ANALYSIS OF THE TROPHIC SUPPORT CAPACITY OF SMITH MOUNTAIN LAKE, VIRGINIA, FOR PISCIVOROUS FISH

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(ABSTRACT)

This investigation examined the adequacy of the forage base to meet current demand of piscivores in Smith Mountain Lake, Virginia. Surplus production, or the maximum sustainable supply, of alewife (*Alosa pseudoharengus*) and gizzard shad (*Dorosoma cepedianum*) were determined using data on the biomass, growth, and mortality of each species. Mean hydroacoustic alewife biomass from 1993-1998 was 37 kg/ha and mean gizzard shad cove rotenone biomass from 1990-1997 was 112 kg/ha. Mean annual alewife surplus production was determined to be 73 kg/ha and mean annual gizzard shad surplus production totaled 146 kg/ha.

Bioenergetics modeling and population density estimates were utilized to derive the annual food consumption (realized demand) of the two most popular sport fish in the system, striped bass (*Morone saxatilis*) and largemouth bass (*Micropterus salmoides*). The striped bass population consumed 46 kg/ha of alewife and 27 kg/ha of gizzard shad annually. Largemouth bass ate 9 kg/ha of alewife and 15 kg/ha of gizzard shad annually. Annual consumption by ancillary predators was estimated to be 13 kg/ha of alewife and 35 kg/ha of gizzard shad.

Prey supply to predators is limited by morphology, behavior, and distribution. The cumulative effect on prey availability of these three factors, in addition to consumption by other predators, was quantified. For largemouth bass, available supply of alewife and gizzard shad exceeded demand by 20% and 53% respectively. For striped bass, available supply of gizzard shad surpassed demand by 30% but available alewife supply was only 4% greater than demand. Annual demand of all predators was 94% of total available clupeid supply.

Striped bass stockings were increased by 50% in 1998 and will remain at this level in the near future. A predator-prey simulation model of alewife and striped bass populations was developed to explore the consequences of increased predator demand. This model incorporated dependencies between alewife abundance and mortality and the mortality, abundance, and growth of striped bass. Model output showed that a 50% stocking increase has a near-zero probability of increasing the mean annual number of legal and citation striped bass in Smith Mountain Lake.

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The time and effort spent writing this onerous/rewarding undertaking is only a portion of the totality of its accomplishment. Many others have had a hand in its completion, and these few pages are devoted to them. This is the one section of the dissertation where humor can hope to escape the editorial scalpel.

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INTRODUCTION

Stocking of sportfish is perhaps the most visible and popular of all fisheries management actions (Heidinger 1993). The general perception is that introducing more fish in addition to those naturally produced should ultimately result in greater catches and increased angler satisfaction. Fisheries agencies culture and stock fish to meet a variety of objectives, including development of self-sustaining populations of non-native species to diversify a fishery, providing instant angler opportunities through put-and-take of catchable-sized fish, and to fortify harvestable populations that experience reproductive failure in a particular body of water. Most often, maintenance stocking involves juvenile fish introduced on a put-grow-take basis (Heidinger 1993).

If a maintenance stocking program is perceived by the public as successful, anglers may demand that the density or frequency of stocking be increased: they perceive that this would lead to better fishing. Hatchery production capability may be expanded to appease angler desires, but the capacity of the receiving water to support fish biomass is finite. At some fish density, habitat and/or food resources will become limiting, affecting not only the growth and survival of the stocked fish, but also of the resident species with which they may compete. Stocking, then, has the potential for diminishing returns, a fact that is not generally well understood or appreciated by the angling public.

The fisheries of North American reservoirs appear to be particularly well-suited for enhancement through stocking. Riverine species are seldom able to successfully colonize recently created pelagic habitat in the period following formation of storage or hydroelectric reservoirs (Rainwater and Houser 1982). In the hopes of establishing additional fishing opportunities, managers often resort to stocking non-native pelagic prey and predators to fill this vacant niche (Radonski and Miller 1986). While the non-native forage fish species must be prolific, stocked predators frequently fail to reproduce, but can be maintained through a put-grow-take program. Choices of suitable species for stocking often are based on perceived characteristics, rather than strong scientific evidence (Kohler et al. 1986). Assessing the consequences of these decisions is difficult due to a lack of consensus for measuring the impact of introduced species (Kohler and Stanley 1984).

Reservoir stocking programs have three potential outcomes (Kohler et al. 1986). At one extreme, an introduced species may fail because its ecological requirements for food or habitat cannot be met (e.g., trout stocked in warmwater lakes). At the other extreme, an introduced species may flourish at the expense of desirable resident species (e.g., Nile perch *Lates niloticus* in Lake Victoria, Africa). The third possibility is that the initial stocking effort is successful in establishing a popular new fishery that appears compatible with the existing sportfishes. If this occurs, anglers may soon demand higher stocking densities. However, the reservoir environment that meets the habitat needs of a new sportfish species will ultimately become food limited as the predator population is inflated.

A wealth of scientific information points to the importance of food supply in limiting sport fish production. Ploskey and Jenkins (1982) found that lack of prey was primarily responsible for reductions in game fish production in typical southern reservoirs. Ney (1990) reiterates the findings of Shelton et al. (1979) and Shuter et al. (1980), namely that overwinter starvation of juvenile centrarchids often determines year-class strength for a cohort. Bottom-up processes have also found support in Hanson and Leggett (1982), Yurk and Ney (1989), and Ogelsby (1977), who have shown that fish production correlates well with nutrient inputs and primary production in lacustrine systems. Despite the commonplace introductions of species into reservoir systems, the population dynamics of the non-natives and their interactions with native fishes are poorly understood (Axon and Whitehurst 1985).

As the prey resource limits of a reservoir are approached, both intraspecific and interspecific competition will intensify. The former will result in lower growth and/or survival of the stocked species, while the latter will affect resident species that share the prey resource. Inasmuch as fisheries for stocked and resident species are each likely to have their own contingent of devotees, the potential arises to escalate a biological conflict into a human dimensions issue. Lest the severity of angler conflicts be taken lightly, one must look no further than recent developments in Norris Lake, Tennessee. In this impoundment, legislation banning striped bass (*Morone saxatilis*) stockings and allowing unrestricted harvest of this species was proposed due to perceptions amongst anglers of detrimental consequences of striped bass presence on largemouth bass (*Micropterus salmoides*), smallmouth bass (*Micropterus dolomieu*), black crappie (*Pomoxis nigromaculatus*), and walleye (*Stizostedion vitreum*) (Tennessee Senate Bills 2823 and 2824).

The ideal maintenance stocking strategy, of course, is to match densities of put-grow-take predators to the capacity of the system to support all resident piscivores, both stocked and native, at desirable levels of growth and abundance. However, achieving this optimal state is problematic. The traditional approach is augmentation of the stocked population until the fishery (for either stocked or native species) suffers a recognizable, cause-and-effect decline. This approach may require a decade to complete (exclusive of the lag time to correct the imbalance) and could exacerbate angler conflicts. A promising emergent alternative is to conduct an analysis of the adequacy of the prey supply to meet present and future predator demand so that stocking rates may be adjusted accordingly, avoiding the consequences of overstocking. To achieve such an analysis, the sustainable supply of available prey must be determined as well as the concomitant demand of the predator assemblage. New techniques for quantifying forage-fish and piscivore abundance have been developed, as well as models to estimate prey consumption (realized demand). The challenge is to combine these techniques and models in a mass-balance analysis that produces accurate and verifiable results for management application.

Others researchers have conducted supply/demand analyses on a variety of species and systems, but all of these ventures leave room for improvement. The Y/C ratio of Swingle (1950) and the AP/P plots of Jenkins and Morais (1978) were early attempts to rectify prey supply with predator demand, but these studies quantified supply and demand only in terms of the biomass of predators and prey. Biomass has since been recognized too static and too coarse a metric on which to base supply/demand investigations (Ney 1990). In addition, only morphological availability of prey to predators was examined, while behavior and distribution were ignored. Ursin (1982) reviewed a variety of approaches to determine prey supply and predator demand in the North Sea. Total prey availability was addressed using an availability coefficient (G) as an indication of the predator's ability to find and capture prey. However, confidence in predator consumption estimates and the reliability of G values has been low (Ney 1990). Carline et al. (1984) and Johnson et al. (1988a) investigated the capacity of largemouth bass to consume gizzard shad (*Dorosoma cepedianum*) production in Ohio reservoirs. Constraints on availability of prey to predators were not completely addressed, however, and changes in predator efficiency with declining prey abundance were overlooked. Hartman and Brandt (1995b) quantified the demand of striped bass, bluefish (*Pomatomus saltatrix*), and weakfish (*Cynoscion regalis*) in Chesapeake Bay, but addressed prey supply through indirect methods and did not investigate prey availability. Stewart et al. (1981) conducted a supply/demand analysis for salmonid stocks and alewife (*Alosa pseudoharengus*) prey in Lake Michigan. Their study was hampered by poor estimates of prey biomass and a lack of information regarding behavioral interactions of predator and prey. Eck and Brown (1985) determined how much additional biomass of lake trout (*Salvelinus namaycush*) could be supported by alewife in Lake Michigan. They also had poor estimates of both consumption and production of prey, and incorporated faulty assumptions concerning utilization of prey biomass by predators (Ney 1990). Lyons and Magnuson (1987) examined the effects of walleye predation on littoral fishes in a small Wisconsin lake, but did not have accurate enough estimates of prey abundance to determine the trophic support capacity of the system for these predators. Miranda et al. (1998) performed bioenergetic modeling to estimate consumption of prey fishes by piscivores in Norris Lake, Tennessee, and used hydroacoustics to assess the prey population in that reservoir. However, they did not examine the sustainable supply of clupeids, and did not discuss availability constraints on predators. Moore (1988) performed a supply/demand analysis for Smith

Mountain Lake, Virginia, but he did not have an accurate means of assessing clupeid abundance, and did not attempt to quantify prey availability.

Smith Mountain Lake (SML) provides an excellent opportunity to apply and refine predator demand versus prey supply analyses. The primary native predators in this system are largemouth bass, black crappie, and catfish (*Ictalurus* and *Ameirus* spp.). The native gizzard shad and the introduced alewife are the primary clupeids, although threadfin shad (*Dorosoma petenense*) were illegally introduced in the early 1990's and reached notable densities in 1993 and 1995. In the late 1960's the Virginia Department of Game and Inland Fisheries (VDGIF) began stocking striped bass into SML. Striped bass are voracious, long-lived piscivores, reaching sizes up to 20 kg and ages of 12+ years. These characteristics suggest that striped bass can impose a heavy toll on the soft-rayed clupeids that are their primary prey (Stevens 1958; Morris and Follis 1978; Combs 1980; Kohler and Ney 1980; Moore et al. 1985; Gustaveson et al. 1993). These pelagic predators displayed excellent growth rates in SML, and a notable fishery emerged. Natural reproduction of striped bass, however, proved futile, so VDGIF engaged in stocking this species annually on a put-grow-take basis. Stocking levels have fluctuated from 40,000 to 850,000/year over the 35-year history of the reservoir, but over the last decade were steady at 300,000/year. At the moment, the SML fishery provides two very popular sportfishing opportunities, one for the stocked striped bass, and one for the native largemouth bass.

In addition to an interesting biological scenario in which to study supply of and demand for forage fish, a wealth of scientific data on the growth, mortality, abundance, and diets of predator and prey species has been collected over the past thirty years on SML by fisheries professionals at the VDGIF and researchers at Virginia Polytechnic Institute and State University. Reliable scientific information is very important for conducting this type of analysis, and much work was saved because of these extensive resources.

My goal in this dissertation is to quantify the available supply of clupeid prey in SML and relate it to the demand for these forage fishes by the SML predator assemblage. Specifically my objectives are:

1. Derive the maximum sustainable supply of alewife and gizzard shad.
2. Calculate annual consumption of clupeids by all major piscivores.
3. Determine the behavioral, morphological, and distributional availability of each clupeid species for each cohort of largemouth bass and striped bass.
4. Make predictions of the consequences of changes in striped bass stocking densities on predator growth and survival, as well as clupeid population dynamics.

This dissertation is organized to address each of these objectives in sequence. Chapter One deals with the derivation of maximum sustainable supply of clupeids in SML. Hydroacoustic surveys were used to derive August biomass estimates for alewife, and cove rotenone surveys were analyzed to determine the average biomass of gizzard shad in late August. Growth and mortality rates for each of these species were determined from cove rotenone data, gillnet samples, and information from previous studies (Tisa 1988; Moore 1988). This information was then utilized to determine the surplus production by each cohort of alewife and gizzard shad. Chapter Two describes the use of bioenergetic modeling to estimate the consumptive demand of largemouth bass and striped bass. Energy intake, in the form of ingested prey, is balanced with energy use by the predator in the form of metabolic requirements, growth, and waste products. Estimation of output allows for the computation of the amount of energy, and thus mass, of food ingested. Food habits, growth and mortality rates, and predator population estimates all play important roles in this computation. Consumption by secondary predators (e.g., catfish, crappie, smallmouth bass, walleye) was also estimated. Chapter Three addresses constraints on the availability of clupeid prey to each age-class of striped bass and largemouth bass. An approach to availability that incorporated morphological, distributional, and behavioral dimensions was adopted. Chapter Four uses modeling simulations to examine the effects of increased striped bass stockings on the alewife population and consequently on striped bass growth and survival.

The Virginia Department of Game and Inland Fisheries has committed to stocking 450,000 striped bass fingerlings (a 50% increase) into SML for the next several years. Determination of predator consumption through bioenergetic modeling, coupled with determination of available clupeid prey through hydroacoustic surveys, and examination of morphological, distributional, and behavioral constraints, will provide information leading to scientifically defensible management recommendations. Ideally, the model output will inform managers of what to expect, and so better prepare them to control and mitigate any problems caused by the stocking increase. Resolution of a user-group conflict thus will be more than political maneuvering, devoid of biological insight. If an adaptive management stratagem of trial-and-error augmentation of the striped bass population has any hope of success, knowing the proximity of the prey supply to overexploitation is critical.

STUDY SITE

The pumpback hydroelectric reservoir known as Smith Mountain Lake was initiated by the Appalachian Power Company in 1963 through impoundment of the Roanoke River. Located about thirty miles southeast of the city of Roanoke, the system receives a great deal of use from a variety of recreationalists throughout the year, but especially during May through September. At full pool, the reservoir encompasses 8340 hectares and has a mean depth of 16.8 meters. The former Blackwater and Roanoke river channels cut the two primary arms of the reservoir, but the system is highly dendritic, having a shoreline development index of 25. The Roanoke arm extends 65 km above the dam, while the Blackwater arm is 32 km long. Retention time is 1.35 years, but pump-back operations induce significant recycling of downlake waters throughout the year.

There are marked differences in the chemistry, morphometry, and ecology of the reservoir depending on distance above the dam. Because of these disparities, previous researchers (Moore 1988; Sutton 1997) have divided the reservoir into uplake, midlake, and downlake regions (Figure S.1). On the Roanoke arm, the uplake region ends at Hales Ford Bridge, while on the Blackwater arm the uplake region is considered approximately all waters above the confluence of the main channel and Gills Creek. The midlake region proceeds from these areas down to the confluence of the Blackwater and Roanoke arms. The downlake region extends from this confluence to the dam. A nutrient gradient exists, with riverine, uplake segments being eutrophic, areas near the confluence of the two river arms being mesotrophic, and the broad, deep pool extending about 10 km above the dam considered oligotrophic (Ney et al. 1990). The bottom in downlake regions often recedes quickly into the profundal zone, with rooted vegetation existing in small patches, if at all. Uplake regions, with bottoms that gradually deepen away from shore, are much more hospitable to littoral flora and fauna. Hypolimnetic uplake waters often become anoxic during summer, while downlake conditions in the hypolimnion stabilize at 2-4 mg/L of O_2. The summer season produces problems for cool-water pelagic fishes, such as walleye, striped bass, and alewife, that must limit their distribution to areas where temperature and oxygen demands can be met. However, summer habitat for these coolwater species has been greatly expanded since installation of an advanced waste treatment plant on the inflowing Roanoke River in the mid-1970's greatly reduced nutrient inputs into SML (Ney et al. 1990).

Ecologically, the system is a varied assemblage of native and introduced fish species (Hart 1978). Indigenous predators include the largemouth bass, crappie, and catfish. Striped bass, smallmouth bass, muskellunge (*Esox masquinongy*), flathead catfish (*Pylodictus olivaris*), walleye, white perch (*Morone americana*), white bass (*Morone chrysops*), and even Pacific salmonids (*Onchorynchus* spp.) have been introduced by the VDGIF during the reservoir's history. Striped bass are the only non-native predator currently stocked at appreciable levels (low densities of muskellunge are stocked), while flathead catfish and walleye could exist at densities great enough to impact the forage base. The main forage species are alewife and gizzard shad, the former introduced and the latter native to the Roanoke river drainage. In addition, assorted cyprinids (*Cyprinella*, *Pimephales*, *Notemigonus*, and *Notropis* sp.), sunfishes (*Lepomis* spp.), catostomids (*Catostomus* sp.), darters (*Etheostoma* sp.), and crayfish (*Oronectes* sp.) are present.

Due to the economic importance and recreational popularity of SML, and the heterogeneous species complex present, many studies have been conducted there. Limnological and water quality measures have been made by Cumming and Estes (1969), Simmons and Neff (1969), LaRoche (1981), Benfield and Hendricks (1975), Obenschain and McLeod (1981), and Whitehurst (1984). Brouha (1974) and Prince (1976) investigated impacts of artificial reefs on fish communities there. Publications concerning various aspects of the species complex and sport fishery are not lacking (Hart 1978; LaRoche 1981; Whitehurst 1984; Ney et al. 1990). Finally, investigations into predator-prey relations among piscine inhabitants are numerous (Moore 1988; Ney et al. 1988; Tisa 1988; Michaelson 1996; Sutton 1997).

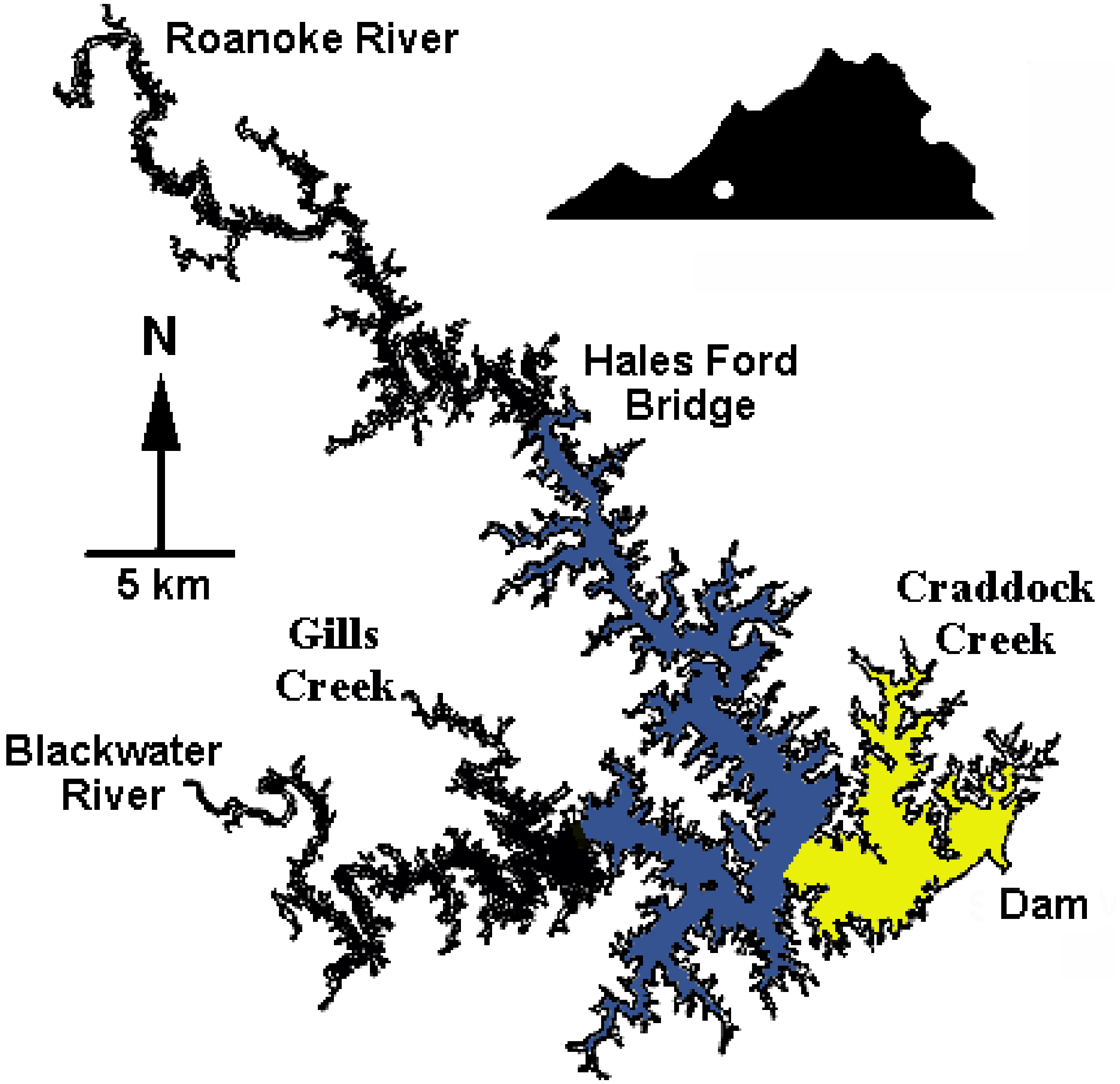

Figure S.1. Map of Smith Mountain Lake, Virginia. The reservoir is located southeast of the city of Roanoke. Black areas represent "uplake" regions, blue areas are "midlake," and the yellow-green area is considered "downlake."

CHAPTER ONE

DETERMINATION OF SUSTAINABLE SUPPLY OF CLUPEIDS IN SMITH MOUNTAIN LAKE

INTRODUCTION

Maximizing sport fish production is a primary management objective in southeastern impoundments (Noble 1981). Many have recognized the need for knowledge of the prey base (recruitment, growth, mortality and production of major forage species) in order to manage predatory sport fish effectively (Ney 1981; Noble 1981; Ney and Orth 1986; DeVries and Stein 1990; Ney 1990). The proliferation of impoundments created in the early 20th century brought recognition of the importance of predator-prey trophic interactions, but research into the dynamics of prey populations progressed slowly (Noble 1981). In the 1950's scientists were just beginning to formulate forage-fish management strategies (Boxrucker et al. 1995). The National Reservoir Research Program, established in 1963, focused scientific inquiry on sport fish harvest and densities in southern impoundments, but directed investigations of prey fishes did not rise to prominence until much later. Jenkins and Morais (1978) were early innovators in the analysis of forage fish adequacy for predator populations. In an ideal lentic system, energy flows efficiently from one trophic level to the next, from phytoplankton to zooplankton to planktivorous fish to piscivorous game fishes. Recognition of predator-prey imbalance and unutilized prey resources led to numerous management efforts directed at forage fish (e.g., chemical control, introductions, supplemental stocking, habitat manipulation) but often without adequate prior baseline data and post-hoc monitoring protocols (Pritchard et al. 1978; Noble 1981; DeVries and Stein 1990).

Once the importance of an adequate forage base was realized, investigators needed to determine the capacity of the prey resource to meet predator demand. To answer this question, the absolute amount of prey biomass and the amount of tissue elaborated in a population per unit of time, including that which dies within that interval, must be estimated (Ney 1990). The latter quantity is termed production, and annual production is the generation of biomass per unit of area, usually reported as kg/ha, during a single year. Production between two time periods can be calculated as

$$P = \ln (W_2 / W_1) * B_M ,$$

where W_2 is the average weight of individuals at the end of the period, W_1 is the average weight of individuals at the start of the period, and B_M is the mean biomass over the elapsed time interval. Total production of a prey population defines the maximum amount of tissue that predators might consume on a sustainable basis (Ney 1990). Not all of this production is truly available to predators, however, due to morphological, behavioral, and distributional constraints (Chapter Three) and death to other causes.

If all of the production of a single prey cohort in its first year of life was consumed by predators, there would be no biomass remaining to perpetuate the cohort. Some of the tissue accumulated in a cohort's first year must remain in order for the cohort to generate production in later years. Ney (1990) used the term *surplus biomass* to delineate the maximum sustainable supply of prey biomass (Ney 1990). In a stable prey population with a balanced age-structure, surplus biomass is that amount of new and previous production that dies during a given time period. Equation 16 of Ney (1990) defines an approximation for surplus biomass as:

$$(N_1 - N_2) * W_1 + [P - N_2 * (W_2 - W_1)]$$

where N_1 and N_2 are the numbers of fish from a specific cohort at the beginning and end of the period, respectively, W_1 and W_2 are the mean weight of these individuals at the start and end of the period, respectively, and P is production during the period. The first term represents biomass produced in previous periods that dies during the period. The second term in brackets represents biomass that is both produced and dies in the period under investigation. From this point forward, I shall refer to this quantity as *surplus production*, rather than surplus biomass, for I believe the former term to be more appropriate.

Rearranging and substituting B_1 for N_1*W_1 and B_2 for N_2*W_2, respectively, we get

$$\text{SURPLUS PRODUCTION} = P - [B_2 - B_1] \qquad (1)$$

where B_1 and B_2 represent total biomass at the beginning and end of the period, respectively, and P is production over the time period. Because all biomass produced eventually dies, surplus production over the lifetime of a cohort will equal total production, but the distribution of each metric across age-classes is not necessarily equal. This is because some of the production that occurs in one time period remains at the end of the period and is later lost, meaning that surplus production is often shifted to older age-classes (Figure 1.1).

Because an estimate of prey population biomass at some point is critical for determining prey production, and thus prey supply, much effort is spent determining the absolute abundance of prey fishes in aquatic systems. Traditional abundance estimation techniques developed for large piscivores (e.g., mark-recapture, creel surveys) were generally found to be inadequate when fragile, extremely abundant prey species were considered (Ney 1990), although some investigators have had success (Isely and Tomasso 1998). Instead, random sampling of subunits of large systems using collection techniques such as rotenone, gill-netting, trawling, seining, electrofishing, and even direct enumeration by underwater observation were employed (Noble 1981; Boxrucker et al. 1995). Fish densities in the subsamples were then extrapolated to system-wide estimates of abundance (Gunderson 1993).

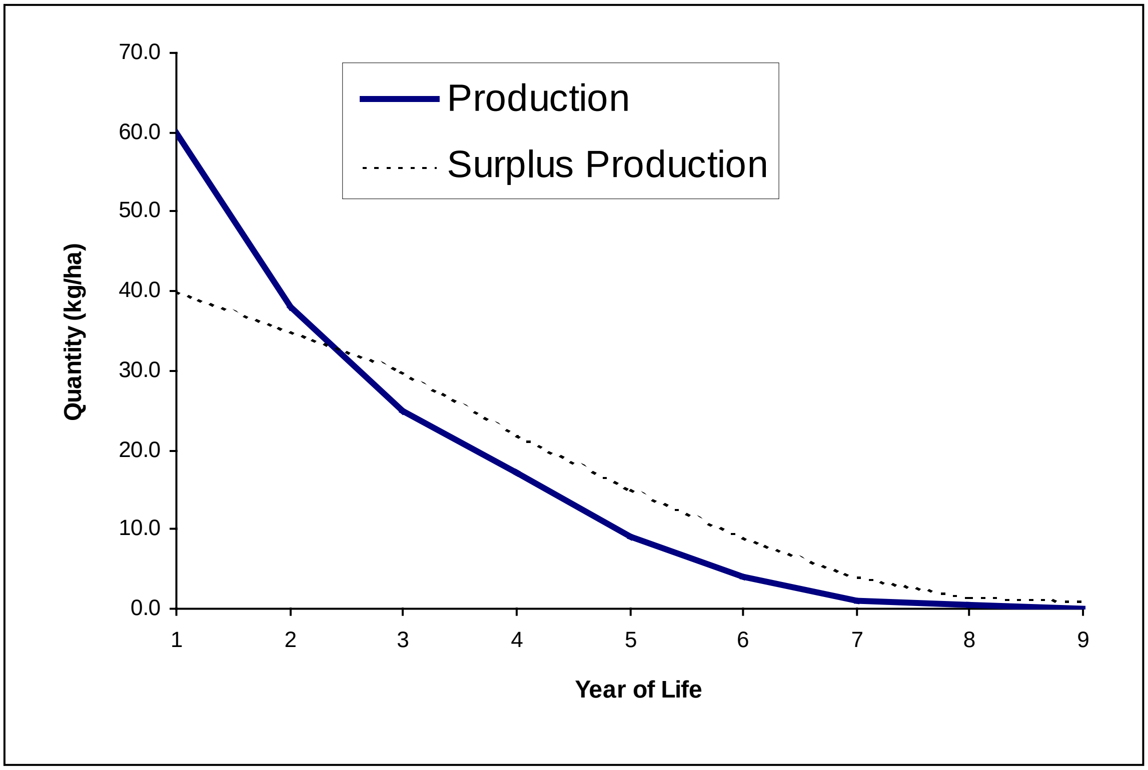

Figure 1.1. Differences in annual surplus production versus production across the lifespan of a hypothetical cohort of prey fish. The area under each curve is equivalent, meaning total surplus production and total production over the lifespan are equivalent.

Of the aforementioned techniques, cove rotenone methodology (Davies and Shelton 1983; Bettoli and Maceina 1996) became the most popular means of assessing littoral species abundance in southern impoundments, due to the perception of total enumeration of fishes within a sampled cove or embayment. The process consists of choosing a number of small coves (usually 0.5-2 ha) and sealing them off from the main lake with a block net. Next rotenone is applied (which disrupts oxygen uptake by fish and generally kills them within 1-9 hours, depending on the species). Finally, collection and measurement (species, length, weight) of all fish recovered within the cove occurs over the next few days. Recognition of bias stemming from high sampling variability, untenable procedural assumptions, and disparity between species in regards to rotenone vulnerability, as well as public-relations problems, left many scientists with little confidence that derived estimates of prey fish densities were representative of actual abundance in the system as a whole (Ney 1990). The Virginia Department of Game and Inland Fisheries (VDGIF) conducted cove rotenone samplings for thirty years on Smith Mountain Lake, but abandoned this methodology after 1997 due to the perception that the data acquired were not worth the considerable effort expended.

Even during the era when rotenone sampling was somewhat popular, researchers recognized that pelagic species were greatly under-represented in littoral coves (Siler et al. 1986). Several attempts were made at open water rotenone application, but with no real improvement over cove techniques in accuracy attained (Hayne et al. 1967; Summers and Axon 1980; Siler 1986; Bettoli and Maceina 1996). Instead, other means of assessing the abundance of pelagic species were developed. Trawling and gill-netting were most intensively investigated as possible replacements, but each was saddled with its own set of liabilities (Van Den Avyle et al. 1995b). Trawling provided more precise estimates and required much less effort than rotenone application demanded, but was only effective in sampling age-0 clupeids (Siler 1986; Michaletz et al. 1995). Gear avoidance of larger individuals was recognized, as well as the inability to sample areas with sunken trees or other obstructions. Gillnets were able to sample a wide range of size classes, but questions were raised concerning size-selectivity of the mesh used, labor requirements, site selection, encounter probabilities, and variations in efficiency caused by subtleties in gear deployment (Van Den Avyle et al. 1995a). Another promising technique for estimating pelagic fish abundance (hydroacoustics) was also coming into prominence at this time, and subsequently has received a great deal of research attention.

