type for each cohort (as proportions by wet weight); and
5) water temperatures.

Estimating consumption with the bioenergetics model required the input of 21 parameters (Table 1), describing energetic equations and algorithms associated with consumption, respiration, excretion, and egestion (see Appendix A and/or Hewett and Johnson 1992 for equations, algorithms, and parameter valuation). Roell (1989)

Table 1. Parameter estimates used in bioenergetics model to estimate consumption by flathead catfish in Byllesby Reservoir, New River, Virginia. All estimates based on Roell (1989) model. Parameter valuation is discussed in detail in Appendix A.

Symbol	Parameter Description	Estimate
	Consumption (C)	
CA	Intercept, C_{max} (g/g/day)	0.25
CB	Slope, C_{max} dependance on weight	-0.20
CQ	Temperature for CK1 (°C)	10
CTO	Temperature for CK2 (°C)	31
CTM	Temperature for CK3 (°C)	32
CTL	Temperature for CK4 (°C)	35
CK1	Proportion of C_{max} at CQ	0.10
CK2,CK3	Proportion of C_{max} at CTO and CTM	0.98
CK4	Proportion of C_{max} at CTL	0.01
	Respiration (R)	
RA	Intercept, R_{max} (gO_2/g/day)	0.01
RB	Slope, R_{max} dependance on weight	-0.36
RQ	Slope, R dependence on temperature	2.1
RTO	Optimum temperature for R (°C)	35
RTM	Maximum temperature for R (°C)	38
ACT	Activity multiplier of R for:	
	Temperatures < 10°C	1.025
	Temperatures ≥ 10°C	1.15
SDA	Proportion of assimilated energy lost to specific dynamic action	0.17

Table 1. Parameter estimates continued.

Symbol	Parameter Description	Estimate
	Egestion	
	Proportion of consumed energy egested for the following prey types:	
IP_1	Centrarchids	0.104
IP_2	Other fish	0.104
IP_3	Insects	0.150
IP_4	Crayfish	0.180
	Excretion	
UA	Proportion of assimilated energy excreted	0.088

developed bioenergetics parameter values for the flathead catfish of Brooks Pool, New River, West Virginia. Roell's (1989) parameter values were used to model the Byllesby Reservoir flathead population.

The bioenergetics model also required input of site-specific information. Water temperature inputs for Byllesby Reservoir were based on water temperatures from the Galax, Virginia gaging station for the years 1982 to 1986 (U. S. Geological Survey 1983, 1984, 1985, 1986, 1987) and surface water temperature data measured during the months of May through October for the years of 1990 through 1992 at Byllesby Reservoir (See **Appendix B**, Table 13). Energy density estimates for both flathead catfish and their prey were established in Brooks Pool, New River, West Virginia and were assumed to be constant through the year (Roell 1989).

Three different time intervals were used to model annual consumption of flathead catfish. These intervals were used to allow separate modeling of periods when flathead catfish and their prey are assumed to have different levels of activity (Roell 1989; Table 2). Lovell and Sirikul (1974) found that channel catfish feed sparingly at temperatures below 10 °C, so it is assumed that flathead catfish behave similarly. Also, crayfish and some aquatic insects are not available to predators at temperatures below 10 °C (Momot 1967; Fast and Momot 1973; Momot and Gowing 1977; Momot 1978; Roell 1989). Thus, each year was divided into growing seasons (water temperatures $\geq$ 10°C) and winter (water temperatures $<$ 10°C). By definition, the day of annulus formation was the first day of the year (simulation day 1) for each cohort; for flathead catfish in Brooks Pool of the New River, Roell (1989) determined this day to be 15 June. It should be nearly the same for Byllesby Reservoir.

Table 2. Intervals used to model Byllesby Reservoir, New River, Virginia flathead catfish population, the landmark events that define the intervals, and the day of the simulation (the day of annulus formation is the first day of each simulation).

Bioenergetic Season	Landmark Event	Simulation Day
Growth Period	Day of annulus formation	1
1	Day before water temperature < 10°C	151
Winter Period	Day water temperature < 10°C	152
	Day before water temperature ≥ 10°C	300
Growth Period	Day water temperature ≥ 10°C	301
2	Day before next annulus formation	365

The first growing period was this day to 12 November (simulation day 151), the day before water temperature drops below 10°C in Byllesby Reservoir. The winter period extended from 13 November (simulation day 152) until 10 April (simulation day 300), the period water temperatures are below 10°C. The final modeling interval was the period from when water temperatures met or exceeded 10°C (11 April, simulation day 301) until the day before next annulus formation (14 June, simulation day 365).

Estimating Consumption with Energetics

Consumption by each cohort was predicted with the bioenergetics computer software program of Hewett and Johnson (1992). Consumption for an average individual for each cohort was calculated and then multiplied by the number of individuals in that cohort for a cohort-level consumption estimate. Summing these estimates across all cohorts resulted in a population-level estimate. Three time intervals were modeled through the year representing periods when activity level, prey availability, and growth differed. A daily time step was used in each simulation.

Estimation of consumption involved two steps, the first being an iterative process to determine the P-value (represents the proportion of maximum ration consumed by the fish over the simulation interval; Hewett and Johnson 1992) necessary to modify maximum consumption so that modeled growth matched estimated growth of Byllesby Reservoir flathead catfish over each time interval. If weights predicted during this first step were not within 0.05 % of observed growth, a new P-value was used in the model and the procedure was repeated until predicted growths matched observed growths. A P-value was determined for each cohort in each interval. The second step of the consumption estimation process involved using the P-values determined for the interval as a constant in the bioenergetics model. The simulation was then run a final time for each interval to estimate how much of each prey type was consumed.

STATISTICAL ANALYSES

Comparisons

Chi-square tests of independence were used to test for differences in the percentages of empty stomachs between small and large flathead catfish and between those sampled in May, June, and July versus those collected in August, September, and October. All comparisons were made with an acceptable type I error rate of $\alpha = 0.05$.

Regression

Simple linear regressions were calculated to evaluate the relation between log-transformed length and weight for all four species of centrarchid and flathead catfish. Length-weight regressions were used to predict weights at given lengths.

RESULTS

FLATHEAD CATFISH

Diet Composition

Of the 45 small and 31 large flathead catfish stomachs examined during 1991 and 1992, 60 % were empty (Table 3). There was no significant difference between the percentage of empty small and large flathead catfish ($P > 0.10$). Flathead catfish sampled in the months of May through July were significantly more likely ($P < 0.025$) to contain food items (48 %) compared to catfish sampled from August through October (21 %).

Fishes were the predominant food item by preserved wet weight in Byllesby Reservoir flathead catfish, contributing 53 % and > 99 % to stomach contents for small and large size classes respectively (Table 3). Crayfishes were of secondary importance in small flathead catfish but were not present in any large individuals. Aquatic insects represented very little of the diet by preserved wet weight for either size class.

Of the fishes consumed, centrarchids represented 95 % and 67 % of the preserved wet weights of small and large catfish stomach contents respectively, but this consisted of a total of only six fish. Five of the six centrarchids were identified as redbreast sunfish with the other being an unidentified *Lepomis* spp. The mean length of consumed centrarchids was 83 mm. The smallest of these sunfish was 15 mm (YOY) in total length (TL) while the largest was nearly 150 mm TL (probably age-2). Of the remaining centrarchids consumed, three were of sizes indicating age-1 and the other probably age-2. Other fishes identified in Byllesby Reservoir flathead diets included a common carp

Table 3. Percent by preserved wet weight contributed by different food items in the diet of small (SM, 300-499 mm TL) and large (LG, ≥ 500 mm TL) flathead catfish in Byllesby Reservoir, 1991 and 1992.

				Diet Composition (%)			
Year	Size Class	Number Examined	% Empty	Centrar-chids	Other Fishes	Aquatic Insects	Crayfish
1991	SM	29	62	59	4	3	33
	LG	22	59	59	41	T[a]	0
1992	SM	16	56	35	2	14	50
	LG	9	67	98	2	T[a]	0
Total	SM	45	60	50	4	7	39
	LG	31	61	66	34	T[a]	0
	ALL	76	61	64	31	1	4

[a] T = Trace =< 0.05 %

(166 mm TL), a channel catfish (145 mm TL), two logperch *Percina caprodes* (73 and 74 mm TL), and two unidentified cyprinids.

Because the low number of flathead catfish sampled and the high incidence of empty stomachs in this study may not have given a representative indication of the diet composition of New River reservoir flathead catfish, data compiled from the Bluestone Reservoir, West Virginia population by Edmundson (1974) were used to corroborate and compliment the Byllesby Reservoir data set. Bluestone Reservoir is an 826 ha impoundment located approximately 168 river kilometers downstream of Byllesby Reservoir. Edmundson's data were reported volumetrically and had to be converted to a wet- weight basis by multiplying the observed volumes by the density (g/ml) of the food item. Densities of fish, crayfish and aquatic insects were determined by comparing the weight of a preserved item and the amount of water displaced by the item. These measurements were made on diet items taken from Byllesby Reservoir catfish. Percentages of the total weights were then determined from these weight values. Edmundson (1974) found fishes to be secondary to crayfish in the diets of small catfish (Table 4). Large flathead catfish from Bluestone Reservoir consumed predominantly fishes (Table 4).

Of the fishes present in stomach contents in the Bluestone sample, centrarchids were the most prevalent by wet weight followed by channel catfish and various cyprinids. Eleven of the 13 centrarchids were identified to the genus *Lepomis*. The remaining two were black crappie *Pomoxis nigromaculatus*.

The diet compositions used for each size class of flathead catfish in the bioenergetics simulations (see **APPENDIX B**, Table 14) for this project resulted from the

Table 4. Diet composition, reported as percentage preserved wet weight, for Byllesby Reservoir, Bluestone Reservoir (Edmundson 1974), and the weighted mean of the combination (Combined) of the two previous accounts for both small (SM, 300-499 mm TL) and large (LG, ≥ 500 mm TL).

Source	Size Class	Number With Food	Diet Composition (%)			
			Centrarchid	Other Fishes	Aquatic Insects	Crayfish
Byllesby	SM	18	50	4	7	39
	LG	12	66	34	T[a]	0
Bluestone	SM	28	12	6	T[a]	81
	LG	48	48	45	T[a]	6
Combined	SM	46	28	5	3	64
	LG	60	51	43	T[a]	5

[a] T = Trace = < 0.05 %

combination of Byllesby and Bluestone Reservoir results (Table 4). For both size groups of flathead catfish, the weights of each prey group from Byllesby and Bluestone Reservoirs were summed and then divided by the total number of catfish in that size group. This resulted in changing the primary diet item by wet weight from fishes to crayfish for small flathead catfish and added crayfish to the diet of large individuals. About one-quarter and one-half of the food consumption by small and large flathead catfish was projected to consist of centrarchids (Table 4).

Age and Growth

Estimates of mean length-at-annulus for the two Byllesby Reservoir flathead catfish were similar to those from Brooks Pool, New River, West Virginia (Roell 1989). All length-at-annulus estimates were within 10 % for each age with the exception of age-1 estimates which differed by 15 %. The two Byllesby fish were age-4 (308 mm TL) and age-7 (466 mm TL). Mean length-at-annulus estimates suggest that Byllesby flathead catfish reach 300 mm TL in their fourth year and should reach 500 mm by age-10, as projected by pattern of growth (Figure 2). These estimates compare favorably with Roell's (1989) data which have Brooks Pool flathead catfish reaching 299 mm at age-4 and 511 mm at age-10 (Figure 2). Although growth was faster through age-3 for New River (both Byllesby and Brooks Pool) flathead catfish, catfish in Lake Carl Blackwell, Oklahoma were predicted to reach 500 mm during their fifth year (Turner 1977). Growth rates beyond age-3 were considerably higher for Lake Carl Blackwell flathead catfish (Figure 2).

Because of the similarity between Brooks Pool and Byllesby Reservoir flathead growth information, age and growth data from Roell (1989) were used in bioenergetics

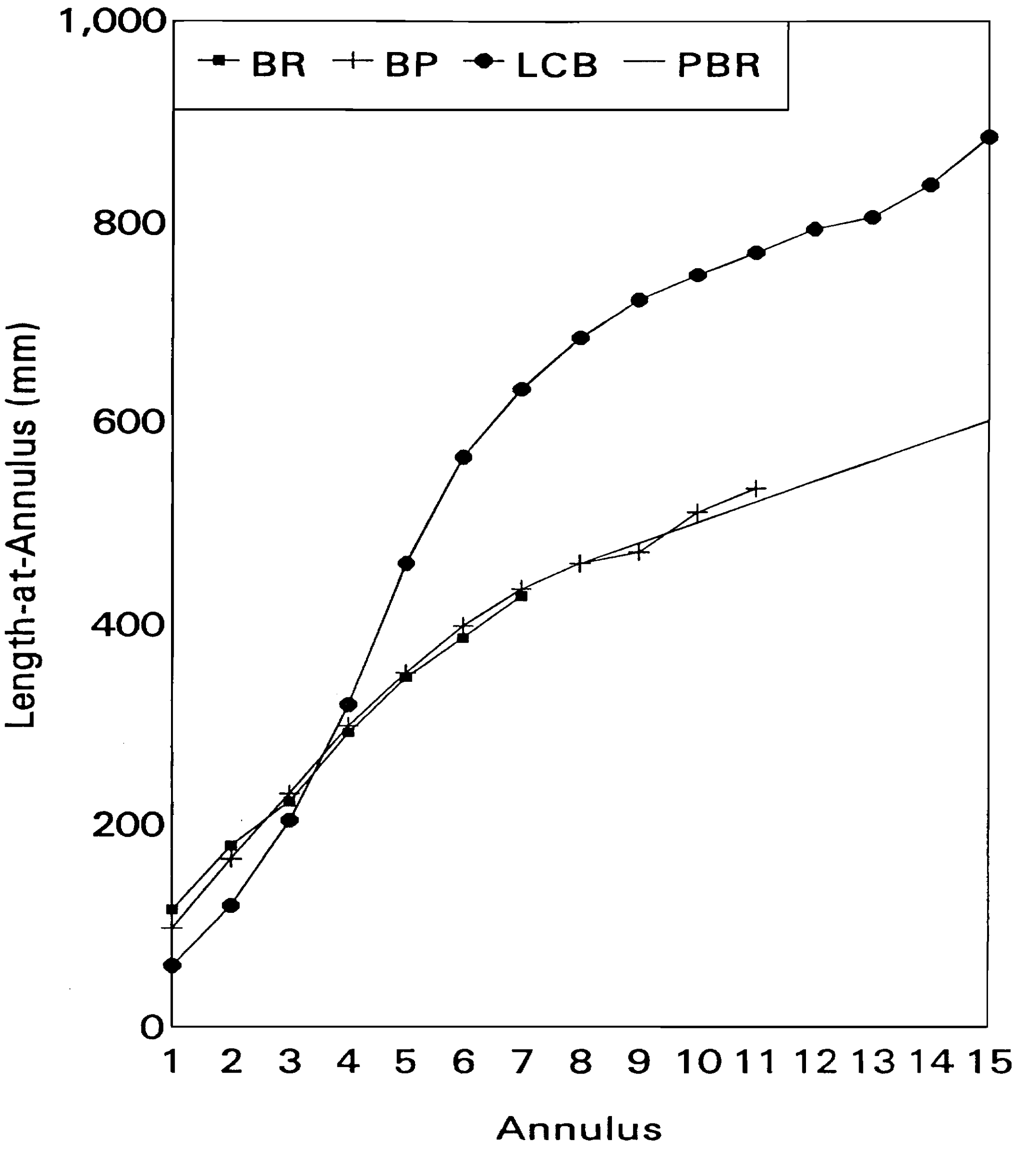

Figure 2. Comparison between mean total lengths-at-annulus (mm) of flathead catfish from Byllesby Reservoir (BR), New River, Virginia, Brooks Pool (BP), New River, West Virginia (Roell 1989), and Lake Carl Blackwell (LCB), Oklahoma (Turner 1977). Predicted Byllesby Reservoir growth (PBR) represents growth used in modeling Byllesby Reservoir flathead population (same as Brooks Pool through age-8).

modeling of Byllesby Reservoir flathead catfish. However, mean length-at-annulus was not estimated for Brooks Pool flathead catfish beyond age 11 (520 mm), with only five of the individuals aged being older than age 8. I captured flathead catfish in Byllesby Reservoir up to 750 mm TL, indicating fish considerably older than 11 years. The mean growth increment for Brooks Pool flathead catfish between age-8 and age-10 was 24.3 mm annually (Figure 3). Similarly, the mean growth increment of Lake Carl Blackwell flathead catfish was 23.3 mm annually between age-10 and age-14 (Figure 3). I assumed that growth increments beyond age 8 were 20 mm annually through age 15, the last age modeled, in the Byllesby Reservoir population. This is a conservative assumption in terms of estimating total annual consumption by a flathead catfish since it likely underestimates annual growth of these older individuals.