HYDROACOUSTICS

Hydroacoustics is a general term for the process of sound generation, transmission, reflection, and detection in water (Ney 1990). The technology associated with acoustical surveys of pelagic fish abundance is rapidly developing (Nero et al. 1990; Brandt et al. 1991; MacLennan and Simmonds 1992; Brandt and Kirsch 1993). For a detailed review of the theory and methodology of all aspects of acoustical studies, see Thorne (1983), Gunderson (1983), MacLennan (1990), and Brandt (1996). Effectiveness is due to the fact that sound waves have the ability to travel much deeper than other wave types in water (radio, light), and thus provide more opportunity to quantitatively observe fish sizes, distribution, abundance, and behavior (Gunderson 1993; Brandt 1996). Unlike most other means of direct assessment, acoustic surveys allow for the continuous recording of data along a series of transect lines. Large volumes of water can be sampled with relatively little effort, and data are collected with minimal disturbance to the stocks and their environment. High sampling rates allow for variations in sampling statistics to be kept low (Brandt 1996). However, the technology is not yet able to discriminate between species, so in most systems, ancillary gears (trawls, gillnets) are used to verify the species, size frequency, age, and sex of targets (Brandt 1996). In addition, unless sound propagation gear is modified, this method as typically employed cannot detect fish that are in the top 1.5 meters of the water column and those that are less than 1 m above the bottom. In shallow water, then, a high proportion of the water column is outside the sampling range. This can be important, for as Van Den Avyle et al. (1995a) showed, densities of threadfin shad and gizzard shad can be greatest in the top 2 meters of the water column. The training required to operate and interpret acoustic data is also fairly intensive.

Developed for military applications, and due to this patronage, sonar technology has advanced rapidly since initial use in World War I submarine tracking devices (Gunderson 1993). Currently, primary applications are in the arena of marine stock assessment, but acoustic technology has been successfully applied in all sizes of lakes, estuaries, coastal areas, and the open ocean (Brandt 1996). Commercial fishermen find acoustic technology very useful for finding concentrations of harvestable fish. More recent applications examine the behavior and ecology of fish, zooplankton, and larger invertebrates (Degan and Wilson 1995; Brandt 1996).

The basic acoustics system consists of four components: a transmitter, a transducer, a receiver-amplifier, and a recorder-control-display module (Thorne 1983). The transmitter produces an electric impulse that is converted to sound by the transducer. The frequency of sound is normally in the range of 12 to 420 kHz, and usually lasts from 0.1 to 1.0 milliseconds. Changes in the frequency affect the wavelength of the sound wave produced, and the sensitivity of the process to various-sized organisms. If frequencies are too low, the sound wave is too long to accurately detect small fish (Michaletz et al. 1995). At high frequencies, detection of non-piscine organisms causes fish abundance to be overestimated (Unger et al. 1987). Research has demonstrated that 120-200 kHz systems work best for estimating the abundance of pelagic fishes, but other frequencies do have their special applications (Degan and Wilson 1995; Brandt 1996).

After the sound wave is produced, it travels downward through the water column, spreading out radially, forming a cone. Thus, sampling volume increases with vertical distance from the transducer. If fish densities at various depths are to be compared, corrections must be made using proper filtering techniques (Brandt 1996). When the wave impinges on an object of a markedly different density than water (e.g., fish’s swim bladder, lake bottom), its energy is scattered, but some portion of it returns towards the transducer. It has been shown that over 90-95% of the acoustic energy reflected from an individual fish target comes from the swimbladder (Brandt 1996).

Target echoes are translated back into electrical signals by the transducer. The receiver-amplifier records the time since transmission (surrogate for depth of the object) and the size of the signal (voltage). Incoming signals also are displayed on an oscilloscope and/or digitally on a computer screen. However, some extraneous factors must be considered. The energy reflected from an object depends on the angle location of the target in relation to the transducer. If directly under the transducer, a target reflects a higher level of energy than if it were off of the perpendicular axis. Techniques for determining the position of a target in the acoustic cone use multi-beam transmissions (dual-beam and split-beam) as well as statistical models (see Brandt 1996). In addition, the energy of the sound wave attenuates the farther it travels. As a result, fish at greater depths reflect less of the initial energy transmitted. Functional relationships between target strength (TS), position in the acoustic cone, and depth are thus used to insure proper readings of actual TS, and therefore fish size (Love 1977).

For mobile acoustic surveys, the transducer is mounted beneath the boat and sampling is done along a chosen surface transect. Survey techniques and transect design are described in Thorne (1983), Gunderson (1993), and Brandt (1996). Transmission, or "ping" rate, depends on water depth (from 1-10 pulses per second), with higher transmission rates occurring in shallow water (Gunderson 1993). A boat moves along the transect at a constant speed, while monitoring the objects detected beneath. The complex physics of sound wave propagation, reflection of energy by variously sized targets at different depths and orientations, and conversion of sound to electrical energy are known well enough for accurate assessment of the volume of water sampled, and absolute fish densities per unit area or volume of water, to be made (Gunderson 1993).

Acoustic data are processed by echo-counting (EC) or, more commonly, echo integration (EI) procedures run on microcomputers (Brandt 1996). The former directly enumerates individual fish targets, while the latter measures fish density by integration over the total returning voltage of all targets (Gunderson 1983). When implementing EC, individuals are counted if their echo voltage exceeds some predetermined level. Fish densities are thus calculated as the number of individuals counted per unit time or volume of water sampled. This technique works best with larger, dispersed fish species, as when Beauchamp et al. (1997) used EC to evaluate the density of sockeye/kokanee salmon (*Oncorhynchus nerka*) in the Sawtooth Valley Lakes of Idaho. Echo integration is used when fish densities are too great to be individually counted, or when individuals are distributionally clumped, as is the case with most small, schooling, pelagic species. Total reflected voltages from EI are converted to absolute areal or volumetric densities by scaling the voltages by the mean back-scattered cross section from individual targets.

For a given fish, TS is a realization of a complex combination of fish size, orientation, physiology, behavior, and acoustic frequency. Conversion of TS to actual fish size depends on body shape and size and orientation of the swim bladder. Brandt (1996) lists over twenty manuscripts devoted to refining this process. Often, regression equations relating TS to fish length are used (Love 1977; Foote 1987; MacLennan and Simmonds 1992). Brandt (1996) cautions that experimental techniques differ among investigators, and TS will vary with fish species, behavior, condition, and position in the beam. In situ measures of TS in the system to be surveyed now are recognized as far superior to measures taken on tethered or caged individuals.

Some investigators believe that TS, being a reflection of an areal measure (the dorsal aspect of the swimbladder), should be more closely related to fish weight than fish length. Fleischer et al. (1997) adopted this stance and were successful in predicting average target weight directly from average TS for bloater (*Coregonus hoyi*), alewife, and rainbow smelt (*Osmerus mordax*) in Lake Michigan. They found that species differences in backscattering properties must be incorporated for accurate estimates of fish biomass. Whatever the method used to determine biomass, estimates are normally given as the kilograms/hectare in the surveyed area. Whole-lake values can then be computed by averaging over all transects surveyed. Tremendous spatial and diel variability in pelagic fish communities can lead to great variability in density estimates between and within acoustic transects (Vondracek and Degan 1995). Bias is kept to a minimum by statistical transect selection designed to sample the range of variability in fish densities, accounting for diel and seasonal fish behavior, stratifying samples by productivity gradients within the system, and by sampling lake regions and limnological habitats in proportion to their true densities (Degan and Wilson 1995; Vondracek and Degan 1995).

In systems with significant species diversity, discerning the species of a target can be the most time consuming and crucial aspect of an acoustic survey (Brandt 1996). Conducting the survey when spatial separation of target species is maximized can greatly facilitate correct identification. Information such as depth and temperature preferences, schooling proclivity, biological sampling at various depths using a variety a capture gear, and statistical analyses of echo shape and size has been used to accomplish this feat (Brandt 1996).

OBJECTIVE

The objective of this chapter is the determination of surplus production, to be interpreted as the maximum sustainable supply of alewife and gizzard shad, under present rates of growth and mortality. Growth and mortality rates of each species were obtained from previous investigations (Tisa 1988) in addition to more recent field sampling done in cooperation with the VDGIF. Estimates of alewife biomass were obtained from hydroacoustic surveys conducted by VDGIF on SML. Gizzard shad biomass was estimated using data from cove rotenone surveys performed by VDGIF. With this information, I reproduced the numbers-at-age and weight-at-age for both clupeid species, leading to annual surplus production estimates for each clupeid species, utilizing equation 1.

METHODS

ESTIMATION OF CLUPEID BIOMASS

Hydroacoustic Procedure

Hydroacoustic surveys were conducted by Mike Duval, VDGIF regional biologist, on SML during late August of 1993 through 1998 using a scientific grade echo sounder with accurate 20 and 40 log R time varied gain (TVG), and a 200 kHz circular dual-beam (6°x15° in 1993 and 1994, 6°x12° thereafter) transducer mounted on a fin near the bow of the sampling vessel. He performed all analyses leading to estimates of number/ha and biomass/ha for each survey. Hydroacoustic systems were calibrated using US Navy standards at the BioSonics, Inc. laboratory in Seattle, Washington. Calibration was also performed at SML using a tungsten carbide reference sphere as a standard target. The transducer was towed 0.5 m deep, and vessel speed was maintained at approximately 8.5 km/h. The time-varied gain (TVG) startup range was 1 m, and post-processing software was set to collect data to within 1 m of the bottom, resulting in data collection from 1.5 m below the surface to 1 m above the bottom. Noise thresholds were implemented to distinguish targets over -60 dB, while ignoring smaller targets. Data were simultaneously recorded onto digital audio tapes using dual-beam signal processing software and a BioSonics model 281 Echo Signal Processor (ESP). This instrument measures the acoustic size (TS) and location (depth and time along transect) of each target and calculates the density of fish by depth strata and location.

Sampling was performed at a rate of 5-10 pings/sec, depending on water depth, using a 0.4-millisecond pulse width and a receiver sensitivity gain of 12 decibels. A zigzagging, shore-to-shore movement pattern along the main channel of the impoundment was utilized. Data were collected continuously as the boat moved upstream, and this large data file was later divided into 500-ping "transects" for calculation of sampling variation. On the Roanoke and Blackwater arms of the reservoir, data collection was initiated at the confluence of the two tributaries, at the edge of the midlake region [see Figure S.1 for the delineation of uplake, downlake, and midlake areas in SML] and proceeded away from the dam until the uppermost river sections (depicted in Figure S.1) were reached. The downlake region of SML, from the foot of the dam to the confluence of the two arms, also was sampled. In certain years, other major reservoir segments (e.g., Craddock Creek, Gills Creek) were surveyed. Data from 1996 were unusable due to software malfunction.

Mr. Duval edited some abnormalities out of acoustic data sets. Many trees were left standing as the river valley was filled following dam construction. These and other remnant structures (barns, tractors, etc.) are easily detected upon visual inspection of the acoustic trace, and a software feature allowing Mr. Duval to manually exclude their presence was utilized. In addition, acoustic data were corrected to eliminate counts of the small aquatic dipteran *Chaoborus*, which have highly reflective gas bladders and so can seriously compromise data garnered from acoustic surveys (Unger et al. 1987). For this reason, a minimum acoustic TS was implemented (-60 dB, or approximately 30 mm TL). As discussed below, this did preclude some clupeids from being sampled.

The areas sampled acoustically were generally pelagic and along the main channel of the reservoir, i.e., few shallow water littoral habitats were examined. Nocturnal observations made during acoustic surveys with a Q-beam spotlight indicated that the tributaries off of the main channel and cove habitats had higher abundances of gizzard shad, at least in the surface waters, than the main-channel areas being sampled. Hayne et al. (1967) found that during the day, gizzard shad abundance in offshore areas was equal to littoral densities of shad in Douglas Lake, Tennessee. However, it was unknown if nocturnal movements of shad would affect the accuracy of acoustic estimates. For this reason, acoustic biomass estimates were assumed to be accurate for alewife only. I did not presume that gizzard shad were not sampled acoustically, merely that their acoustically-derived biomass might not be indicative of their of lakewide abundance. The findings of Hayne et al. (1967) led me to conclude that cove rotenone biomass estimates of gizzard shad density in SML could be considered good estimates of their whole-lake abundance.

Acoustic sampling of pelagic regions was done well after sunset and completed well before dawn to prevent crepuscular changes in fish distribution from affecting the samples (Levy 1990; Luecke and Wurtsbaugh 1993). Night samples were chosen because during the day pelagic prey species like alewife often form dense schools that can cause underestimation of fish densities (Gunderson 1983; Degan and Wilson 1995; Vondracek and Degan 1995), as well as affecting the variability of density estimates (Kimura and Lemberg 1981; Hammond 1997). At night when schools disperse, fish are more uniformly distributed and accuracy of density estimates is consequently increased (Brandt 1996). In order to determine fish densities in the top meter and a half of the water column, several transects in 1997 and 1998 were run with the transducer oriented to send out acoustic signals horizontally, parallel to the water surface. In 1993 through 1995, when horizontal placement of the transducer was not utilized, no density estimates for the top 1.5 meters of water were made. For these years, estimates of fish density in the top 1.5 meters were derived from information from later surveys. For example, if the density of fish in the top 1.5 meters in later surveys averaged 30% of the density of fish in the water column below 1.5 meters, the density of fish in the top 1.5 meters in 1993, 1994, and 1995 would be set to 30% of the density of fish sampled below 1.5 meters in each respective year.

Acoustic data were processed by dual-beam (DB) and echo-integration (EI) analyses. The former is used to determine the acoustic size of individual targets, and the latter to measure fish densities. The total reflected voltages from EI were converted to absolute densities (#/ha) by scaling the measured voltages by the average back-scattered cross section (determined from DB analysis) of the sampled targets. This methodology has the potential to bias estimates of fish density and biomass. The severity of the error depends on how well the average-backscattering cross section describes the actual size of fishes in the surveyed area. Hammond (1997) recognized that fish with larger TS are detected with greater probability that fish with low TS, so the average TS measure could be too large. If this is the case, then fish densities and biomass would be underestimated. In years where TS distributions were available, actual size distributions of targets were compared to estimated clupeid size distributions, derived from simulated numbers-at-age (Results section, Table 1.3), to determine if serious bias occurred due to the use of erroneous average TS.

The average TS (measured in decibels) of individual targets was transformed into fish length using Love's "Any Aspect" equation (Love 1977):

$$\text{Total Length (cm)} = 10^{\,(TS + 69.23) / 20}$$

This equation accounts for various orientations of individual targets in the water column. A general length-weight relationship for SML clupeids, developed by Mr. Duval from gillnetted individuals, was used to convert mean total length (mm) to mean weight (g):

$$W = 0.000005 * L^{3.1069}$$

With average target weight and fish densities measured, areal estimates of biomass (kg/ha) were made. At this point, Duval transferred the data files to me for further processing.

Allocation of Acoustically-Determined Biomass Between Species

Experimental gillnets set concurrently with acoustic sampling supported the assumption that virtually all small (< 250 mm TL) pelagic targets were clupeids. Gizzard shad were found exclusively in the top seven meters of water, while alewife were found down to ten meters, the maximum depth of the nets. It was assumed that all ages of clupeids were sampled in proportion to their true abundance in these pelagic areas. Examination of TS distributions, as discussed later, supported this assumption.

Due to the presence of non-clupeid fishes, the possibility existed that attributing all of acoustic biomass to clupeids would be inappropriate. Based on maximum clupeid sizes (170 mm TL for alewife and 350 mm TL for gizzard shad) and vertical distributions of alewife and gizzard shad in the water column, I decided that targets in water seven meters or less and greater than 350 mm TL, and targets deeper than seven meters and over 170 mm TL, were non-clupeids. Judging by their size and position in the water column, these fish were probably pelagic predators such as striped bass, black bass, crappie, catostomids, or walleye. In 1993, 1994, 1997, and 1998 only 1.6%, 3.6%, 0.5%, and 2% of targets, respectively, fit the non-clupeid criteria. Because number and biomass estimates are a function of the average TS, the non-clupeid targets had little affect on biomass estimates. In 1993, when the average TS was computed first for clupeids, and then for all targets, it increased less than 0.3%. For this reason, acoustic biomass was assumed to consist exclusively of clupeids.

Once total clupeid biomass in each year was estimated, it was partitioned by species using distributional data reported by Tisa (1988), and based on information collected since 1995 (from gillnets set in pelagic areas as acoustic surveys were performed) on clupeid distributions in SML. Longitudinally, gizzard shad biomass was 99% of the total in uplake regions, but alewife began to compose a larger proportion of the fish in sampling gear as one progressed downlake. From a vertical perspective, gizzard shad were found exclusively in the top seven meters of water in all years. Alewife were found from the surface down to ten meters of water. Nets were not set below ten meters, but the assumption that alewife occupy these depths was made. One problem with using gillnet data for species allocation, however, is that the smallest mesh-size used (12.5 mm bar mesh) only captures fish over 85 mm TL. Growth data showed that virtually no age-0 alewife are this large in late August (Tisa 1988), so a correction for their absence had to be made.

For both Blackwater and Roanoke arm surveys, 99% of the biomass in the first uplake transect in the top seven meters of the water column was attributed to gizzard shad. As transects proceeded downlake, the proportion of biomass allocated to alewife in the top seven meters of the water column was increased in a linear manner. The biomass of alewife in downlake gillnets in all years averaged 35%, but these nets were set approximately 15 km above the dam. Not only was 35% thought to be an underestimate of alewife biomass in the sampled regions due to the inability to catch age-0 alewife in gillnets, but alewife abundance would be expected to increase as one approached the dam. For these reasons, I estimated alewife biomass in the top seven meters of water near the dam to be 70% of total biomass sampled there. In all years, any biomass deeper than seven meters was attributed to alewife, regardless of the longitudinal location of the transect. Using this progressing proportional scale, estimates of transect biomass were allocated to the two clupeid species. For 1993-1995, 25% of whole-lake biomass in the top 1.5 meters was allocated to alewife, and 75% to shad. These were the average percent of alewife and gizzard shad biomass for 1997 and 1998 horizontal surveys in the top 1.5 meters of water.

Rotenone Procedure

During August of most years between 1973 and 1997, the VDGIF performed rotenone analysis on SML in four coves per year, representing littoral areas of the upper, middle, and lower regions of the reservoir. Fish were collected from each cove for a period of three days after treatment. For a complete description of general rotenone methodology, see Bettoli and Maceina (1996). For prolific species such as gizzard shad, weighing and measuring thousands of recovered individuals was too time consuming, so sub-sampling was performed. The surface area of each cove was known, so numbers and biomass of fish per hectare, after correction for non-recovery rates, could be calculated (Table A.1). Recovery rates refer to the proportion of fish of each species that were tagged prior to rotenone application, released into the cove, then subsequently recovered. For example, if 80% of gizzard shad that were tagged and released into the cove prior to rotenone application were recovered, density estimates were divided by 0.8 to arrive at the final estimate. The magnitude of shad standing stock (kg/ha) in rotenone coves was assumed to give accurate whole-lake standing stock estimates due to the findings of Hayne et al. (1967), who showed that shad abundance in offshore habitats (during the day) was very similar to shad abundance in rotenone coves in Douglas Lake, Tennessee, a deep storage reservoir similar to SML.

ANNUAL PREY PRODUCTION

As discussed previously, surplus production (equation 1) of a prey population indicates the maximum sustainable supply of prey for predator consumption, and over the lifetime of a cohort equals total production (Ney 1990). Surplus production for clupeid cohorts was estimated using information on biomass, growth, and mortality from acoustic and rotenone surveys, prior research findings on Smith Mountain Lake (Tisa 1988), and more recent gill-netting data. For the first growth season of each clupeid cohort, data on population size and individual weight were simulated daily. After this point, however, population biomass and individual weights were only estimated for a single time period each year (late August).

Age-0 Dynamics

Following the research of Tisa (1988), each age-0 clupeid cohort was assumed to consist of twelve sub-cohorts, spawned one week apart. For alewife, the first sub-cohort hatched on 1 June, and the last on 22 August. For gizzard shad, the first sub-cohort began life on 1 May, and the last on 22 July. The magnitude of each sub-cohort was determined by referring to data collected by Tisa (1988) on the relative contribution of each week's spawn to the overall number of fish hatched in a given year (Figure 1.2). At hatching, both gizzard shad and alewife were assumed to have a length of 5 mm. Alewife grew 0.84 mm per day until 31 August, and 0.3 mm per day thereafter until growth for the season ceased (30 November). Gizzard shad grew 1.33 mm per day until 1 September, whereupon their growth rate changed to 0.2 mm per day until growth cessation on 30 November. To translate total length (TL, in millimeters) into weight (W, in grams), the following relationships were used (Tisa 1988):

Alewife < 20 mm TL: $W = 0.0000001893 * TL^{3.91}$

Alewife ≥ 20 and < 32 mm TL: $W = 0.00000002775 * TL^{4.64}$

Alewife ≥ 32 mm TL: $W = 0.00001177 * TL^{2.91}$

Shad < 20 mm TL: $W = 0.0000001696 * L^{3.98}$

Shad ≥ 20 and < 50 mm TL: $W = 0.0000003216 * L^{3.9}$

Shad ≥ 50 mm TL: $W = 0.0000085464 * L^{3.01}$

Age-0 clupeids were found to have the following daily mortality rates (Tisa 1988):

Alewife < 30 mm TL = 0.071
Alewife ≥ 30 and < 60 mm TL = 0.02
Alewife ≥ 60 mm TL = 0.01

Shad < 17 mm TL = 0.127
Shad ≥ 17 and < 30 mm TL = 0.083
Shad ≥ 30 and < 60 mm TL = 0.02
Shad ≥ 60 mm TL = 0.01

Initially, I partitioned an arbitrarily number of larvae amongst the twelve sub-cohorts of each clupeid species. Using growth and mortality rates, daily dynamics of each age-0 sub-cohort could be followed throughout the growth season. On any given day, average length and weight of the entire cohort could be calculated, as well as population biomass and surplus production occurring since the previous day. Here, surplus production for the age-0 cohort is equivalent to biomass dying in the previous 24 hours.

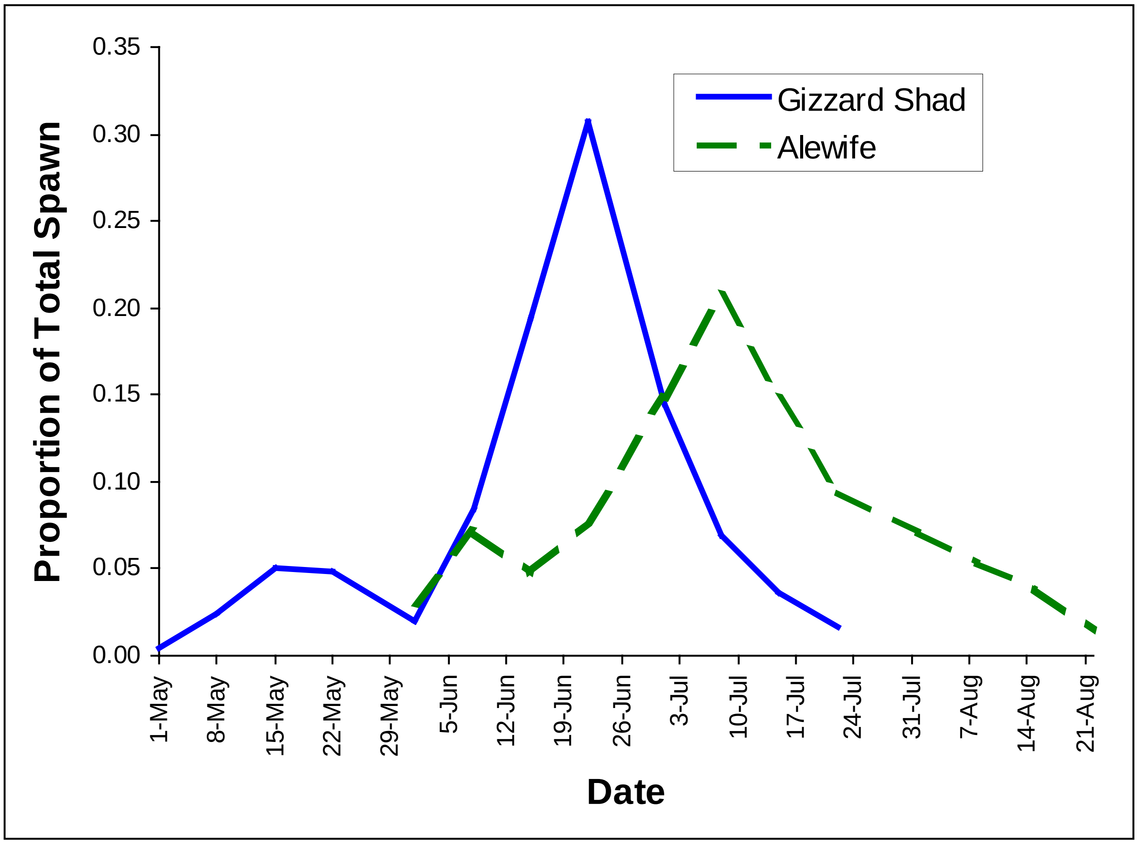

Figure 1.2. Percent of total spawn hatched on a weekly basis for clupeids in Smith Mountain Lake. From Tisa (1988).

After their initial growth season, numbers-at-age and average weight-at-age for the year-class were estimated in late August of each successive year. Previous data collected from sampling efforts of Tisa (1988) and VDGIF had shown that there were four age-classes of alewife present in the reservoir (ages 0-3), and eight age-classes of gizzard shad (ages 0-7). In addition, annual mortality rates of 80% for age-1+ alewife and 70% for age 1+ gizzard shad had been previously determined (Tisa 1988). In order to move from an arbitrary cohort size of 1 million individuals to a real average cohort size, actual population biomass at a certain point in time was needed. Acoustic survey data provided me this population biomass estimate for alewife, and rotenone data presented me with an estimate for the gizzard shad population. Once numbers-at-age and weight-at-age over the lifespan of the cohort were estimated, it was a simple matter to iteratively modify the initial cohort size until late August biomass of the simulated alewife or shad population equaled late August biomass seen in acoustic or rotenone surveys.

At this point, a minor adjustment needed to be made. Previously, it was discussed how acoustic targets less than about 30 mm TL were ignored. From growth data (Tisa 1988), I determined that some age-0 alewife (no age-0 gizzard shad) would be less than 30 mm TL in late August, and would be excluded from the acoustic data. I therefore had to match the acoustic biomass of age-0 alewife not to the entire simulated cohort of age-0 alewife, but only to the simulated biomass of only those age-0 alewife > 30 mm TL. Cohort simulations revealed that alewife < 30 mm TL made up 52% of the total number of age-0 alewife in late August, but only 2% of the total age-0 biomass at this time.

RESULTS

ACOUSTIC BIOMASS ESTIMATES

Annual estimates of kilograms per hectare, for targets at each depth interval, are given in Table 1.1. These are the mean values for all transects performed in the stated year. In each year, nearly all targets were located above 25 meters, and the bulk of these occurred in the top ten meters of water. There were differences in vertical target distributions between years. For example, the biomass in the top meter of water in 1998 was twice that of biomass below 2 meters of water. In 1997, the biomass in the surface meter was only 20% of the biomass below 2 meters. These disparate values had to be reconciled in order to estimate the biomass of clupeids in the top 1.5 meters of water, which was not surveyed in 1993, 1994, and 1995. When comparison of biomass in each one meter depth stratum below 2 meters was examined for 1993 and 1997, 1994 and 1997, and 1995 and 1997, the average correlation coefficient was 0.97. When these same comparisons were computed for 1993 and 1998, 1994 and 1998, and 1995 and 1998, the average correlation was 0.72. This was taken as an indication that the depth distributions of targets in the early surveys were more like 1997 than 1998. In 1997, the biomass in the top 1.5 meters equaled 29.5% of the biomass below 1.5 meters, so this value was used to project biomass in the top 1.5 meters in 1993, 1994, and 1995.

Total biomass in the five sampling periods was greatest in 1998, and lowest in 1994. Biomass across the five surveys had a mean of 114 ± 13.1 kg/ha, where 13.1 is the standard error of the mean (Table 1.2). Alewife biomass during the period averaged approximately 37 ± 4.5 kg/ha. Gizzard shad biomass was twice as great, averaging 77 ± 10.1 kg/ha. However, this survey technique was assumed to underestimate gizzard shad abundance due to sampling location bias. The average biomass of gizzard shad in cove rotenone samples during the period 1990-1997 was 112 ± 18.5 kg/ha (Table A.1), and this value was used to construct the "average" gizzard shad cohort.

Table 1.1. Estimates of clupeid biomass (kg/ha) in SML from hydroacoustic assessments, 1993-1998.

Depth (m)	1993	1994	1995	1997	1998
0-1	20.1	16.4	8.7	13.5	112.8
1-2	9.0	6.8	8.0	20.7	9.0
2-3	21.5	10.0	7.2	19.5	3.5
3-4	26.9	27.2	31.6	31.0	6.2
4-5	11.7	18.6	21.3	19.0	7.9
5-6	4.3	4.2	1.4	5.9	5.4
6-7	3.9	1.8	0.4	1.4	2.7
7-8	2.4	1.7	0.3	1.0	1.0
8-9	1.9	0.8	0.3	0.2	0.7
9-10	1.5	0.6	0.9	0.2	0.8
10-11	1.4	0.5	1.4	0.2	1.1
11-12	0.8	0.3	0.2	0.1	1.4
12-13	0.7	0.2	0.6	0.1	1.3
13-14	0.5	0.2	0.6	0.2	1.4
14-15	0.5	0.2	1.8	0.1	1.6
15-16	0.4	0.1	3.5	0.2	1.4
16-17	0.3	0.1	0.3	0.3	1.6
17-18	0.3	0.1	0.2	0.1	1.1
18-19	0.2	0.1	0.8	0.1	0.8
19-20	0.1	0.0	1.1	0.1	0.6
20-21	0.1	0.0	1.3	0.1	0.4
21-22	0.1	0.0	0.9	0.1	0.3
22-23	0.0	0.0	1.3	0.2	0.2
23-24	0.0	0.0	0.0	0.1	0.1
24-25	0.0	0.0	0.0	0.1	0.1
25-26	0.0	0.0	0.0	0.1	0.0
26-27	0.0	0.0	0.0	0.0	0.0
27-28	0.0	0.0	0.0	0.0	0.0
28-29	0.0	0.0	0.0	0.0	0.0
29-30	-	-	-	0.0	0.0
30-31	-	-	-	0.0	0.0
31-32	-	-	-	0.0	0.0
32-33	-	-	-	0.0	0.0
33-34	-	-	-	0.0	0.0
34-35	-	-	-	0.0	0.0
35-36	-	-	-	-	0
36-37	-	-	-	-	0
37-38	-	-	-	-	0
38-39	-	-	-	-	0
39-40	-	-	-	-	0
Totals	109	90	94	115	163

Table 1.2. Mean and variability of acoustical biomass estimates, with biomass separated by clupeid species. “Corrected” biomass estimates refer to the addition of biomass in the top 1.5 meters to the 1993, 1994, and 1995 surveys, which lacked such data.

			Year				**Standard**
	1993	**1994**	**1995**	**1997**	**1998**	**Mean**	**Error**
Average kg/ha	88	73	85	115	163	105	16.0
Corrected kg/ha	109	90	94	115	163	114	13.1
Alewife kg/ha	39	28	40	28	52	37	4.5
Shad kg/ha	70	62	54	87	111	77	10.1

POPULATION DYNAMICS OF ALEWIFE AND GIZZARD SHAD

The dynamics of alewife and shad populations in SML were simulated based on the growth and mortality rates of clupeids, as well as acoustic biomass estimates in late August (Table 1.3). The addition of alewife less than 30 mm TL (these were neglected by acoustic surveys) increased the biomass estimate very little. The initial alewife cohort size was 2 billion individuals, and age-0 fish in late August made up 40% of the total standing stock. The age-1 cohort had a late-August biomass that was slightly greater than the age-0 biomass at this time. Biomass decreased greatly after this point. The biomass of the age-3 cohort was about 1.3 kg/ha.

The initial cohort of gizzard shad numbered 715 million fish, about one-third the cohort size of alewife. Age-0 shad made up about 41% of the total August standing stock of shad, a value very similar to the age-0 alewife cohort. By the end of the growth season, age-0 shad numbers had dropped to under 18 million individuals, but age-0 alewife were now only about twice as numerous. By August of their third growth season, there were almost as many gizzard shad remaining as alewife. August biomass of shad peaked with the age-0 cohort, at over 45 kg/ha. Biomass of shad age-4 and older was only about 7 kg/ha.

Table 1.3. Number and biomass of successive cohorts of alewife and gizzard shad in SML, as estimated by information on growth and mortality rates. Initial number of larvae for each species was iteratively adjusted until the simulated August standing stock matched that determined by acoustic and rotenone sampling efforts.

Alewife

Age & Date	Number	Mean Weight (g)	Biomass (kg/ha)
larvae at hatching	2000000000	0.0001	0.02
0 - Aug 25th	240854481	0.53	15.0
0 - Dec 1	37338827	4.2	18.63
1 - Aug 25th	11166914	11.7	15.64
2 - Aug 25th	2233383	18.6	4.99
3 - Aug 25th	446677	25.3	1.36
		August kg/ha	**37.1**

Gizzard Shad

Age & Date	Number	Mean Weight (g)	Biomass (kg/ha)
larvae at hatching	715000000	0.0001	0.009
0 - Aug25	46916559	8.1	45.4
0 - Dec1	17642263	16.3	34.4
1 - Aug25	7151468	36.8	31.6
2 - Aug25	2145441	72.1	18.6
3 - Aug25	643632	124.8	9.6
4 - Aug25	193090	177.9	4.1
5 - Aug25	57927	244.3	1.7
6 - Aug25	17378	325.5	0.7
7 - Aug25	5213	388.5	0.2
		August kg/ha	**112.0**

For gizzard shad, numbers of YOY peaked at almost 180 million in late June (Figure 1.3). Biomass of the cohort was highest in the first week of September, at just over 440,000 kg, then decreased to 287,000 kg by the end of November. Average total length of age-0 fish at the end of the growth season (30 November) was 118 mm and average weight was just over 16 g. Considering that the total number of larvae hatched was 715 million, and population size on 30 November was about 17.6 million, mortality for the growth season was 97.5%.

Maximum numbers of age-0 alewife occurred in the third week of July, reaching almost 500 million individuals (Figure 1.4). Population biomass rose steadily from first hatch through August, then began to level out at just over 150,000 kg. The apex was not attained until late November, however, at 156,000 kg. On 30 November, the average total length of alewife was 78.3 mm and their average weight was 4.2 g. At this time, there were 37.3 million age-0 alewife remaining, translating to a mortality of 98.1% for the growth season.

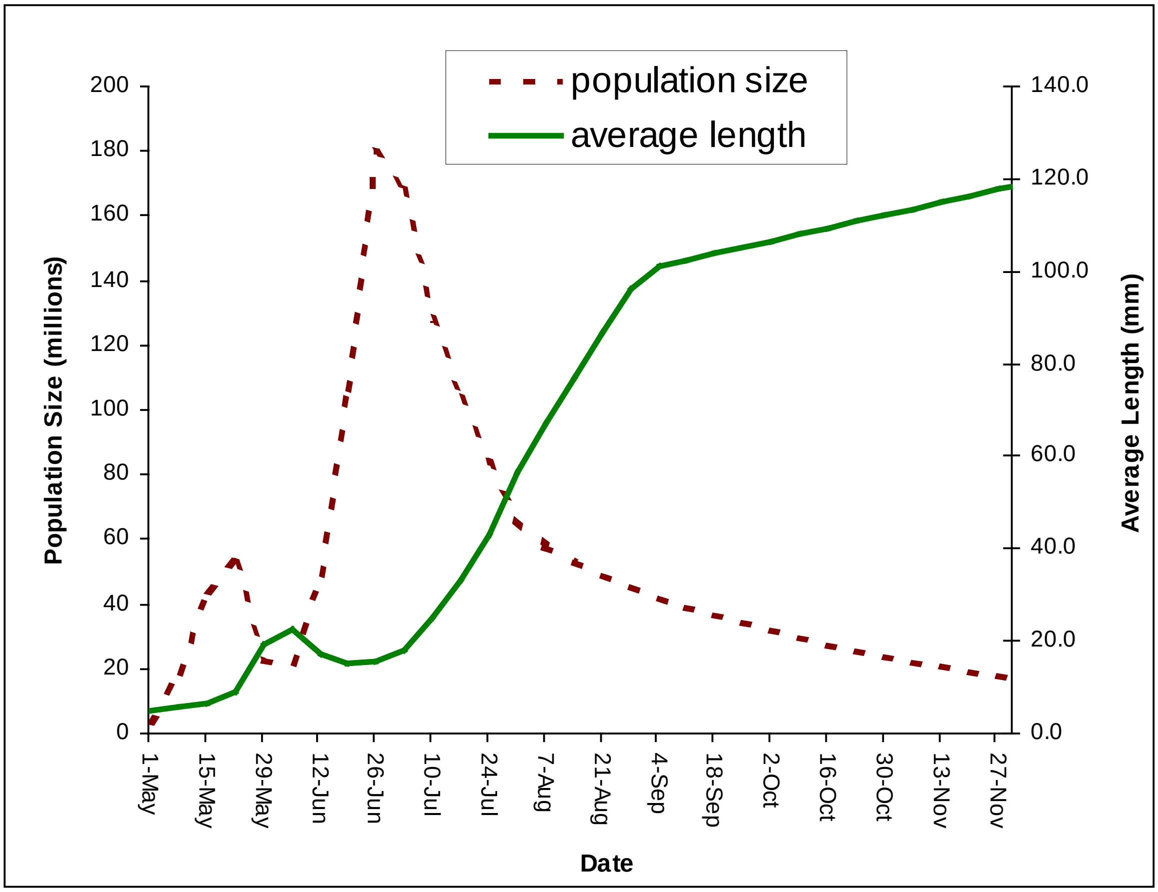

Figure 1.3. Numbers and mean length of the age-0 gizzard shad cohort during the growth season.

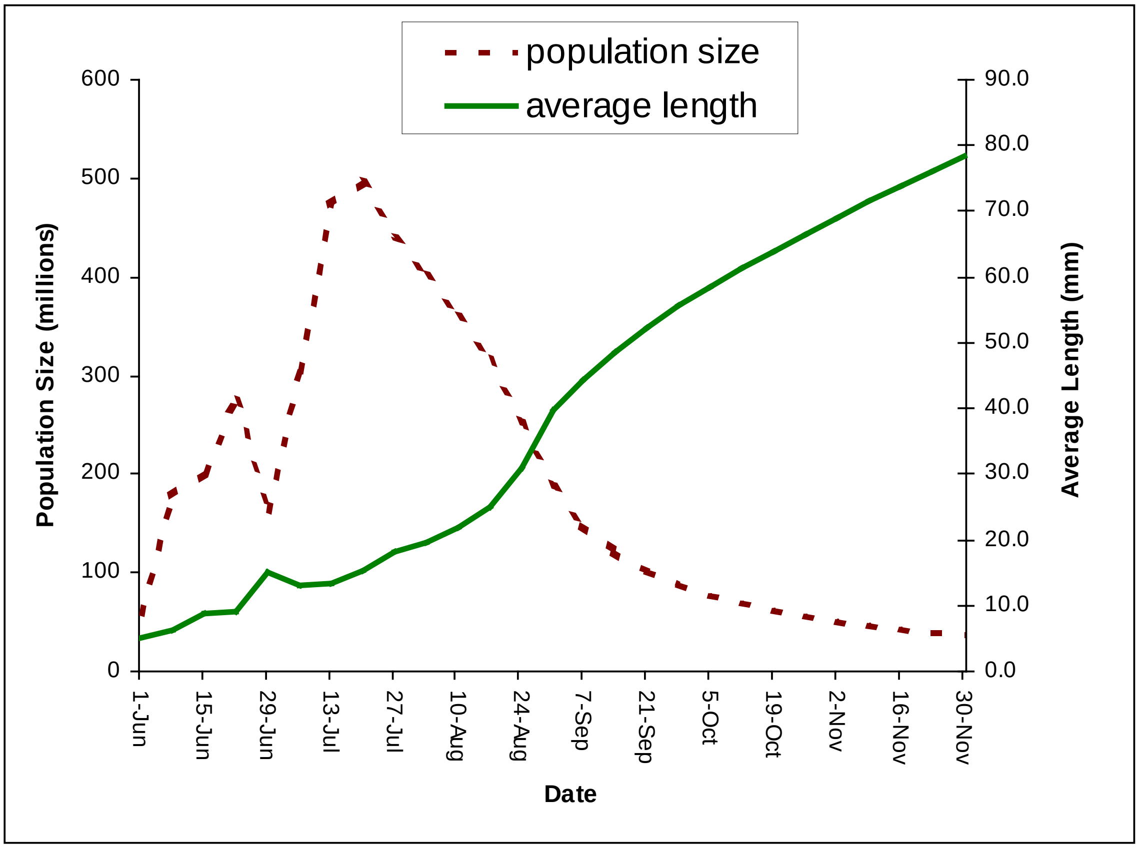

Figure 1.4. Numbers and mean length of the age-0 alewife cohort during the growth season.

PRODUCTION OF ALEWIFE AND GIZZARD SHAD

I estimated total production over the lifetime of an alewife cohort at 55-102 kg/ha, and 82-307 kg/ha for gizzard shad. These ranges were developed by examining the lowest and highest biomass estimates from acoustic surveys for alewife (28 and 52 kg/ha), and rotenone sampling for gizzard shad (62 and 231 kg/ha). For alewife, initial cohort sizes that resulted in these production values were 1.5 billion and 2.8 billion individuals. For gizzard shad, initial cohort size ranged from 400 million to 1.5 billion. Using mean initial cohort sizes (2 billion for alewife, 715 million for shad), mean total production over the lifetime of the cohort was 73 kg/ha for alewife and 147 kg/ha for gizzard shad (Figure 1). For the longer-lived shad, 39% of the production of a cohort occurs as surplus, i.e. dies, during the first growth season. For alewife, surplus production of the age-0 cohort was 42% of lifetime production. Age-0 shad surplus production during their first growth season is approximately 83% greater than age-0 alewife surplus production, and after this time surplus production of the shad cohort was more than twice the alewife cohort's surplus production. Only about 15% of the surplus production of a shad cohort occurs after their third growth season, and over 80% of total alewife surplus production occurs in their first two growth seasons.

The production to biomass ratio (P/B) for the alewife population was approximately 2.0, and for shad it was 1.3. Production here refers to true production, defined as instantaneous growth times mean biomass between two time periods, while biomass is the standing stock of the population in August.

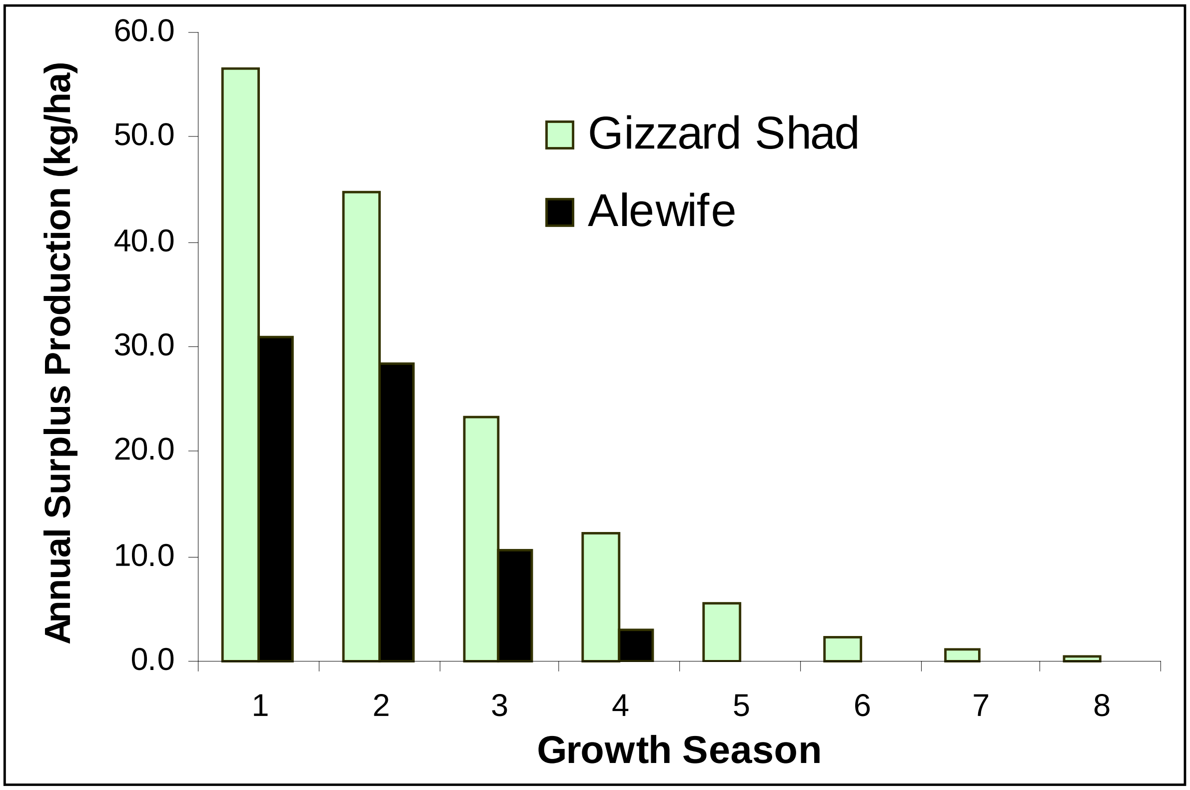

Figure 1.5. Mean annual surplus production of alewife and gizzard shad populations for the period 1993-1998, exclusive of 1996, for alewife and 1990-1998 for gizzard shad.

DISCUSSION

VALIDITY OF METHODOLOGY

Hydroacoustic Procedures

Hydroacoustic technology offers the research scientist the best hope of quantifying pelagic prey fish abundance, but the technique is far from flawless. Bias in target strength (TS) measures and species identification methodology can both result in misleading data and misrepresentation of the pelagic community. Hammond (1997) recognizes that unbiased TS measures are essential for echo integration to properly assess fish biomass and density. Average TS can be overestimated because fish with greater TS are more readily detected than fish with low TS. A technique called off-axis angle thresholding can be used to lessen this bias, but it has its own set of associated problems (Hammond 1997). When fish aggregations are clumped into densely-packed schools, a number of errors can occur (Brandt 1996). "Shading" is a term to describe the inability to detect fish deepest within the school due to the presence of so many others between them and the impinging sound wave. Conversely, echoes from unresolved targets can lead to an overestimation of fish density. Echoes from adjacent fish, if interpreted as one impulse, can lead to an overestimate of TS. The denser and deeper the school, the more accentuated these failings. Filtering algorithms do exist but these have been shown to be imperfect, often leading to the wrongful discarding of single target echoes especially if they are created by large individuals (Soule et al. 1995; Hammond 1997). Finally, acoustic echoes tell the researcher nothing about the species of fish under the transducer. For this, ancillary gear must be set to determine species composition. The selectivity biases and limitations of sampling gear such as trawls or gill-nets are thus invoked. Studies by Fleischer et al. (1997) and McClatchie et al. (1996) have shown the importance of accounting for species differences in determining fish size from TS measures. Variations in morphology, physiology, and behavior of various species can profoundly affect TS fish-size relationships. These studies recommend utilizing species-specific TS fish-size relationships in systems with a heterogeneous species array, provided some method to classify echoes into likely originator species can be developed. Most often this has been done based on differences in depth distributions of various fish species within the water column (Fleischer et al. 1997).

Fortunately, there were aspects of the survey design and the SML system that limited these potential errors. First, surveys were performed at night when pelagic schools of prey tend to disband and adopt a more uniform distribution in upper surface layers of the water column, allowing for better detection of individual targets (Brandt et al. 1991; Brandt 1996; Beauchamp et al. 1997). Secondly, gillnets indicated that nearly all pelagic targets were either gizzard shad or alewife. These two clupeids do have minor morphological differences, but are not nearly as disparate as would warrant concern based on the findings of Fleischer et al. (1997). A single relationship between TS and fish size therefore would cause no major bias in biomass estimates. Finally, if small targets were less likely to be detected than larger ones (Hammond 1997) then biomass of clupeids in SML could be overestimated.

Target strength distributions generally supported the conclusion that clupeids were sampled in proportion to their true size distributions. Clupeid population dynamic simulations indicate that age-0 alewife should be the most abundant pelagic entity in the system, and the age-0 alewife large enough to be sampled acoustically should average approximately 50 mm TL. In addition, the next most abundant pelagic inhabitant should be age-0 gizzard shad with the vast majority between 60-110 mm TL. Targets between 40-100 mm TL should therefore be most plentiful. That is exactly what is seen upon examination of the TS size distributions for 1993, 1994, and 1997 (no TS distribution was available for 1995). In 1998, while 50% of targets were below 100 mm TL, 30% were between 120 and 200 mm TL, a much greater percentage than in other years. This was probably caused not only by a much larger number of age-2 shad than in other years, but also by a paucity of age-0 gizzard shad in SML. This cohort was basically absent from gillnets set at the time acoustic sampling was performed.

Acoustic Sampling Areas

Zigzagging shore-to-shore transects were performed along the main channel from the dam to uplake regions on both the Roanoke and Blackwater river arms. If clupeid biomass was very different in coves and minor tributary arms, estimates could be biased. For this study, I assumed acoustic surveys produced whole-lake estimates of alewife biomass only, although it was determined that reasonable estimates of shad biomass were produced as well. The average gizzard shad standing stock in cove rotenone samples, which is assumed to estimate whole-lake biomass well (Hayne et al. 1967), in the four years that acoustic data also were gathered, was 76.1 kg/ha, as compared to the 69 kg/ha acoustic average for these four years. It appears, therefore, that acoustic estimates only slightly underestimated whole-lake gizzard shad biomass. Examining rotenone data that shows very little alewife biomass in coves; one might conclude that acoustic estimates of their abundance are an overestimate of whole-lake alewife biomass. The problem, however, with comparing rotenone data with acoustic estimates is that confounding occurs. The spatial and temporal factors that influence clupeid distribution cannot be separated. Rotenone samples are representative of inshore areas during the day, while acoustic surveys sampled offshore areas at night. It is therefor improper to compare inshore to offshore densities of alewife using rotenone and acoustic estimates because one represents densities during the day and one represents nocturnal densities. In fact, Kelso and Ney (1983) found large numbers of alewife feeding in coves at night from early July through August in Claytor Lake, Virginia. Because block nets are set across rotenone coves in the early morning, however, any differences in onshore/offshore distributions due to nocturnal movements cannot be identified. To draw conclusions regarding spatial differences in abundance, the proper intensive approach as used by Hayne et al. (1967) and Summers and Axon (1980) is to sample onshore and offshore areas simultaneously.

Biomass Partitioning

It is difficult to determine the accuracy of the methodology used to partition acoustically-derived biomass between gizzard shad and alewife. Gillnet data were available for 1993-1995, and 1997-1998, but age-0 alewife are not sampled by the gear and age-0 shad were nearly absent in 1994, 1995, and 1998 gillnets. In all of these years, however, gizzard shad dominated uplake nets while alewife biomass increased in the downlake nets. Rotenone data also indicated that the further downlake the cove, the higher the ratio of alewife to gizzard shad biomass. In years that both age-0 alewife and age-0 shad are present in average numbers, I would not expect this spatial pattern to change. I would not expect to see drastic changes in the water column distribution of gizzard shad either (most plentiful in the top four meters of water, intermediate densities between four and seven meters, and non-existent below seven meters). The metric subject to most scrutiny is the percentage of alewife biomass in downlake regions. In each year, alewife biomass was between 25-35% of total clupeid biomass in gillnets set in the top seven meters of water 15-20 km uplake of the dam. This is an underestimate of alewife presence due to the inability of the gear to sample age-0 individuals. In addition, fewer of the mesh sizes used are appropriate to catch alewife, so their probability of being caught is lower. These factors suggest that the percentage of alewife biomass in downlake areas must be increased from what is seen in gillnets. The accuracy of my estimate of 70% alewife biomass in the furthest downlake areas unfortunately could not be directly validated.

ASSESSMENT OF RESULTS

Clupeid Biomass

It is ecologically appealing that gizzard shad biomass was estimated to be greater (by almost three times) than alewife biomass. Gizzard shad both live longer and grow larger than alewife in SML. Simulated total number of alewife per hectare, however, were about 2.5 times as high as gizzard shad densities in August. This is a result of the large numbers of juvenile alewife present at this time of year. Of the 16,700 alewife per hectare (> 30 mm TL) estimated to be in SML in August, only about 1,650 per hectare are age-1 and older fish. For gizzard shad, total numbers in August are approximately 7,000 per hectare, with about 1,200 of these being age-1 and older. So, despite the numerical dominance of young alewife, gizzard shad biomass supercedes that of alewife. Isely and Tomasso (1998) utilized mark-recapture methodology to estimate the population density of adult blueback herring (*Alosa aestivalis*) at 3,200 per hectare. This is 12% greater than the 2,850 adult clupeids per hectare I estimated for SML, but total biomass of adult clupeids would be similar in the two systems because adult blueback herring attain a maximum size in freshwater impoundments between that of alewife and gizzard shad in SML (Prince and Barwick 1981).

Average annual clupeid biomass in SML (about 150 kg/ha) is far from either extreme of the less than 1 to over 475 kg/ha range of average clupeid densities in 116 U.S. reservoirs (Jenkins 1967, cited in Michaletz 1998a). Smith Mountain Lake, however, has an annual average total phosphorus concentration of only 20 ppb, as does Thurmond Reservoir (U.S. Army Corps of Engineers, Waterways Experiment Station, Trotters Shoals Limnological Research Facility). This value, while defining a system on the edge of the mesotrophic/eutrophic delineation, would put SML nearer the lower extreme of the 5-100 ppb range of phosphorus concentrations for U.S. reservoirs reported by Ney (1996). Miranda et al. (1998) reported that an acoustic assessment in October of 1997 in Norris Lake, Tennessee, produced clupeid biomass estimates of 236 kg/ha. This was surprising because Norris Lake phosphorus levels averaged only 8 ppb. A survey later in the growth season would, however, tend to give higher biomass than one conducted earlier in the growth season. Rotenone surveys indicated that clupeid biomass averaged 160 kg/ha in Norris Lake during 1960-1997, while in SML from 1979-1997 it averaged 150 kg/ha. These values are also not very congruent with the productivity differences in the two systems. From these data, it appears that either clupeid biomass was incredibly high in 1997 in Norris Lake, or very low in the 1990's in SML. Because clupeid densities in Norris were derived from a single, first-time hydroacoustic assessment of the system, results could be less certain as well.

Based on an empirical relationship between total phosphorus and rotenone fish standing stocks in reservoirs (Yurk and Ney 1989), the mean total fish biomass in cove habitats in SML should be 377 kg/ha, with a 95% confidence interval of 316-449 kg/ha. Total fish biomass collected in rotenone coves averaged 290 kg/ha during 1990-1997 (Table A.1). This is below the lower bound of the confidence interval, and the lesser value in SML might be an indication of its predator-prey assemblage. For a given amount of primary productivity, systems with a higher percentage of top-level predators would be expected to have a lower total fish biomass due to the inefficiency of energy transfer between trophic levels (Diana 1995). From 1993-1997 rotenone data, I calculated that the mean piscivore-to-total fish biomass ratio (P/TFB) was 0.19 and the clupeid-to-total fish biomass ratio (CL/TFB) was 0.27. Using a massive data set on rotenone surveys performed in almost 200 reservoirs across the Unites States (obtained from a database compiled by the National Reservoir Fisheries Group of the United States Fish and Wildlife Service), I determined that the mean annual CL/TFB was 0.39 with a standard error of the mean (SEM) of 0.013 in reservoirs containing clupeids (about 2,100 reservoir-years examined). The mean P/TFB ratio in these reservoirs was 0.16, with an SEM of 0.008. Smith Mountain Lake therefore has a higher percentage of predators and a lower percentage of clupeid prey than the average US reservoir, and thus should exhibit lower total fish biomass estimates than predicted. Ratios of sport fish to total fish biomass typically decline with increasing nutrient input in reservoir systems (Jenkins 1982). Because SML is on the low end of the nutrient gradient seen in US reservoirs, this could partially explain the higher P/TFB. The SML total fish biomass could also be lower than predicted if SML had a higher biomass of pelagic and semi-pelagic species (alewife, striped bass, walleye, smallmouth bass) than the reservoirs studied by Yurk and Ney (1989). This would tie up more of the system’s productivity in offshore species that were much less susceptible to rotenone evaluation.

P/B ratios

Stewart and Binkowski (1986) assumed that Lake Michigan alewife would have a P/B ratio of approximately 1, but this species lives longer (up to seven years) in the Great Lakes. Waters et al. (1990) found that an inverse relationship existed between P/B ratios and the number of age-classes for three species of trout in a Minnesota stream. Rainbow trout (*Oncorhynchus mykiss*) had three age-classes and a ratio of 2.2, brook trout (*Salvelinus fontinalis*) had four age-groups and a ratio of 1.7, and brown trout (*Salmo trutta*) had six age-classes and a ratio of 0.9. The P/B ratio of smallmouth bass in a Minnesota stream was determined by Waters et al. (1993) to be 1.6 in 1985-86 and 0.9 in 1987-88. During the earlier period there were four age-classes of bass, while seven age-groups were seen in the latter period. Alewife have four age-classes and shad have seven to eight age-groups in SML. It is not surprising for SML clupeid P/B estimates to be slightly higher, because alewife and shad are forage species rather than top piscivores, and fish in the former category could be expected to have greater mortality rates leading to faster biomass turnover, and thus higher P/B ratios. Shad have a lower P/B ratio relative to alewife because there is a good deal of shad biomass (and thus former production) tied up in slower-growing, old individuals. Alewife, on the other hand, grow fast and die young, so alewife biomass is recycled more quickly than gizzard shad biomass. On a cohort-by-cohort basis, P/B ratios are greatest for age-0 fish, and decline for each age-class that follows. This pattern was suggested by Mann and Penczak (1986) in their review of production in riverine fish populations. In this investigation, for example, the age-7 gizzard shad cohort had the smallest P/B ratio, a paltry 0.46. Waters et al. (1993) concluded that P/B ratios should decrease as the longevity of a population increases.

Annual Variability

Production calculations were performed assuming an average cohort size for both alewife and gizzard shad, as well as with the high and low biomass seen in acoustic and rotenone surveys. Data from SML show that both shad and alewife abundance can vary considerably from year to year. Annual clupeid abundance and year-class strength have been found to be notoriously variable in some systems and fairly consistent in others (Brown 1972; Kohler and Ney 1981; Crecco et al. 1983; O'Gorman and Schneider 1986; Willis 1987; Rainwater and Houser 1982; Michaletz 1998a; Sammons et al. 1998). I used the reservoir data set referenced earlier to determine the average coefficient of variation (CV=SD/Mean) of gizzard shad standing stock within a system to be 0.75. For alewife the value was 0.93. Only reservoirs that had at least five total years of data, and for which the species of interest was detected in at least three of those years, were used. For gizzard shad, this resulted in 140 reservoirs being examined, but for alewife only three reservoirs fit these criteria. In SML since 1979, when current nutrient levels were established, CV's for gizzard shad and alewife standing stock were lower than this national average, at 0.46 and 0.79, respectively. These are still high numbers, and along with demonstrating the variability common to rotenone surveys (Bettoli and Maceina 1996), these wide fluctuations no doubt result from actual changes in clupeid recruitment from year to year in SML. These variations in clupeid abundance mean that predators must utilize other sources of prey when clupeid populations are greatly reduced, or suffer consequences in terms of growth and survival (see Chapters Three and Four).

DYNAMICS OF CLUPEID SUPPLY

Intensive predation on clupeids in SML might be keeping them well below their carrying capacity. If predation mortality were reduced, cohort sizes of alewife and gizzard shad might increase accordingly, and growth would likely slow as a result of increased intra-specific competition for food. Given the borderline eutrophic productivity levels in SML, growth of the current cohorts of alewife and gizzard shad is not likely to be food-limited, considering the intense predation mortality that each cohort undergoes throughout its first growth season. It is therefore plausible to hypothesize that current clupeid growth rates in SML are near their maximum for the system, and not likely to increase without changes in environmental variables like temperature and nutrient loadings. If food availability, and not predation, was driving clupeid growth and survival, and primary production were to increase, the effects on clupeid growth rates would depend on the life-stage. Dicenzo et al. (1996) found that growth rates and condition factors of age-1 and older gizzard shad were lower in more eutrophic Alabama impoundments. They hypothesized that increased food resources allowed a greater number of juvenile shad to survive to adulthood. This led to increased intra-specific competition for food among adults, resulting in decreased growth and condition of these fishes. Michaletz (1998a) found similar results in Missouri reservoirs. He determined that first-year shad growth was greater in eutrophic reservoirs, while growth after age-1 was reduced in less productive systems. The shad in eutrophic systems reached sizes great enough to allow them to survive their critical first winter. Large numbers of age-1 shad then began to grow more slowly than their counterparts in oligotrophic systems due to increased intra-specific competition for food. In oligotrophic systems, many young shad died over their first winter because food resources would not permit them to accumulate enough energy reserves. Those age-0 shad that did survive were released from the confines of competition in their second growth season and beyond.

A disturbing trend of declining clupeid abundance in SML from the late 1970's to the late 1990's is evident. During 1979-1991, rotenone data indicated that average clupeid biomass was 180 kg/ha, but between 1992 and 1997 it was only 90 kg/ha (Table A.1). Because gizzard shad make up over 95% of clupeid biomass in rotenone coves, this reduction primarily reflects their decline. This abatement occurred long after a 65% decline in phosphorus levels between 1975 and 1980, subsequent to an advanced waste treatment plant that was built on the Roanoke River just below the city of Roanoke in 1975 (Ney et al. 1988). It is true that average rotenone abundance of shad was 500 kg/ha during 1973-1977. Ney et al. (1988) primarily attributed the decline of clupeid, and indeed total fish, standing stock in the 1980's to decreased phosphorus levels. Since 1979, however, nutrients levels in the system have remained stable. The most likely explanation of this recent biomass decrease is biological, from increased predation on age-0 clupeids by an expanding predator population. The latter scenario will be explored by examining predator demand (Chapter Two) and its relation to gizzard shad supply (Chapter Three).

CHAPTER TWO

DETERMINATION OF PREY CONSUMPTION BY THE PREDATOR ASSEMBLAGE OF SMITH MOUNTAIN LAKE

INTRODUCTION

The striped bass has been widely introduced into freshwater systems across the United States. Designated to fill the pelagic void created by a river's impoundment, striped bass have indeed provided many quality sport fishing opportunities that would have otherwise been absent (Bettoli et al. 1995). However, ignorance concerning the amount of pressure these piscivores place on the forage base has limited the success of many managed populations (Axon and Whitehurst 1985). These long-lived fish feed primarily on clupeids, and have been shown to overcrop prey in various systems (Bailey 1975; Morris and Follis 1978; Keith 1986; Summerfelt 1986). Concern has increased concomitant with awareness that an adequate forage base plays a crucial role in the successful maintenance of valued sport fisheries (Ney 1990), and that a lack of available prey to predators is primarily responsible for unrealized sport-fish production in southeastern reservoirs (Ploskey and Jenkins 1982).

The striped bass is one of the primary piscivores in Smith Mountain Lake, and feeds nearly exclusively on two resident clupeids, alewife and gizzard shad. The Virginia Department of Game and Inland Fisheries stocks striped bass on a put-grow-take basis because these fish do not naturally reproduce in the system. Annual stocking numbers have varied greatly since the mid-1960's, but in the last decade they have been approximately 300,000 fingerlings per year. It would seem essential in systems as SML, where striped bass play a vital role in the economics and ecology of the fishery, significant hatchery resources of the Virginia Department of Game have been allocated, and there is a genuine uncertainty as to the long-term ability of the forage fish population to meet predator demand, to accurately estimate the amount of prey being consumed by the assemblage of piscivorous fishes. Serious overexploitation of prey resources, especially clupeids, leading to reduced growth and survival of a number of predatory species, would be ecologically and economically dangerous to the SML fishery. The lake also holds large populations of largemouth bass, catfish, and crappie, with lesser numbers of other predators (smallmouth bass, walleye, muskellunge), that depend partly on clupeid prey to meet energetic requirements. All of these species provide angling opportunities, and each species' consumption should be included to accurately assess total clupeid consumption.

My objective in this chapter was to quantify annual prey consumption by the suite of piscivorous fishes in SML. Differences between the terms "demand" and "consumption" should be noted. Demand, as defined by Ney (1990) and Hartman and Brandt (1995b), refers to the amount of prey that would be consumed by a predator population if each individual were feeding at maximum capacity, exhibiting a genetic growth potential unconstrained by food limitation. Wild fishes seldom, if ever, are presented with enough available prey to have their energetic demands completely fulfilled. Consumption, then, is the portion of demand that is realized. Each individual will consume a lesser amount of prey than satiation would require, leading to lesser growth rates than the maximum possible. Population consumption is then the summed consumption by each individual.