Weights used in the bioenergetics model (see figure 2 and **APPENDIX B**, Table 15) were determined by using lengths-at-annulus from Brooks Pool in the length weight equation developed for Byllesby Reservoir flathead catfish (Figure 4). The length-weight equation for Byllesby Reservoir flathead catfish had a coefficient of determination (r^2) of 0.98 (Table 5).

Abundance and Mortality

Direct estimates of abundance and mortality of Byllesby Reservoir flathead catfish were unsuccessful due to the low number of specimens collected. During the two summers of sampling, 73 flathead catfish were marked (50 in 1991 and 23 in 1992) while only three catfish were recaptured (one in 1991 and two in 1992). The two recaptures in 1992 were the same individual. Because direct estimates of flathead

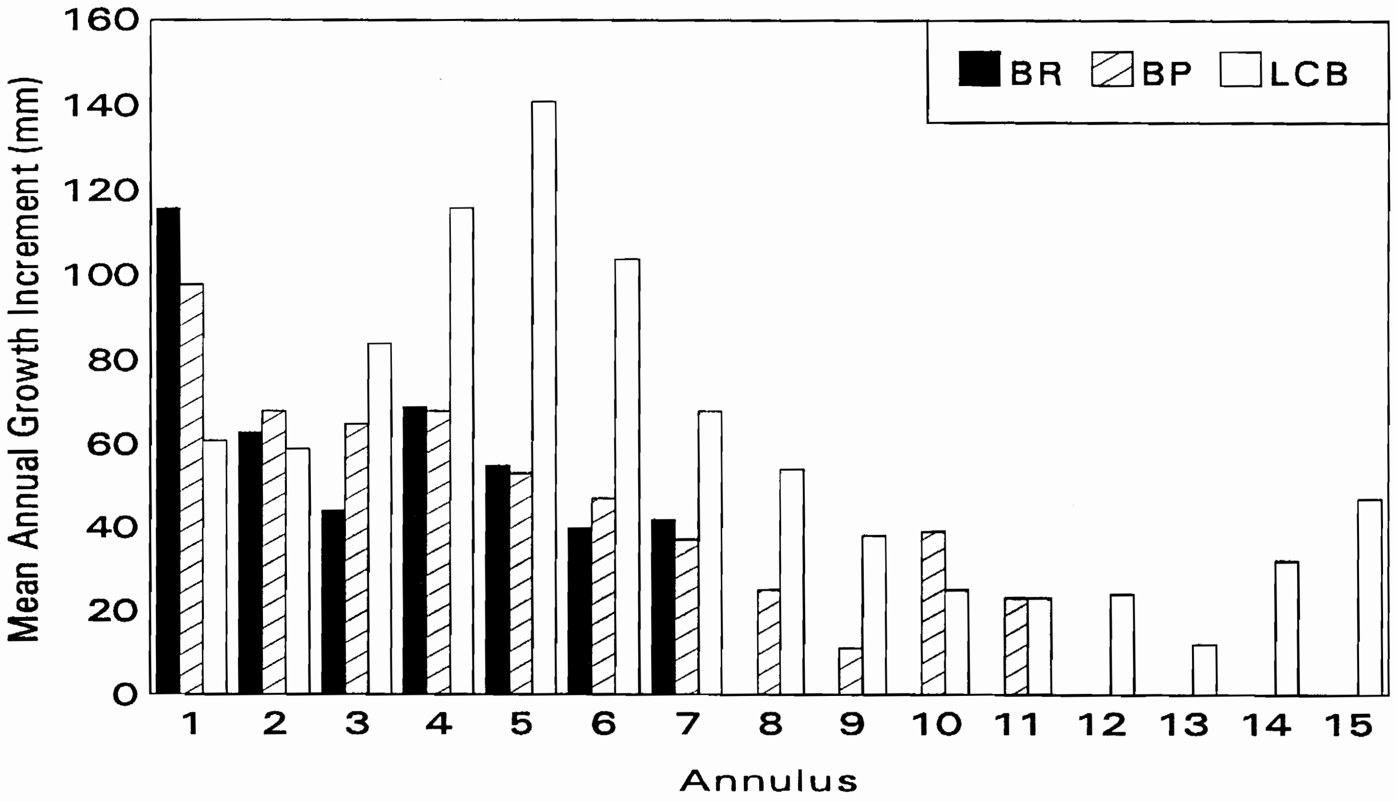

Figure 3. Comparison between annual growth increments of flathead catfish from Byllesby Reservoir (BR), New River, Virginia, Brooks Pool (BP), New River, West Virginia (Roell 1989), and Lake Carl Blackwell (LCB), Oklahoma (Turner 1977).

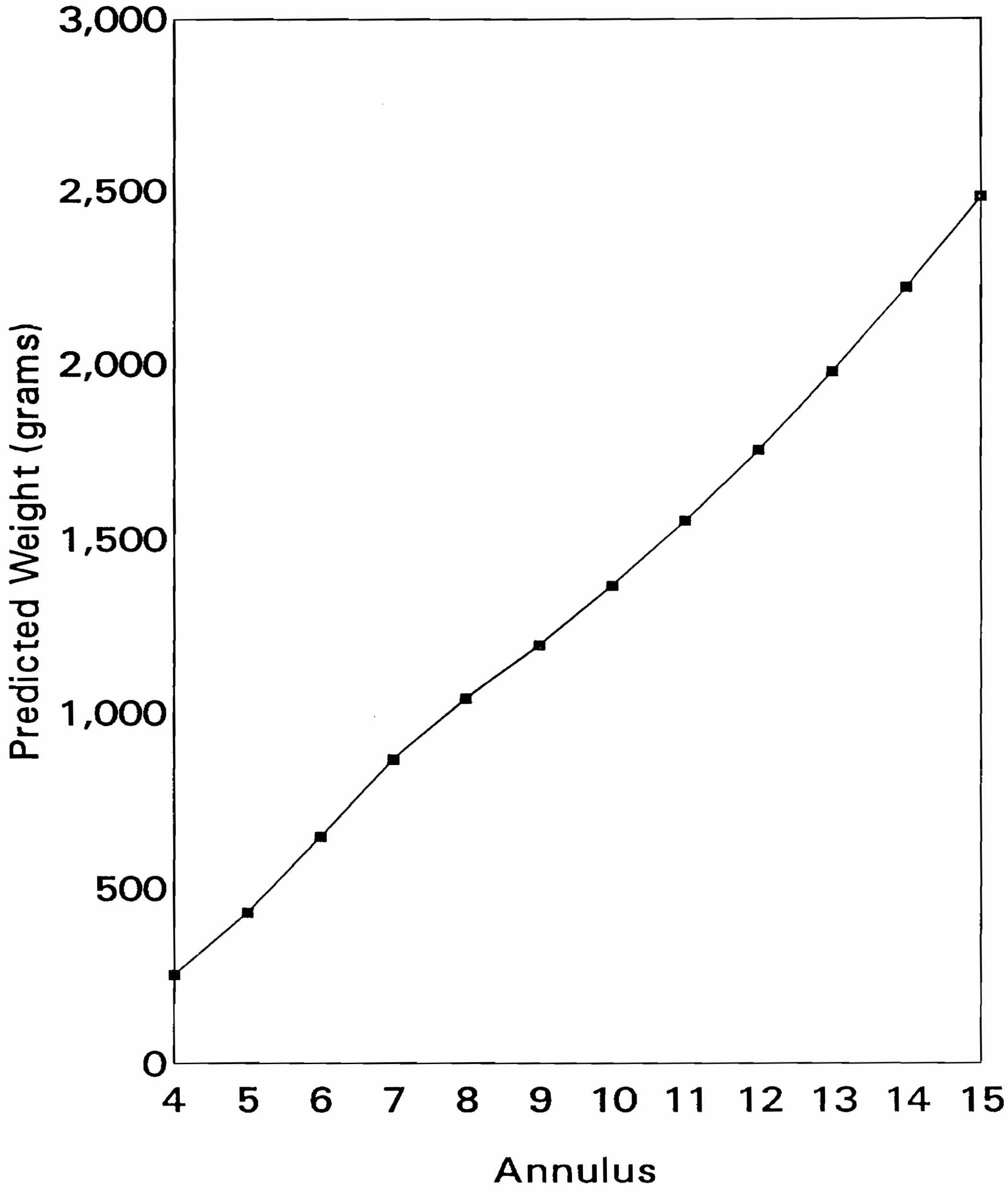

Figure 4. Weights-at-annulus predicted from length-at-annulus data using length-weight equation developed for Byllesby Reservoir flathead catfish.

Table 5. Length-weight equations for the predominant centrarchids and flathead catfish of Byllesby Reservoir, New River, Virginia. All lengths were measured in millimeters and weights in grams.

Species	Predictive Equation	N	r^2
Bluegill	$\log_{10}W = -5.07 + 3.17 \cdot \log_{10}L$	160	0.94
Redbreast Sunfish	$\log_{10}W = -5.21 + 3.25 \cdot \log_{10}L$	243	0.98
Smallmouth Bass	$\log_{10}W = -5.28 + 3.17 \cdot \log_{10}L$	165	0.98
Spotted Bass	$\log_{10}W = -5.32 + 3.18 \cdot \log_{10}L$	129	0.99
Flathead Catfish	$\log_{10}W = -5.73 + 3.28 \cdot \log_{10}L$	74	0.98

catfish abundance and mortality were not obtained, reported values from large river and reservoir systems in the southeastern United States (systems approximating Byllesby) were used to model the Byllesby Reservoir flathead population.

Density estimates for flathead catfish > 300 mm in southeastern river and reservoir systems ranged from 3.5 flathead catfish per ha in Claytor Lake, New River, Virginia (Hart 1981) to 14 flathead catfish per ha in the Flint River, Georgia (Quinn 1988) (Table 6). The other density values reported in the literature are grouped toward the lower end of this range. Notably, Roell (1989) estimated a density of 5.8 catfish ≥ 300 mm per ha for modeling Brooks Pool flathead catfish based on mark-and-recapture work he conducted. The values defining the range of flathead densities (3.5 and 14.0) in the southeastern rivers and reservoirs and an intermediate value, skewed toward the lower end of the range (6.1 catfish per ha, the density marking the lower quarter of the range), were used in simulations. The most plausible density for Byllesby Reservoir flathead catfish was assumed to be 6.1 flathead catfish per ha because this value is close to the Brooks Pool estimate, and most of the reported densities were in the lower quarter of the range. Flathead catfish density from Claytor Lake was not used because the fish were collected by cove-rotenone, a technique biased against collecting this species. Assuming this density, Byllesby Reservoir would support a population of 601 flathead catfish > 300 mm (see Appendix B, Figure 13 for abundance-at-age for modeled populations).

Only two values were found in the literature for flathead catfish mortality in southeastern rivers and reservoirs (Table 6). Quinn (1988) estimated an

Table 6. Reported estimates of density (# per ha) and instantaneous total mortality for river and reservoir populations of flathead catfish in the southeastern United States and assumed values for Byllesby Reservoir.

Location	Source	Density	Mortality
Claytor Lake	Hart 1981	3.5[a]	NA
An Oklahoma Reservoir	Weeks and Combs 1981	4.1[b]	NA
Flint River, GA	Quinn 1987	14.0[a]	0.490
Brooks Pool	Roell 1989	5.8[c]	0.818
Byllesby Reservoir[d]	This Study	6.1[a]	0.654

[a] = Density of flathead catfish > 305 mm TL.

[b] = Density of flathead catfish > 201 mm TL.

[c] = Density of flathead catfish older than age 4 (299 mm TL).

[d] = population parameters used to model Byllesby Reservoir.

instantaneous annual mortality (Z) of 0.49 while Roell (1989) calculated an estimate of 0.82. To describe Byllesby flathead mortality, the midpoint of these two values was used ($Z = 0.65$) as a compromise. This converts to a finite annual mortality (A) of 0.48. Roell's (1989) mortality estimate was not used because he reported a low number of large flathead catfish ($\geq$ 500 mm TL) while 41 % of the Byllesby Reservoir flathead catfish sampled in this study were over 500 mm TL, with 9 fish being between 600 and 799 mm TL. This suggests that mortality in Byllesby Reservoir is lower than in Brooks Pool, New River, but it could be a result of differences in sampling gear used (Roell 1989 used boat electrofishing). Mortality was assumed to be constant for all cohorts and through all seasons.

CENTRARCHIDS

Abundance

A total of 326 centrarchids was marked during late July in 1992. Eighty one redbreast sunfish, 102 bluegill, 60 smallmouth bass, and 83 spotted bass were marked respectively (Table 7).

Modified Petersen abundance estimates were determined for all four centrarchid species (Table 7). Based on the mark-recapture data collected in 1992, bluegill was the most abundant centrarchid in Byllesby Reservoir. Redbreast sunfish was the next most abundant followed by the two bass species. Insufficient numbers of recaptures precluded age- or size-class-specific abundance estimates.

Catch-per-efforts (CPUE) declined from 1990 to 1992 for all species but bluegill (Table 7). Thus, each species' CPUE adjustment factor (ratio of 1992 CPUE/1990 CPUE) was greater than 1 except for bluegill. Catch-per-effort decreased most dramatically for smallmouth bass, declining

Table 7. Modified Petersen abundance estimates of age 1 and older centrarchids in Byllesby Reservoir, New River, Virginia, in 1992. Values are shown for each abundance estimate (N), number marked (M), corresponding recaptures (R), 95 % confidence intervals (95 % CI), respective adjustment factor (ADJ*, ratio of 1990 to 1992 catch-per-effort), and the adjusted abundance estimate (ADJ N).