I used bioenergetics models to derive annual consumption by individual striped bass and largemouth bass of each age group, then multiplied those estimates by the number extant in each age group to attain annual consumption by each cohort. Bioenergetics is the balancing of energy inputs and outputs, and has been applied in numerous systems for over two dozen species of fish and other aquatic taxa, addressing both autecological and synecological questions (Moore et al. 1993). This concept has been implemented at time scales ranging from evolutionary to metabolic cellular processes, and on spatial scales from controlled aquaculture systems to ecosystem contexts (Hanson et al. 1997). The proliferation of applications in fisheries can be traced to the development and subsequent microcomputer packaging of the Wisconsin bioenergetics model (Kitchell et al. 1977; Hewett and Johnson

1987). The basic innovation was to estimate actual consumption as a percentage of maximum ration for a fish of a given species and weight at a given temperature. This model is discussed in detail below. The array of scientists who have found novel ways to utilize updated versions of Wisconsin's modeling software is a testament to its versatility, flexibility, quantitative output, intuitive nature, cost-effectiveness, and previous successes (Stewart et al. 1983; Brandt and Hartman 1993; Hansen et al. 1993; Ney 1993; Hanson et al. 1997).

My traditional implementation, as in most fisheries applications, adopted a mass-balance approach in which energy consumed by the organism must equal the sum of energy metabolized, stored, and eliminated. Inputting values for these parameters resulted in an estimate of individual consumption, which was then coupled with estimates of predator densities, thereby defining prey consumption by the total predator population. Using this same procedure, Stewart et al. (1981) quantified the impact of stocked salmonids on the forage base of Lake Michigan, Carline et al. (1984) examined potential demand of largemouth bass populations for gizzard shad in Ohio reservoirs, Hartman and Margraf (1992) studied impacts of walleye on the prey assemblage of Lake Erie, Hartman and Brandt (1995b) estimated consumption by striped bass, bluefisf, and weakfish in Cheasapeake Bay, and Rudstam et al. (1995) assessed prey consumption by the burbot (*Lota lota*) in Green Bay.

In addition to using a bioenergetics approach for determining individual consumption, I examined population dynamics of largemouth bass and striped bass. This task was performed to permit determination of population consumption by these predators. Population dynamics of a species will here refer to estimates of growth and survival rates, as well as numbers at age. The tremendous effort traditionally expended to accurately determine the dynamics of reservoir predator populations is directly correlated to the necessity of having good data in order to effectively manage fisheries in these complex systems (Moore 1988).

Population dynamics of black basses in reservoirs have been extensively investigated, usually requiring intensive sampling of the population using techniques such as rotenone, mark-recapture, electrofishing, or angler surveys (Hanson 1962; Cole 1966; Bryant and Houser 1971; Aggus and Rainwater 1975; Hickman and Hevel 1975; Ager 1978; Yeager and Van Den Avyle 1978; Harris et al. 1979; Dewey and Moen 1981; Farman et al. 1982; Dent 1986). Investigations of striped bass population dynamics in reservoirs, however, have not been as extensive (Axon and Whitehurst 1985; Bulak et al. 1995). When these studies have been performed, the majority deal with growth, food habits, or distribution of stocked fish (Sutton 1997). Carlander (1997) is a comprehensive source of information on the striped bass, presenting a review of published data on growth, condition, and reproduction. Bulak et al. (1995), in an investigation concerning consequences of management actions, performed yield-per-recruit and Leslie matrix analyses in Santee-Cooper Reservoir, South Carolina, requiring estimation of adult mortality rates and reproductive output. Factors affecting juvenile recruitment in Santee-Cooper also were examined (Bulak et al. 1997). Moore (1988) and Moore et al. (1991) examined striped bass population dynamics in SML, while Sutton (1997) investigated growth and mortality of age-0 striped bass in this system. Recently, however, a supply-demand study was completed on Norris Lake, Tennessee (Miranda et al. 1998). The objectives of that study were to determine how much extra prey would be available to other predators if striped bass stocking was discontinued. This required an estimate of striped bass annual consumption, as well as annual clupeid prey supply.

The pelagic nature of striped bass, and lack of both fiscal and technological resources, have been blamed for the relative dearth of freshwater striped bass investigations (Moore 1991). Fortunately, because striped bass do not naturally reproduce in most reservoirs, researchers modeling these systems have the luxury of knowing the exact numbers of striped bass stocked annually. Knowing the numbers stocked, and having data on age-specific survival rates, will allow the investigator to recreate the numbers-at-age for each cohort of striped bass present in the system. Precise knowledge of population size obviously is crucial if population consumption is to be extrapolated from individual consumption estimates derived from bioenergetics modeling (Ney 1990).

METHODS

BIOENERGETICS

Mass-balance bioenergetics models have grown in popularity in the past decade. Despite the existence of many different model variations, all rely on a number of input parameters to describe the physiology and metabolism of the organism, namely consumptive processes, respiration, and egestion/excretion. Much laboratory research has gone into developing species-specific parameter estimates to insure that these processes are appropriately depicted. When novel species are modeled for which parameters have not been previously defined, "species borrowing" occurs, where values for species similar in morphology or ecology are substituted (Ney 1990). In addition to species-specific inputs, site-specific inputs are also implemented to incur greater accuracy. These inputs are most often water temperature, diet composition, growth rates, and energy content (cal/g) of predator and prey. Capturing seasonal variations in these metrics is generally considered to improve the estimation of consumption. Before delving into the specifics of my model's inputs, I first present the mathematics behind the specific model I chose to utilize.

The mathematical underpinnings of bioenergetics models begin simply with the basic balanced energy equation of Winberg (1956):

Consumption = **G**rowth + **R**espiration + **S**pecific**D**ynamic**A**ction + **E**gestion + **E**xcretion

For fishes, growth includes both somatic and gonadal gains, respiration is standard plus active metabolic costs, specific dynamic action refers to the energy released in deamination of proteins and other digestive processes, egestion is energy lost to solid waste products, and excretion is the energy in excreted products such as urea and ions passed over the gill lamellae. Egestion is often represented by the letter **F** (feces), and excretion by the letter **U** (urea). Components on the right side of the equation are modeled as functions of various physiological parameters of the organism.

Researchers at the University of Wisconsin expanded on this basic equation (Kitchell et al. 1977), and estimated consumption (C) as a proportion of the maximum daily ration for a given species at a given weight and temperature. I chose to use their approach for a number of reasons, primarily due to the availability of a microcomputer program to run the model, and the availability of species-specific model parameters for striped bass and largemouth bass. The basic consumption equation that drives their system is:

$$C = C_{max} * P * f(T)$$

[Nomenclature for symbols from Hanson et al. (1997)]

C_{max} is maximum daily consumption at the species' optimal temperature, and is an allometric power function ($C_A * W^{C_B}$) of the weight of the fish, where C_A is the intercept of the mass dependence function for a 1 gram fish at 0° C and C_B is the mass dependence coefficient. P (referred to as the P value) is a proportion of maximum ration whose value can be manipulated so predicted growth curves closely match observed growth curves of the species in question, limiting potential for estimation error (Bartell et al. 1986). The term f(T) is a temperature-dependent proportional scalar of consumption rate and requires knowledge of optimum and maximum feeding temperatures of the species. For largemouth bass, f(T) took the following form, used previously for modeling warmwater species (Kitchell et al. 1977):

$$f(T) = V^X * e^{(X*(1-V))}$$

where

$$V = (C_{TM} - T) / (C_{TM} - C_{TO})$$

$$X = (Z^2 * (1 + (1 + 40 / Y)^{1/2})^2) / 400$$

$$Z = \ln(C_Q) * (C_{TM} - C_{TO})$$

$$Y = \ln(C_Q) * (C_{TM} - C_{TO} + 2)$$

The maximum water temperature that consumption will occur at is C_{TM}, C_{TO} is the optimal temperature for consumption, T is ambient temperature, and C_Q is the slope of the relationship between consumption and temperature at relatively low temperatures.

For striped bass, f(T) was of a more complex form, used to model cool-water species (Stewart and Ibarra 1991):

$$\mathbf{f(T) = K_A * K_B}$$

where

$$K_A = (CK_1 * L_1) / (1 + CK_1 * (L_1 - 1))$$

$$L_1 = e^{(G_1 * (T - C_Q))}$$

$$G_1 = (1 / (C_{TO} - C_Q)) * \ln((0.98 * (1 - CK_1)) / (CK_1 * 0.02))$$

$$K_B = (CK_4 * L_2) / (1 + CK_4 * (L_2 - 1))$$

$$L_2 = e^{(G_2 * (C_{TL} - T))}$$

$$G_2 = (1 / (C_{TL} - C_{TM})) * \ln((0.98 * (1 - CK_4)) / (CK_4 * 0.02))$$

These relationships define the product of two sigmoid curves, one fitting the increasing portion of the temperature dependence function (K_A) and the other modeling the decreasing component (K_B). The water temperature at which the temperature dependence is a small fraction (CK_1) of the maximum rate is C_Q, and C_{TO} is the water temperature at which consumption is 0.98 of maximum. The upper temperature at which dependence is some reduced fraction (CK_4) of the maximum rate is C_{TM} (Hanson et al. 1997).

Respiration (R) depends on fish weight, water temperature, and activity. Total metabolic costs are calculated by summing costs of respiration (standard plus active) and costs of deamination of proteins (specific-dynamic action, or SDA). Specific-dynamic action is modeled as a constant proportion of assimilated energy, with values usually between 0.15 and 0.20 (Hanson et al. 1997). The basic form of the respiration function is:

$$R = R_A * W^{R_B} * f(T) * ACTIVITY$$

where W is fish mass, R_A and R_B are the intercept and slope of the allometric mass function, respectively, f(T) is the temperature dependence function, T is water temperature, and ACTIVITY is the activity multiplier. For both largemouth and striped bass, f(T) and ACTIVITY took the following forms:

$$f(T) = e^{(R_Q * T)}$$

$$ACTIVITY = e^{R_{TO}}$$

R_Q approximates the Q_{10} (the rate at which f(T) increases at low water temperatures) and R_{TO} is the coefficient for swimming speed dependence on metabolism.

For both predator species, waste losses (egestion and excretion) were modeled as a constant proportion of energy consumed (FA and UA, respectively), which is the conventional approach:

Egestion: $F = FA * C$

Excretion: $U = UA * (C – F)$

Reproductive tissue gain and loss were not modeled because of a lack of accurate data on the phenomenon in this system. Without this component, fourteen and seventeen input parameters were required for largemouth bass and striped bass, respectively. I used parameters values developed for largemouth bass (Rice et al. 1983) and striped bass (Hartman and Brandt 1995a) (Table 2.1). I slightly modified the striped bass parameters to more appropriately reflect temperature preferences of reservoir populations of striped bass (Moore et al. 1993). Ecological ramifications of model output were used to judge model validity. For instance, if average food conversion efficiency of a predator species were found to be excessive (e.g. 50%), this would be taken as an indication of model inadequacy, incongruent with published material on the energy budgets of piscivores (Winberg 1956; Webb 1978; Brett and Groves 1979; Diana 1995).

Simulation Specifics

Documentation for the Windows™-compatible software used to implement the bioenergetic investigation is detailed by Hanson et al. (1997). The software was utilized to predict individual consumption from species-specific metabolic parameters (discussed in the previous section) and site-specific inputs on predator diets, growth rates, water temperature, and energy content of predators and prey. The starting and ending weight of an individual over a given time span was input, and the software iteratively determined a P value to arrive at the proper end weight. At one extreme, values for site-specific inputs need only be given for the starting and ending day of the period. Values for all days between the two endpoints are then determined by linear interpolation. At the other extreme, values can be given for every day in the period, thus requiring no interpolation. Any level of precision between these two extremes can be accommodated. My own input methods are presented later.

The software evaluated time by reference to the day of the simulation. I arbitrarily chose Day 1 to be 15 June, approximating the day when striped bass fingerlings are stocked, and a few weeks after largemouth bass are hatched (Moore 1988). For both largemouth bass and striped bass, I modeled 11 cohorts (age-0 through age-10).

Table 2.1. Physiological parameter values input into Wisconsin bioenergetics models for estimation of predator consumption. Parameter definitions given in the text and Hanson et al. (1997).

Source	Rice et al. 1983		Hartman and Brandt 1995			
Species	Largemouth Bass		Striped Bass			
Age	YOY	Adult	YOY	Age-1	Age-2	Adult
CONSUMPTION						
CA	0.33	0.33	0.3021	0.3021	0.3021	0.3021
CB	-0.325	-0.325	-0.2523	-0.2523	-0.2523	-0.2523
CQ	2.3	2.65	2.6	6.6	6.6	7.4
CTO	29	27.5	21.6	19	18	15
CTM	37	37	22.7	28	29	28
CTL	*	*	28.3	30	32	30
CK1	*	*	0.047	0.262	0.255	0.323
CK4	*	*	0.713	0.85	0.9	0.85
RESPIRATION						
RA	0.0015	0.0028	0.00146	0.0028	0.0028	0.0028
RB	-0.4	-0.355	-0.2702	-0.218	-0.218	-0.218
RQ	0.09	0.0811	0.08339	0.076	0.076	0.076
RTO	0.04	0.0196	0.9014	0.5002	0.5002	0.5002
SDA	0.163	0.163	0.172	0.172	0.172	0.172
EGESTION/EXCRETION						
FA	0.104	0.104	0.104	0.104	0.104	0.104
UA	0.068	0.068	0.068	0.068	0.068	0.068

Both species may live longer in SML, but numbers in these oldest age-classes are too small to have an appreciable impact on prey consumption by their respective populations.

Sutton (1997) reported that the SML age-0 striped bass cohort develops a bimodal length distribution in its first growth season. He hypothesized striped bass that begin feeding on fish prey soon after stocking grow faster than members of their cohort that feed on less energetically-profitable benthic invertebrates. This size discrepancy increases through time, and by the spring after stocking only the larger striped bass (> 150 mm TL) of the cohort remain. The smaller individuals likely suffer high starvation mortality over-winter from insufficient energy reserves. For this reason, I chose to model age-0 striped bass using two distinct groups of individuals, those that consume fish almost immediately and have faster growth and lower mortality (large mode group), and those unfortunate individuals who primarily consume benthic invertebrates, grow slowly, and are gone by the following April (small mode group).

Individual consumption using a single P value for a 365-day period was approximately 5% greater than individual consumption using multiple P values to describe seasonal growth patterns (Table A.2). The latter approach utilizes separate P values to adjust for changes in trophic interactions and environmental conditions from season to season. The similarity of the two estimates reflect the fact that a single, immutable annual P value will overestimate consumption at certain times, and underestimate consumption at other times. The requirement that simulated ending weight precisely match input ending weight in essence puts a limit on the error that can occur (Bartell et al. 1986). This would seem to indicate that modeling intra-seasonal growth patterns is not necessary. However, Rice et al. (1983) demonstrated that intra-seasonal consumption dynamics are misrepresented by using a single annual P value. In other words, despite fairly consistent estimates of annual consumption regardless of whether seasonal growth periods are used, temporal patterns of consumption can be highly inaccurate if seasonal changes in feeding and prey availability occur and are not addressed.

If a starting weight and an ending weight for a certain period are input, and simulation shows that weight steadily increases from beginning to end, as opposed to fluctuating above and below the desired ending weight, it is an indication that a single P value is adequate to model weight gain during the period (Rice et al. 1983). If weight fluctuates non-linearly, however (primarily due to changes in water temperature or diet of the predator over the modeled period), it is an indication that the period should be divided into shorter intervals of constant weight gain (or loss).

Determination of the temporal locations of similar intra-annual growth periods for striped bass and largemouth bass proceeded using this technique: one P value was initially input for the entire 365 days, and then simulated weight of an individual was plotted over time. Intra-annual periods of linear, monotonically-changing weight were exhibited. During these intervals, temperature and diet of the predator were fairly constant. These temporal terms were assumed to be well-described by a unique P value. Largemouth bass exhibited two different growth trajectories annually, while striped bass evinced four distinct periods (Figures 2.1 and 2.2). Thus, for adult striped bass, annual consumption was estimated during the four recognized periods: Spring (15 March to 31 May), Summer (1 June to 14 October), Fall (15 October to 14 December), and Winter (15 December to 14 March). Consumption by both large and small young-of-the-year (YOY) striped bass was estimated in only three periods, as they were not present in the spring. For these age-0 fish, fall and winter periods were identical to those of older striped bass, but the summer period began on 15 June. Adult largemouth bass cohorts were modeled using only two periods, the growth season (15 April to 31 October) and the "torpid" season of minimal growth (1 Nov to 14 April). Age-0 largemouth also required two periods of consumption to be estimated: 15 June to 14 August, and 15 August to 31 March. The growth season for age-1 largemouth bass thus spanned from 1 April to 31 October, slightly longer than the growth period for older largemouth bass.

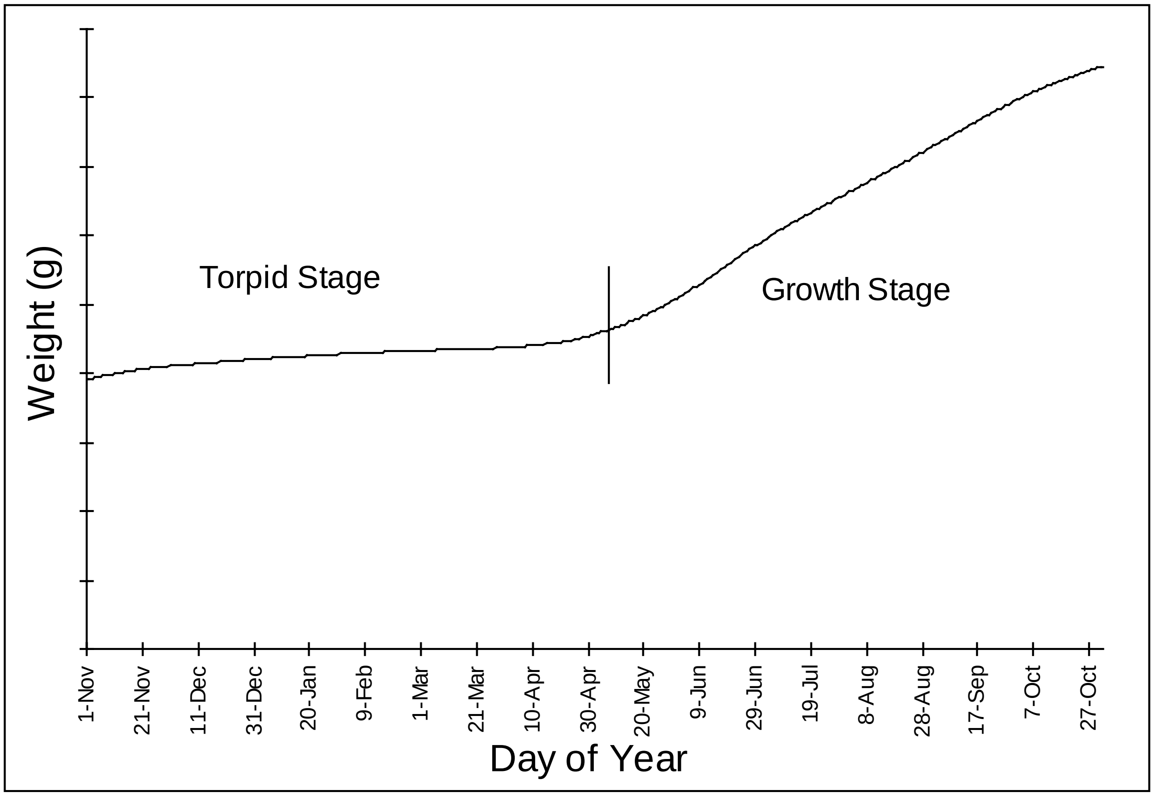

Figure 2.1. Modeled pattern of change in weight of an adult largemouth bass over the course of one year using the bioenergetics model and a single constant P value.

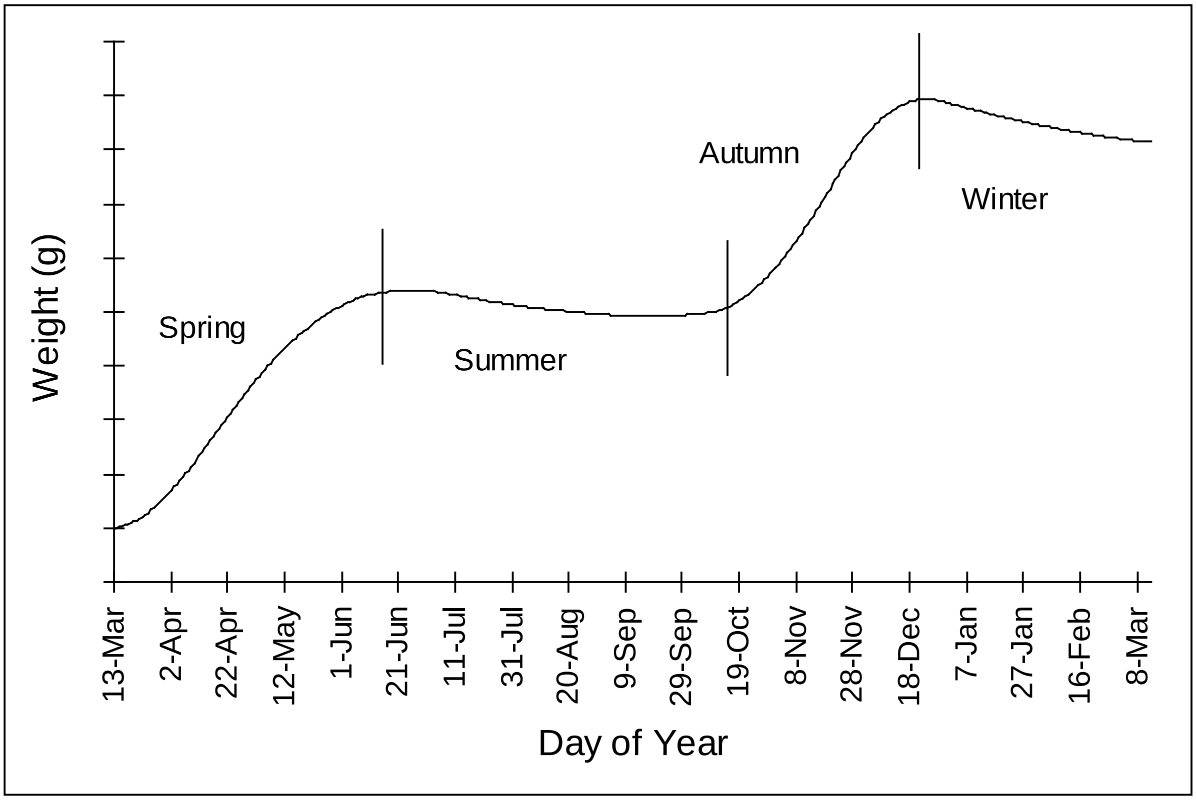

Figure 2.2. Modeled pattern of change in weight of an adult striped bass over the course of one year using the bioenergetics model and a constant P value.

Site-Specific Inputs to the Bioenergetics Model

Diet. Stomach contents were examined from striped bass and largemouth bass to quantify predator diets. These fish were captured in 1995 through 1998, from uplake, downlake, and mid-lake locations. Largemouth bass were sampled in April through October while striped bass were collected in May through March. Electrofished largemouth bass had their stomach contents removed using an acrylic tube inserted into the stomach via the esophagus (Van Den Avyle and Roussel 1980). Individuals were released after this procedure with little immediate post-release mortality witnessed. Stomach contents were bagged and placed on ice for later analysis. Striped bass stomachs were excised from individuals caught in gill-nets or harvested by anglers. They subsequently turned these parts in at a collection site where they were kept frozen until collection. A comprehensive collection record is presented in Table 2.2.

In the laboratory stomach contents were thawed, blotted dry, and weighed to the nearest tenth of a gram. Prey were identified to the lowest possible taxa and the mean percent weight of each prey item was classified according to predator species and season of collection. Special effort was made to identify clupeids (alewife and gizzard shad) from other fish prey, and distinctive morphological characteristics (body shape, mouth, scales, peritoneum color, presence of gizzard) facilitated separation of the two clupeid species (Manooch 1973). In cases where unidentifiable prey material was found, weight was allocated to the various prey taxa based on the mean contents in the stomachs of fish collected at the same time and location. Care was taken to insure stomach contents from angler-harvested striped bass had not been bait used by the angler. These contents were removed from tabulation if they prey item was particularly fresh and clear evidence of a hooking wound on the prey could be found. Total length and backbone length were recorded for recognizable prey specimens to allow for questions concerning morphological availability of prey to be addressed, e.g., as an indication of prey size-selectivity for predators of various lengths.

Table 2.2. Record of adult predators collected for analysis of stomach contents.

Species	Year	Season	Sampling Locations	Collection Method	Number Collected
Striped Bass	1995	Fall	Upper, Middle, Lower	Gillnets	169
	1996	Fall	Upper, Middle, Lower	Gillnets	156
	1996	Winter	Upper, Middle, Lower	Angler Returns	8
	1997	Spring	Upper, Middle, Lower	Gillnets, Angler Returns	40 , 35
	1997	Summer	Middle, Lower	Gillnets, Angler Returns	32 , 146
	1997	Fall	Upper, Middle, Lower	Gillnets, Angler Returns	103 , 5
	1997	Winter	Upper, Middle, Lower	Angler Returns	8
	1998	Spring	Upper, Middle, Lower	Angler Returns	15
	1998	Summer	Middle, Lower	Angler Returns	50
Largemouth Bass	1996	Spring	Upper, Middle, Lower	Electrofishing	59
	1996	Summer	Upper, Middle	Electrofishing	235
	1996	Fall	Upper, Middle	Electrofishing	128
	1997	Spring	Upper, Middle, Lower	Electrofishing	41
	1997	Summer	Upper, Middle, Lower	Electrofishing	79

Water Temperatures. Daily water temperatures in SML were modeled using a trigonometric function modified from Dalton (1987) by Sutton (1997). This equation was fitted to observed weekly temperatures taken in 1994-1995 and 1995-1996 at a depth of 1 m from both littoral and pelagic areas. Sutton (1997) found differences in water temperatures in these two reservoir zones to be statistically insignificant (Chi-square, $p = 0.11$). The model is:

$$\mathbf{T = 15.94 - 9.07 * \cos(0.0172 * D) - 6.10 * \sin(0.0172 * D)}$$

where T is temperature in degrees Celsius and **D** is the Julian calendar date. It is not these daily water temperatures that are input into the model, but rather the temperatures occupied by individuals of each cohort over the modeled time period. These values were determined by referring to the preferred temperatures for consumption of each species and life stage (C_{TO}, Table 2.1). It was assumed predators would inhabit waters closest to, but not exceeding, their preferred temperature for respiration (Table 2.3). When surface waters exceeded optimum temperatures, it was assumed cooler, adequately oxygenated waters were present in the lower reaches of SML throughout the summer period (Ney et al. 1990).

Table 2.3. Temperatures occupied by predators throughout the year in Smith Mountain Lake. Values based on trigonometric temperature function of Sutton (1997) and temperature preferences presented in Moore (1988).

	Actual	**Largemouth**	**Striped Bass**		
Date	**Water Temp**	**All Ages**	**YOY**	**Ages 1-2**	**Ages 3+**
15-Jun	22.9	22.9	22.9	22.0	20
15-Jul	26.2	26.2	25.0	22.0	20
14-Aug	26.7	26.7	25.0	22.0	20
13-Sep	24.5	24.5	24.5	22.0	20
13-Oct	20.0	20.0	20.0	20.0	20
12-Nov	14.5	14.5	14.5	14.5	14.5
12-Dec	9.4	9.4	9.4	9.4	9.4
11-Jan	6.0	6.0	6.0	6.0	6.0
10-Feb	5.1	5.1	5.1	5.1	5.1
12-Mar	7.0	7.0	7.0	7.0	7.0
11-Apr	11.3	11.3	11.3	11.3	11.3
11-May	16.7	16.7	16.7	16.7	16.7

<u>Predator/Prey Caloric Values</u>. Knowledge of energy content (either joules/g or cal/g) of predators and prey are necessary before bioenergetic simulations can be run. While some investigators have chosen to use constant caloric values for predator and prey (Kitchell et al. 1977; Rice et al. 1983; Bevelhimer et al. 1985), seasonal changes in energy content for both predator and prey have been shown to be significant (Soofiani and Hawkins 1985). The five major prey categories for which energy content was needed were gizzard shad, alewife, crayfish, other fish, and insects/invertebrates. Gizzard shad and alewife caloric values were taken from a study performed on Watts Bar Reservoir, Tennessee (Adams et al. 1982a), crayfish values were taken from Nielsen and Orth (1984), non-clupeid fish values were found in Adams et al. (1982a), and insect values came from Penczak (1985). Table 2.4 gives the seasonal caloric values for the five prey groups input into the bioenergetics model.

Information on proximate composition and energy content of primary prey items in SML is more readily available than for predator species, especially freshwater populations of striped bass. Hartman and Brandt (1995b) give a detailed account of seasonal energy content for the Chesapeake Bay striped bass stock, but these saltwater specimens have a completely different diet than their freshwater brethren. For this reason, I adopted the approach of Rottiers and Tucker (1982), who stated that energy content of predators could be well estimated by examining the energy content of their prey. To determine seasonal energy content for largemouth bass and striped bass, I used a weighted average of the energy content of prey items, the weights being the relative contribution (measured as percent of total stomach content mass) of each prey item to the predator’s diet in a given season (Table 2.5). Obviously, this constrained the number of times that predator energy content could be calculated to those dates on which predator diet composition was known. This technique limits the extent that predators can have much higher or lower energy content than their diet would grant.

Table 2.4. Energy content (cal/g wet weight) of the five major prey items of predators in Smith Mountain Lake.

Date	Alewife	Gizzard Shad	Crayfish	Other Fish	Insects
15-Jun	1504	1433	923	1150	972
15-Jul	1367	1301	923	1000	972
15-Aug	1394	1301	923	1118	972
15-Sep	1361	1349	923	1090	972
15-Oct	1421	1391	923	1118	972
15-Nov	1540	1409	923	1160	972
15-Dec	1606	1433	923	1130	972
15-Jan	1666	1463	923	1110	972
15-Feb	1725	1469	923	1090	972
15-Mar	1827	1493	923	1090	972
15-Apr	1588	1229	923	1030	972
15-May	1552	1337	923	1080	972
15-Jun	1504	1433	923	1150	972

Table 2.5. Seasonal energy content (cal/g wet weight) of largemouth and striped bass. Values are derived using a weighted average of prey energy content, with percent of items in the predator diet as the weights. Predator energy content values could thus only be calculated on dates for which diet composition was known.

	Largemouth Bass			**Striped Bass**			
Date	**YOY**	**Age-1**	**Adult**	**Small YOY**	**Big YOY**	**Age-1**	**Adult**
15-Mar	-	1285	1150	-	-	1765	1681
1-May	-	1197	1398	-	-	1532	1444
15-Jun	1088	-	-	1061	1061	-	-
15-Jul	-	1221	1149	-	-	1352	1280
1-Aug	1046	-	-	1033	1033	-	-
15-Oct	-	1333	1122	1119	1391	1364	1395
1-Nov	1131	-	-	-	-	-	-
15-Dec	-	1110	1323	-	-	1395	1442

Growth Rates. Samples of 413 largemouth bass collected via electrofishing in 1993 and 1996, and 95 striped bass captured in the fall of 1997 using gill-nets, were used to develop growth curves for each species. Mike Duval, VDGIF biologist, took length, weight, and scale/otolith samples on these fish. He conducted age determination using common hard-part analysis techniques (Jearld 1983). I fit a modified von Bertalanffy growth function (Moreau 1987) to his average lengths-at-ages using a non-linear sum of squares minimization fitting technique. This equation has the flexibility to represent intra-seasonal growth patterns commonly seen in many fish subject to variations in the environment they occupy (Moore 1988). The equation is:

$$L_t = L_\infty * (1 - e^{(-K*(t - t_0)+S_t)})$$

where L_t is the length (mm) at time t, L_∞ is the maximum length for individuals of that species in the system, K determines how fast they reach this maximum size, t_0 is the time when individuals are hatched, and S_t controls the amplitude and timing of the seasonal growth fluctuations. S_t can be any function of time, for example a sine function (Moore 1988). If S_t=0, size at that time is the same as if no adjustment to the von Bertalanffy equation were made. If S_t is a negative value, size at that time is less than the unaltered equation would have produced. If S_t is positive, size at that time is greater. As the magnitude of S_t is increased, the deviation of size-at-age from the basic growth equation is augmented.

Due to the periodicity of annual growth (Figures 2.1 and 2.2), I needed to estimate length-at-age for two days during the year for largemouth bass (15 April and 1 November) and four days for striped bass (15 March, 1 June, 15 October, and 15 December). For each one of these dates, an S_t value was needed. My goal was to choose values of S_t such that modeled individuals would grow during spring, summer, and fall, but have little to no growth over-winter.

Few striped bass over age five and largemouth bass over age seven were captured. Due to inadequate representation of older fishes, I used length-at-age for older largemouth bass and striped bass collected from previous investigations on SML (Smith and Kauffman 1982; Banach 1989). For these older predators, I used the 75th percentile of length-at-age to fit the growth equation rather than the reported median length-at-age to err on the liberal side of consumption estimation. To conservatively estimate consumption would carry more risk for the fishery, as an overly optimistic supply/demand investigation would justify management actions that could lead to overexploitation of the forage base. Because the majority of population consumption is performed by the numerous individuals of young ages, inaccuracy in modeling the growth of older predators would not lead to major errors in consumption estimation. The modified von Bertalanffy equation did not produce length estimates that matched empirical observation for age-0 striped bass and age-0 largemouth bass. Instead, mean length values for age-0 striped bass were taken from Sutton (1997), who performed biweekly sampling throughout the growth season. Mean length for age-0 largemouth in mid-August was derived from rotenone data from the Virginia Department of Game and Inland Fisheries.

In order to derive weight-at-age from length-at-age, length-weight relationships were derived from 73 largemouth bass sampled during spring 1996 electrofishing, and 178 striped bass gill-netted in the fall of 1995. A variety of curves types was examined to find the best fit to the scatter of data. Fit was judged primarily by the amount of variation explained by the trendline and ecological interpretation of the resulting equation. With the information gathered up to this point, the data requirements for estimation of individuals consumption by both largemouth bass and striped bass were satisfied.

POPULATION ABUNDANCE

To induce population consumption from individual consumption, the number of predators at each age must be known. Estimates of annual morality rates and initial numbers of age-0 predators are primary inputs for this procedure. My goal was to describe the typical densities of predator populations in SML, and using mean abundance would seem to facilitate this development, rather than having focused on annual fluctuations in predator densities (see Table A.1).

Initial numbers of striped bass were set at 300,000 fingerlings, the mean number stocked annually during the period 1982-1997. Since 1973, gill-net surveys have been used by the VDGIF in October, November, and December to estimate population sizes of age-1 striped bass. Average survival to this time is approximately 21% of fish stocked, or about 63,000 fish (Duval 1996). I found that I could approximate this number using reasonable survival rates for age-0 striped bass if I partitioned the initial cohort into 200,000 individuals that would soon become piscivorous, with concomitantly higher growth and survival than another group of 100,000 individuals who did not become piscivorous until much later, if ever. The latter group would suffer near-complete mortality by the following April (Sutton 1997), requiring no further demarcation between the two. Duval (1996) performed cohort analysis on gillnetted striped bass to estimate 28% survival from age-1 to age-2, and catch-curve methodology to estimate annual survival of striped bass ages 2-6 at 37%. Using growth data, I determined that Duval's (1996) survival estimates for age-1 fish appeared too low to allow for sufficient numbers of older, larger fish to reconcile average numbers of citation fish reported over the history of the fishery (about 185 per annum, Figure A.1). [Anglers are given certificates of merit, or citations, by the Virginia Department of Game and Inland Fisheries for catching striped bass over 9.1 kg, or 20 pounds.] If any drastic change in annual mortality occurs for age-1+ fish, it would seem logical for it to happen when they are recruited to a size harvestable by anglers (508 mm TL). In addition, having sub-legal fish, which sampling showed not to be emaciated, suffering mortality higher than fish fully recruited and undergoing intensive harvest by anglers was not intuitively appealing. For these reasons, I increased annual survival rates for all pre-recruits, including large age-0 striped bass, to 50%, while using Duval's estimate of annual survival for legal striped bass (37%, Table 2.6).

A 50% mortality rate for pre-recruits was chosen because Moore (1988) used catch-curve analysis to estimate that mean survival of age-1 striped bass during 1973-1983 was approximately 50%. Changes in the SML fishery have occurred since his study, but survival of pre-recruit striped bass should have been fairly stable if foraging conditions were also steady. Prey availability and the severity of winter most likely limit pre-recruit striped bass survival (Sutton 1997). Pre-recruit striped bass depend on alewife for the majority of their diet (Moore 1988; Sutton 1997). Alewife abundance in rotenone coves during the 1980's and 1990's in SML was similar. In addition, there is no evidence that drastic climatic changes have occurred between these two decades. I therefore concluded that the mean pre-recruit mortality value of Moore (1988) could be used without incurring great bias. I would expect survival of legal striped bass, due to its contingence on fishing pressure, to be more time-dependent. Because angler effort levels have increased substantially in the past decade (M.C. Duval, VDGIF, unpublished data), I would be more hesitant to use survival rates for legal-size striped bass from previous decades.

Density and biomass of age-0 to age-3 largemouth bass in late August were estimated from rotenone surveys (for rotenone sampling methods, see Chapter One) conducted by the Virginia Department of Game and Inland Fisheries during 1989-1997. Older, larger bass were perceived to be incompletely sampled using rotenone methods due to a preference for cooler water, which caused them to move further offshore in late summer (Hayne et al. 1967; Summers and Axon 1980; Hightower et al. 1982). To convert largemouth bass size to age, I used the following conversions, based on data from cove rotenone largemouth bass samples: Age-0 = 0-149 mm, Age-1 = 150-224 mm, Age-2 = 225-299 mm, Age-3 = 300-350 mm.

Table 2.6. Survival rates for striped bass of various ages. Modified from Duval (1996) to fit average number of citation fish caught in the last ten years.

Age-Class	Period	Survival Rate
"Small" YOY	15 June to 15 December	0.40
"Small" YOY	15 December to 15 March	0.001
"Big" YOY	15 June to 15 March	0.50
Age-1 to Age-3	15 March to 15 March	0.50
Age-3+	15 March to 15 March	0.37

It was assumed that rotenone density estimates, averaged across the four coves per year, accurately represented lake-wide littoral densities of age-0 to age-3 largemouth bass (Bettoli and Maceina 1996). Open-water densities of these age-classes still needed to be determined in order to derive whole-lake density estimates. Previous investigators have researched the problem of adjustment of littoral densities to open-water densities of fish species sampled using rotenone (Jenkins and Morais 1978; Hightower et al. 1982). The most extensive attempts were conducted by Hayne et al. (1967) in Douglas Lake, Tennessee, and Summers and Axon (1980) in Barkley Lake, Tennessee. They found very different species-specific adjustment factors, and critics recognized this as indicative of a wide discrepancy in basin morphometry and limnological characteristics between the two systems, as well as possible differences in experimental methodology and environmental stochasticity (Bettoli and Maceina 1996). Since this time, further rotenone research has indicated that the relationship between open water and littoral densities of fish is site-specific; no single adjustment factor is nearly appropriate for all lakes and reservoirs (Bettoli and Maceina 1996).

In the absence of site-specific data, the following adjustment factors were applied to SML rotenone biomass estimates to arrive at open-water biomass estimates: Age-0 = 0.1, Age-1 = 0.75, Age-2 = 0.8, Age-3 = 1.0. These values were based on the ecological reasoning that few age-0 largemouth bass would be found in off-shore habitats, while an increasing percentage of larger, older bass, might be expected to occupy these zones (Hayne et al. 1967; Jenkins and Morais 1978; Summers and Axon 1980; Hightower et al. 1982; Annett et al. 1996). For age-1 and older bass, these expansion factors are similar to those reported by Hayne et al. (1967) for Douglas Lake, which is limnologically much closer to SML than Barkley Lake. My correction factor for age-0 bass is between the Douglas Lake and Barkley Lake values. Because no convincing evidence exists to suggest that pelagic densities of 80-100 mm largemouth bass are more than a small fraction of densities in littoral regions in SML, I decided the age-0 correction factor from Douglas Lake was too generous. Multiple years of gillnetting in open-water areas of SML did not capture a single largemouth bass less than 150 mm TL, while striped bass from 100-150 mm TL were readily caught in some of the mesh sizes utilized.

For my purposes, the littoral region of the lake sampled by rotenone was defined as the volume of the reservoir that was 7 meters or less in depth from surface to bottom, to agree with the maximum depth in the cove sites sampled. Hipsometric data from the Army Corps of Engineers showed this region to be 25% of the total volume of the system at full pool. To compute a whole-lake population estimate of age-0 to age-3 largemouth bass, I multiplied the cove density estimates by the number of littoral hectares (2084), and took the product of open-water densities and the number of pelagic hectares (6253), then summed the two quantities. In order to estimate the number of largemouth bass hatched on 15 June, I would have had to estimate survival rate from hatching to late August. Because largemouth bass during this life stage feed on zooplankton and benthic fauna, rather than fish prey (Sutton 1997), arriving at some number was not deemed critical. Individual consumption for this life-stage was estimated, but cohort consumption was not.

CONSUMPTION BY OTHER PREDATORS

Other predators in SML include smallmouth bass, walleye, crappie, catfishes, and muskellunge. Adults of each species likely consume clupeids during certain times of the year, but population densities and diet must be estimated before impact can be assessed. In general, accurate diet assessment and population estimates are severely lacking for predators other than largemouth and striped bass. Due to resource and data constraints, I could not determine consumption by these ancillary predators using bioenergetics modeling, but rather used assorted information on their population density, consumption, and diet to arrive at reasonable estimates.

Smallmouth bass prefer cool water habitat and reach large adult size (> 400 mm TL). These characteristics point to their capability of consuming clupeids, especially alewife, in significant numbers (Moore 1988). Walleye overlap distributionally to an even greater extent with alewife, and rely almost exclusively on this prey item in SML (Moore 1988), but the density of these predators has fallen off significantly since stocking was discontinued nearly a decade ago. Black crappie, although they have smaller adult sizes, probably do have some impact on age-0 clupeids. Due to gape limitation, only the larger adult crappies could feed on clupeids, however, and would likely be limited to predation on age-0 prey. Adult catfishes are large, benthic, nocturnal piscivores. Their habitat preferences likely limit the amount of their clupeid consumption, but they would certainly consume alewife and shad if the opportunity presented itself. The state of Virginia does stock low numbers of muskellunge into SML, but these large, littoral, ambush predators are at such low densities that no serious impact on clupeid prey can be inferred.

Population densities of these predators in SML could only be assessed through examination of cove rotenone standing stock estimates. Data were analyzed identically to the method given for largemouth bass. Open water biomass could be very different from cove biomass, depending on the habitat preference of the predator. A species-specific expansion factor was used to develop open-water biomass estimates from cove rotenone biomass. I derived these expansion factors from examination of the Douglas Lake data presented in Bettoli and Maceina (1996). Unique expansion factors were given for various size-classes within each predator species, so I estimated a mean expansion factor for the species. I utilized the Douglas Lake findings because that reservoir is morphometrically similar to Smith Mountain Lake.

The recommended average expansion factor for crappie was approximately 2.0, meaning open-water biomass was twice that of cove biomass. For catfishes, the recommended expansion factor was approximately 1.0. The expansion factor for black basses (smallmouth and largemouth) was approximately 1.0, but smallmouth bass prefer cooler water and are more offshore oriented than largemouth bass (Smith and Crossman 1973). I therefore increased the smallmouth bass expansion factor to 2.0. Walleye primarily inhabit benthic pelagic habitat in SML, and Bettoli and Maceina (1996) had no recommended expansion factor for a truly open-water species. I chose an expansion factor of 10.0. No adult muskellunge were sampled in the eight years of rotenone data collected so a population density estimate for this species was not attempted.

Once whole lake population estimates were made, annual consumption to August biomass (C/B) ratios were used to calculate population consumption for ancillary predators. These ratios for largemouth bass and striped bass populations were estimated via bioenergetic modeling to be 2.6 and 4.7, respectively. A greater ratio for striped bass was likely due to higher annual growth and mortality relative to largemouth bass, leading to a higher turnover rate (more biomass produced and lost each year) and a higher production to biomass ratio. In addition a lower food conversion efficiency, possibly due to the increased metabolic costs of being a more active, roaming predator, would increase the ratio. Striped bass also become much heavier than largemouth bass, and food conversion efficiency decreases at increased weight. I decided to set all of the other predator C/B ratios to 3.5, a value slightly more similar to largemouth bass than striped bass, instead imposing unwarranted levels of precision based on broad depictions of predator lifestyles.

Finally, to partition consumption between three prey components (alewife, shad, and other), diet information was needed. For smallmouth and walleye, data from Moore (1988) were used. He found alewife and gizzard shad to be 39% and 33% of the annual smallmouth bass diet, respectively. His information on the diet of walleye ages 4-8 (67% alewife, 26% gizzard shad) was used to partition consumption for this predator species between its prey items. However, alewife and shad are not primary prey items for age-0 walleye for part of their first growth season. Instead, age-0 walleye rely on zooplankton and benthic invertebrates until they are large enough to consume age-0 clupeids, at about 60 mm TL (Maloney and Johnson 1957; Johnson et al. 1988b). The fraction of total population consumption that can be attributed to age-0 walleye is unknown (age-0 largemouth bass and striped bass contribute very differently to total clupeid consumption, see Figures 2.7, 2.8). Due to this possible bias, the percent of alewife and gizzard shad in the walleye population diet was lowered by 10% from the values given in Moore (1988). For catfishes, crappie, and muskellunge, very little information on diet in SML was available. For this reason, investigations of these predators in other systems were examined.

Crappie dietary selection in lentic systems has been extensively investigated, and evidence that clupeids can be important prey is not lacking. Hale (1996) demonstrated that adult white crappie (*Pomoxis annularis*) utilize both age-0 threadfin shad and gizzard shad to meet nutritional demands in two Kentucky reservoirs. Michaletz (1998b) reports that age-0 shad serve as the primary prey for adult crappie during summer and early fall in certain Missouri reservoirs. Huish (1957) reported that threadfin shad were a major forage component for adult crappie during the summer months in Lake George, Florida. Dendy (1946, Norris Reservoir, Tennessee), Ball and Kilambi (1973, Beaver Reservoir, Arkansas), and Ager (1976, Lake Okeechobee, Florida) found adult black crappie to consume primarily fish in later summer and fall, and invertebrates, such as aquatic insects and earthworms, during spring and early summer. Ball and Kilambi (1973) report that threadfin shad were the primary fish species eaten, with lesser amounts of gizzard shad and brook silversides (*Labidesthes sicculus*). The predominance of threadfin shad in the diet was attributed to their great abundance and smaller average size as compared to gizzard shad. In that study, as in Hale (1996) and Michaletz (1998b), it was noted that crappies are gape-limited and mostly consume smaller age-0 individuals of each prey species. Ager's (1976) data showed that fish were primarily consumed by crappies greater than 240 mm TL, while smaller crappie consumed mainly crustaceans and insects. Hale (1996) found crappies as small as 150 mm to consume age-0 shad early after the shad hatch. The window of morphological vulnerability of shad to crappie was not open very long, however. Scott and Crossman (1973) state that prey fish over 65 mm TL were never found in black crappie stomachs. Unfortunately none of these studies were performed on systems with alewife present, as in SML. Threadfin shad are morphologically similar to alewife and generally inhabit pelagic areas (Ney et al. 1982), so the assumption that the two could be considered equivalent forage species is not unreasonable. Based on these findings total crappie consumption was partitioned as follows: 10% alewife, 15% gizzard shad, and 75% other items. This reflects both the fact that clupeid prey are only consumed during certain seasons and that only the larger adult crappie feed on these fish.

Wahl and Stein (1991) report that age-0 muskellunge in five Ohio reservoirs primarily utilized age-0 gizzard shad, especially in the fall months after these predators were stocked. As gizzard shad grew too large to consume, however, these muskellunge began to consume larger quantities of centrarchids and cyprinids. Muskellunge have been shown to prefer soft-rayed species such as cyprinids and clupeids over spiny centrarchids (Wahl and Stein 1988). For this reason, and because of their littoral nature, it was assumed that muskellunge would choose gizzard shad as a primary dietary component in SML. In addition the near-shore presence of alewife during their protracted summer spawn likely makes them attractive prey during this season, although their small size is likely not appealing to the large adults. No doubt catostomids, centrarchids, and cyprinids are also preyed upon to some extent. Muskellunge diet was segmented into 40% shad, 20% alewife, and 40% other. With no rotenone data on muskellunge density, total consumption for muskellunge was set to 1% of largemouth bass consumption. While the former predator reaches substantially larger adult sizes, its population density is a minute fraction of the latter's.

The final predator group is the catfishes of SML; the flathead, white (*Ictalurus catus*) and channel (*Ictalurus punctatus*) species. Stevens (1960) found adult white catfish in Santee-Cooper Reservoir, South Carolina, to feed predominantly on clupeid fishes such as various shad species and herring, while channel catfish had a more diverse diet, with other catfish species being the primarily item ingested. Herring (*Alosa* spp.) were utilized to some extent but shad were virtually ignored. Carlander (1968) reports that channel catfish became piscivorous near 100 mm TL and calls attention to another study performed in Ouachita River, Louisiana, in which channel catfish did not utilize abundant shad resources. However, in Norris Lake, Tennessee, and Canton Reservoir, Oklahoma, channel catfish did consume appreciable quantities of gizzard shad (Carlander 1968). Minckley and Deacon (1959) report that flathead catfish under 100 mm TL in a Kansas reservoir were insectivorous while individuals from 100-250 mm TL become increasingly piscivorous. Individuals over 250 mm TL were nearly exclusively piscivorous, but shad were not present in this system so their contribution to flathead diets could not be assessed. Miranda et al. (1998) learned that shad were the dominant prey item in the stomachs of channel catfish during March in Norris Lake, Tennessee. This investigation also found that flathead catfish consumed alewife during the latter's inshore spring spawning movements. Flathead catfish are benthic, structure-oriented predators, and thus would seem to be spatially separated from pelagic clupeid prey fishes at other times of the year. From these data it appears as if clupeids are likely a sizeable component of white catfish diets in SML, somewhat less important to channel catfish, and least important to flathead catfish. The exception would be during the alewife spawn when alewife move inshore and are more vulnerable to littoral predators. Most catfish biomass is concentrated in uplake areas (M.C. Duval, VDGIF, personal communication). This information would suggest that gizzard shad are more susceptible to catfish predation than alewife. Of the total biomass of these three ictalurids, rotenone data indicated that channel catfish made up 42%, flathead catfish 35% and white catfish 23%. Based on this partitioning and the relative contributions of clupeids to the diets of the three species the following diet percentages were used: alewife 5%, shad 25%, other 70%. A summary of various estimates used to derive consumption by ancillary predators can be found in Table 2.7.

Table 2.7. Parameters used to estimate consumption by ancillary predators in Smith Mountain Lake.

Predator	**Littoral Biomass (kg/ha)**	**Open-Water Conversion**	**Whole-Lake Biomass (kg/ha)**	**B/C Ratio**	**Diet Percentages**		
					alewife	**shad**	**other**
Catfish spp.	27.9	1.0	27.9	3.5	0.05	0.25	0.70
Crappie	10.0	2.0	17.5	3.5	0.10	0.15	0.75
Muskie	*	*	*	3.5	0.20	0.40	0.40
Smallmouth	0.5	2.0	0.9	3.5	0.39	0.33	0.28
Walleye	0.0	10.0	0.2	3.5	0.60	0.23	0.17

RESULTS

SITE-SPECIFIC INPUTS

Diet Composition

Seasonal and age-related changes occurred in the diets of largemouth bass and striped bass in Smith Mountain Lake. These variations are primarily the result of changes in prey availability to different cohorts of predators. Age-0 largemouth bass consumed primarily non-clupeid fishes such as cyprinids and centrarchids, as well as benthic invertebrates during their first year of growth (Table 2.8). Early next spring clupeids and crayfish began to show up in the diet and during their second growth season age-0 shad appeared to be most heavily utilized. The diet of adult largemouth bass usually consisted of over 60% shad and crayfish. The exception to this is during late spring to mid-summer when alewife and non-clupeid fishes were consumed in greater quantities.

The small age-0 striped bass ate almost entirely non-clupeid fishes and benthic invertebrates during their first growth season, with only a few consuming alewife in late fall (Table 2.9). Large age-0 fish had a similar diet during summer but moved offshore and began consuming alewife nearly exclusively in the fall. This continued until the fall of their second growth season when age-0 shad became an appreciable component of the diet. For adult striped bass alewife were most heavily utilized from March through September, while gizzard shad were the primary prey item at other times of the year. Crayfish were the only other prey item to make up more than 5% of the diet and this was the case only during the early summer period. Although I did not examine consumption of specific age-classes of prey, Moore (1988) found age-0 alewife to compose 10%, 80%, 30%, and 20% of alewife biomass ingested annually by all largemouth bass, and age-0, age-1, and adult striped bass, respectively. His data as well as my own stomach analyses showed that nearly all gizzard shad consumed by predators were less than approximately 160 mm TL, a size that they reach in the middle of their second growth season.

Table 2.8. Diet summary for largemouth bass cohorts. Table entries are the percent weight of each prey item in the diet.

YOY

Prey Species	mid-June	early August	early November	mid-March	early May
Alewife	0.00	0.00	0.00	0.12	0.17
Shad	0.00	0.00	0.00	0.39	0.33
Crayfish	0.00	0.00	0.00	0.27	0.16
Other Fish	0.65	0.85	0.95	0.22	0.32
Other	0.35	0.15	0.05	0.01	0.01

Age-1

Prey Species	15-Jul	mid-October	mid-December	mid-March	early May
Alewife	0.00	0.00	0.02	0.05	0.63
Shad	0.75	0.85	0.33	0.22	0.11
Crayfish	0.06	0.08	0.63	0.39	0.06
Other Fish	0.19	0.07	0.02	0.34	0.19
Other	0.00	0.00	0.00	0.00	0.00

Adult

Prey Species	15-Jul	mid-October	mid-December	mid-March	early May
Alewife	0.30	0.00	0.01	0.05	0.63
Shad	0.19	0.37	0.75	0.22	0.11
Crayfish	0.23	0.49	0.19	0.39	0.06
Other Fish	0.29	0.14	0.05	0.34	0.19
Other	0.00	0.00	0.00	0.00	0.00

Table 2.9. Diet summary for striped bass cohorts. Table entries are the percent weight of each prey item in the diet. Percentages in each distinct column sum to one.

Small YOY

Prey Species	mid-July	early August	mid-October
Alewife	0.00	0.00	0.10
Shad	0.00	0.00	0.00
Crayfish	0.00	0.00	0.00
Other Fish	0.50	0.70	0.70
Other	0.50	0.30	0.20

Large YOY

Prey Species	mid-June	early August	early November	mid-March	early May
Alewife	0.00	0.00	0.90	0.88	0.90
Shad	0.00	0.00	0.00	0.07	0.05
Crayfish	0.00	0.00	0.00	0.00	0.00
Other Fish	0.50	0.70	0.10	0.05	0.05
Other	0.50	0.30	0.00	0.00	0.00

Age-1

Prey Species	mid-June	mid-October	mid-December	mid-March	early May
Alewife	0.95	0.54	0.06	0.61	0.60
Shad	0.02	0.36	0.78	0.36	0.36
Crayfish	0.02	0.07	0.00	0.01	0.01
Other Fish	0.01	0.03	0.16	0.03	0.03
Other	0.00	0.00	0.00	0.00	0.00

Adult

Prey Species	mid-June	mid-October	mid-December	mid-March	early May
Alewife	0.68	0.36	0.07	0.61	0.71
Shad	0.11	0.62	0.93	0.36	0.21
Crayfish	0.21	0.00	0.00	0.01	0.05
Other Fish	0.00	0.02	0.00	0.03	0.03
Other	0.00	0.00	0.00	0.00	0.00

Growth

Aging analysis from collections of largemouth bass and striped bass in 1993, 1996, and 1997 allowed the 95% confidence intervals for mean length-at-age for each species to be determined (Table 2.10). The parameters of the modified von Bertalanffy growth equation (presented below) were determined by non-linear least squares fitting to these mean lengths-at-age in addition to the 75th percentile of length-at-age for striped bass over age-5 and largemouth bass over age-7 from Smith and Kauffman (1982) and Banach (1989).

	L_∞	K	t_0
Largemouth Bass	660	0.22	-0.45
Striped Bass	1200	0.19	-0.25

For largemouth bass, S_t on 15 April was set to -0.27, while S_t on 1 November equaled 0.22. This resulted in all growth occurring from April to November with individuals maintaining their length between November and April. For striped bass, March, June, October, and December S_t values were -0.03, -0.1, -0.15, and 0.09, respectively. In the absence of reliable data describing intra-seasonal growth of striped bass in SML these values simply resulted in striped bass having near-constant weight increase during the growth season and weight maintenance over-winter.

When relationships for length and weight of predators were examined power functions ($W = a*L^b$) were found to provide the best fit to both largemouth and striped bass data ($r^2 = 0.981$ and 0.987, respectively). These equations were:

Largemouth Bass $W = 0.0000017*L^{3.356}$
Striped Bass $W = 0.000064*L^{2.712}$

where W is weight in grams and L is total length in millimeters. Judging by the exponents of the power functions one can deduce that largemouth bass are generally more plump for their length than striped bass. The former develops a football-shaped morphology as it ages while the latter tends to stay more streamlined.

Modeled growth in length and weight across the lifetime of largemouth bass and striped bass is shown in Figures 2.3 and 2.4, respectively. Based on these growth rates the average largemouth bass would reach a legal size (356 mm TL) during its fourth growth season while the average striped bass would reach a legal size (508 mm TL) during the latter part of its third growth season. Duval (1996) comes to the same conclusion concerning the timing of striped bass recruitment to the fishery. The average striped bass would reach citation size (9075 g) late into its tenth growth season.

Using this growth data I derived an estimate of the number of legal and citation striped bass size (508 mm TL and 9075 g, respectively) in SML on an annual basis. A certain percentage of fish can be expected to reach these milestones earlier than average and a certain percentage will surpass them somewhat behind schedule. I used a Gaussian cumulative probability function to model the cumulative percentage of striped bass having reached these hallmark sizes at various ages. This Gaussian variable had a mean equal to the size that the fish would be legal or citation and a standard deviation set to some percentage of the mean. For citation striped bass the standard deviation was set to 25% of the mean because weight-at-age of these older fish can fluctuate a great deal due to exponential weight changes with deviations in length. The standard deviation for legal striped bass was set to 15% of the mean because length-at-age when individuals are young is much less variable. This variation about mean length and mean weight-at-age was consonant with the findings of Moore (1988). Using this methodology the percentage of individuals reaching the milestone was near-zero for fish three standard deviations below the appropriate size, increased according to the Gaussian cumulative distribution function to 50% when the average individual was exactly legal or citation size, then rose to almost 100% where the average individual was three standard deviations above the appropriate size. Numbers of striped bass estimated to have reached these special sizes are presented in the section entitled "Population Abundance."

Table 2.10. Mean length-at-age (mm) for largemouth bass and striped bass collected in SML, with 95% confidence intervals. SEM is the standard error of the mean. Largemouth bass were collected in early May and striped bass were caught in late October.

Largemouth Bass

Age	Mean	SEM	Lower Bound	Upper Bound	N
0.9	144	4	136	151	41
1.9	252	4	245	260	125
2.9	330	4	322	337	92
3.9	371	3	366	377	81
4.9	418	5	408	428	42
5.9	442	6	429	454	16
6.9	462	15	432	491	11
7.9	508	16	476	539	5

Striped Bass

Age	Mean	SEM	Lower Bound	Upper Bound	N
1.4	416	7	402	429	24
2.4	510	3	503	517	55
3.4	626	19	588	664	8
4.4	632	16	601	664	6
5.4	739	24	692	785	2

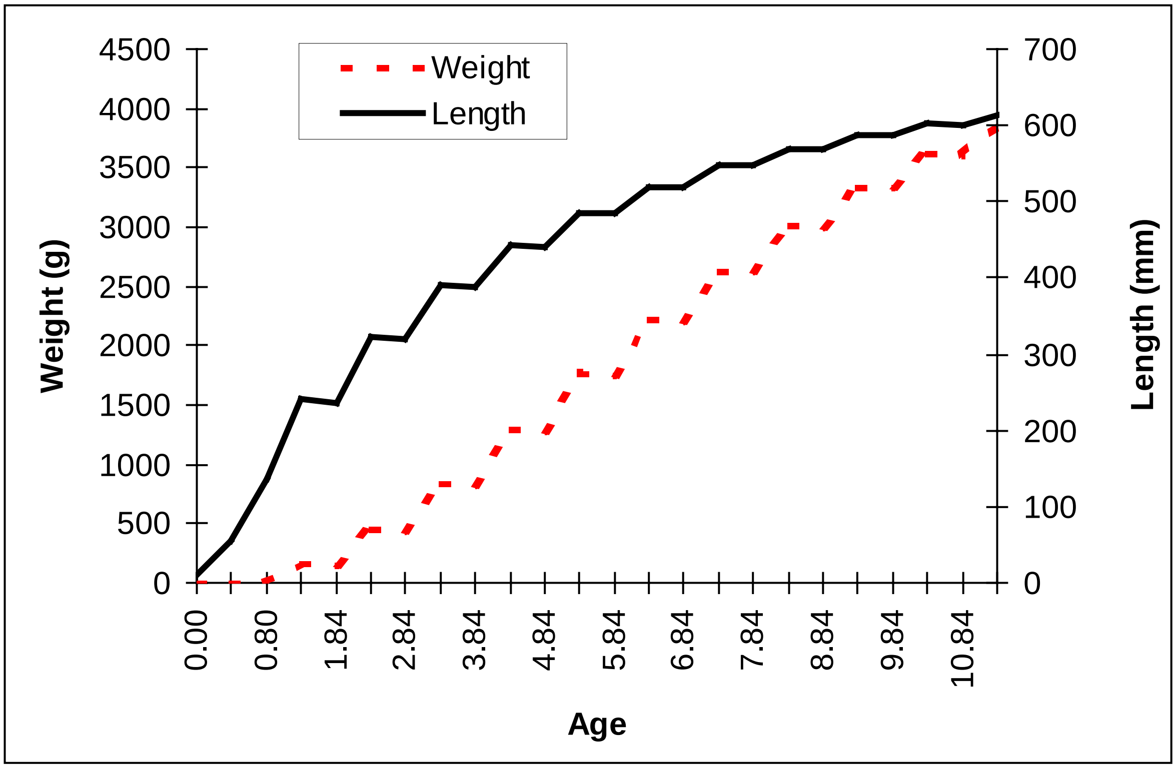

Figure 2.3. Median length and weight-at-age for modeled largemouth bass over their lifetime. Data points for age-1 and older individuals are taken at 15 April and 1 November of each year. Using model terminology, largemouth bass have a birthday on June 15 of each year, so on April 15, 0.84 years have elapsed since their last birthday.