Species	N	M	R	95 % CI	ADJ*	ADJ N
Bluegill	1880	102	7	976-3957	0.17	320
Redbreast Sunfish	1212	81	8	649-2479	1.68	2036
Smallmouth Bass	641	60	5	303-1478	3.81	2440
Spotted Bass	696	83	6	346-1523	2.44	1698

from 0.61 to 0.16 smallmouth bass per shocking minute. A near six-fold increase in CPUE, from 0.08 to 0.46 individuals per shocking minute, occurred for bluegill from 1990 to 1992. When these adjustment factors were applied to the abundance estimates from 1992, relative abundances among the four centrarchid species were altered (Table 7). Based on these adjusted abundance estimates, smallmouth bass became the most abundant centrarchid in Byllesby Reservoir, followed by redbreast sunfish, spotted bass and bluegill.

Length and Weight

Back-calculated lengths-at-annulus (ages 1 through 4) for the four centrarchid species are reported in Table 8. Coefficients of determination (r^2) associated with length-weight equations developed for each centrarchid species ranged from 0.94 for bluegill to 0.99 for spotted bass (Table 5). Midpoint length values were calculated between consecutive ages for each of the centrarchid species. These midpoint lengths were then used with the appropriate length-weight equation to estimate mean weight for each age of each centrarchid species (Table 9). These weights were used in determining number of centrarchids consumed by modeled catfish populations.

CONSUMPTION PATTERNS

Estimates of Individual Consumption

Crayfish were the principal energy source of the modeled Byllesby Reservoir flathead catfish ages-4 through 9 (Table 10). The next most important food item category was centrarchid, followed by other fishes, and aquatic insects. Centrarchid was the most important food item category for

Table 8. Mean back-calculated lengths-at-annulus, sample sizes (N), and standard deviations (S.D.) of predominant centrarchids ages-1 through 4 in Byllesby Reservoir, New River, Virginia.

	Annulus I			Annulus II		
Species	N	Mean (mm)	S.D.	N	Mean (mm)	S.D.
Redbreast Sunfish	56	64.7	12.0	29	127.9	18.1
Bluegill	50	70.1	12.2	39	103.5	18.8
Smallmouth Bass	45	115.4	21.0	21	171.3	33.2
Spotted Bass	80	112.8	29.2	46	189.5	30.5
	Annulus III			Annulus IV		
Species	N	Mean (mm)	S.D.	N	Mean (mm)	S.D.
Redbreast Sunfish	4	174.5	3.7	1	202.1	-
Bluegill	15	141.9	20.7	6	161.8	25.1
Smallmouth Bass	9	269.2	16.9	2	293.3	-
Spotted Bass	19	257.3	23.9	9	295.9	16.4

Table 9. Average weight (grams) of ages-1 through 3 centrarchids used to determine number of each species consumed annually by modeled flathead catfish populations.

Species	Weight (grams)		
	Age-1	Age-2	Age-3
Bluegill	11.9	35.6	70.1
Redbreast Sunfish	17.0	73.8	150.6
Smallmouth Bass	36.0	140.7	305.3
Spotted Bass	41.8	145.3	286.2

flathead catfish ≥ 500 mm, followed by other fishes, crayfish, and aquatic insects (Table 10).

Seasonal patterns of estimated consumption were similar for all flathead catfish cohorts. Estimated consumption of all prey types decreased during the winter interval due to decreasing water temperatures (Figure 5). Peak consumption occurred in July and August due to high water temperatures (25 °C). Increasing water temperatures following the winter season prompted increasing individual consumption rates.

Total amount (g) of food consumed annually per individual increased with increasing age (Table 10 and Figure 6). Gross conversion efficiency (ratio of weight gained by individual flathead catfish to weight of food consumed during a year) ranged from 0.29 for age-4 to 0.17 for age-8 and 9 flathead catfish (Figure 6). Gross conversion efficiencies were highest for younger age classes and then decreased with age. Although reaching a low at age-8, gross conversion efficiencies were slightly higher and fairly stable for those age classes that consumed primarily fishes (ages-10 through 15; Figure 6). Individual age-10 flathead catfish were predicted to eat 1.7 times as many grams of centrarchid and 7 times as many grams of other fishes annually compared to age-9 catfish. This is due primarily to the change in diet composition at age-10 (500 mm TL).

Estimates of Population Consumption

General

Estimates of individual consumption were calculated daily by the Wisconsin bioenergetics model and multiplied by age-specific flathead catfish abundance, resulting in a daily estimate of consumption for each prey type by the entire flathead catfish population. By summing across all

Table 10. Annual consumption of each prey type for individual flathead catfish (g per individual per year) by each age class in Byllesby Reservoir, New River, Virginia.

Age Class	Centrar-chid	Other Fishes	Aquatic Insects	Crayfish	Total
4	190	38	19	371	618
5	243	49	23	448	763
6	275	55	26	504	860
7	279	56	26	503	864
8	292	59	27	515	893
9	317	64	30	568	979
10	533	446	10	24	1013
11	578	484	10	27	1099
12	626	525	11	28	1190
13	675	566	12	30	1283
14	728	610	13	33	1384
15	782	655	14	35	1486
Life-span	5518	3607	221	3086	12432

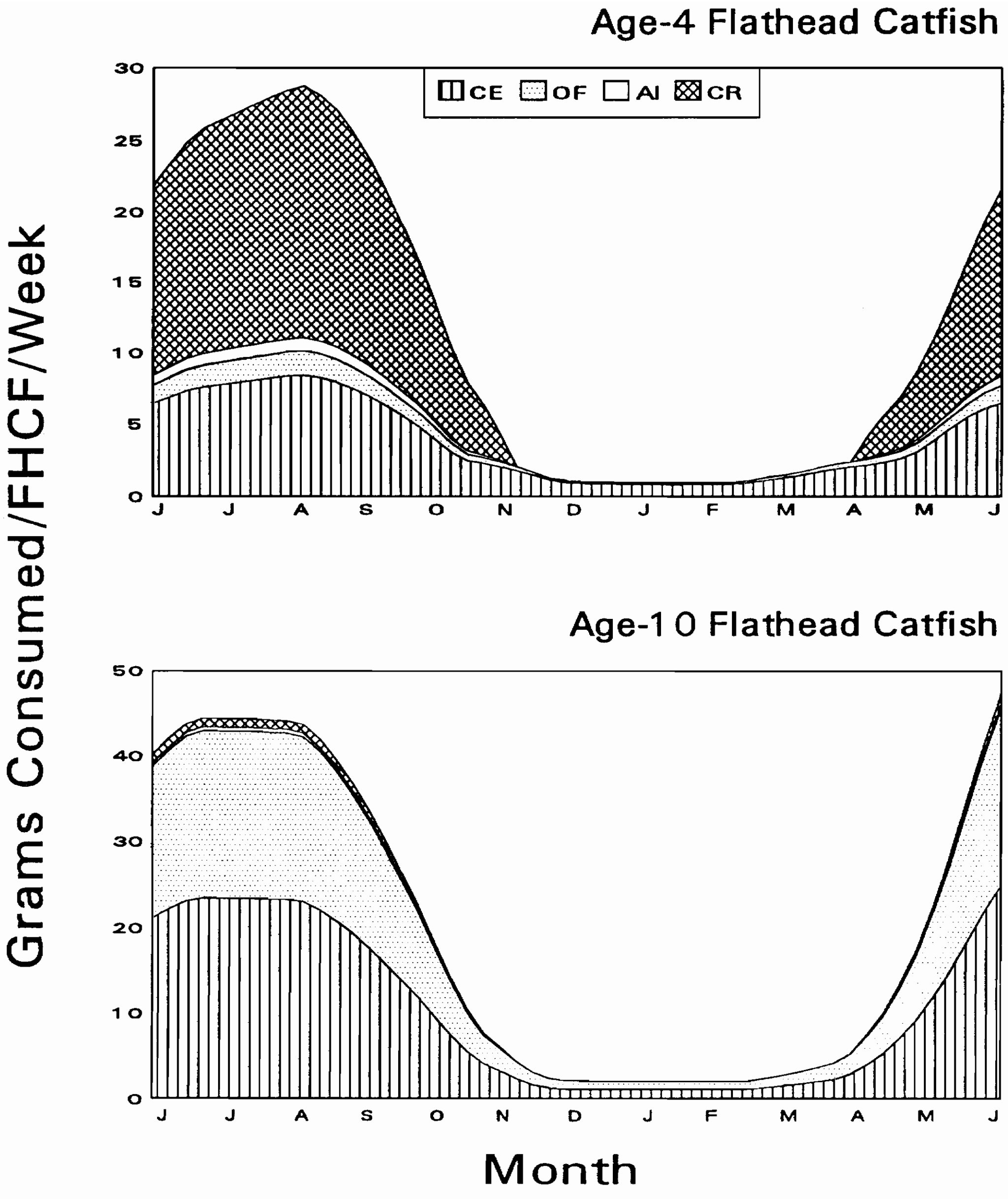

Figure 5. Predicted consumption (g per flathead catfish per week) of aquatic insects (AI), centrarchid (CE), crayfish (CR), and other fish (OF) by modeled age-4 and age-10 flathead catfish in Byllesby Reservoir, New River, Virginia.

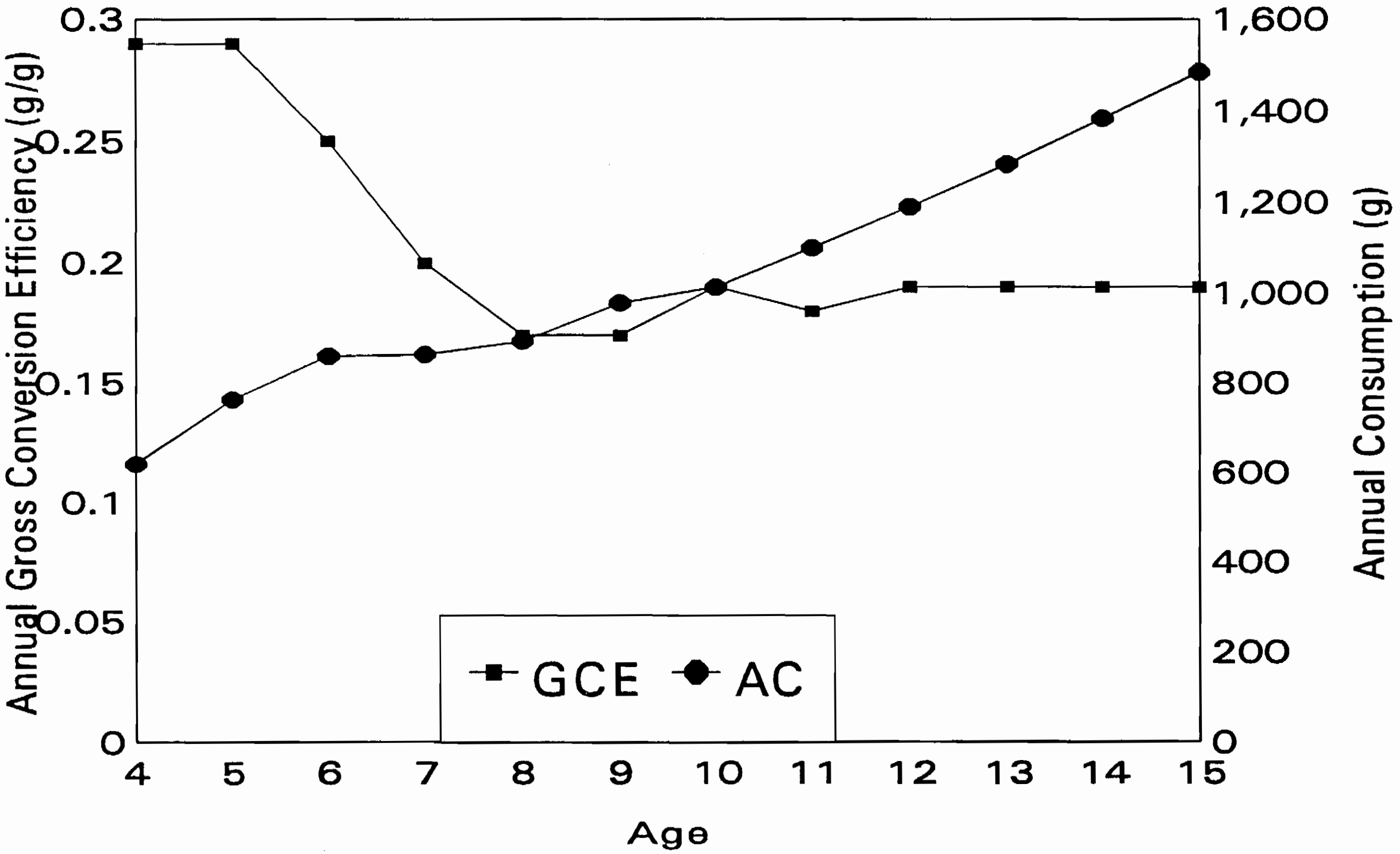

Figure 6. Gross conversion efficiencies (GCE), annual consumption (AC), and weight-at-annulus of modeled flathead catfish (ages-4 through 15) of Byllesby Reservoir, New River, Virginia.

the days of the year, an annual estimate of all the food consumed by the Byllesby Reservoir flathead population was obtained. Annual consumption estimates of this type were calculated for three different flathead catfish populations. The flathead population characteristics were: (1) a density of 3.5 per ha and an annual instantaneous mortality of 0.82; (2) a density of 14.0 per ha and an instantaneous annual mortalities of 0.49; and (3) a density of 6.1 per ha and an annual instantaneous mortality of 0.65. These populations represented (given the range of values for density and annual instantaneous mortality) the smallest possible population, the largest possible population, and a population assumed to be the most probable for Byllesby Reservoir (an intermediate density and annual instantaneous mortality) (see **Appendix B**, Figure 13).

Centrarchids

To determine the number of each species of centrarchid consumed annually by the modeled populations of flathead catfish, the weight consumed annually had to be partitioned by species and age-class of centrarchid. The low absolute number of centrarchids recovered from Byllesby Reservoir flathead stomachs precluded confident partitioning by age-class. By examining the lengths and weights of centrarchids consumed by flathead catfish from two sources (Ashley and Buff (1987) in the Cape Fear River, North Carolina and this project), the weight of centrarchids consumed was partitioned among age classes YOY through age-3. Centrarchids consumed by Cape Fear River, North Carolina flathead catfish were aged based on their lengths compared to lengths-at-age for Byllesby Reservoir centrarchids. Of the centrarchids consumed by Cape Fear River catfish, the percentages of the wet weight assumed to be YOY, and age-1 through age-3 were 5, 16, 44, and 36 % respectively. In Byllesby Reservoir catfish, 1 % of the total weight of centrarchids consumed was YOY, 26 % was age-1, 73 % was age-2, and 0 % was age-3. When results of these two data sources were combined by aggregating weights in each age-class and dividing the combined weight from both sources, 4 % of the weight was YOY, 19 % was age-1, 52 % was age-2, and 24 % was age-3. For the purposes of this model, 5, 20, 50, and 25 % of the estimated weight of centrarchid consumed were assumed to be YOY through age-3 respectively. Although all centrarchids consumed by Cape Fear River and Byllesby Reservoir flathead catfish were sunfish, the same percentages were used to partition weight of consumed black bass between age-classes. Because black bass reach greater lengths-at-age than sunfish, it is likely that a greater percentage of the weight consumed would be younger fish. Thus, the weight partitioning for black bass likely underestimates the number consumed by partitioning too much weight into older age-classes.