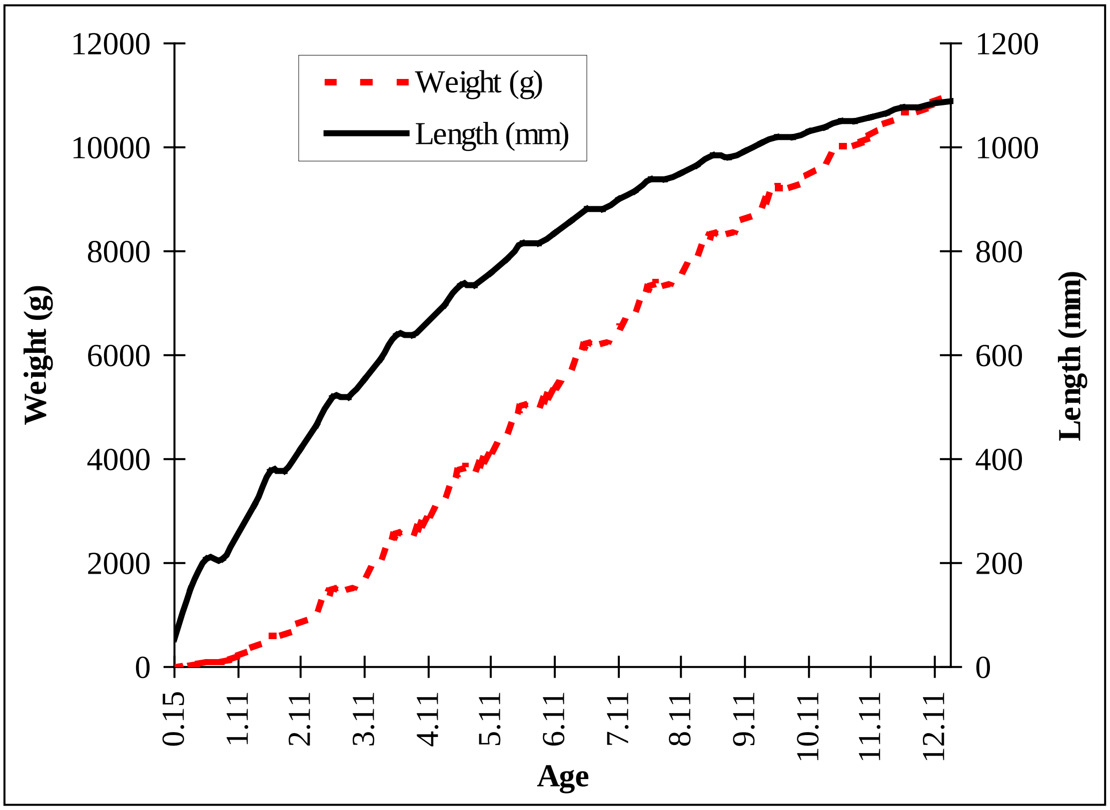

Figure 2.4. Median length and weight-at-age for modeled striped bass over their lifetime. Data points for age-1 and older fish are taken at 15 March, 1 June, 15 October, and 15 December of each year. Using model terminology, striped bass are considered “hatched” on May 1 of each year, so on June 1 it has been 0.11 years since their last birthday. At stocking time (considered to be June 15), YOY striped bass are 0.15 years old.

INDIVIDUAL CONSUMPTION

Quantitative estimates of consumption were of primary concern. These were tabulated for each age-class of largemouth and striped bass during the various seasonal growth stanzas occurring during a given year of life. The following tables and figures summarize the grams of each prey type consumed by an individual of a given species and age-class during a given season.

Largemouth Bass

Not surprisingly, consumption during the growth season for age-1 and older fish was almost four times consumption during the torpid season (Table 2.11). This period ran from 15 April to 1 November for fish age-2 and older and from 1 April to 1 November for age-1 largemouth. For age-0 fish this period ran only from June through July, so consumption was much lower than in the latter period. In both seasons total consumption by individuals increased with age. In the growth period consumption ranged from about 415 grams for age-1 fish to over 3100 grams eaten by age-10 fish. For adult largemouth bass during the growth season diet breadth was rather wide, with alewife, gizzard shad, crayfish, and other fish species composing nearly equal portions of all items consumed. Age-1 fish derived most of their nutritional requirements from age-0 gizzard shad during this period. Age-0 largemouth bass ate primarily non-clupeid fishes and benthic invertebrates.

For age-1 and older individuals the torpid period began on 1 November and ran until 15 April. For age-0 fish this inappropriately-named period was from 15 August to 1 April. For largemouth age-2 and older gizzard shad were the primary prey item in this season followed by crayfish and non-clupeid fishes (Table 2.11). Alewife were not consumed in great quantities. Age-1 largemouth consumed nearly equivalent quantities of crayfish and gizzard shad with lesser contributions from non-clupeid fishes and alewife. Age-0 fish relied most heavily on non-clupeid fishes but some gizzard shad, crayfish, insects, and alewife were consumed. Annual consumption ranged from 56 grams for age-0 fish to 840 grams for age-10 individuals.

Annual consumption increased as largemouth bass aged but the rate of increase declined (Figure 2.5). Crayfish, gizzard shad, alewife, and other fish were all primary prey of adult largemouth bass. Annual consumption peaked at about 4000 grams for an age-10 fish. This compares with only five hundred grams eaten by an age-1 individual. By taking the average weight of age-0 alewife, adult alewife, and gizzard shad ingested by largemouth bass (2.5, 13, and 3.33 grams, respectively), determined from my own diet analyses and Moore (1988), I could calculate the number of alewife and shad eaten by various ages of largemouth bass in a single year. These values increased from cohort to cohort and ranged from one alewife and two gizzard shad for an age-0 bass to 67 alewife and 335 gizzard shad for an age-10 bass.

Table 2.11. Individual largemouth bass consumption (grams) of each prey item during the growth and torpid seasons.

Growth						
Cohort	Alewife	Gizzard Shad	Crayfish	Miscfish	Other	Total
YOY	0	0	0	2.9	0.6	3.5
1	8.2	308.2	37.1	63.5	0.9	417.9
2	220.7	235.8	290.5	207.6	0.0	954.6
3	358.5	355.0	435.4	323.2	0.0	1472.3
4	480.3	456.5	558.4	423.3	0.0	1918.5
5	579.3	537.0	655.9	503.8	0.0	2276.0
6	656.5	598.6	730.3	565.8	0.0	2551.3
7	715.5	645.0	786.2	612.9	0.0	2759.6
8	759.6	679.0	827.3	647.7	0.0	2913.7
9	792.1	703.7	857.0	673.2	0.0	3026.0
10	816.9	722.5	879.6	692.7	0.0	3111.8

Torpid						
Cohort	Alewife	Gizzard Shad	Crayfish	Miscfish	Other	Total
YOY	2.3	7.5	5.2	37.7	2.8	55.5
1	6.5	35.4	38.5	12.6	0.0	93.1
2	11.8	94.7	60.0	34.9	0.0	201.4
3	18.1	144.8	91.9	53.5	0.0	308.2
4	24.3	194.3	123.3	71.9	0.0	413.8
5	30.1	240.0	152.4	88.9	0.0	511.4
6	33.2	242.1	152.5	84.0	0.0	511.7
7	37.3	272.1	171.5	94.4	0.0	575.3
8	41.1	299.6	188.8	104.0	0.0	633.5
9	46.8	373.0	236.9	138.3	0.0	795.1
10	49.5	394.0	250.3	146.1	0.0	840.0

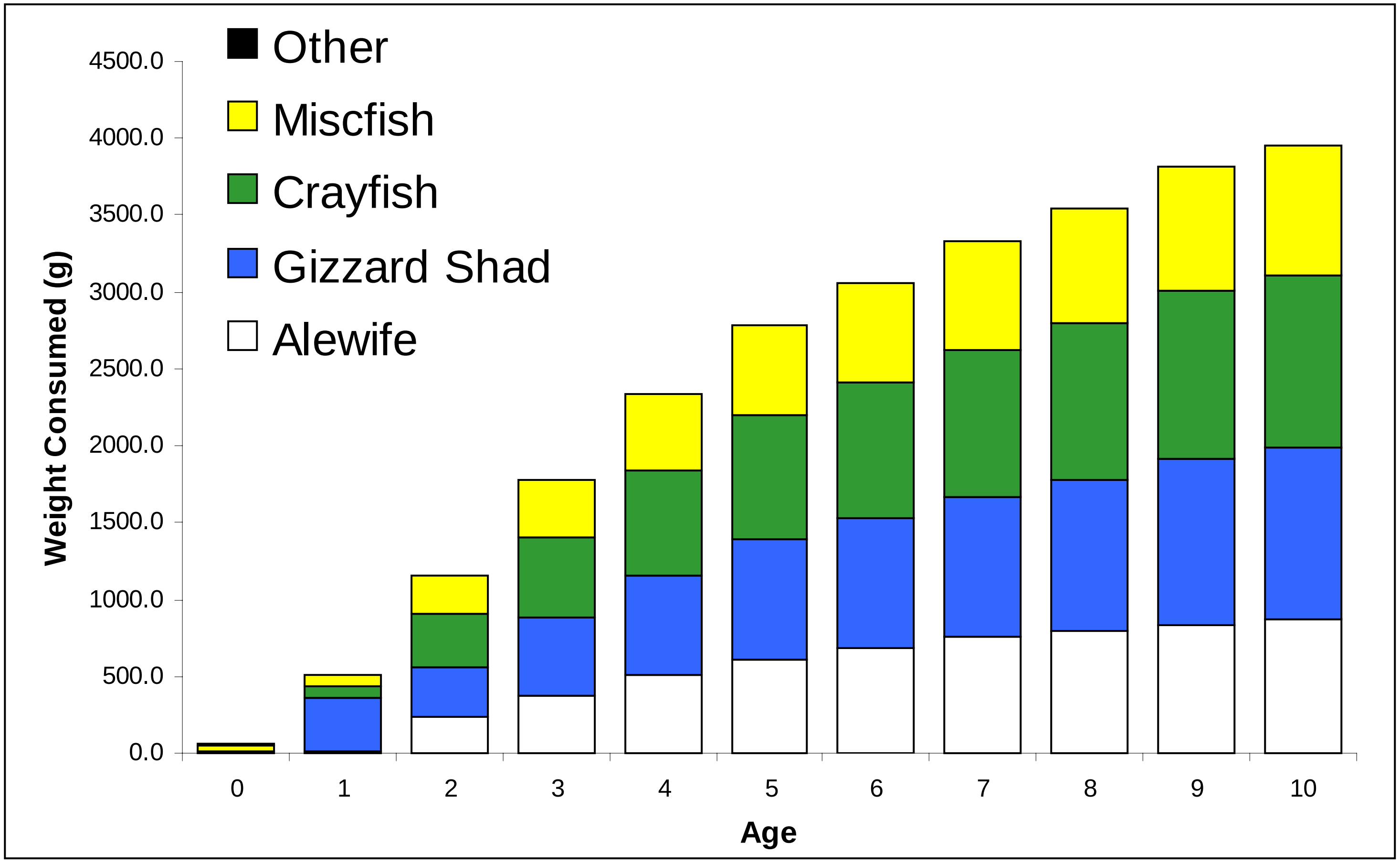

Figure 2.5. Annual consumption (grams/year) by individuals of each cohort of largemouth bass.

Striped Bass

Consumption by striped bass was estimated during four seasons: spring, summer, fall, and winter. In each season individual consumption increased as fish aged. The spring period began on 15 March and ended on 1 June for all cohorts except age-0 fish, which were not stocked into the system until 15 June. Individuals consumed primarily alewife during this period, especially age-1 striped bass (Table 2.12). For older striped bass gizzard shad were also a primary component of ingested prey taxa. Both crayfish and non-clupeid fish contributed only minor amounts. Total consumption during the spring period ranged from approximately 320 grams for age-1 fish to about 4.6 kilograms for age-10 fish.

The summer period for age-1 and older striped bass began on 1 June and ended on 15 October. For both small and large YOY the period began with stocking on 15 June and ended on 15 October. For age-2 and older fish alewife made up more than half of the diet, while shad were about 30% and crayfish were 12.5% (Table 2.12). Age-1 striped bass ate mainly alewife while small age-0 fish ate primarily non-clupeid fishes and insects. Large age-0 striped bass ate non-clupeid fishes and alewife after an initial post-stocking period where benthic invertebrates were primarily consumed. Consumption by individual large YOY was three times that of small YOY during the period. Consumption by older age-classes ranged from about 1200 grams for age-1 fish to approximately 13.7 kilograms for age-10 individuals. For age-1 fish summer consumption was almost four times that of spring consumption, while for older age-classes the former was about three times the latter.

For each cohort the fall period began on 15 October and ended on 15 December. Gizzard shad were about 75% of the diet amongst all cohorts except YOY (Table 2.13). Large YOY ate mainly alewife while the small YOY consumed primarily non-clupeid fishes. Consumption by large YOY was about five times that of small YOY. Adult striped bass continued to utilize alewife but only for about 23% of their diet. Consumption during the fall was greater than spring consumption for young individuals but this gap closed as striped bass aged. For fish age-6 and older spring consumption was actually greater than fall consumption.

The winter period began on 15 December and ended on 15 March for all cohorts. Alewife were the primary item consumed by large age-0 largemouth bass (Table 2.13). The dwindling numbers of small YOY continued to eat mainly non-clupeid fishes. Age-1 and older individuals ate primarily gizzard shad and alewife, the former making up more than twice the amount consumed compared to the latter. Individual consumption was lowest in winter, ranging from only 13 grams for small age-0 fish to just over 2.8 kilograms for age-10 fish.

Annual individual consumption also increased from cohort to cohort for striped bass, but at a slightly decreasing rate (Figure 2.6). Clupeids composed the bulk of striped bass diets for all age-classes but YOY. Age-1 fish consumed about twice as much alewife as gizzard shad biomass over the year, but this difference was not as great for older striped bass. For these individuals alewife made up about 51% of the diet, gizzard shad were about 40%, and crayfish were approximately 8%. Individual annual consumption ranged from a mere 100 grams for small YOY to over 25 kilograms for age-10 fish. I could calculate the number of each prey species consumed by individual striped bass annually given that the average age-0 alewife consumed by striped bass weighed 3 grams, the average adult alewife consumed weighed 15 grams, and the average gizzard shad weighed 7.5 grams. These values increased from cohort to cohort and for alewife ranged from approximately two age-0 alewife consumed by small YOY to 860 age-0 alewife and 690 adult alewife consumed by an age-10 striped bass. Numbers of gizzard shad ingested annually ranged from 0 for small YOY to about 1,350 for age-10 fish.

Table 2.12. Consumption (grams) of each prey item by individual striped bass during the spring and summer.

Spring						
Cohort	Alewife	Gizzard Shad	Crayfish	Miscfish	Other	Total
1	289.4	16.7	0.8	13.5	0.0	320.4
2	608.6	202.3	52.6	23.1	0.0	886.6
3	1028.8	346.0	86.7	39.3	0.0	1500.8
4	1447.0	488.2	121.2	55.4	0.0	2111.7
5	1835.9	620.5	153.2	70.4	0.0	2680.0
6	2180.9	737.9	181.6	83.7	0.0	3184.1
7	2482.9	840.8	206.4	95.3	0.0	3625.4
8	2741.6	929.0	227.6	105.3	0.0	4003.5
9	2962.3	1004.2	245.7	113.8	0.0	4326.0
10	3149.3	1067.9	261.0	121.0	0.0	4599.2

Summer						
Cohort	Alewife	Gizzard Shad	Crayfish	Miscfish	Other	Total
Small YOY	2.0	0.0	0.0	37.7	16.7	56.5
Big YOY	58.8	0.0	0.0	76.1	34.0	168.9
1	938.5	175.6	45.8	24.4	0.0	1184.3
2	1654.6	860.2	356.3	29.1	0.0	2900.2
3	2484.9	1280.4	536.2	43.5	0.0	4345.0
4	3492.7	1785.7	755.2	60.9	0.0	6094.5
5	4448.8	2263.4	963.1	77.3	0.0	7752.6
6	5324.0	2700.1	1153.5	92.3	0.0	9270.0
7	6102.6	3087.9	1323.0	105.6	0.0	10619.2
8	6785.9	3428.1	1471.7	117.4	0.0	11803.1
9	7374.7	3720.9	1599.9	127.4	0.0	12823.0
10	7880.1	3972.2	1709.9	136.1	0.0	13698.3

Table 2.13. Consumption (grams) of each prey item by individual striped bass during the fall and winter.

Fall						
Cohort	Alewife	Gizzard Shad	Crayfish	Miscfish	Other	Total
Small YOY	3.2	0.0	0.0	22.1	6.3	31.6
Big YOY	140.1	1.1	0.0	18.2	1.4	160.9
1	231.8	404.7	29.4	65.8	0.0	731.6
2	300.7	1001.7	2.6	17.1	0.0	1322.2
3	429.4	1431.5	3.8	24.4	0.0	1889.1
4	548.2	1816.7	4.8	31.1	0.0	2400.9
5	651.1	2149.5	5.7	37.0	0.0	2843.3
6	737.9	2429.8	6.4	41.9	0.0	3216.1
7	811.0	2665.4	7.1	46.1	0.0	3529.6
8	870.9	2858.6	7.6	49.5	0.0	3786.6
9	921.0	3019.8	8.0	52.4	0.0	4001.2
10	962.1	3151.9	8.4	54.7	0.0	4177.0

Winter						
Cohort	Alewife	Gizzard Shad	Crayfish	Miscfish	Other	Total
Small YOY	1.3	0.0	0.0	8.8	2.5	12.6
Big YOY	46.8	2.4	0.0	3.7	0.0	52.9
1	101.7	192.4	1.1	32.1	0.0	327.3
2	197.8	422.5	2.4	8.8	0.0	631.5
3	303.2	655.8	3.7	13.5	0.0	976.3
4	409.7	886.0	5.0	18.3	0.0	1318.9
5	510.6	1104.0	6.3	22.8	0.0	1643.7
6	603.0	1303.6	7.4	26.9	0.0	1940.8
7	685.0	1480.8	8.4	30.5	0.0	2204.8
8	758.0	1638.5	9.3	33.8	0.0	2439.6
9	820.8	1774.1	10.1	36.6	0.0	2641.6
10	874.9	1890.8	10.7	39.0	0.0	2815.4

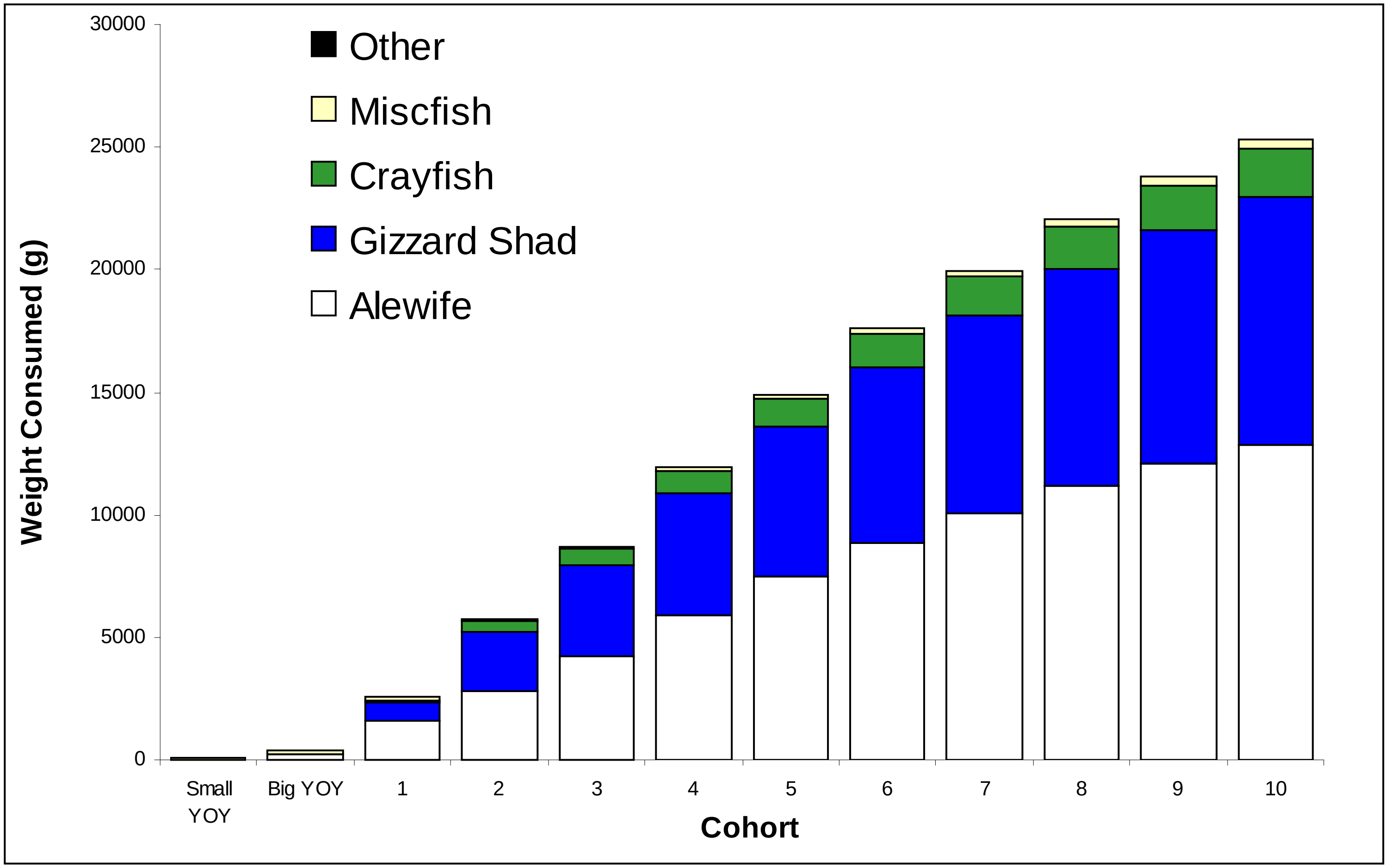

Figure 2.6. Annual consumption (grams/year) by individuals of various cohorts of striped bass.

POPULATION ABUNDANCE

Once individual consumption had been estimated, numbers-at-age for largemouth bass and striped bass were used to derive estimates of population consumption. For striped bass annual stocking numbers were coupled with estimates of striped bass annual mortality to accomplish this task. After stocking 300,000 fingerlings cohort size dips below 10,000 individuals during the winter after their fourth growth season (Table 2.14). Early into their seventh growth season the cohort was reduced to fewer than 1000 fish. At the end of their eleventh growth season the cohort has only about ten members remaining. These estimates are typical of a cohort of striped bass in SML, but not necessarily the pattern that all cohorts would follow.

Numbers-at-age derived from rotenone data indicated that survival for largemouth bass between late August of their first growth season and late August of their second growth season was approximately 8%. For the next two years annual survival of bass was approximately 60%. This value was also used for annual survival of older bass. I recreated the typical largemouth bass population in SML given the estimates of numbers-at-age for largemouth bass ages 0-3 from rotenone and these estimates of annual mortality rates (Table 2.15). The number of age-0 bass in mid-August was the starting point for the cohort because no attempt to estimate survival from hatching to mid-August was made. In early November of their first year almost 840,000 bass were present. One year later that number was down to approximately 98,000. About 10,000 members of the cohort remained at the beginning of their seventh growth season and numbers sank below 1,000 individuals near the end of their eleventh growth season.

Table 2.14. Numbers at various times during the year for modeled age-classes of striped bass. Age-0 cohort numbers include both “big” and “small” individuals. Age-1 individuals on March 15 are entirely composed of formerly-labeled “big” YOY.

Age	15-Mar	15-Jun	15-Oct	15-Dec
0		300000	200823	165270
1	96066	82840	63985	56986
2	48033	41420	31992	28493
3	24017	19419	13407	11355
4	8886	7185	4961	4201
5	3288	2659	1835	1554
6	1217	984	679	575
7	450	364	251	213
8	167	135	93	79
9	62	50	34	29
10	23	18	13	11

Table 2.15. Numbers-at-time for various ages of Smith Mountain Lake largemouth bass, determined from cove rotenone surveys and estimated mortality rates.

Age	**15-April**	**1-November**
0	*	838747
1	263958	97882
2	77699	58729
3	46619	35237
4	27972	21142
5	16783	12685
6	10070	7611
7	6042	4567
8	3625	2740
9	2175	1644
10	1305	986

POPULATION CONSUMPTION

Largemouth Bass

From a population perspective alewife, shad, crayfish, and non-clupeid fishes all played significant roles as prey items. During the growth season over 60 thousand kilograms of each was consumed by age-1 and older largemouth bass (Table 2.16). Consumption was greatest for age-2 largemouth, followed by age-3 fish, age-1 fish, and age-4 fish. Over 70% of total population consumption was done by fish age-4 and younger.

Consumption by age-0 individuals during this period could not be estimated accurately because their initial density was unknown. I generated consumption estimates using a range of survival values from time of hatching to mid-August. These estimates varied inversely with survival values because the lower the survival, the more individuals must have hatched to lead to a given number of survivors in August. If survival from hatching to mid-August was as low as 1% consumption for age-0 fish during this period was almost 30,000 kilograms. If survival increased ten-fold to 10%, consumption dropped considerably to 9,500 kg. If survival was as high as 50%, consumption was just under 5,000 kilograms. Finally, if survival was 75% consumption was 4,300 kg. Regardless the magnitude of their consumption, bass during this period preyed entirely upon invertebrates and non-clupeid fishes and thus had no direct impact on clupeid populations.

Population consumption during the torpid season was less than a third of consumption during the growth season (Table 2.16). Age-0 fish consumed the most food during this period but the time encompassed is very different for this cohort, so comparisons to other cohorts are not valid. Among the other age-classes patterns of consumption were identical to the growth period: age-2 fish consumed the most, followed by age-3 fish, age-1 fish, and age-4 fish. Due to the prominence of age-0 consumption non-clupeid fishes were eaten in greatest quantity. Disregarding this fact, gizzard shad and crayfish provided the bulk of the largemouth bass diet for age-1 and older individuals.

Total annual consumption for the entire largemouth bass population was about 400,000 kilograms, or just over 48 kg/ha (Figure 2.7). This is an underestimate because consumption by age-0 individuals during their first three months of life was not included. Depending on their survival during this period, consumption could increase anywhere from one half to almost four kilograms per hectare. Without this consumption factored in age-2 individuals were the top consumers at almost 75,000 kg. Consumption declined for each cohort after age-2, reaching a nadir at age-10 with about 4,250 kg consumed. For the entire population gizzard shad, non-clupeid fishes, and crayfish were eaten in the greatest quantities but alewife were not far behind. Age-2 and older bass had a balanced diet, utilizing shad, alewife, crayfish, and other fish in nearly equal proportions. Age-1 bass consumed mainly shad while age-0 fish ate primarily non-clupeid fishes. The largemouth bass population consumed 8.5 kg/ha of alewife annually and 14.8 kg/ha of gizzard shad. I divided the weight of clupeids consumed by the largemouth bass population by the average weight of alewife and gizzard shad eaten to estimate that about 700,000 age-0 alewife, 6.2 million adult alewife, and 37.4 million gizzard shad were consumed annually.

Table 2.16. Consumption (kilograms) by various cohorts of largemouth bass during the growth and torpid seasons.

Growth						
Cohort	Alewife	Gizzard Shad	Crayfish	Miscfish	Other	Total
YOY	*	*	*	*	*	*
1	1551	36750	4830	8762	156	52049
2	15346	15257	18726	13879	0	63209
3	15011	13841	16905	13023	0	58780
4	12088	10704	13035	10258	0	46084
5	8759	7567	9198	7334	0	32858
6	5960	5066	6151	4948	0	22125
7	3899	3277	3976	3218	0	14370
8	2484	2071	2511	2041	0	9108
9	1555	1289	1561	1273	0	5678
10	962	794	962	786	0	3504
Total	67616	96616	77855	65522	156	307764

Torpid						
Cohort	Alewife	Gizzard Shad	Crayfish	Miscfish	Other	Total
YOY	1084	3495	2448	33001	2747	42776
1	526	3259	3453	1063	0	8302
2	572	5133	3191	1790	0	10686
3	527	4709	2929	1645	0	9810
4	425	3791	2359	1326	0	7902
5	316	2810	1749	984	0	5859
6	208	1718	1061	559	0	3545
7	140	1159	716	377	0	2392
8	93	765	473	249	0	1580
9	64	566	352	198	0	1180
10	40	359	223	126	0	748
Total	3995	27765	18954	41320	2747	94781

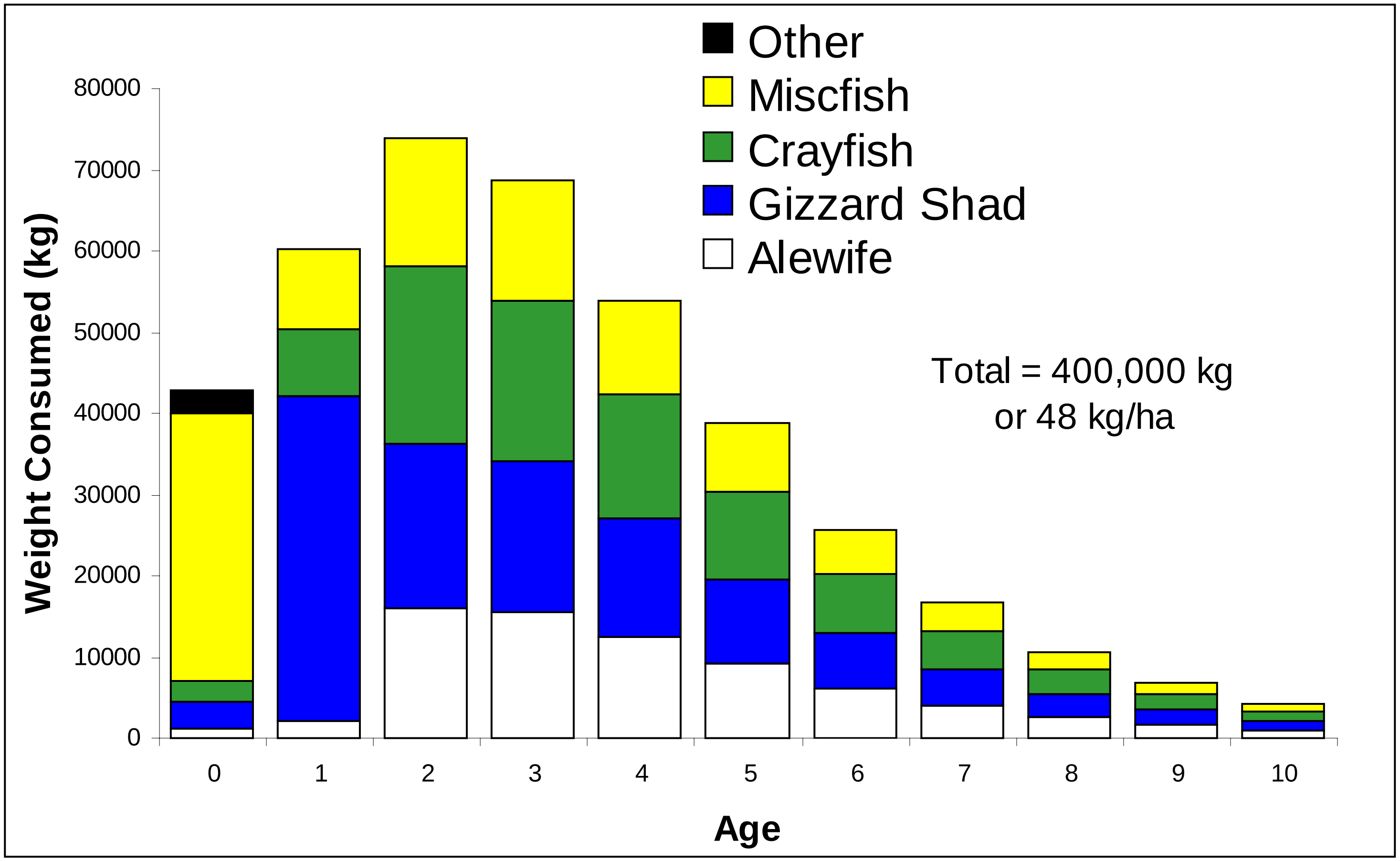

Figure 2.7. Annual consumption (kilograms/year) by each cohort of largemouth bass.

Striped Bass

During the spring the striped bass population consumed about 130,000 kilograms of prey items and age-2 fish contributed the largest share, just ahead of the age-3 cohort (Table 2.17). Alewife dominated the diet during this period and nearly 95,000 kilograms were consumed. In comparison, gizzard shad consumption totaled approximately 25,000 kilograms. Consumption during the summer was 2.8 times as much as during the spring (Table 2.17). Age-2 fish were again responsible for the largest amount followed by the age-1 and age-3 cohorts. During summer both large-mode and small-mode age-0 striped bass combined to consume only about 32,000 kilograms. Alewife and gizzard shad again were the primary forage with the biomass of alewife consumed almost three times that of gizzard shad. Crayfish, although still only a supplemental prey item, were eaten in relatively greater quantities than in any other season.