Three scenarios were examined to proportion the weight between the four abundant centrarchid species of Byllesby Reservoir. The first scenario assumed that centrarchid species were consumed in proportion to their relative abundances (this works out to 36 % of the total centrarchid weight consumed being sunfishes and 64 % of the weight being black basses and will be abbreviated as 36/64). Only two of the previous accounts reporting centrarchids in the diets of flathead catfish found evidence of black bass (Turner and Summerfelt 1970 and Quinn 1987). Centrarchids were found in the diets of flathead catfish in half of the six reservoir surveyed by Turner and Summerfelt (1970). In two of the reservoirs, only sunfish or crappie were present in flathead stomachs. In the other, largemouth bass *Micropterus* *salmoides* represented 34 % of the centrarchid weight consumed, but only 2.1 % by weight of the total diet. Of the centrarchids consumed by Flint River flathead catfish, 0 % and 37 % by weight were *Micropterus* sp. for catfish between 301 and 600 mm TL and those greater than 600 mm TL respectively (Quinn 1987). It seems that sunfish and crappie may be more vulnerable to flathead predation than the black basses, perhaps due to habitat preferences or activity levels. The second scenario addresses this by having the two sunfish species being consumed 1.4 times their relative abundances while the two black bass species are consumed at a rate 0.6 times their relative abundances (abbreviated as 57/43). In the final scenario, only sunfish are consumed, as none of the flathead catfish in this study or Edmundson's (1974) had black bass present in their stomach contents (abbreviated as 100/0). In this scenario, the two sunfish species are consumed in proportion to their relative abundances. All estimates of the number of individual centrarchids consumed, reported below, are age-1 and older centrarchids only.

Assuming that centrarchids are eaten in proportion to their relative abundances (the 36/64 scenario), estimates for the number of each species consumed per hectare by the flathead catfish population in Byllesby Reservoir were 4.2, 0.6, 5.1, and 3.5 for redbreast sunfish, bluegill, smallmouth bass, and spotted bass respectively (Table 11). Predicted consumption estimates (presented as # per hectare) from the extreme flathead populations ranged from 2.2 to 11.2 for redbreast sunfish, 0.3 to 1.7 for bluegill, 2.6 to 13.4 for smallmouth bass, and 1.8 to 9.3 for spotted bass.

If sunfish were assumed to be consumed more frequently than black bass (the 57/43 scenario), the Byllesby flathead population was predicted to consume 7.7 redbreast sunfish, 1.2 bluegill, 4.0 smallmouth, and 2.8 spotted bass per hectare annually (Table 11). The numbers of each species estimated to be consumed by the low density-high mortality catfish population modeled were 4.0 redbreast sunfish, 0.6 bluegill, 2.1 smallmouth bass, and 1.5 spotted bass per hectare. Estimates from the high density-low mortality population were 20.5 for redbreast sunfish, 3.2 for bluegill, 10.5 for smallmouth bass, and 7.5 for spotted bass per hectare.

Assuming only sunfish were consumed by flathead catfish, the modeled Byllesby Reservoir population was predicted to consume 20.8 redbreast sunfish and 3.3 bluegill per hectare annually (Table 11). The range of consumption estimates from the bounding flathead catfish populations using this assumption were 10.8 to 55.1 per hectare for redbreast sunfish and 1.7 to 8.6 per hectare for bluegill.

IMPACT OF FLATHEAD CATFISH PREDATION ON CENTRARCHID ABUNDANCE

Annual mortality due to predation by flathead catfish on abundances of age-1 and older centrarchids in Byllesby Reservoir was estimated to be 20 % for all species, assuming centrarchids were consumed in proportion to their relative abundances (36/64 scenario) (Table 11 and Figures 6 through 9). Since the centrarchid species were consumed in proportion to their relative abundances, the percentages of each species consumed were equivalent. If sunfish were assumed to be consumed more frequently than black bass (57/43 scenario), then annual mortality due to flathead predation for the two sunfish species increased to 37 % while impacts on black bass decreased to 16 % (Table 11 and Figures 6 through 9). The final scenario assumed that black

Table 11. Annual impact, defined as percentage of age-1 and older individuals of each species consumed, of flathead catfish predation on four centrarchid species. Prey vulnerability to predation is expressed as 36/64 for the scenario assuming equal vulnerability, 57/43 for the scenario assuming sunfish are more vulnerable than black bass, and 100/0 for the scenario assuming only sunfish are vulnerable. Densities are reported as number per ha and annual mortalities are instantaneous. Numbers of each species predicted to be consumed per ha by the flathead catfish population are reported in parentheses.

Flathead Catfish			Impact		
Density	Mortality	Species	36/64	57/43	100/0
3.5	0.818	Redbreast Sunfish	0.10 (2.2)	0.19 (4.0)	0.52 (10.8)
		Bluegill	0.10 (0.3)	0.19 (0.6)	0.52 (1.7)
		Smallmouth Bass	0.10 (2.6)	0.08 (2.1)	0 (0)
		Spotted Bass	0.10 (1.8)	0.08 (1.5)	0 (0)
6.1	0.654	Redbreast Sunfish	0.20 (4.2)	0.37 (7.7)	1.00 (20.8)
		Bluegill	0.20 (0.6)	0.37 (1.2)	1.00 (3.3)
		Smallmouth Bass	0.20 (5.1)	0.16 (4.0)	0 (0)
		Spotted Bass	0.20 (3.5)	0.16 (2.8)	0 (0)
14.0	0.490	Redbreast Sunfish	0.54 (11.2)	0.98 (20.5)	2.67 (55.1)
		Bluegill	0.54 (1.7)	0.98 (3.2)	2.67 (8.6)
		Smallmouth Bass	0.54 (13.4)	0.43 (10.5)	0 (0)
		Spotted Bass	0.54 (9.3)	0.43 (7.5)	0 (0)

bass were not consumed by flathead catfish (100/0). Using this scenario, the percentage of the sunfish population age-1 and older consumed by flathead catfish was 100 % (Table 11 and Figures 5 and 6). This is unlikely in Byllesby because the reservoir maintains populations of both redbreast sunfish and bluegill. However, it is probable that the reservoir sunfish populations are bolstered by downstream immigration to some degree.

Given the range of flathead catfish population characteristics examined, a range of impact estimates were generated (Table 11 and Figures 6 through 9). Assuming all centrarchids were consumed in direct proportion to their relative densities (36/64), annual mortality due to flathead predation ranged from 10 % to 54 %. When sunfish were assumed to be consumed more frequently than either of the black bass species, modeled flathead catfish consumed between 19 and 98 % of the sunfish and 8 and 43 % of the smallmouth and spotted bass per year. If flathead catfish were assumed to eat only sunfish, the population was estimated to consume 52 to 267 % of the redbreast sunfish and bluegill annually.

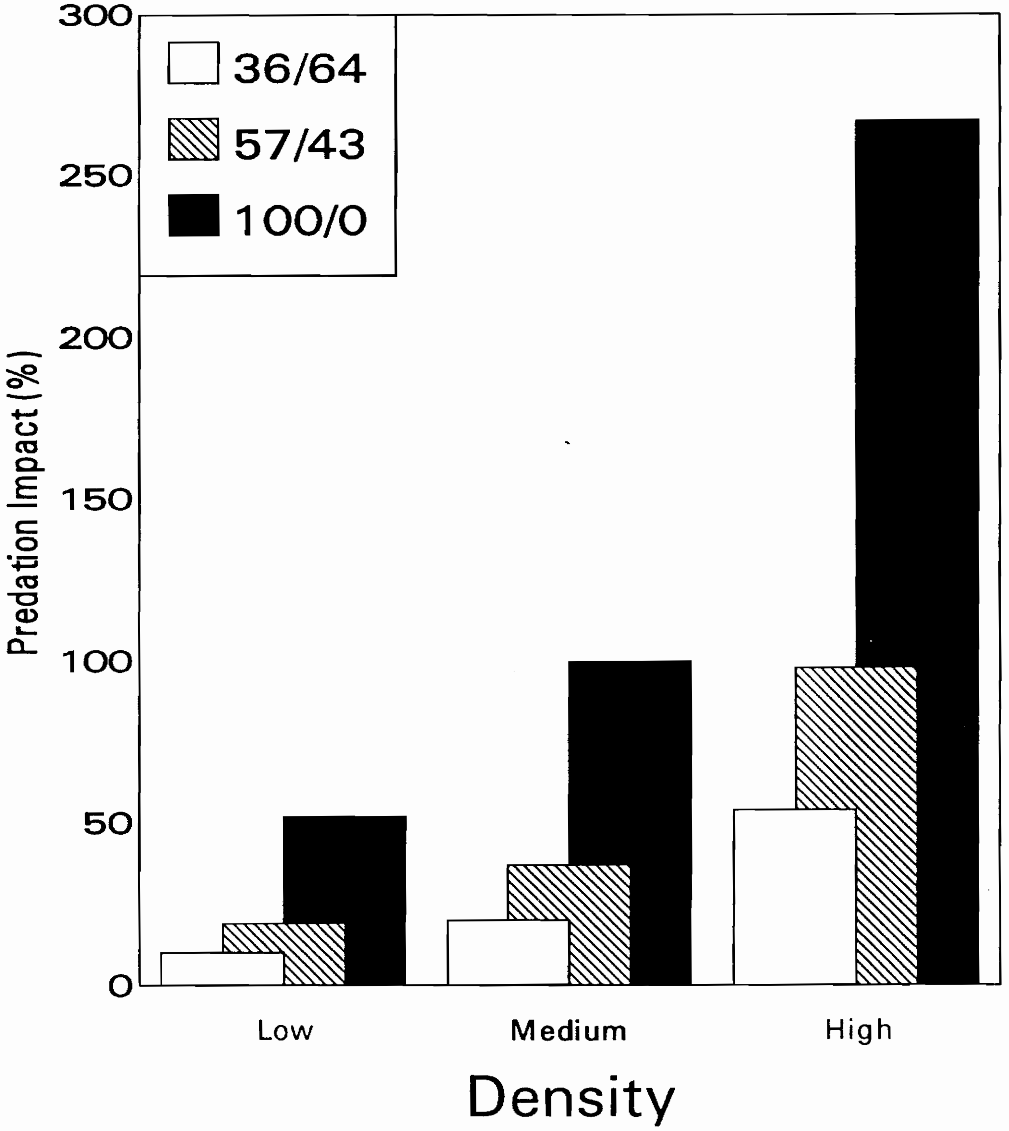

Figure 7. Predation impact (% of estimated prey abundance consumed annually) of three modeled flathead catfish populations (low, medium, and high density) on the Byllesby Reservoir, New River, Virginia redbreast sunfish population following three consumption scenarios. Equal vulnerability to predation by all species is represented by 36/64, greater vulnerability to predation for sunfish is represented by 57/43, and no vulnerability to predation for black bass is represented by 100/0.

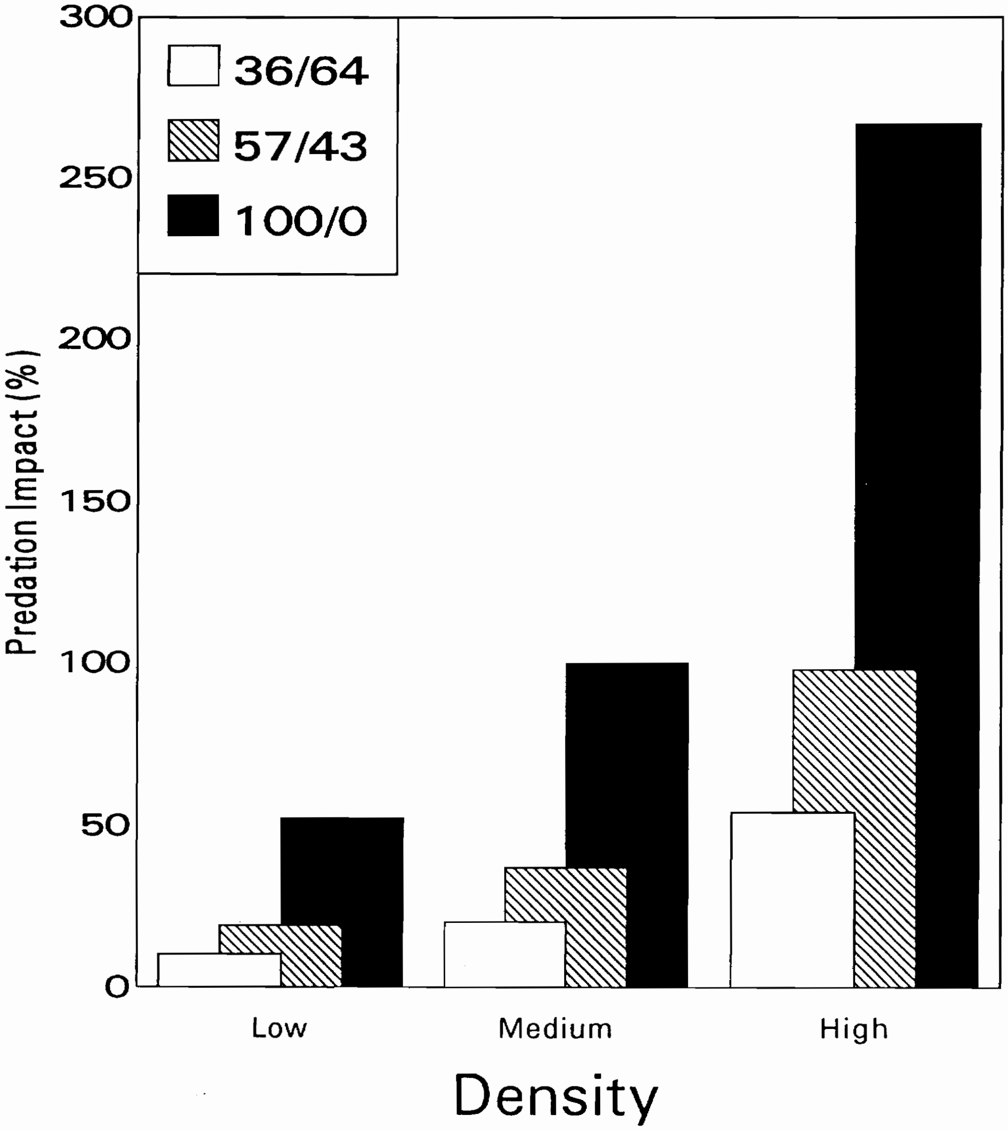

Figure 8. Predation impact (% of estimated prey abundance consumed annually) of three modeled flathead catfish populations (low, medium, and high density) on the Byllesby Reservoir, New River, Virginia bluegill population following three consumption scenarios. Equal vulnerability to predation by all species is represented by 36/64, greater vulnerability to predation for sunfish is represented by 57/43, and no vulnerability to predation for black bass is represented by 100/0.

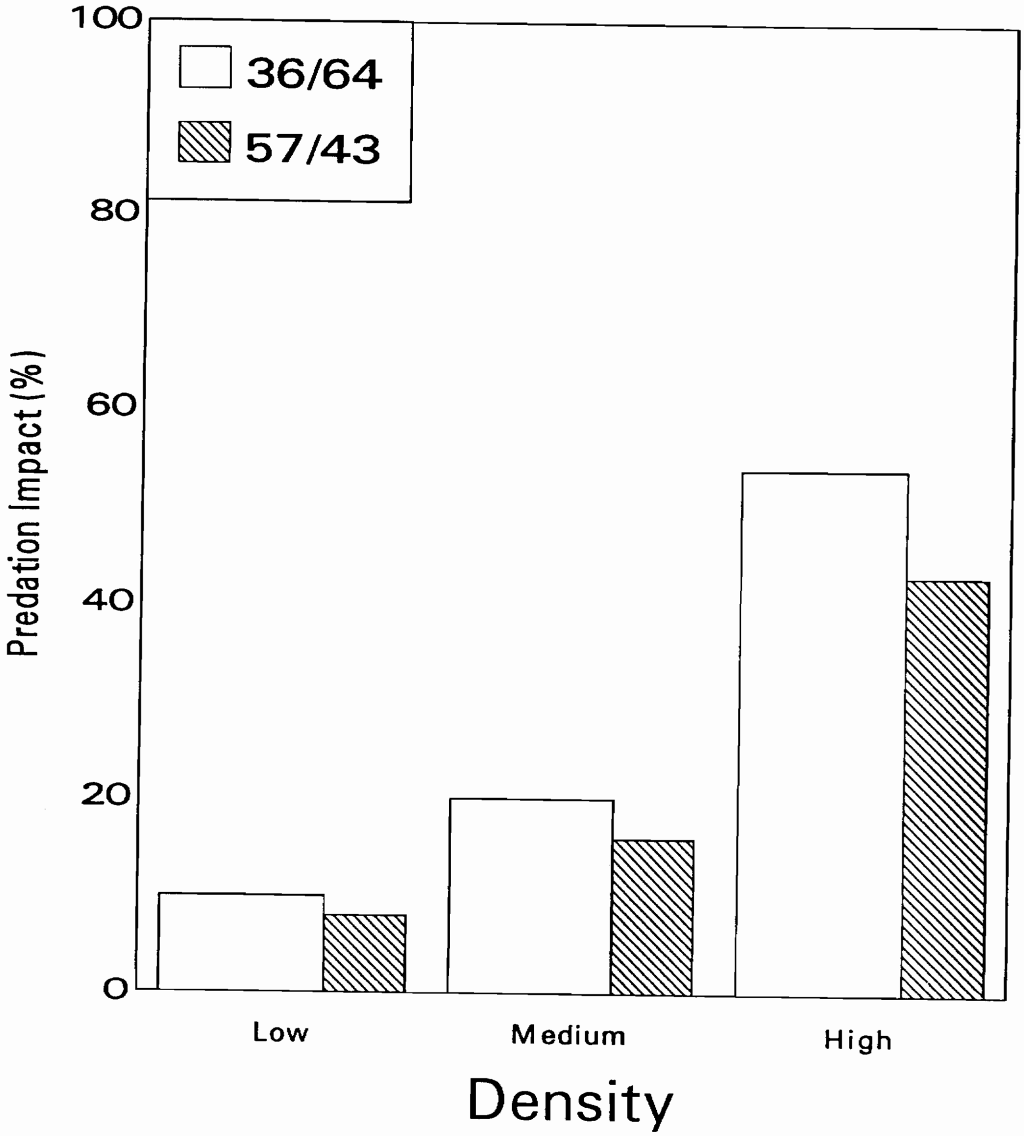

Figure 9. Predation impact (% of estimated prey abundance consumed annually) of three modeled flathead catfish populations (low, medium, and high density) on the Byllesby Reservoir, New River, Virginia smallmouth bass population following three consumption scenarios. Equal vulnerability to predation by all species is represented by 36/64 and greater vulnerability to predation for sunfish is represented by 57/43.

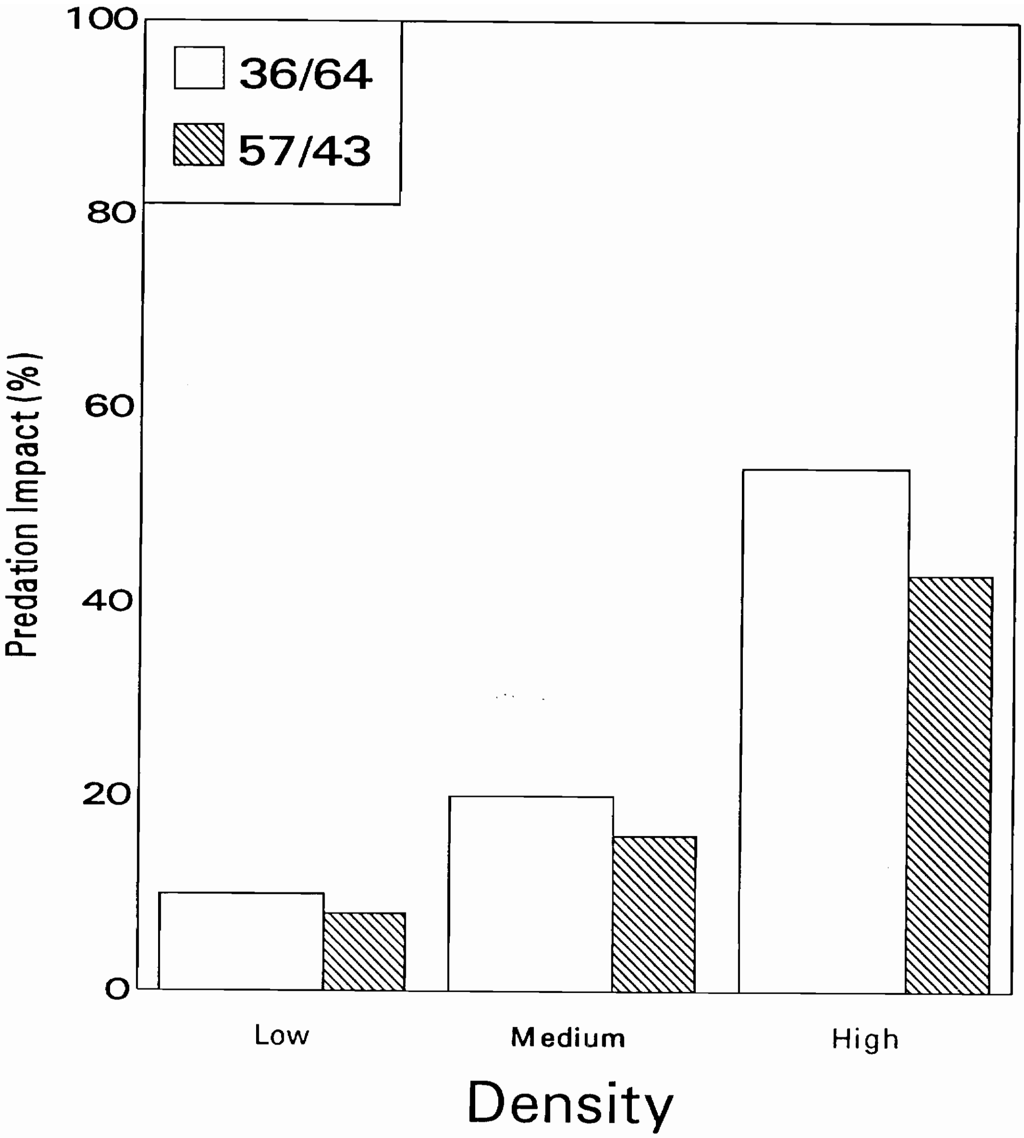

Figure 10. Predation impact (% of estimated prey abundance consumed annually) of three modeled flathead catfish populations (low, medium, and high density) on the Byllesby Reservoir, New River, Virginia spotted bass population following three consumption scenarios. Equal vulnerability to predation by all species is represented by 36/64 and greater vulnerability to predation for sunfish is represented by 57/43.

DISCUSSION

EVALUATION OF INPUT DATA

Flathead Catfish

Diet Composition

Although only 39.5 % of the stomachs of the Byllesby Reservoir flathead catfish examined contained food, those that did ate primarily centrarchids and other fishes. This was especially true of catfish greater than 499 mm TL, but also held for individuals between 250 and 499 mm TL. Flathead catfish of the smaller size group had a higher percentage of crayfish and aquatic insects present in their diets.

Most previous studies reported percentages of flathead catfish with food being less than 60 % (Turner and Summerfelt 1970; Edmundson 1974; Ashley and Buff 1987; Quinn 1987), with values ranging from 45 to 77.5 % (Ashley and Buff 1987; Minckley and Deacon 1959). Of those studies examining only flathead catfish greater than 300 mm (TL), the mean percentage of flathead catfish with food was 50 % (Turner and Summerfelt 1970; Edmundson 1974; Ashley and Buff 1987; Quinn 1987). Although the percentage of flathead catfish with empty stomachs in Byllesby is slightly lower than all other reported values, it is not considerably lower. Flathead catfish with small or scant food items may have been counted as empty in this research because of using tubes to remove stomach contents instead of excising stomachs. More than half of the catfish sampled in this study were collected with passive sampling gear. Nets were checked every 12 hours, so fish captured at the beginning of a set may have finished digesting the food in their stomachs by the time they were removed from the sampling gear.

However, this is unlikely unless the food item(s) was nearly digested when the flathead was captured. Hungry flathead catfish may be more vulnerable to capture by passive gear because they are moving in search of food more than non-hungry catfish. Of the studies presented above, only Turner and Summerfelt (1970) and Edmundson (1974) used passive sampling gear to collect flathead catfish, though percent of empty stomachs were not lower in these studies versus those using active sampling methods (electroshocking).

The trend observed in Byllesby Reservoir flathead diets is typical of what most previous research regarding flathead diet composition has found. In general, flathead catfish eat aquatic insects and crayfish until they reach a length of about 250 mm TL at which time they begin eating fishes (Minckley and Deacon 1959; Lee and Terrell 1987; Quinn 1987). However, Swingle (1964) noted flathead catfish as small as 51 mm consuming fishes, indicating that even YOY can be piscivorous. As flathead catfish length increases above 250 mm, fishes become a more predominant component in the diet. By a size of near 500 mm TL, flathead catfish are almost entirely piscivorous, as Byllesby Reservoir fish were (Edmundson 1974; Quinn 1987).

Results of flathead catfish diet composition studies conducted on southeastern rivers and reservoirs are consistent with my findings for the Byllesby Reservoir population with the exception of a study conducted on Brooks Pool, New River, West Virginia (Roell 1989). Diet composition of Brooks Pool flathead catfish was primarily crayfish (> 90 % by wet weight) for catfish between 250 and 461 mm with less than 5 % of the wet weight being fish. Although Roell (1989) did not examine stomach contents of flathead catfish over 500 mm (TL), there was no evidence of fishes becoming more prevalent in the diets as the size of catfish increased.

Diet composition was consistent with results of other studies even with respect to percentage of the wet weight for major diet items (*eg*. crayfish, fish, aquatic insects). Quinn (1987) found fish to make up 52 % of the stomach contents (by wet weight) for flathead catfish between 300 and 599 mm TL, while 96 % of the diet in catfish larger than 599 mm was fish in the Flint River, Georgia. Similarly, Ashley and Buff (1987) found 46 and 97 % of the diet items by wet weight was fish for flathead catfish from the Cape Fear River, North Carolina between 300 and 499 mm TL and greater than 499 mm TL, respectively. These results were mirrored by the diet composition of both Byllesby flathead catfish and the combination of Byllesby and Bluestone (Edmundson 1974) data.

The percentage of the diet made up of centrarchids, however, was higher in both Byllesby and Bluestone Reservoir catfish than in flathead catfish from either the Cape Fear or Flint Rivers. This discrepancy may be due to differential availability of centrarchids in these systems and the abundance of clupeid prey in the Cape Fear and Flint Rivers. Clupeid prey were not present in Byllesby or Bluestone Reservoirs when diet studies were conducted. Flathead catfish tend to prey on fish species in relation to their availability (Minckley and Deacon 1959; Turner and Summerfelt 1970; Davis 1985; Ashley and Buff 1987). Ney et al. (1990) reported high abundances of centrarchids in Byllesby Reservoir relative to other potential prey species. Edmundson (1974) speculated that the shallow nature of Bluestone Reservoir may have made sunfishes available to foraging catfish, accounting for the abundance of centrarchids in the diets of flathead catfish of this reservoir. However, contrary to diet composition data, largemouth bass were shown to be preferred by flathead catfish over white catfish, green sunfish, and goldfish in plastic-lined tanks during a prey preference study (Hackney 1965). Centrarchids are likely to be a major prey resource in systems where their abundance is high relative to other potential prey.

Bioenergetic Parameters

Little research has been done to determine the bioenergetic parameters for flathead catfish. Therefore, many of the parameters used by Roell (1989) and Roell and Orth (1993) in modeling the bioenergetics of this catfish were chosen based on parameter values determined for other species. In those cases where little information about flathead catfish was available, values were chosen such that consumption estimates could not be overestimated (Roell and Orth 1993). This conservative modeling approach strengthens the results regarding impact on centrarchids by underestimating annual consumption (thus, the number of centrarchids consumed is likely greater than estimated with this model). Examples of conservative modeling are exclusion of reproductive energy costs and use of low activity metabolism multipliers (Roell 1993).

Abundance and Mortality

Because I was unable to directly estimate abundance and mortality for the Byllesby Reservoir population, three separate flathead catfish populations were modeled incorporating four density/abundance estimates and three estimates of mortality. The values bounding the ranges of abundance and mortality are estimates from other studies on flathead catfish conducted in large reservoirs and large rivers the southeastern United States. Therefore, the populations modeled in these simulations should bound the range of annual prey consumption of actual river and reservoir flathead populations in this region of the country. A maximum density estimate of 14 flathead catfish per ha (Quinn 1988) coupled with the lowest rate of annual instantaneous mortality, 0.490 (Quinn 1988), resulted in the largest flathead catfish population modeled, while the minimum density of 3.5 catfish per ha (Hart 1981) and the highest rate of annual instantaneous mortality, 0.818, described the lowest population modeled. A population with a density skewed toward the lower end (6.1 catfish per ha) and an intermediate annual instantaneous mortality (0.654) was assumed to be the most probable for Byllesby Reservoir based on both qualitative and quantitative observations. Differing densities should not have any effect on annual consumption of individual flathead catfish unless the food resource is limiting.