Fall brought a decrease in population consumption when compared to summer, but at approximately 150,000 kg it was higher than spring consumption (Table 2.18). Consumption by age-0 striped bass is non-existent during the spring period, however. In autumn the age-1 cohort contributed the largest amount to population consumption followed closely by the age-2 cohort, the age-3 cohort, and large-mode YOY. Alewife biomass consumed by the striped bass population was 60% of gizzard shad biomass eaten. It would have been only 38% if not for large age-0 striped bass, whose dietary requirements were almost entirely met by feeding on alewife. Consumption during winter was lower than during other seasons, totaling only about 59,000 kilograms (Table 2.18). As top consumers, age-1 and age-2 cohorts ingested nearly the same weight of prey items. Large YOY consumed only about 5,900 kilograms during the period and declining numbers of the small YOY ate only about 100 kilograms of prey. As in the fall, gizzard shad and lesser amounts of alewife made up the bulk of the diet for age-1 and older bass while large YOY consumed primarily alewife.

The age-2 cohort consumed the greatest amount on an annual basis and consumption declined for every subsequent cohort (Figure 2.8). Age-1 consumption placed between age-2 and age-3 consumption. Neither size of age-0 fish consumed a great amount on an annual basis but, as expected, large YOY ate much more that small YOY. Not only was their growth rate much greater but they were more numerous. Total population consumption was approximately 700,000 kilograms annually or about 84 kg/ha. Alewife were the bulk of this, amounting to approximately 387,000 kilograms or 47 kg/ha. Consumed gizzard shad biomass totaled 227,000 kg or approximately 27 kg/ha. These estimates indicate that annual striped bass population consumption is more than 75% greater than largemouth bass. If annual consumption estimates for striped bass are translated into numbers of age-0 alewife, adult alewife, and gizzard shad eaten annually, values of 36, 19 and 30 million are produced, respectively. Compared to largemouth bass, striped bass consume more than fifty times as many age-0 alewife annually and more than three times as many adult alewife. Largemouth bass consume about 7 million more gizzard shad despite the fact that striped bass eat 103,000 more kilograms of gizzard shad annually. The perplexing outcome can be explained, however, because the average-sized gizzard shad consumed by striped bass is more than twice as heavy as the averaged-sized shad consumed by largemouth bass.

Table 2.17. Consumption (kilograms) by various cohorts of striped bass during spring and summer.

Spring						
Cohort	Alewife	Gizzard Shad	Crayfish	Miscfish	Other	Total
1	25393	1480	68	1190	0	28130
2	26761	8984	2269	1021	0	39036
3	21854	7459	1790	842	0	31945
4	11371	3893	926	439	0	16629
5	5341	1832	433	206	0	7812
6	2349	807	190	91	0	3436
7	989	340	80	38	0	1447
8	405	139	33	16	0	593
9	163	56	13	6	0	238
10	64	22	5	2	0	94
Total	94689	25012	5807	3852	0	129360

Summer						
Cohort	Alewife	Gizzard Shad	Crayfish	Miscfish	Other	Total
Small YOY	124	0	0	2715	1279	4118
Big YOY	9119	0	0	12812	5855	27785
1	68861	12070	3195	1753	0	85878
2	61071	30136	13331	1039	0	105576
3	41019	19608	9017	684	0	70329
4	21356	10129	4703	355	0	36543
5	10074	4755	2221	167	0	17216
6	4463	2100	984	74	0	7622
7	1893	889	418	31	0	3231
8	781	366	172	13	0	1332
9	314	147	69	5	0	536
10	121	57	27	2	0	206
Total	219196	80256	34137	19649	7134	360372

Table 2.18. Consumption (kilograms) by various cohorts of striped bass during fall and winter.

Fall						
Cohort	Alewife	Gizzard Shad	Crayfish	Miscfish	Other	Total
Small YOY	158	0	0	1108	317	1583
Big YOY	18795	146	0	2475	205	21621
1	14253	24383	1811	3939	0	44386
2	9242	30326	80	525	0	40174
3	5437	17737	47	309	0	23529
4	2430	7880	21	138	0	10469
5	1129	3648	10	64	0	4851
6	474	1526	4	27	0	2031
7	192	619	2	11	0	824
8	77	246	1	4	0	328
9	30	95	0	2	0	127
10	12	38	0	1	0	51
Total	52228	86644	1976	8603	521	149973

Winter						
Cohort	Alewife	Gizzard Shad	Crayfish	Miscfish	Other	Total
Small YOY	10	0	0	67	19	96
Big YOY	5180	260	0	412	0	5852
1	5210	10276	55	1732	0	17273
2	5069	11308	63	226	0	16665
3	2959	6823	37	132	0	9951
4	1479	3410	18	66	0	4974
5	682	1572	9	30	0	2293
6	298	687	4	13	0	1002
7	125	289	2	6	0	422
8	51	119	1	2	0	173
9	20	47	0	1	0	69
10	8	19	0	0	0	28
Total	21092	34809	188	2688	19	58796

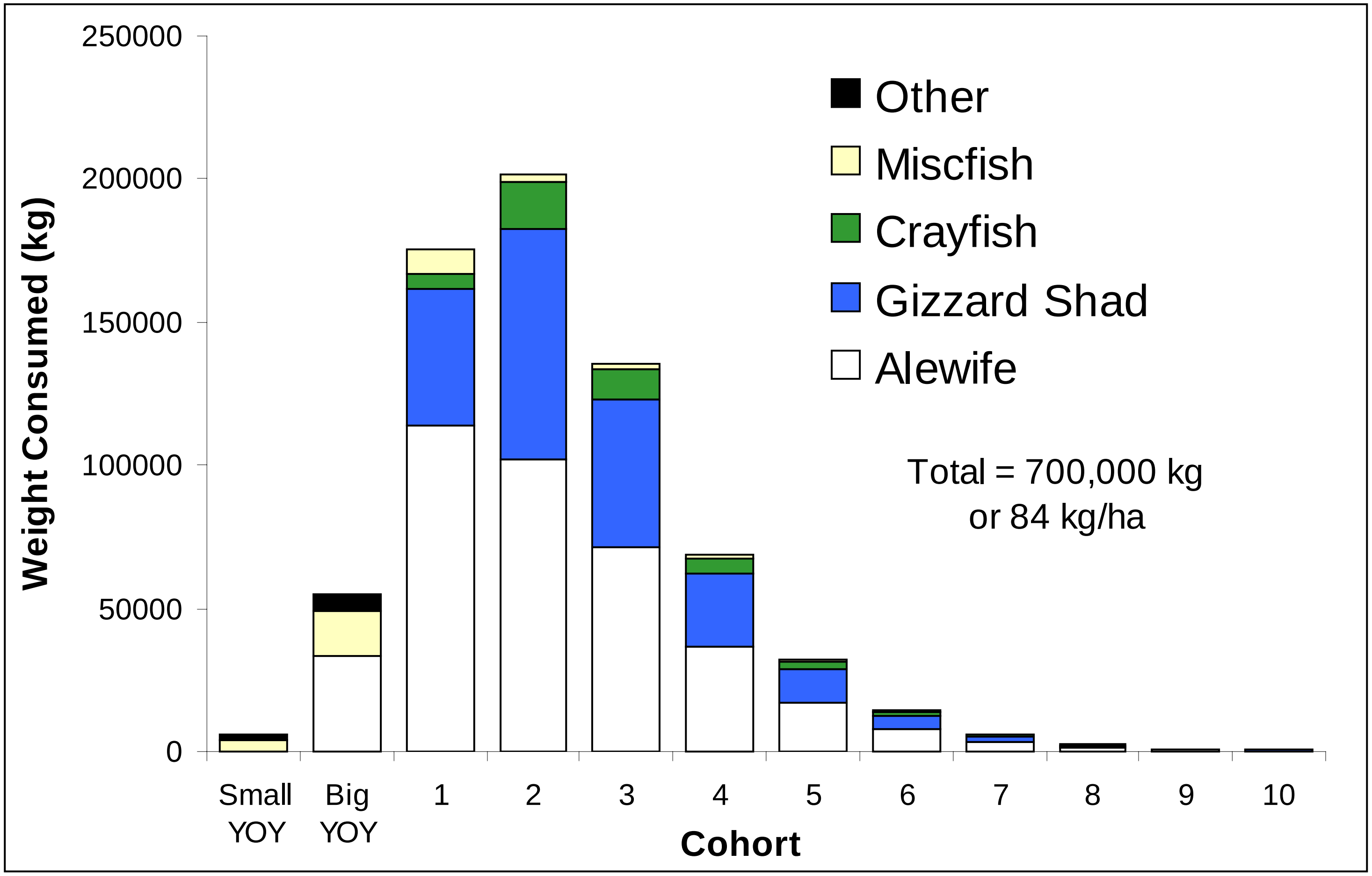

Figure 2.8. Annual consumption (kilograms/year) by each cohort of striped bass.

ANCILLARY MODEL OUTPUT

Food Conversion Efficiency

Food conversion efficiencies, or the ratio of growth that occurs to the weight of food consumed, are important model output to examine. Extremely high or low efficiencies can be an indication of poor model specification. Estimates of the conversion efficiency for both largemouth bass and striped bass were made for each of the seasonal periods modeled and for each cohort within each species.

For largemouth bass during the "growth" season (approximately April through October for age-1 and older bass), the expected pattern of declining efficiency with age was seen (Figure 2.9). Efficiency varied from about 34% for age-0 and age-1 fish to only 9% for age-10 individuals. Efficiencies during the "torpid" season were negative values for all but age-0 largemouth bass because weight was lost over this timespan. For age-0 bass, however, the period spanned from 15 August to 1 April and total conversion efficiency was estimated at almost 43%. Age-0 largemouth bass were most efficient on an annual basis, converting over 40% of ingested matter to body weight. There was a sharp decline to 28% for age-1 fish and then a steady decrease throughout successive cohorts, bottoming out with age-10 fish, which operated at about 7% efficiency for the year. Taking a weighted average of efficiencies (numbers-at-age used as the weights) led to an annual population efficiency of approximately 35% if the large number of age-0 fish were included, and 23% if not.

Striped bass food conversion efficiencies as determined by the bioenergetics model also declined with age. Food conversion values were generally lower than those of largemouth bass (Figure 2.10). During the spring efficiencies ranged from 30% for age-1 fish to 5% for age-10 fish. Age-0 fish were not stocked until 15 June and so were not included in this period. Summer efficiency of small YOY was 10% while for large YOY it was 28%. During this period small YOY ate mainly benthic invertebrates which provide a lower percentage of assimable energy than the fish that large YOY consumed. Age-1 fish had a conversion efficiency of 13% and efficiency declined steadily to 2% for age-10 individuals. Conversion efficiency was highest in the fall and ranged from almost 44% for large YOY to about 7% for age-10 individuals. Large YOY again had much greater efficiency than small YOY. Small age-0 fish lost a great deal of weight during the winter and as a result had a large negative conversion efficiency. All other age classes had nearly zero efficiency because weight was only maintained, not increased. As a percentage of body weight, however, it took less prey to maintain an individual's weight over the winter. An age-1 fish had to consume more than 50% of its body weight over winter in order not to lose weight, while an age-10 individual had to consume only 28% of its body weight to accomplish the same task.

For small YOY annual efficiency was just under 10%, while it was more than three times as high for large YOY. I attributed this difference to a diet of invertebrates for the former versus a diet of fish for the latter. For age-1 striped bass annual conversion efficiency was about 21% and declined to 3% for age-10 fish. Using the same weighted-average technique as performed on largemouth bass (numbers-at-age used as the weights), annual food conversion efficiency for the entire striped bass population was found to be approximately 23%. If age-0 striped bass were excluded population conversion efficiency was 16%.

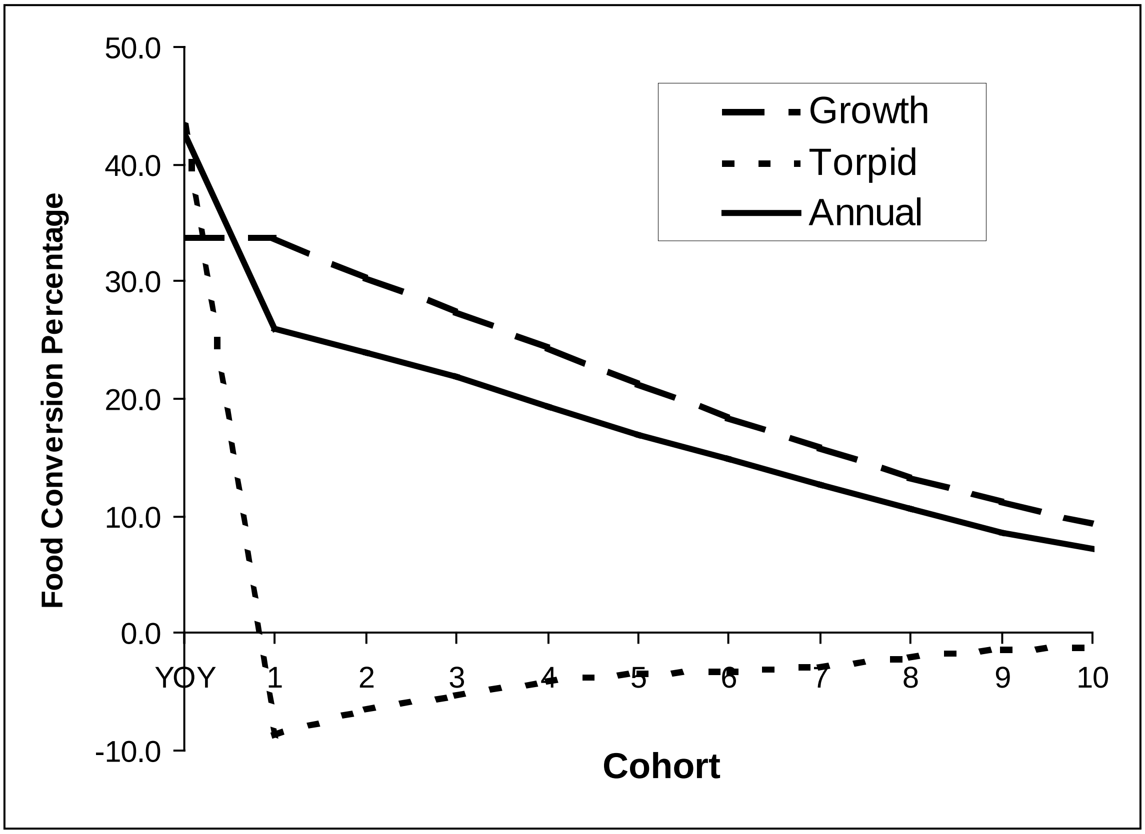

Figure 2.9. Seasonal and annual food conversion efficiencies for largemouth bass.

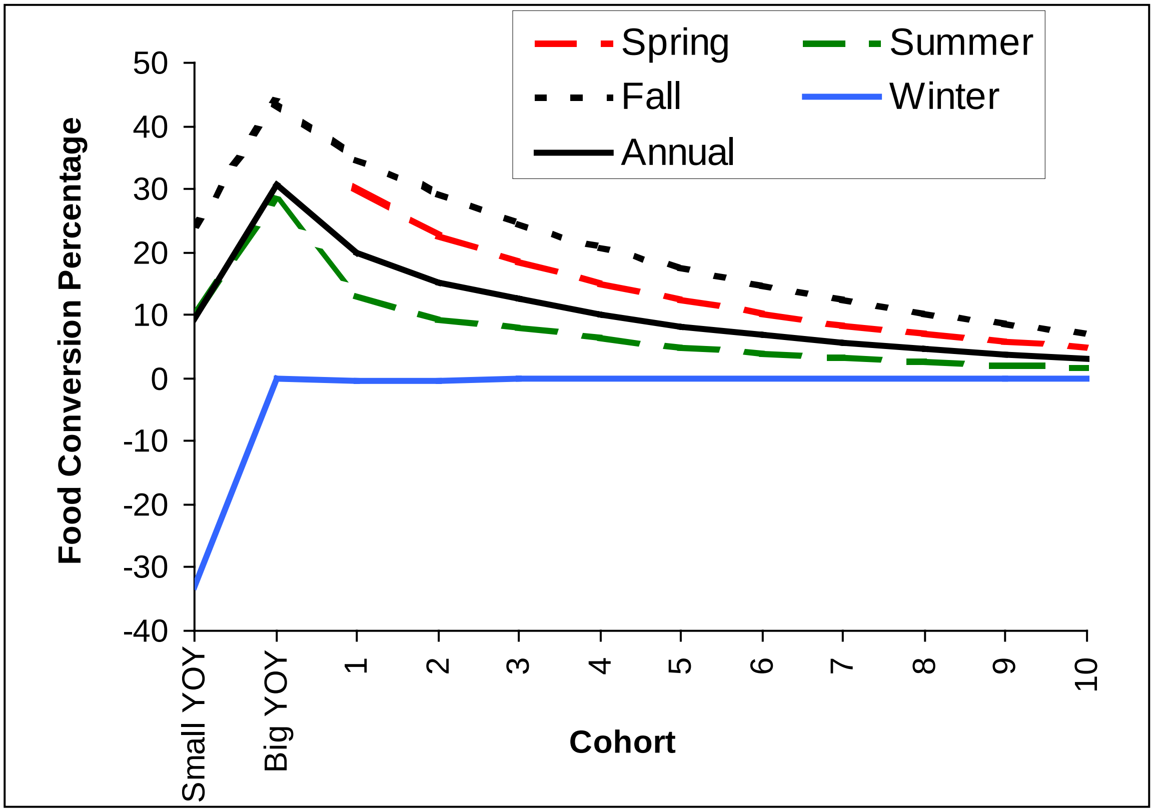

Figure 2.10. Seasonal and annual food conversion efficiencies for striped bass.

Predator P Values

The bioenergetics software uses a proportionality constant (P) to model the proportion of maximum daily ration realized. An iteratively-adjusted P value allows the user-defined end weight to be precisely attained. Once the appropriate P value has been determined it is used for each day during the modeled period. P values thus would be changed daily if starting and ending weights were input on a daily basis. If starting weight is input for day 1 and the ending weight is given for day 50, only one P value would be used. Ecological interpretations of these values are plentiful but some consensus has been reached that they reflect prey availability and can be used as an index of the feeding efficiency of the predator (Cochran and Rice 1981; Rice et al. 1983; Hanson et al. 1997).

The P values determined for largemouth bass during both the growth and torpid seasons ranged from 0.5 for age-0 fish during their first summer to 0.25 for age-10 fish during the growth season (Figure 2.11). A value of 0.5 means that each day the individual consumed 50% of the its maximum ration, the latter being a function of the individual's physiology, body weight, and environmental variables such as water temperature. Largemouth bass P values declined from cohort to cohort during the "growth" season but showed a slightly more complex pattern during the torpid season. The P values were greater during the growth season as compared to the torpid season for age-0 to age-5 fish but the reverse was true for age-6 to age-10 individuals.

Similar patterns in P values were seen for striped bass (Figure 2.12). These P values in spring, summer, and fall generally declined from age-0 to age-10. During the coldest period of the year, however, P values were highest for the oldest fish and declined with decreasing age. Age-0 striped bass had the highest P values in summer while age-1, age-2, and age-3 fish had the highest values in the fall. P values were greatest during winter for striped bass age-4 and older. Estimates ranged from 0.60 for large YOY in summer to 0.28 for the oldest two age-classes in spring.

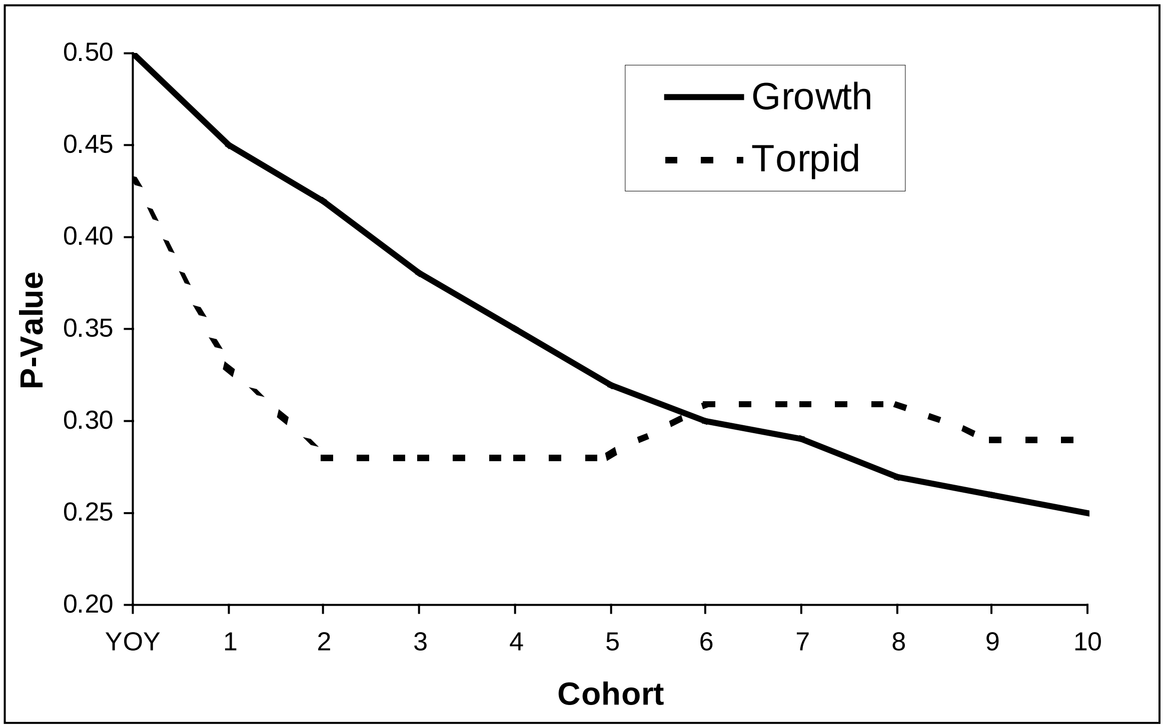

Figure 2.11. Seasonal P values for largemouth bass determined from the bioenergetics software to insure modeled ending weight matches user-input ending weight for an individual predator.

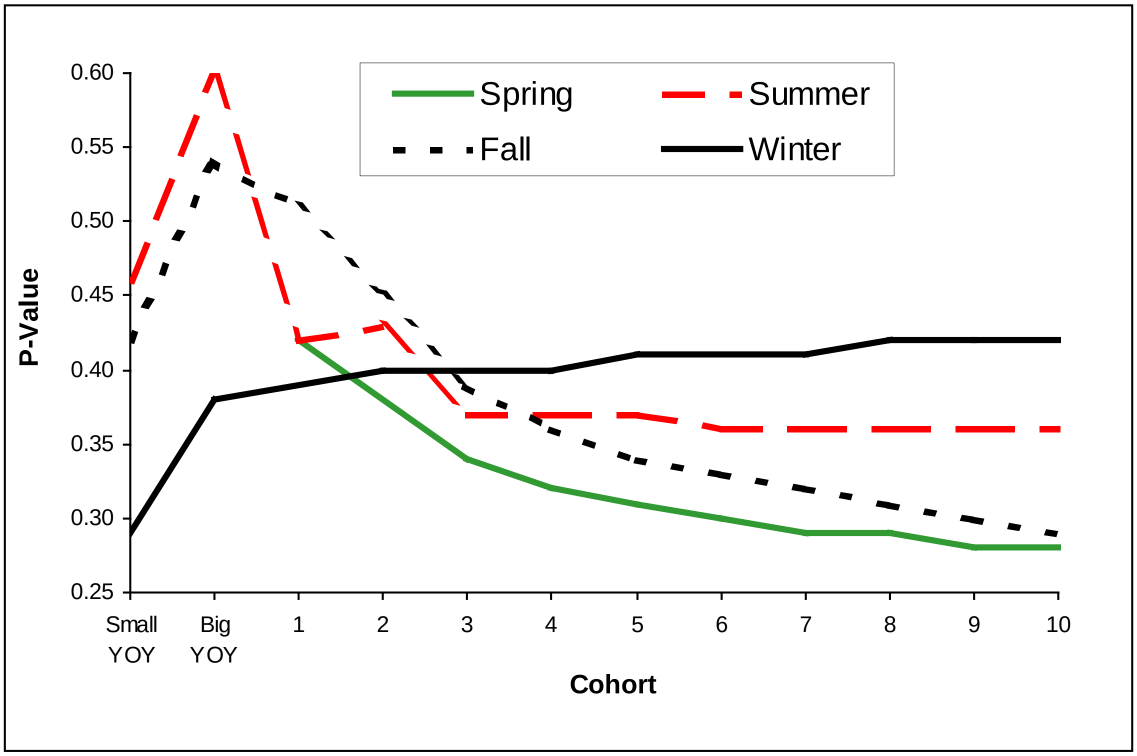

Figure 2.12. Seasonal P values for striped bass determined from the bioenergetics software to insure modeled ending weight matches user-input ending weight for an individual predator.

CONSUMPTION BY SECONDARY PREDATORS

Estimated total annual consumption (kg/ha) by catfish, crappie, smallmouth bass, walleye, and muskellunge was approximately 163 kg/ha (Table 2.19). Thirteen kg/ha of this amount was alewife biomass and 35 kg/ha was gizzard shad. Catfish and crappie were responsible for over 97% of the consumption by ancillary predators. Smallmouth bass had only 3 kg/ha of annual consumption, and total consumption by muskellunge and walleye totaled only 1 kg/ha. The speculative nature of these estimates stem primarily from the uncertainty surrounding cove to open water expansion factors, C/B ratios, and diet proportions of these predatory groups (Table 2.7) was discussed in this chapter's methods section. Estimates of consumption by striped bass and largemouth bass, determined by bioenergetic modeling and more intensive attempts to quantify population dynamics, hypothetically should be more accurate.

Approximately 70% of the 68 kg/ha of alewife biomass ingested by predators annually could be attributed to striped bass. Largemouth bass, crappie, and catfish were second, third, and fourth in annual alewife consumption, albeit distantly. Striped bass and catfishes combined to eat 52 kg/ha of shad annually, while other predators consumed only 25 kg/ha. Ingestion of "other" items (predominantly non-clupeid fishes and crayfish) was led by the catfishes, with 68 kg/ha of annual consumption. Crappie were second, largemouth bass third, and striped bass were a distant fourth in this category. Catfish consumed more biomass on an annual basis than any other predator species. Striped bass were second, crappie third, and largemouth bass fourth.

Clupeids accounted for approximately 50% of the total prey "pie" for all SML game fishes. Alewife and gizzard shad still accounted for over 33% of the ingested material of game fishes if striped bass were ignored.

Table 2.19. Annual consumption (kg/ha/year) of the various prey types for the major piscivores in Smith Mountain Lake. The category "Other" includes primarily crayfish and non-clupeid fishes.

	Prey Species			
Predator	**Alewife**	**Shad**	**Other**	**Total**
Striped Bass	46.4	27.2	10.1	83.8
Largemouth Bass	8.6	14.9	24.8	48.3
Smallmouth Bass	1.2	1.0	0.9	3.1
Walleye	0.4	0.1	0.1	0.6
Catfish spp.	4.9	24.4	68.4	97.7
Crappie	6.1	9.2	45.9	61.3
Muskie	0.1	0.2	0.2	0.5
Total	68	77	150	295

DISCUSSION

ASSESSMENT OF INDIVIDUAL CONSUMPTION ESTIMATES

There are a number of model inputs that significantly affect the bioenergetic estimates of individual predator consumption. Although the physiological parameters that I used for striped bass and largemouth bass were derived from members of the same species, extrapolation to populations in other water bodies could introduce bias. Striped bass values (Table 2.1) were taken from Hartman and Brandt (1995a), who examined fish from Chesapeake Bay. The only changes made to their proposed values was in the optimum temperature for consumption and respiration for various age-classes. These values were replaced with those of Moore (1993), which were based on landlocked rather than anadromous striped bass populations (Coutant and Carroll 1980; Schaich and Coutant 1980). The values for largemouth bass were first presented in Rice et al. (1983) and have withstood critical scrutiny since that time (Bartell et al. 1986; Moore 1988; Whitledge and Hayward 1997). Undesirable "species borrowing" (Ney 1990) is generally avoided when modeling largemouth and striped bass. This term refers to the adopting of physiological parameters from ecologically or morphologically similar species when the species of interest has not been studied.

Error in the caloric content of predators could have led to bias in consumption estimates. The use of the caloric content of prey items ingested to determine predator caloric content could come under scrutiny. Stewart and Binkowski (1986), Stewart et al. (1983), and Elliott (1976) all indicate that predators can have significantly higher energy content than the prey they ingest. They even draw a distinction between food conversion efficiency and energy conversion efficiency due to this phenomenon. The energy content of striped bass in SML as directly determined by Moore (1988) ranged from 90% to 106% of the values I used.

Analyses showed that little difference in consumption estimates occurred when his values were substituted for my own.

Given reasonable physiological parameterization the most important input for accurately determining individual consumption via bioenergetics is predator growth rates (Ney 1990; Hanson et al. 1997). Errors in the estimation of individual consumption are restricted when using the Wisconsin bioenergetics model by accurate information on the growth history of the species under consideration (Bartell et al. 1986; Stewart and Binkowski 1986). The growth of largemouth bass and striped bass in their first five years, when the majority of population consumption occurs, was estimated using a large number of individuals collected in the 1990's from SML, and modeled growth matched empirical observations closely. The mean lengths-at-age for age-1 through age-10 largemouth bass in Maryland, North Carolina, and Virginia, reported in Carlander (1977), ranged from 94% to 102% of the values used in this study. Lengths-at-age of age-1 through age-10 striped bass in six Virginia reservoirs, reported in Carlander (1997), ranged from 93% to 103% of those used in this study.

One aberration in predator growth modeling was apparent. My model indicated that age-0 largemouth bass experienced near-constant growth from mid-August to early the following April. Over-winter growth of these relatively small predators would be unusual so another explanation must exist. A situation in which a bimodal size distribution of age-0 individuals develops as the growth season wears on (similar to striped bass in SML) is likely involved. Average size of age-0 largemouth bass collected in the late fall would then be somewhere between the large mode and small mode of fishes. The small mode fishes are gone when spring sampling occurs so average size increases and growth appears to have occurred. This very phenomenon has been seen in a number of largemouth bass populations in the United States (Aggus and Elliot 1975; Timmons et al. 1980; Adams et al. 1982b; Miranda and Hubbard 1994). These studies indicate that small age-0 individuals suffer much higher over-winter mortality than larger age-0 fishes. Size distributions of largemouth bass cohorts can therefore drastically change from late fall to early spring. If this phenomenon does occur in

SML, annual consumption estimates by age-0 largemouth bass would not be affected to a great degree because consumption by large YOY would be underestimated and consumption by small YOY would be overestimated. Age-0 largemouth bass also consumed very few clupeids and so were not extremely relevant to this investigation. The severity of the possible error should have been contained as long as growth was accurately depicted beyond the first growth season.

ASSESSMENT OF POPULATION CONSUMPTION ESTIMATES

Errors in population estimates of predators in SML could severely bias population consumption estimates, so some validation of the modeled population sizes and mortality rates had to be made. I estimated that the average annual number of legal striped bass in SML was approximately 31,200 fish, or 3.7 harvestable fish per hectare. This was accomplished by combining modeled numbers-at-age with growth rates for striped bass and using the Gaussian cumulative probability functions discussed earlier. A 1998 creel survey estimated that about 18,000 striped bass were harvested that year (M.C. Duval, VDGIF, unpublished data). Legal striped bass would have an annual fishing mortality of 58% and an annual natural mortality of about 5% (assuming total annual mortality of 63%). I estimated the average annual abundance of citation-sized striped bass (> 9.1 kg), which are a small subset of all legal fish, to be 285. Annual fishing and natural mortality of citation-sized striped bass was also estimated to be 58% and 5%, respectively, based on the average annual number of citations reported in the 1990's (approximately 165).

My mortality rate of 50% for pre-recruit striped bass was judged to be more plausible than Mike Duval's 1996 estimate of 70% given that these fish were not suffering fishing mortality, this mortality rate was supported by historic data (Moore 1988), and it produced numbers of legal and citation-sized striped bass that corroborate creel survey information. Gill-net sampling methods used to develop survival estimates for pre-recruits could be biased by gear selectivity for larger, older individuals, although experimental gill-nets utilizing a range of mesh sizes end-to-end were used to sample striped bass. Younger striped bass could have different behavior and distribution patterns which affect gillnet catches as well.