Age and Growth

Mean lengths-at-annuli were not different by more than 10 % between Byllesby Reservoir and Brooks Pool flathead catfish except at age-1, where Byllesby catfish were 15.5 % longer than Brooks Pool flathead catfish. Although growth rates from the two Byllesby Reservoir flathead catfish examined were similar to those determined by Roell (1989) for Brooks Pool, New River catfish, using the Brooks Pool data could have biased model results in an unpredictable manner; there is no way to know if the fish sampled from Byllesby Reservoir were representative of the entire population. However, although it is possible that flathead catfish of Byllesby Reservoir grow more slowly than those of Brooks Pool, it is not likely. Brooks Pool flathead catfish exhibited slower growth rates than any others reported

(Roell 1989). Further, the fish diet of Byllesby Reservoir flathead catfish, as opposed to aquatic invertebrates in Brooks Pool, should confer greater growth due to better energetic profitability (Brett and Groves 1979), unless consumption rates are considerably different. Thus, it is likely that Byllesby Reservoir catfish have nearly the same or a slightly faster growth rate than Brooks Pool individuals, and the use of Brooks Pool growth data probably resulted in underestimation of annual consumption to some degree.

Energy Density

Energy densities for both predator and prey were modeled as unchanging values seasonally and ontogenetically. Roell (1989) modeled flathead catfish and the New River prey base in the same manner. No evidence exists to support this assumption. Several models have incorporated fluctuations in energy densities for both predators and prey fishes (Craig 1977; Mills and Forney 1981; Stewart et al. 1983; Flath and Diana 1985; Stewart and Binkowski 1986). Stewart and Binkowski (1986) examined the error in consumption estimates for alewives if changing energy densities are modeled as static. They found maximum seasonal consumption errors of 88 % when using constant energy densities. However, there was only 7 % difference between annual consumption estimates from constant versus changing energy density models. Thus, if only annual consumption is desired, as in this case, constant energy density is probably adequate (Stewart and Binkowski 1986).

Water Temperature

Bartell et al. (1986) found through sensitivity analysis that the equations defining temperature dependence, for both maximum consumption and standard respiration, and the water temperature input data have considerable influence in the bioenergetics model when predicting consumption. Much of the water temperature profile developed for Byllesby in this model was taken from data collected at the gaging station at Galax, Virginia, located approximately 21 river km upstream of Byllesby Dam, and should be similar to surface temperatures in the impoundment. The remainder of the water temperature profile (months May through October) was developed from site-specific surface water temperatures. Although the temperature data from Galax may be consistent with Byllesby Reservoir surface temperatures, many of the flathead catfish sampled at Byllesby Reservoir were collected in water greater than 5 m deep. However, since Byllesby Reservoir is essentially isothermic, flathead catfish at depth are experiencing water temperatures nearly the same as those temperatures measured at the surface (Ney 1989).

Centrarchids

Abundance

Because the number of fish marked and recaptured in this study was low, the population estimates for the four centrarchid species are not reliable. The density estimate for smallmouth bass ≥ 100 mm in Byllesby compared favorably to the mean estimate generated from Claytor Lake (a mainstream, New River impoundment located downstream of Byllesby) cove-rotenone data (Claytor Lake estimate was 1.23 times as large as the Byllesby estimate; Hart 1981). Comparisons of Claytor Lake and Byllesby Reservoir densities for the other centrarchid species, however, were not so close. The mean Claytor Lake spotted bass ≥ 100 mm density was three times as large as the Byllesby estimate while the combined mean densities of sunfishes ≥ 70 mm (bluegill, green, and pumpkinseed sunfishes) was 83 times higher in Claytor Lake than the combined redbreast and bluegill density in Byllesby Reservoir (Hart 1981). It is not suprising that Claytor Lake supports greater densities of centrarchids than Byllesby because Claytor Lake is more fertile and contains better habitat for centrarchids (ie. contains more coves and has more woody debris). Flathead catfish predation could also be responsible for maintaining low centrarchid abundances in Byllesby Reservoir.

Age and Growth

Mean back-calculated length-at-annulus of smallmouth bass and spotted bass were similar to values from around the state of Virginia (Table 12). Smallmouth bass and spotted bass from Byllesby exhibited growth rates as fast or faster than those reported as the Virginia state average by Banach (1989). Smallmouth bass from Byllesby Reservoir also had growth rates slightly higher than the western Virginia average (Banach 1989). However, while Byllesby spotted bass grew at the same rate as those from Claytor Lake, smallmouth bass from Claytor Lake grew considerably faster than Byllesby smallmouth (Kohler 1980). Although the United States average lengths-at-age-1 for both smallmouth and spotted bass were much larger than those determined for Byllesby Reservoir, the reported United States average lengths-at-ages-2 through 4 were similar to Byllesby black bass estimates (Carlander 1977).

Growth rates of sunfish did not compare as well with those reported in other studies as did the black bass. Redbreast sunfish from Byllesby Reservoir grew much faster than the Virginia state average and the average for western

Table 12. Comparison of mean back-calculated lengths-at-annulus (mm TL) for bluegill, redbreast sunfish, smallmouth bass, and spotted bass in Byllesby Reservoir, New River, Virginia with averages from other localities in Virginia.

		Bluegill				Redbreast Sunfish			
Location	Source	I	II	III	IV	I	II	III	IV
Byllesby Reservoir	This Study	70	103	142	162	65	128	175	202
Claytor Lake	Banach (1989)	45	87	130	160	-	-	-	-
Western Virginia	Banach (1989)	43	85	122	150	50	100	138	156
Virginia State	Banach (1989)	42	87	128	155	50	101	138	163

		Smallmouth Bass				Spotted Bass			
Location	Source	I	II	III	IV	I	II	III	IV
Byllesby Reservoir	This Study	115	171	269	293	113	189	257	296
Claytor Lake	Kohler (1980)	95	188	302	401	104	185	268	288
Western Virginia	Banach (1989)	94	169	228	283	-	-	-	-
Virginia State	Banach (1989)	97	174	243	291	92	168	232	278

Virginia (Table 12; Banach 1989). Redbreast sunfish from Byllesby Reservoir grew much faster than those reported for New York and North Carolina, although mean age-1 North Carolina redbreast sunfish were 51 mm longer than Byllesby redbreast sunfish (Carlander 1977). Byllesby Reservoir bluegill also grew faster than the Virginia state average, western Virginia average, and representatives from Claytor Lake (Table 12; Banach 1989). Byllesby bluegill were 1.5 times longer at the first annulus than any of the previously mentioned groups. Byllesby bluegill grew at a about the same rate as those from Maryland (Carlander 1977), but were smaller (on the order of 30 mm) than the United States and southeastern United States mean lengths for ages-1 and 2. By age-3, back-calculated lengths-at-annulus were nearly the same as the national and regional averages. Because abundance estimates were low for Byllesby sunfish, it is unlikely that these populations are experiencing any stunting due to overcrowding, which could be responsible for growth rates greater than other Virginia waters.

IMPACT OF FLATHEAD CATFISH PREDATION ON CENTRARCHID ABUNDANCE

The amount, in grams, of centrarchid biomass consumed annually by a flathead catfish population depended on the density and mortality rate of the population in that simulation (three combinations in my simulations). In turn, the predicted impact of flathead predation on the four centrarchid species in Byllesby Reservoir also depended on whether sunfish were assumed more vulnerable to catfish predation, all centrarchids were assumed equally vulnerable, or only sunfish were assumed vulnerable to predation. The product of three density-mortality combinations times three centrarchid vulnerability scenarios resulted in nine simulations of predation impact. Impact, the percentage of a centrarchid species population consumed annually, on the two black bass species ranged from approximately 9 to 55 %. The most probable result (assumed to be density of 6.1 flathead catfish per ha, annual instantaneous mortality rate of 0.654, and consuming more sunfish than bass (57/43)) was 16 %. Estimated impacts of flathead catfish predation on redbreast and bluegill were considerably higher, based on the predation vulnerability assumption. For sunfish species, impacts ranged from just over 11 to 100 %, which cannot occur, though the most probable impact was 37 %.

Although annual mortality rates were not determined for the centrarchid species of Byllesby Reservoir, annual mortality estimates from other sources were gathered for comparison with predation impacts. Carlander (1977) reported annual mortality estimates for adult (age-II and older) bluegill ranging from 57 to 99 %, with a mean estimate of 77 %. No estimates of redbreast sunfish annual mortality were available, so they will be considered to be the same as bluegill. Assuming the mean annual mortality estimate for sunfish is that experienced in Byllesby, then the probable impact of flathead catfish predation contributes nearly 50 % of the mortality. Mortalities of this magnitude due to predation are not unusual. Lyons and Magnuson (1987) reported that walleye predation accounted for nearly 100 % of the adult darter annual mortality when YOY yellow perch densities were low.

Reported annual mortality estimates for adult smallmouth bass ranged from 53 to 69 %, with a mean of 62 % (Carlander 1977). Estimates of spotted bass annual mortality were not available and were assumed to be the same as smallmouth bass. The probable mortality due to flathead catfish predation in Byllesby Reservoir contributes 26 % of the assumed total annual mortality.

Because there was a large discrepancy in estimated abundance of sunfish populations of Claytor Lake and Byllesby Reservoir, the densities of flathead catfish necessary to produce the same impacts on Claytor Lake (assuming model parameters and flathead mortality rate used for Byllesby Reservoir apply to Claytor Lake) were estimated. A density of 406 flathead catfish per ha would be necessary to consume 37 % of the age-1 and older Claytor Lake sunfish, given that sunfish are more vulnerable to predation than black bass (Figure 11). Assuming black bass and sunfish are equally vulnerable to flathead predation, a density of 742 catfish per ha would be required to eat 37 % of the sunfish (Figure 11). If the only centrarchids consumed are sunfish, a density of 153 flathead catfish per ha is needed to produce a 37 % impact on the Claytor Lake sunfish population (Figure 11). Densities of these magnitudes have not been reported for flathead catfish. The highest density reported was 14 catfish per ha (Quinn 1987), more than one-tenth the density required to consume 37 % of the Claytor sunfish assuming they are the only centrarchid eaten.

Densities of flathead catfish required to produce 16 % annual mortality on the spotted and smallmouth bass populations in Claytor Lake were 8.6 flathead catfish per ha given equal vulnerability of black bass and sunfish, and 10.8 catfish per ha assuming sunfish were more vulnerable to predation than black bass (Figure 12). Both of these density estimates are within, or close to, the upper end of the reported range of flathead densities.

Density estimates of flathead catfish from Claytor Lake were 3.5 per ha (Hart 1981), much lower than those needed to

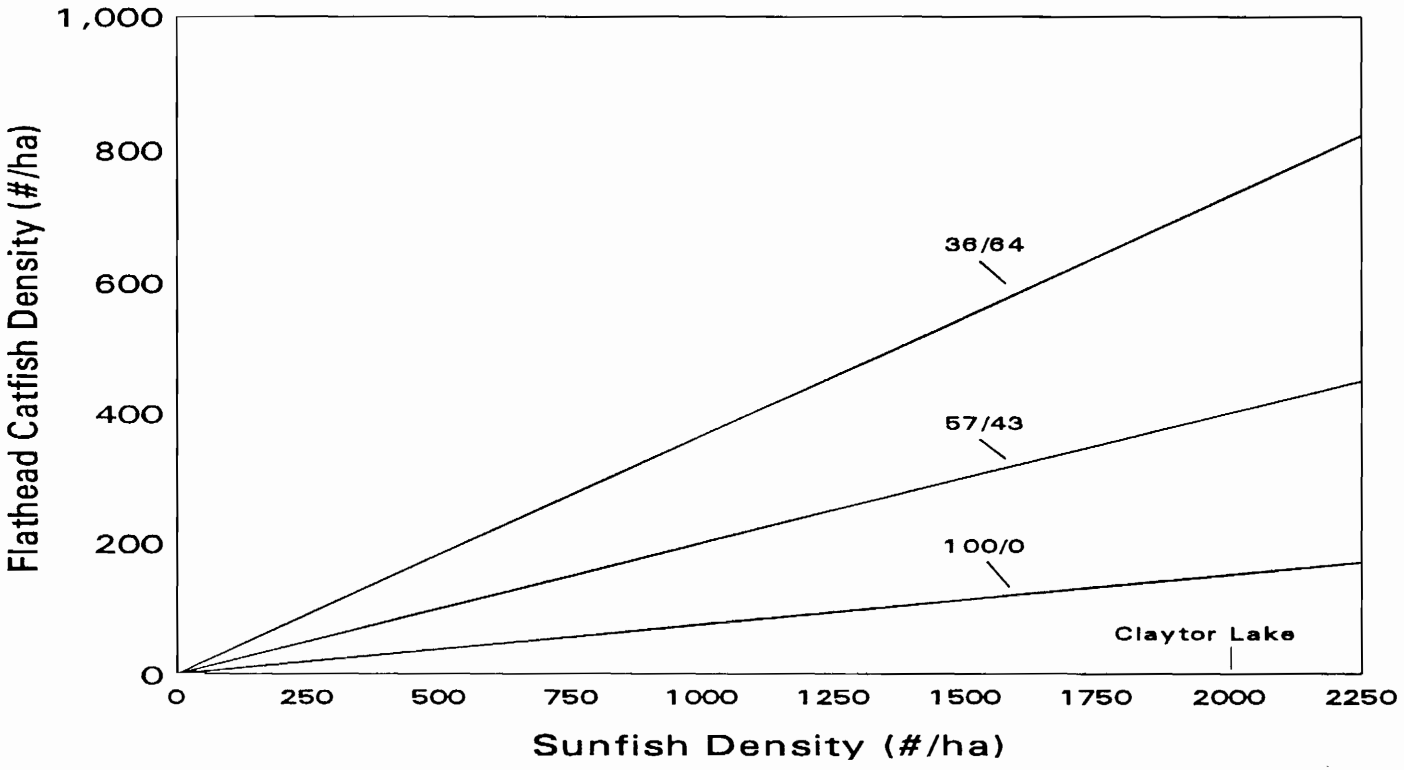

Figure 11. Density of flathead catfish necessary to consume 37 % of the sunfish at different sunfish densities given model parameters and flathead mortality same as used in Byllesby Reservoir bioenergetics model. Line marked 36/64 assumes the number of sunfish eaten per catfish as in equal vulnerability scenario in Byllesby model while 57/43 assumes sunfish more vulnerable to flathead predation than black bass. Sunfish density of Claytor Lake is noted (Hart 1981).

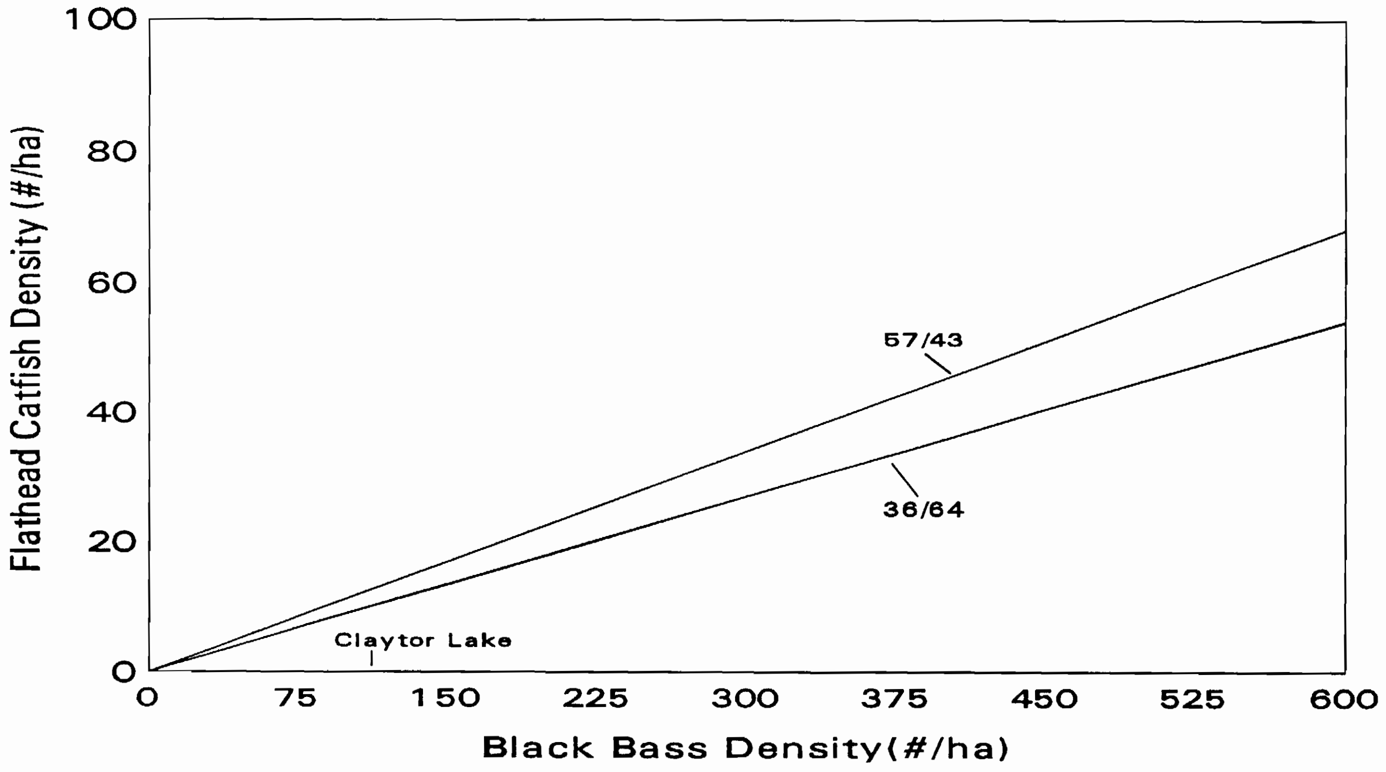

Figure 12. Density of flathead catfish necessary to consume 16 % of the black bass at different black bass densities given model parameters and flathead mortality same as used in Byllesby Reservoir bioenergetics model. Line marked 36/64 assumes number of black bass eaten per catfish as in equal vulnerability scenario in Byllesby model while 57/43 assumes black bass less vulnerable to flathead predation than sunfish. Black bass (smallmouth and spotted bass) density of Claytor Lake is noted (Hart 1981).

produce impacts equivalent to those predicted in Byllesby Reservoir. This estimate was based on cove-rotenone data, a technique not conducive to accurate estimation of flathead abundance. Even so, densities in Claytor Lake should be well below those needed to consume 37 % of the sunfish, and should be lower than those to produce 16 % impact on black bass, especially if the 57/43 scenario holds. The range of densities required to produce 16 % impact on black bass (having a density of nearly 10 fish per ha) are below the maximum reported density for flathead catfish of 14 catfish per ha by Quinn (1987).

The few experiments conducted on efficacy of flathead catfish predation in controlling overcrowded sunfish populations met with limited success (Hackney 1965 and Swingle et al. 1965). However, in these trials, catfish were stocked as fingerlings or sub-adults at rates higher than modeled in these simulations. It is possible that these fish were not yet eating predominantly fishes, if eating fish at all. Trials were run for less than a year. This species, especially when stocked at a small size, has large predator inertia, the time it takes from entry into the system until most of the predatory impact has occurred (Stewart et al. 1981). Thus, the ability of flathead catfish to control sunfish populations should not be judged on such a short-term when stocking small individuals. Davis (1985) reported drastic shifts in abundance of several of the predominant species in a Minnesota lake within two years following the introduction of adult flathead catfish. Introduction of adult flathead catfish, rather than fingerlings, is likely to produce immediate changes in the abundances of prey.

Bioenergetics modeling has helped elucidate interactions and dynamics between predaceous fishes and their prey (Stewart et al. 1981; Carline et al. 1984; Kitchell and Crowder 1986; Lyons and Magnuson 1987; Roell 1989; Hartman and Margraff 1992; Roell and Orth 1993). In the case of Byllesby Reservoir, it appears that the centrarchids and flathead catfish have achieved some degree of balance such that (barring complete reproductive or recruitment failure of one or more of the centrarchid species) flathead predation should not eliminate or cause severe declines in prey populations. However, if a sudden reproductive boon occurs for flathead catfish and their densities approach or exceed 9 per ha while centrarchid abundances remain unchanged, then the flathead population is predicted to consume greater than 50 % of the sunfish and greater than 25 % of the black bass age-1 and older annually. Losses of this magnitude may, through time, reduce sunfish and/or black bass populations to extremely low levels, placing a strain on management of the recreational fishery in Byllesby Reservoir. This, in turn, may cause reductions, or oscillations, in flathead catfish densities, such that balance is once again achieved.

SUMMARY AND CONCLUSIONS

SUMMARY

1. Of the 76 flathead catfish examined for diet composition from Byllesby Reservoir, 60 % were empty. There were no significant differences between the percentages of empty small (300 to 499 mm TL) and large (≥ 500 mm TL) flathead catfish ($P > 0.10$), but catfish sampled in the months May through July were significantly more likely to contain food than those collected form August through October ($P < 0.025$).

2. The predominant food item found in small flathead catfish from Byllesby Reservoir was fish of the centrarchid family (50 % by wet weight). Crayfish made up 39 % of the diet for catfish of this size group with aquatic insects and other fishes contributing 7 and 4 % respectively.

3. Large flathead catfish from Byllesby Reservoir were found to be almost entirely piscivorous with the predominant prey being centrarchids (66 % by wet weight). Other fishes made up 34 % of the weight while aquatic insects and crayfish made up < 0.05 % and 0 % respectively.

4. Because of the small sample size of flathead catfish containing food used to develop diet composition for Byllesby Reservoir, data from Bluestone Reservoir flathead catfish were integrated with the Byllesby results to determine diet composition for use in the bioenergetics model. Percentages by wet weight for

small flathead catfish following combination of Byllesby and Bluestone Reservoirs data were 27, 5, 3, and 65 % for centrarchids, other fishes, aquatic insects, and crayfish respectively. Diet composition used for large flathead catfish was 51, 43, 0, and 5 % centrarchids, other fishes, aquatic insects and crayfish.

5. Spines from only two Byllesby Reservoir flathead catfish were available for age and growth analysis. Mean back-calculated lengths-at-annulus suggest that Byllesby Reservoir flathead catfish reach 300 mm TL by age-4 and were predicted to reach 500 mm TL by age-10, based on growth trend projections.

6. It was not possible to generate accurate abundance estimates of flathead catfish > 300 mm possible in Byllesby Reservoir. A range of values was developed from reported densities in the literature. The minimum value was 3.5 catfish per ha while the maximum density was 14.0 per ha. Intermediate values used in modeling were 6.1 and 8.7 flathead catfish per ha. The value of 6.1 per ha was assumed to be the most plausible for Byllesby Reservoir.

7. An estimate of mortality rate was also unable to be determined. Again, literature reported values were used to develop a range of values with the minimum instantaneous rate of mortality being 0.49 and the maximum being 0.82. The mean value of 0.65 was chosen to represent mortality of Byllesby Reservoir flathead catfish.

8. Modified Petersen abundance estimates, corrected to pre-flood levels using a comparison based on catch-per-effort ratios, were used to determine abundances of the four predominant centrarchids in Byllesby Reservoir. Abundance estimates were 320, 2036, 2440, and 1698 for age-1 and older bluegill, redbreast sunfish, smallmouth bass, and spotted bass respectively.

9. Results from bioenergetics modeling showed that the amount of food consumed per individual flathead catfish increased with increasing age but gross conversion efficiency was highest for age-4 catfish (0.29) and decreased to a stable 0.19 for age-10 and older flathead catfish. Peak individual consumption occurred in late July and early August, when water temperatures were highest. Individual consumption was lowest during the cold winter months of January and February.

10. The number of age-1 and older bluegill, redbreast sunfish, smallmouth bass, and spotted bass predicted to be consumed annually by the flathead population of Byllesby Reservoir were 64, 417, 499, and 347, assuming that all centrarchid species were consumed in proportion to their relative abundances. If the sunfish species were assumed to be more susceptible to predation than the bass species, then the predicted number consumed annually by the Byllesby flathead population were 118, 764, 392, and 279 for bluegill, redbreast sunfish, smallmouth bass, and spotted bass respectively. If only sunfish were consumed by Byllesby Reservoir catfish, then the number of bluegill and redbreast sunfish consumed annually by flathead catfish were predicted to be 321 and 2050 respectively.

11. Impact of estimated flathead catfish consumption on centrarchid populations in Byllesby Reservoir (based on the most probable population) was 20 % for all species if consumed in proportion to their relative abundances, 37 % for the sunfishes and 16 % for the basses if sunfishes were assumed to be more susceptible to predation than black basses, and 100 % for sunfishes if black bass were not susceptible to predation.

12. Flathead catfish densities of 742, 406, and 153 per ha would be required to consume 37 % of the Claytor Lake sunfish given that sunfish are consumed as in the modeled population for Byllesby Reservoir under the equal vulnerability, sunfish more vulnerable than black bass, and sunfish only vulnerable consumption scenarios, respectively. Catfish densities of 8.6 and 10.8 per ha would be required to consume 16 % of the black bass in Claytor Lake for the equal vulnerability and sunfish more vulnerable than black bass scenarios, respectively.

CONCLUSIONS

The results of this study indicate that flathead catfish predation may cause substantial declines in the abundances of prey fishes. In Byllesby Reservoir, the abundance of centrarchids, specifically bluegill, redbreast sunfish, smallmouth bass, and spotted bass, make them the probable primary prey of flathead catfish. Diet composition results suggested that sunfish were the most important food item, by wet weight, for flathead catfish from Byllesby Reservoir, especially for those catfish over 500 mm TL.

The flathead catfish bioenergetics model estimated considerable impact on age-1 and older centrarchid populations in Byllesby due to flathead predation. Using the most likely population parameters (6.1 flathead catfish per ha and an instantaneous mortality of 0.65) and consumption scenario (assuming sunfish are more vulnerable to predation by flathead catfish than black bass), approximately 37 % of the bluegill and redbreast sunfish and 16 % of the smallmouth and spotted bass were predicted to be consumed annually by the flathead population of Byllesby Reservoir. Impact estimates from extreme modeled populations ranged from 19 to 98 % for sunfish and 8 to 43 % for black bass, again assuming sunfish more vulnerable to predation than black bass.

Based on annual consumption estimates generated in these simulations, it is unlikely that flathead catfish will have considerable impact on their prey in most bodies of water. The exceptions would be in systems having low abundances of prey animals and few or no alternative prey or where flathead populations reach extremely high densities. The effect of competition between flathead catfish and other piscivores on a prey base is unknown.

The results of this research indicate that flathead catfish can be used as an auxiliary predator to largemouth bass in ponds to reduce overcrowded sunfish populations. Previous attempts at using flathead catfish in this capacity have proven ineffective, but small catfish were stocked and time periods were less than one year. Stocking flathead catfish of at least 200 mm (300 mm would be better) would prove more effective in thinning crowded sunfish populations relatively quickly.

Prior to the introduction of flathead catfish, inventory of existing species and their relative abundances should be determined and then monitored following catfish release. Knowledge of the piscivorous nature of flathead catfish and the effects their predation could have on abundant game and non-game species should be taken into account. If the depletion of a species or group of species is unwanted, flathead catfish should not be stocked.

If declining abundances of fish (or other probable flathead prey) occur and are not desired, increased harvest of flathead catfish can be used to decrease the catfish population and reduce the impact of their predation. Increased harvest can be achieved by promotion the flathead catfish fishery or by relaxing creel limits on the species. Conversely, if flathead prey are overabundant and a large fishery for catfish exists, tighter regulations on this species should allow increasing flathead abundance. At greater population sizes, predatory impact on prey will be greater.

Many of the parameters used in modeling flathead catfish are based on guesswork. In this research, some of the site-specific inputs to the model were also borrowed from alternate sources. Prior to further bioenergetics modeling, better estimates of physiological parameters for flathead catfish should be determined to provide more accurate results. Growth, abundance, and mortality of populations should be also determined more accurately prior to making annual consumption estimates with bioenergetics models. In these simulations, unknown physiological parameters and growth rate were chosen such that resultant consumption estimates were conservative. However, because annual instantaneous mortality and density of the probable Byllesby Reservoir population were based on no empirical data, the predation impact estimates on centrarchid populations are likely inaccurate.

Continued research on the interactions of flathead catfish and their prey is warranted. Results of bioenergetics modeling suggest that flathead catfish could be used to manage certain nuisance species (overcrowded/stunted sunfish populations or abundant gizzard shad populations). Although previous research has yielded little positive evidence on the efficacy of using flathead catfish as an auxiliary predator (Hackney 1965 and Swingle et al. 1965), the sizes of flathead catfish stocked and the time periods of the trials contributed to the ineffectiveness of this form of control. Bioenergetics results suggest that sufficiently large populations of large flathead catfish can exert suitable predatory levels to reduce prey populations. Experimentation with overcrowded and stunted sunfish populations and large flathead catfish should be conducted in easily controlled ponds to further develop this as management practice. Analysis of competitive interactions between flathead catfish and other piscivores would also prove useful in assessing the practice of introducing this fish.

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APPENDIX A

COMPONENTS OF THE BIOENERGETICS MODEL

Balanced Energy Equation

The bioenergetics model used to estimate consumption by flathead catfish in Byllesby Reservoir was based on the following formula (as in Hewett and Johnson 1992):

$$C = (R + S) + (F + U) + (\Delta B + G), \qquad [A1]$$

where C = consumption, R = respiration, S = apparent specific dynamic action, F = egestion, U = excretion, ΔB = somatic growth, and G = gonadal growth. Each component of the balanced energy equation is calculated as a daily specific rate (g per g per day). These specific rates can be converted to absolute estimates for a catfish through multiplication by catfish weight. Each component was calculated with algorithms taken from the literature as recommended by previous attempts at flathead bioenergetic modeling (Roell 1989 and Roell and Orth 1993); parameter estimates used in algorithms and models are listed in Table 1. The effect of reproductive energy (G) on fish energetics is not well understood (Ursin 1979) and was ignored in this model, resulting in an underestimation of consumption by this model.

Consumption

Consumption was modeled as a function the maximum specific feeding rate at the optimum temperature (C_{max}), a scalar value denoting proportion of the maximum feeding rate exhibited (P-value (P)), and a water temperature dependence function for consumption ($f(T_C)$):

$$C_D = C_{max} \cdot P \cdot f(T_C) \qquad [A2].$$

Maximum consumption was modeled as a function of flathead catfish weight (W), the intercept of the weight dependence function (CA), and the weight dependence coefficient (CB):

$$C_{max} = CA \cdot W^{CB} \qquad [A3].$$

Estimates for these parameters have not been determined specifically for flathead catfish. The values used for these parameters were 0.25 for CA and -0.20 for CB (Roell 1989). Parameters values were chosen by Roell (1989) based on the values determined for other species for this model. A midpoint value was used for CA because none of the species served as a sufficient surrogate for flathead catfish. The value chosen for CB was based on values used previously on larger piscivores (Roell 1989).

A Thornton and Lessem (1978) algorithm was used to model water temperature dependence ($f(T_C)$). This function models the product of two sigmoid curves; in this case, the two curves represent the relation of consumption at temperatures below and above an optimal water temperature range. The range of temperatures at which maximum consumption could occur were based on hypothesized temperature preference by Gammon (1973) (as in Roell 1989). Maximum consumption was hypothesized to occur between temperatures of 31 (CTO) and 32 (CTM) °C. Proportion of C_{max} declined markedly at water temperatures below 10 (CQ, lower minimum-rate temperature) and above 35 (CTL, upper minimum-rate temperature) °C. The proportion of maximum consumption assigned to the various temperatures (0.10 at CQ, 0.98 at both CTO and CTM, and 0.01 at CTL) were based on literature values (Thornton and Lessem 1978; Roell 1989; Hewett and Johnson 1992; and Roell and Orth 1993).

Respiration

Respiration (R) was modeled the same as consumption with one exception. Instead of having a scalar value, respiration was modified by an activity multiplier (R_A):

$$R = R_s \cdot R_A \cdot f(T_R) \qquad [A4]$$

where R_s = standard weight-specific standard respiration and $f(T_R)$ = water temperature dependence function.

Standard respiration was modeled based on flathead weight (W), an intercept value (RA, measured in g O_2 per g per day), and a slope relating dependence of standard respiration to weight (RB):

$$R_s = RA \cdot W^{RB} \qquad [A5].$$

Values for parameters used in this algorithm were described by Roell (1989). The value for RA used in modeling flathead catfish was an arbitrarily chosen compromise of 0.01 (range of known values for this parameter is 0.002 to 0.015). The RB value used for flathead catfish in this model was -0.36 based on values determined for largemouth bass (Roell 1989).

The temperature dependent maximum respiration adjuster was modeled with parameters defining optimum temperature for respiration (RTO), maximum temperature for respiration (RTM), the coefficient describing dependence of water temperature and respiration (Q), and actual water temperature:

$$f(T_R) = V^X \cdot e^{(X \cdot (1 - V))} \qquad [A6]$$

where

$V = (RTM - T) / (RTM - RTO)$,

$X = (Z^2 \cdot (1 + (1 + 40 / Y)^{0.5})^2) / 400$,

$Z = \log_e(RQ) \cdot (RTM - RTO)$,

$Y = \log_e(RQ) \cdot (RTM - RTO + 2)$.

Optimum and maximum temperatures for respiration were derived by the Kitchell et al. (1977) method and were estimated to be 35 and 38 °C respectively (Roell 1989 and Roell and Orth 1993). A value of 2.1, standard for piscivores, was used estimate the slope for standard respiration dependence on temperature (Kitchell et al. 1974; Kitchell et al. 1977; Kitchell and Beck 1980).

An activity multiplier (ACT) was estimated for flathead catfish in water less than 10 °C (ACT = 1.025) and greater than or equal to 10 °C (ACT = 1.15) by Roell (1989) and Roell and Orth (1993); these estimates were also used in this model. The activity multipliers were based on flathead activity compared to that of smallmouth bass and were estimated via field observation by Roell (1989).

Specific Dynamic Action

Specific dynamic action, or SDA, is the energy used in absorption, digestion, transportation, and deposition of assimilated energy (Beamish 1974). A value of 0.17, standard for piscivores, was used for SDA.

Egestion

Egestion was modeled as a function of consumption (C), prey indigestibility (IP_i), and proportion of each prey item in the diet (P_i):

$$F = FA \cdot C, \qquad [A7]$$

where

$$FA = \Sigma(P_i \cdot IP_i).$$

The proportion of consumed energy egested is 0.18 for crayfish (Stein and Murphy 1976, Kelso 1972), 0.15 for aquatic insects (Elliott 1976), and 0.104 for all fishes consumed (Beamish 1972).

Excretion

Excretion was modeled as a constant proportion of assimilated energy:

$$U = UA \cdot (C - F), \qquad [A8]$$

where

UA = the proportion of assimilated food excreted (for all prey).

A value of 0.088 was estimated as the proportion of assimilated energy excreted for largemouth bass, another large piscivore, by Rice et al. (1983). Roell (1989) and Roell and Orth (1993) used this value for flathead catfish.

Energy Density

Energy density estimates for both flathead catfish and prey items were based on previously reported results. Flathead catfish were assumed to have a energy density of 998.6 calories/g wet weight (Roell 1989, Roell and Orth 1993). Energy densities of 998.6, 1356.6, and 898.8 calories per g wet weight were used for all fish prey, centrarchids and other, aquatic insects, and crayfish respectively (Kelso 1972; Vannote and Ball 1972; Roell and Orth 1988). Predator and prey energy densities were assumed to be constant through the year.

APPENDIX B

SEASONAL AND AGE-SPECIFIC BIOENERGETICS INPUTS

Table 13. Water temperature (°C) values used in modeling flathead catfish bioenergetics.

Simulation Day	Date	Water Temperature (°C)
1	15 June	22.5
21	07 July	25.0
66	19 August	23.5
119	11 October	16.0
152	12 November	10.0
161	21 November	8.5
175	06 December	5.0
210	11 January	1.0
252	21 February	6.0
301	11 April	10.0
339	19 May	17.0
365	14 June	22.5

Table 14. Proportion of diet items, by preserved wet weight, used in bioenergetics model for flathead catfish from Byllesby Reservoir, New River, Virginia. Proportions based on weighted means of Byllesby Reservoir and Bluestone Reservoir, New River, West Virginia flathead catfish diet composition data.

		Fishes			
Age	Day[1]	Centrarchids	Other	Aquatic Insects	Crayfish
4	1-151	0.28	0.05	0.03	0.64
	152-300	0.85	0.15	0.00	0.00
	301-365	0.28	0.05	0.03	0.64
5	1-151	0.28	0.05	0.03	0.64
	152-300	0.85	0.15	0.00	0.00
	301-365	0.28	0.05	0.03	0.64
6	1-151	0.28	0.05	0.03	0.64
	152-300	0.85	0.15	0.00	0.00
	301-365	0.28	0.05	0.03	0.64
7	1-151	0.28	0.05	0.03	0.64
	152-300	0.85	0.15	0.00	0.00
	301-365	0.28	0.05	0.03	0.64
8	1-151	0.28	0.05	0.03	0.64
	152-300	0.85	0.15	0.00	0.00
	301-365	0.28	0.05	0.03	0.64
9	1-151	0.28	0.05	0.03	0.64
	152-300	0.85	0.15	0.00	0.00
	301-365	0.28	0.05	0.03	0.64

[1] Simulation day 1 is 15 June, the day of annulus formation; Simulation day 152 is 12 November, the day water temperature drops below 10 °C; Simulation day 301 is 11 April, the day water temperature equals or rises above 10 °C.

Table 14. Proportion of diet items for modeled flathead catfish, continued.

		Fish			
Age	Day[1]	Centrarchids	Other	Aquatic Insects	Crayfish
10	1-151	0.51	0.43	0.01	0.05
	152-300	0.54	0.46	0.00	0.00
	301-365	0.51	0.43	0.01	0.05
11	1-151	0.51	0.43	0.01	0.05
	152-300	0.54	0.46	0.00	0.00
	301-365	0.51	0.43	0.01	0.05
12	1-151	0.51	0.43	0.01	0.05
	152-300	0.54	0.46	0.00	0.00
	301-365	0.51	0.43	0.01	0.05
13	1-151	0.51	0.43	0.01	0.05
	152-300	0.54	0.46	0.00	0.00
	301-365	0.51	0.43	0.01	0.05
14	1-151	0.51	0.43	0.01	0.05
	152-300	0.54	0.46	0.00	0
	301-365	0.51	0.43	0.01	0.05
15	1-151	0.51	0.43	0.01	0.05
	152-300	0.54	0.46	0.00	0
	301-365	0.51	0.43	0.01	0.05

[1] Simulation day 1 is 15 June, the day of annulus formation; Simulation day 152 is 12 November, the day water temperature drops below 10 °C; Simulation day 301 is 11 April, the day water temperature equals or rises above 10 °C.

Table 15. Weights, both starting and final, and iteratively-fit P-values for each interval of each bioenergetically modeled flathead catfish cohort.

		Weight (grams)		
Age	Days	Starting	Final	P-value
4	1-151	251	429	0.181
	152-300	429	403	0.115
	301-365	403	429	0.129
5	1-151	429	647	0.158
	152-300	647	613	0.107
	301-365	613	647	0.121
6	1-151	647	866	0.132
	152-300	866	824	0.099
	301-365	824	866	0.113
7	1-151	866	1040	0.094
	152-300	1040	993	0.104
	301-365	993	1040	0.107
8	1-151	1040	1195	0.092
	152-300	1195	1147	0.093
	301-365	1147	1195	0.108
9	1-151	1195	1366	0.086
	152-300	1366	1310	0.088
	301-365	1310	1366	0.101

[1] Simulation day 1 is 15 June, the day of annulus formation; Simulation day 152 is 12 November, the day water temperature drops below 10 °C; Simulation day 301 is 11 April, the day water temperature equals or rises above 10 °C.

Table 15. Flathead catfish weights and P-values, continued.

Age	Days	Weight (grams)		P-value
		Starting	Final	
10	1-151	1366	1554	0.086
	152-300	1554	1492	0.088
	301-365	1492	1554	0.101
11	1-151	1554	1758	0.085
	152-300	1758	1691	0.087
	301-365	1691	1758	0.099
12	1-151	1758	1981	0.083
	152-300	1981	1908	0.084
	301-365	1908	1981	0.097
13	1-151	1981	2222	0.082
	152-300	2222	2144	0.083
	301-365	2144	2222	0.095
14	1-151	2222	2484	0.081
	152-300	2484	2400	0.082
	301-365	2400	2484	0.094
15	1-151	2484	2766	0.079
	152-300	2766	2676	0.080
	301-365	2676	2766	0.092

[1] Simulation day 1 is 15 June, the day of annulus formation; Simulation day 152 is 12 November, the day water temperature drops below 10 °C; Simulation day 301 is 11 April, the day water temperature equals or rises above 10 °C.

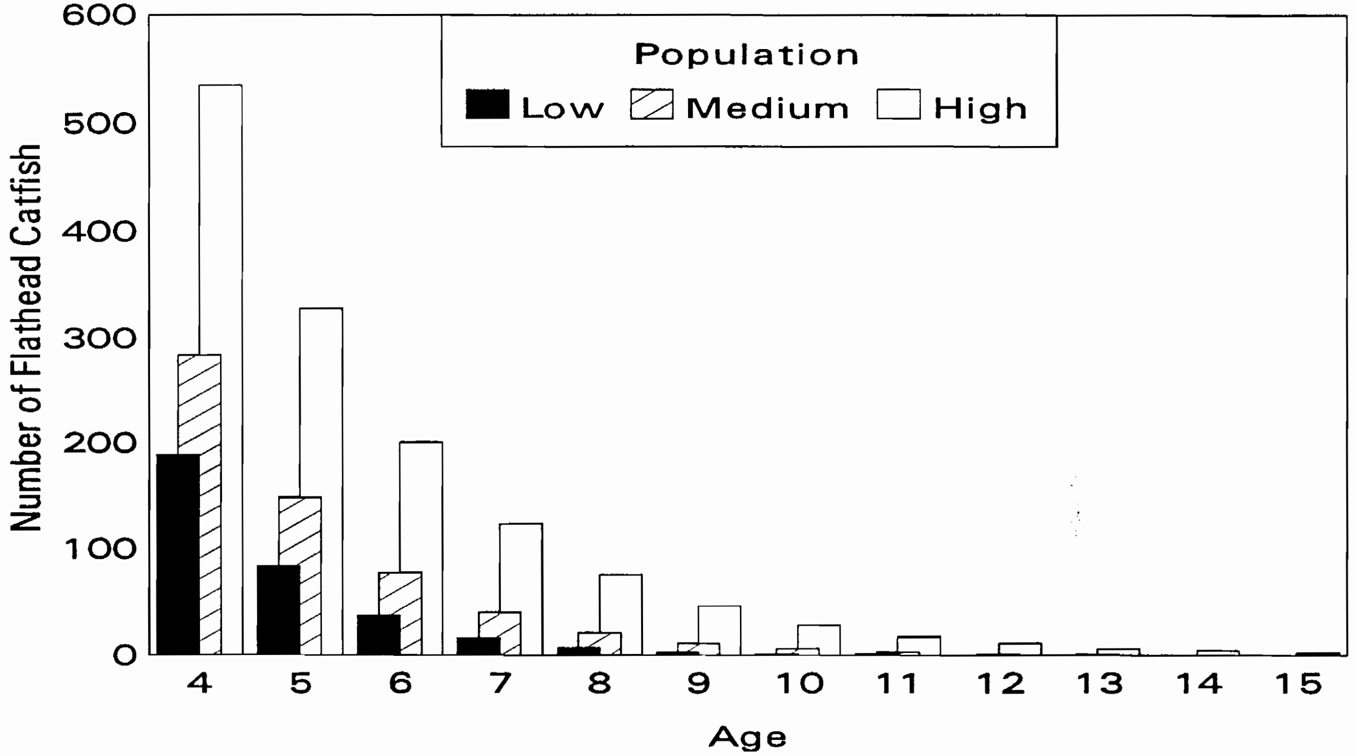

Figure 13. Number of flathead catfish at each age (ages-4 through 15) for the three modeled populations. The small population had a density of 3.5 flathead catfish per ha and an instantaneous annual mortality of 0.82. The medium population had a density of 6.1 flathead catfish per ha and an instantaneous annual mortality of 0.65. The large population had a density of 14.0 flathead catfish per ha and an instantaneous annual mortality of 0.49.

VITA

Brian Robert Barr was born (29 September, 1968) and raised in Arlington Heights, Illinois. In fall of 1986, following graduation from Buffalo Grove High School, he enrolled at Miami University, Oxford, Ohio. In May 1990, a Bachelor of Science degree was earned in Zoology. After graduating, Brian moved to Blacksburg, Virginia, working as a technician for Drs. Paul L. Angermeier and John J. Ney on a survey of fishes in four reservoirs. Graduate study in Fisheries and Wildlife Science began in January 1991 at Virginia Polytechnic Institute and State University under the direction of Dr. John J. Ney.

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