The 40% annual mortality used here for age-1 and older largemouth bass is equal to the estimate determined by Duval (1996) from catch curve analysis using 1993 electrofishing data. It also fell well within the range of annual survival rates of largemouth bass populations in other systems (8% - 80%, mean = 41%, Carlander 1977). In many of these systems fishing mortality was a large component of total mortality whereas in SML creel survey data indicate the black bass fishery is overwhelmingly catch and release (LaRoche and Duval 1993). The average natural mortality rates for bass populations reported in Carlander (1977) was 35%, which would be slightly lower than for bass in SML if absolutely no fishing mortality occurred. Adult largemouth bass in SML suffer less annual mortality relative to adult striped bass. This can likely be attributed to the catch-and-release habits of most black bass anglers on this system. The annual survival rate of this species will likely remain below that of largemouth bass as long as the striped bass fishery remains primarily harvest-oriented. Striped bass tend to be susceptible to angling-induced mortality, especially during the warmer summer months (Harrell 1988; Nelson 1998). Annual mortality therefore would still be expected to remain higher for these pelagic predators even if catch-and-release efforts of striped bass anglers increase.

I determined that approximately 244,000 largemouth bass over 200 mm TL are present in SML in November using largemouth bass growth rates. This body size, according to creel survey data (LaRoche and Duval 1993), is also the approximate size when largemouth first become susceptible to the gear of the majority of black bass anglers. The 1992 survey also indicated that approximately 135,000 black bass were caught (most were subsequently released) by anglers. An largemouth bass greater than 200 mm TL would have approximately a 55% chance of being captured each year (assuming each individual were caught at most once per year). The probability of an individual being caught would decrease if some individuals are caught multiple times in a given year. The extent of the reduction in capture probability would depend on the prevalence of multiple capture events for individuals. I estimated there to be 41 bass per lakewide hectare, and 163 bass per littoral hectare in SML, excluding age-0 fish and averaging population size in April and November. Carlander (1977) reported densities of bass in other reservoirs systems across the United States to range from just over one to almost 300 per hectare. The median value reported was approximately 47 bass per hectare, but the text was not always specific enough to determine if the estimates were for littoral or total lake area and what size/age of bass were included. My estimates for SML nonetheless appear reasonable. I estimated that the largemouth bass population in SML averages approximately 18 kg/ha annually using information on numbers-at-age and weight-at-age. Carlander (1977), summarizing studies in other North American reservoirs, reports a median and mean biomass of 8 and 19 kg/ha, respectively, with a range of 0.1 to almost 250.

Population consumption by striped bass and largemouth bass is dominated by young fishes. Many researchers (Moore 1988; Ney 1990; Rudstam et al. 1994; Hartman and Brandt 1995b) reported a similar demographic pattern for piscivorous fish populations. Consumption increases greatly from year to year on an individual basis, but this increase cannot counteract effects of the rapid decline in numbers-at-age, which leads to decreases in cohort consumption for older age-classes. It is therefore most important for researchers to accurately characterize the metabolism, growth, and diet for these younger life-stages. Similar estimation errors for older fish would have much less impact on prey demand calculations.

Seasonal consumption by striped bass varied considerably despite the modeling of constant weight gain throughout the growth season. Consumption during the summer far exceeded that of any other season. Elevated water temperatures in June, July, and August meant much larger respiration costs at this time of year. Much more food would have to be ingested than during cooler periods in order to attain a given weight increase during these months. It could be possible that weight gain for striped bass during the growth season is not linear but rather occurs primarily in spring and fall, with simple weight maintenance during the hottest months when striped bass are confined to sufficiently oxygenated waters of the hypolimnion in the lower lake. Simulations indicated that even if weight were only maintained, however, consumption by the striped bass population during the summer would still be slightly higher than consumption during spring and fall. Alewife were eaten nearly exclusively by temperature-restricted striped bass during the summer, so this prey population endured the majority of the increase in striped bass consumption.

There is little doubt that estimates of winter consumption by both striped bass and largemouth bass are most speculative. It was assumed that weight maintenance would occur during the coldest months. Moore (1988) found that lengths of adult largemouth bass did not significantly change from mid-December through March, but individual weight was not assessed. Coutant (1975) and Cox and Coutant (1981) indicate that growth of largemouth bass and striped bass below 10 °C is negligible. Lack of information on predator diets during winter adds to the uncertainty of consumption estimates during this season. The SML Striped Bass Club did turn in over 120 stomachs from striped bass caught during December through March but 80% were empty. The fact that fishermen had continued success, however, is an indication that these predators do indeed continue feeding during the coldest months of the year. Bioenergetic simulations have been shown to be most imprecise in winter (tending to overestimate consumption) due to bias in physiological parameters at cold temperatures (Minton and McLean 1982; Adams et al. 1982a; Hartman and Brandt 1995a). My estimates of winter consumption should thus be viewed as upper limits to consumption of these species in this season. Error induced from imprecise winter consumption would not be critical because winter consumption was only 8% of annual consumption for striped bass and 13% of annual consumption for largemouth bass.

CONVERSION EFFICIENCIES AND P VALUES

Conversion efficiencies for largemouth bass and striped bass followed expected patterns and had reasonable magnitudes. The pattern of declining food conversion efficiency with age is a common ecological phenomenon (Webb 1978; Adams et al. 1982a; Pauly 1986; Stewart and Binkowski 1986; Diana 1995). Metabolic and reproductive demands of older fish simply require a larger proportion of incoming energy relative to young fish. Lane et al. (1979) summarized a number of studies that reported food conversion efficiencies of fish ranging from 1% to over 60%, but most adult populations of piscivores are considered to operate in the vicinity of 20% (Ursin 1979; Diana 1995). The average conversion efficiency for age-1 and older striped bass in SML appeared to be approximately 20% less than this benchmark. A 20% conversion efficiency would be a slight underestimate for age-1 and older largemouth bass. Differences in diet, physiology, activity levels, behavior, and any number of other interacting forces could be responsible. The important result is that striped bass not only grow to greater sizes than largemouth bass, but must eat more food per gram of added mass. Striped bass population consumption thus is much greater than largemouth bass, even though largemouth bass are present in larger numbers in the system.

Both largemouth bass and striped bass had an average P value during the growth season in SML of approximately 0.35. The P values in fall were higher than in the spring. The appearance of age-0 prey fishes in late summer must lead to a higher availability of prey for most species of predators, especially younger piscivores. Winter P values tended to be the greatest of any season for older fish, possibly because maximum consumption levels were so low at cold temperatures that any consumption became a large percentage of the maximum. Moore (1988) also found that striped bass and largemouth bass had average P values of 0.35 across the growth season in SML. Miranda et al. (1998) found that the average P value for striped bass across the growth season was about 0.36 in Norris Lake, Tennessee. The largemouth bass population in their study had an average P value of 0.33. Rice et al. (1983) found that P values of adult largemouth bass in Par Pond, South Carolina, ranged from 0.16

to 0.75 over the year but did not report a mean value. Johnson et al. (1988) found that the largemouth bass population had an average P value of 0.42 during June through September in Kokosing Lake, Ohio. This is 20% higher than in SML, but their values do not include the spring period and P values in SML were lower at this time. Rice and Cochran (1984) report that age-3 largemouth bass in Lake Rebecca, Minnesota, had an mean P value of approximately 0.5 during the growth season. It is possible that latitudinal differences in annual thermal regimes could be responsible for the higher P values in Ohio and Minnesota. A given level of consumption in lower water temperatures would produce a higher P value.

It cannot be known precisely why these two predator species in SML only realize 35% of their maximum daily ration on average during the growth season. Prey availability must obviously be limited to some extent, either due to behavioral interactions, morphological limitations, or spatial separation. Seasonal changes in any one of these dimensions cause prey availability to be altered. All three factors interact and evolve as new prey cohorts are hatched, grow, and begin their patterned movements within the large system.

COMPARISON OF CONSUMPTION ESTIMATES TO OTHER INVESTIGATIONS

Agreement was equivocal between my predator consumption estimates and those of Moore (1988), who performed a bioenergetics analysis of SML predators. He concluded that the majority of striped bass consumption occurred during the summer but his model also determined that striped bass conversion efficiency was greatest during this period. The modified von Bertalanffy growth equation he utilized resulted in the greatest growth occurring in summer, while my modification led to near constant growth from spring to fall. I concluded that this disparity in summer conversion efficiency could only be due to the different equations used to model respiration and consumption as functions of temperature. The equations I adopted were specifically recommended for cool-water species (Hanson et al. 1997) while his equations were developed for warm-water species. Hartman and Brandt (1995a) defended these cool-water equations for striped bass, described in detail the major differences between this model and the Moore (1988) model, and concluded that the Moore

(1988) model would lead to higher consumption for a given growth trajectory. However, my estimates of consumption by striped bass during the growth season were much greater than those of Moore (1988). He estimated that the striped bass population of SML consumed 282,000 kg of clupeid prey from March to December while my estimate was twice that. The discrepancy cannot be explained away by differences in diet, water temperatures occupied, or population abundance, as these were similar between the two studies. Length-at-age of older striped bass was approximately 10% greater in my analysis, but this would not make a tremendous difference. Growth rates for younger fish (up to age-5) were similar and, as stated previously, the great bulk of consumption is done by these cohorts. I found that his conversion efficiencies for age-5 and younger striped bass were approximately twice mine. The gap lessened for older cohorts but total consumption by these fish was basically negligible. These differences in food conversion efficiency are enough to account for most of the discrepancy in consumptive demand. If Hartman and Brandt (1995a) were correct in their analysis, conversion efficiency using the Moore (1988) model should be lower, not higher. I ran the Moore (1988) model without changing any other input parameters (diet, caloric content, water temperature, population abundance) and did indeed find that consumption was slightly higher for each age-class and season. I could not therefore replicate the results of Moore (1988) using his inputs.

My estimates of clupeid consumption by the largemouth bass population during the growth season were about one-half of Moore’s (1988) values. My estimate of alewife biomass consumed was slightly greater than his, however, while his estimate of gizzard shad biomass consumed was 2.4 times greater than my own. This occurred despite my largemouth bass growth rates being slightly higher than those used in his study. No major differences in conversion efficiency of each age-class were seen. Disagreement arose due to diet information and population estimation. Moore (1988) estimated that over 50% of the diet of age-0 largemouth bass consisted of gizzard shad, while my diet data for this age-class, taken from a more recent study (Sutton 1997), indicated that age-0 largemouth eat almost no clupeids in their first growth season. They instead rely mainly on centrarchids, cyprinids, and invertebrates. Age-0 largemouth are not large enough to eat most shad present in SML judging by analyses of morphological vulnerability (Chapter Three). The difference in alewife consumption can also be partially explained by diet differences between the two studies. Moore (1988) determined that alewife compose less than 10% of largemouth bass diets in SML at any point during the year, while more recent diet data (Michaelson 1996 and this investigation) indicate alewife can be as much as 60% of the diet of adult largemouth bass during the protracted spawn of these clupeid prey fishes.

The other factor responsible for the large difference in gizzard shad consumption between the two studies is our respective estimates of population size. My estimates of the abundance of age-0 and age-3 and older largemouth bass are not very different than Moore (1988), but my estimates of the abundance of age-1 and age-2 fishes were about 50% less in both cases. Both of our derivations of the abundance of fish age-2 and younger were from cove rotenone data, his from 1979-1983, mine from 1989-1997. Densities of largemouth bass might actually have changed in SML during the decade between our studies, but adjustment of cove abundance to reflect whole-lake densities was also handled differently between the two studies. Using my methodology whole-lake age-0 abundance was approximately 33% of cove abundance, while the methods of Moore (1988) estimated this percentage to be about 36%. For age-1 adjustment my percentage was about 81%, his was 77%. For age-2 fish mine was 85%, his was 182%. He stopped there, deriving abundance of age-3 fish from mortality estimates. I continued to the next age-class, using rotenone data to generate estimates of age-3 fish with an adjustment factor of 100%. The obvious difference in the derivation of two-year-old fish abundance explains why his age-2 density was twice that of mine. My whole-lake adjustment should have led to a slightly higher abundance of age-1 largemouth bass, however (assuming actual abundance of these fish was commensurate during the two periods). This would seem to indicate a real decrease in the abundance of age-1 largemouth bass in SML between the early 1980's and the 1990's.

I perceive an air of confusion to surround cove versus open-water adjustment factors published from two studies on dissimilar reservoirs (Hayne et al. 1967; Summers and Axon 1980). Not only have these metrics been criticized as notoriously study-specific and unreliable for extrapolation to other systems (Bettoli and Maceina 1996), they can be inappropriately used for the direct calculation of whole-lake abundance from cove abundance while bypassing an important intermediate step (e.g., Jenkins and Morais 1978; Hightower et al. 1982). It is inappropriate to convert a cove abundance to a whole-lake abundance without knowing the ratio of cove-to-open water in the system unless it is assumed that the lake under investigation has the approximate cove-to-open water ratio as either Barkley or Douglas Lake (likely based on morphometric and limnological characteristics of each). This assumption must be clearly stated if it is made. A system with 60% cove habitat could not have applied to it the same whole-lake adjustment factors as a system with 25% cove habitat. To proceed correctly the cove abundance should first be adjusted to an open-water abundance, then a weighted average of each habitat taken to arrive at a whole-lake abundance estimate. I do not believe Moore (1988) appropriately utilized the correction factors. His error only appeared to make a large difference in calculating the density of age-2 largemouth bass.

Miranda et al. (1998) conducted a comparable study of predator consumption in Norris Lake, Tennessee, a southeastern reservoir with a similar predator assemblage compared to SML. They estimated largemouth bass consumption to be approximately 64 kg/ha and striped bass consumption to be 65 kg/ha on an annual basis, versus 48 kg/ha and 84 kg/ha determined here for these SML predators, respectively. Their population abundance estimates of largemouth bass and striped bass were 19 and 15 kg/ha, respectively, as compared to 17.5 and 16 kg/ha for SML. Largemouth bass consumption was 33% higher in Norris Reservoir at an 8% higher population biomass. Consumption by striped bass was 30% greater and striped bass biomass was 6% greater in SML. These different findings can be explained by examining the modeled population age structures and growth rates of these predators in each system. The largemouth bass population age-structure was similar between Norris Reservoir and SML, but largemouth bass in Norris were larger until the start of their fourth growth season. Consumption would have to be higher to reach the larger size and conversion efficiency should be less at these larger sizes. This growth difference is important because it occurs in the early age-classes when fish are most abundant and can affect population consumption greatly. Size-at-age for striped bass was slightly greater in Norris than in SML until fish reached their sixth growth season. This should have lead to more consumption by Norris Lake striped bass. The striped bass population in Norris was more heavily skewed towards older individuals, however, meaning there were many more small striped bass in SML. Numbers of striped bass in SML were estimated to be 50% greater (31/ha vs. 20/ha). This situation, despite slower growth in Smith Mountain, led to the greater consumption that I estimated by the SML striped bass population.

TOTAL PREDATOR CONSUMPTION

Total consumption by catfishes and crappie approached 160 kg/ha annually. These predators consumed only 45 kg/ha of clupeids annually, compared to 73 kg/ha for striped bass. Diet data for catfishes and crappie in SML were not available, however, so prey-partitioning of their total ingested biomass could be heavily biased. Rotenone data indicated that channel catfish were most abundant, followed by flatheads and whites. The literature suggests that white catfish have the highest proclivity towards clupeid consumption followed by channels and flatheads (Minckley and Deacon 1959; Stevens 1960; Carlander 1968). I speculated that clupeids were 30% of the diet of these three catfish species. Further study will be needed to determine the accuracy of this estimate. Adult crappie, while not attaining extremely large sizes, still have sufficient gapes to feed on small age-0 clupeids. Attributing only 25% of the crappie population’s diet to clupeids was deemed reasonable because only the larger adults feed on clupeids (Ager 1976; Hale 1996; Michaletz 1998b) and spatial separation between these littoral predators and age-0 alewife was thought likely. Based on the uncertainties regarding their total food consumption, more detailed information on the diet, growth rates, and population abundance of catfish and crappie in SML would seem to be a logical progression towards accurately assessing total predator demand for clupeids in SML.

The fact that striped bass consume over 50% of all clupeids eaten by piscivores in SML was not surprising. Striped bass diet data indicated that over 90% of striped bass prey were clupeids. Striped bass have evolved to most effectively feed on schooling prey fishes, to the point of near starvation when clupeid populations decline (Matthews et al. 1988). Diet analyses of largemouth bass from SML and literature investigations on food habits of catfish and crappie in other systems showed their diets to be more varied, including large quantities of crayfish and non-clupeid fishes, depending on the season.

Moore (1988) ignored catfish and crappie but included smallmouth bass and walleye in his investigation. He found, as here, that consumption by the latter two predator species was minor compared to striped bass and largemouth bass. Walleye stocking has been discontinued since 1984 and their quiet presence in the system indicates either migration from upstream locations on the Roanoke and Blackwater or minor natural reproduction occurring in the impoundment. The low density of smallmouth bass in the reservoir is somewhat puzzling, but the scarcity of deep, rocky areas for adults and shallow gravel beds for spawning is thought to play some part (M.C. Duval, personal communication). It is also apparent that unless management initiatives change drastically muskellunge will not play a large role in defining clupeid demand in the near future.

It is also worthwhile to compare these consumption results with those of Miranda et al. (1998) for predators in Norris Reservoir, Tennessee (Table 2.20). Crappie were found to consume more prey than any other predatory group in Norris (over 114 kg/ha). Crappie consumption in SML was estimated to be 61 kg/ha. The population biomass of crappie in SML was estimated to be 20% greater than in Norris. This difference should lead to greater crappie consumption in SML, unless most crappie biomass in Norris was old adults with low food conversion efficiencies and most crappie biomass in SML was very young fish with high conversion efficiencies. Ninety percent (by number) of the crappie population of Norris Lake, however, was estimated to be age-0 fish. Miranda et al. (1998) performed a bioenergetic analyses for this species, so arguably their results could be more accurate, but the standard error of their crappie consumption estimate was 194 kg/ha, far higher than for any other predator species examined in that study. Catfish were not considered in Norris Reservoir but consumption by smallmouth and spotted bass in that system was 60 and 31 kg/ha, respectively. Spotted bass are not found in Smith Mountain Lake and SML smallmouth bass consumption was estimated at only 3 kg/ha. The population density of smallmouth bass in Norris was determined to be fourteen times that of smallmouth in SML, and modeled growth rates and maximum sizes were very high for this species in Norris. A higher population density and good growth are enough to explain this difference in consumption. Walleye consumption in Norris was 64 kg/ha compared to less than 1 kg/ha in SML. Population density of walleye in Norris was more than thirty five times that in SML, but this is not a large enough difference to explain the 70-fold difference in consumption. It is striking that the estimated biomass of predators shown in Table 2.20 (excluding catfish, which are found in Norris but whose abundance was not quantified) is 23 kg/ha greater (45% greater) in Norris, a less nutrient-rich system, than in SML.

SUMMARY

My estimate of total annual consumption of alewife by piscivores in Smith Mountain Lake was 68 kg/ha (Table 2.19). I estimated that annual consumption of gizzard shad by predators was 77 kg/ha. I estimated in Chapter One that total annual surplus production, which equals the maximum sustainable prey supply, was 73 kg/ha for alewife and 146 kg/ha for gizzard shad. Total surplus production of clupeid prey thus appears adequate to meet predator demand (Figure 2.13). Alewife surplus production is only 7% greater than current predator demand, however, while gizzard shad surplus production is 90% greater than current predator demand. Some of this prey surplus, however, was unavailable to each predator cohort due to behavioral, morphological, and distributional constraints. The importance of these factors in determining true prey availability to each predator cohort will be investigated in Chapter Three.

Table 2.20. Annual consumption (kg/ha) and average abundance (kg/ha) of the major predator species investigated by Miranda et al. (1998) in Norris Reservoir, Tennessee, and Smith Mountain Lake. An asterisk means consumption for that species was not estimated, or that the species is not present in the system.

	Consumption (kg/ha)		Abundance (kg/ha)	
Predator	Norris	SML	Norris	SML
Largemouth Bass	64	48	19.0	17.5
Smallmouth Bass	60	3	13.5	1.0
Spotted Bass	31	*	5.5	*
Striped Bass	65	84	15.0	15.0
Crappie	114	61	14.5	17.5
Walleye	64	1	7.0	0.2
Catfish	*	98	*	27.9

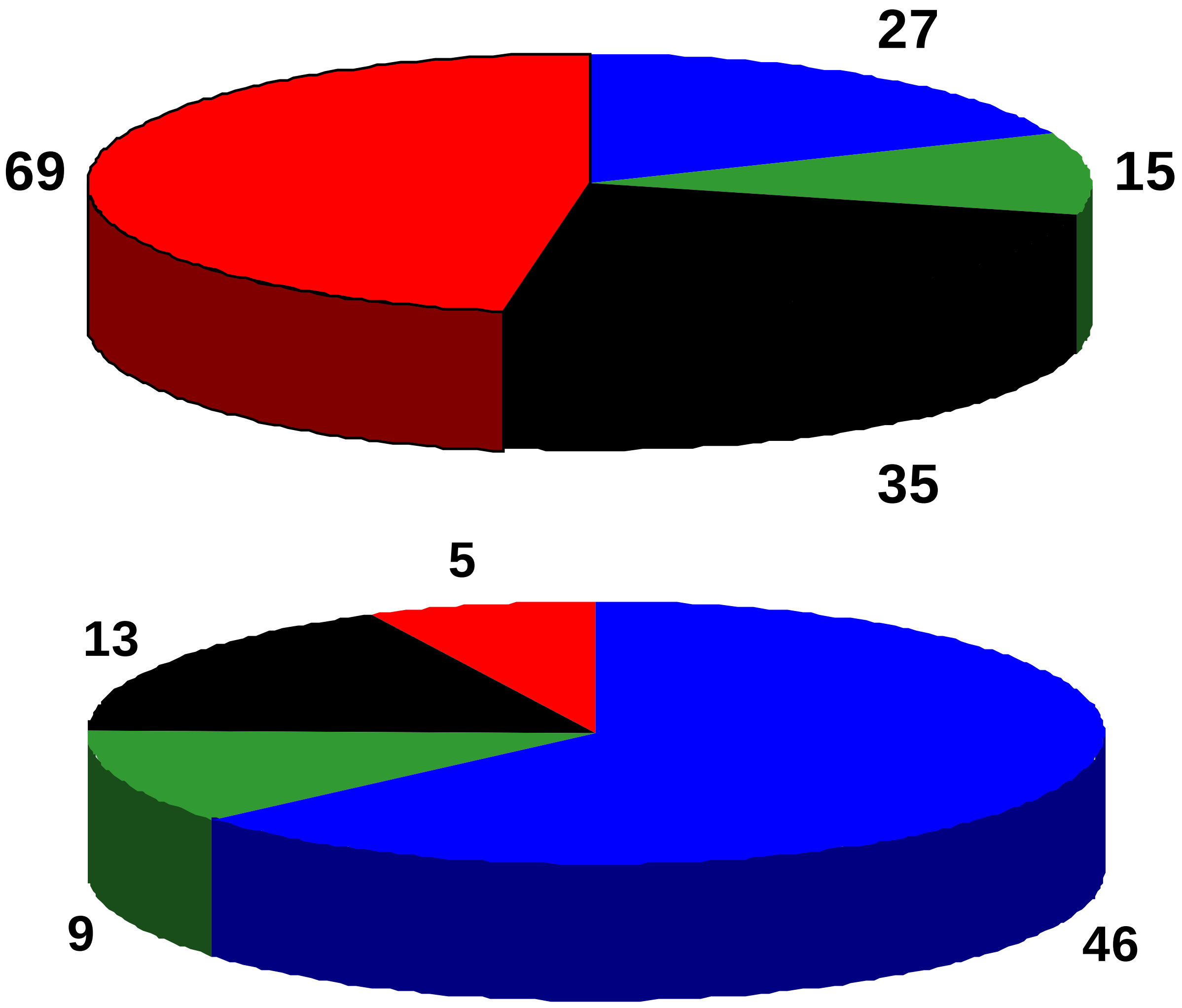

Figure 2.13. Fate of alewife and gizzard shad surplus production. The top pie chart represents gizzard shad surplus, and the bottom chart is for alewife surplus. The blue area is surplus eaten by striped bass, the green area is surplus eaten by largemouth bass, the black area is surplus eaten by other predators, and the red area is surplus that is not eaten. Numbers beside the pie are the kg/ha of surplus production in each respective piece.

CHAPTER THREE

AVAILABILITY OF CLUPEID PREY TO MEET PREDATOR DEMAND IN SMITH MOUNTAIN LAKE

INTRODUCTION

Chapter One was devoted to determination of annual surplus production (the maximum sustainable supply) of alewife and gizzard shad in Smith Mountain Lake. Total annual production of the alewife and gizzard shad populations was apportioned among cohorts as surplus production. I quantified the annual consumption by SML piscivores for alewife and gizzard shad in Chapter Two. An additional analytic step is required before the adequacy of the forage-fish supply can be definitively related to present predator demand; availability of the potential supply must be addressed.

Total annual production overestimates the actual prey supply to the extent that some prey may be too large for some predators to ingest (morphological availability), spatially isolated from predators (distributional availability), and/or difficult for predators to catch (behavioral availability). These three availability factors are not only species-specific for predators, but also cohort-specific within a predator species. One cannot simply reduce the total clupeid supply to meet total predator demand because of this cohort specificity. The work in this chapter instead is an examination of the adequacy of total available supply to meet cohort demand for each of the primary SML piscivores, largemouth bass and striped bass.

Prey availability has not been fully considered in previous supply/demand analyses (e.g., Eck and Brown 1985; Brandt and Kirsch 1993; Hartman and Brandt 1995b). A few studies have included prey/predator size limitations (Jenkins and Morais 1978; Michaletz 1997b, 1998b; Miranda et al. 1998), but none have examined distributional and behavioral limits. I first review the extant literature regarding morphological, distributional, and behavioral limitations on prey availability in this chapter. I then analyze how these components limit the availability of the alewife and gizzard shad supply to the SML piscivores. Finally, I assess the adequacy of the available prey supply to meet current average consumptive demand of striped bass and largemouth bass cohorts in SML.

LIMITS ON PREY AVAILABILITY

Morphology

A prey item is morphologically available if the predator is physically capable of swallowing it. A successful post-attack feeding event is primarily determined by such prey features as maximum body depth and presence of dorsal and/or anal fin spines, coupled with predator morphology in throat diameter and maximum gape. This is the case because most piscivores ingest prey whole (Hobson 1979). Fewer and fewer prey items are too large to be ingested as a predator ages and grows larger. It is therefore younger, smaller piscivores that are most affected by morphological constraints on consumption (Jenkins and Morais 1978; Timmons and Shelton 1980; Noble 1981; Gutreuter and Anderson 1985; Adams and DeAngelis 1987; Ney 1990; Hale 1996; Michaletz 1997b, 1998b). Changes in growth of prey fishes will thus affect their availability to predators, and researchers have found this to be very important to the survival and growth of young sport fishes (Sutton 1997; Michaletz 1997b, 1998b; Garvey and Stein 1998). Reservoir researchers of the southeastern U.S. are well aware of the effects of morphological availability due to the dominance of gizzard shad in these systems and their tendency to outgrow the window of vulnerability quickly (Noble 1981; Moore et al. 1985; Adams and DeAngelis 1987; Hambright et al. 1991; Stein et al. 1995; DiCenzo et al. 1996; Michaletz 1997b, 1998a, 1998b).

Lack of morphologically-available prey for age-0 piscivores has been shown to have a variety of deleterious consequences. Young piscivores grow faster and reach greater lengths if small fish are available as prey (Shelton et al. 1979; Timmons et al. 1980; Keast and Eadie 1985;

Michaletz 1998b) than if benthic invertebrates, containing fewer calories per unit of mass, must be substituted (Aggus and Elliott 1975, Prus 1975, Forney 1976, Penczak et al. 1984, Moore 1988, Sutton 1997). Michaletz (1998a) reports that the growth of largemouth bass and white crappie in Missouri reservoirs was inversely related to the growth of gizzard shad, especially the age-0 shad cohort. These sport fish grew more slowly in productive reservoirs where age-0 gizzard shad grew quickly than in deep, less productive reservoirs where age-0 shad grew more slowly. Slow growth of age-0 piscivores can negatively affect later recruitment if these smaller piscivores suffer higher predation mortality. This consequence has been demonstrated for walleye (Chevalier 1973, Madenjian et al. 1991), largemouth bass (Minton and McLean 1982), and yellow perch (Nielsen 1980, Post and Prankevicius 1987).

Attaining a larger body size, and thus accumulating a greater amount of energy reserves, enhances an age-0 fish's probability of over-winter survival (Carline et al. 1984; Adams and DeAngelis 1987; Thompson et al. 1991; Johnson and Evans 1996). Lipids are metabolized more slowly for larger individuals (Shuter et al. 1980; Henderson et al. 1988; Post and Evans 1989), who also have lower metabolic requirements per unit of mass (Paloheimo and Dickie 1966). Larger individuals also have higher probabilities of finding appropriately-sized prey items when water temperatures and metabolic requirements rise the following spring (Adams et al. 1982a; Adams and DeAngelis 1987). Largemouth bass recruitment in some systems has been shown to be heavily dependent on the relative timing of largemouth bass and shad spawning (Timmons and Shelton 1980; Gutreuter and Anderson 1985; Adams and DeAngelis 1987). Young shad become invulnerable to the later-spawned age-0 largemouth bass when gizzard shad spawn well before largemouth bass. Age-0 largemouth bass consequently grow poorly and later suffer high over-winter mortality.

Lawrence (1958) quantitatively assessed the maximum size of various forage fishes that largemouth bass could swallow. He developed relationships between prey body depth and bass throat diameter. Jenkins and Morais (1978) modified his work, developing functional relationships to estimate the maximum ingestible length of a prey item for a given predator species and length. The investigators then used these relationships to examine cove rotenone standing stock estimates and length distributions for various predator and prey species. They developed graphical depictions (termed AP:P plots) to assess whether or not sufficient production of ingestible prey was available to predators of various sizes. Their technique became standard assessment protocol among reservoir biologists but has also come under criticism for being too simplistic (Ney 1990). It does not address behavioral aspects of predator-prey interactions nor the distributional availability of prey, while providing an excellent means of identifying ingestibility limits for various-sized predators.

Distribution

Distributional availability requires that the predator and prey overlap sufficiently in space and time to allow frequent encounters between the two. Fish mobility assures that encounters between piscivores and ingestible prey occur but frequency of these meetings is determined by habitat preferences of the species involved (Ney 1990). Alewife and striped bass, for example, are coolwater pelagic species while gizzard shad and largemouth bass are more littoral, warm water species. Alewife/striped bass and gizzard shad/largemouth bass encounters are thus much more frequent on an annual basis than alewife/largemouth bass and gizzard shad/striped bass meetings. In addition, age-0 alewife and age-0 striped bass both prefer similar water temperatures (which are warmer than the adults of their species; Stewart and Binkowski 1986; Moore et al. 1993; Hartman and Brandt 1995a). This could lead to differences in encounter rates between different life stages of predator and prey. Ney et al. (1990) noted that cool, oxygenated waters needed for adult striped bass and adult alewife are scarce from mid-summer to mid-fall in the upper Roanoke and Blackwater arms of SML, but this habitat is more plentiful in downlake areas. This demarcation mirrors the fertility gradient within the system. If significant habitat partitioning between predator and prey exists, either spatially or temporally, encounter rates would be low.

Environmental variables such as temperature, oxygen, light levels, and food availability play critical roles in determining species distributions in freshwater systems (Fry 1947; Kerr 1980; Crowder et al. 1981). The lack of internal physiological temperature regulation in most fishes means they must actively find and maintain position in areas with preferred temperatures (Magnuson et al. 1979; Crowder et al. 1981; Coutant 1990). Predators can attempt sojourns into areas with higher prey densities to meet nutritional requirements if these areas do not contain sufficient food resources (Diana 1995). This phenomenon would be comparable to stream fishes moving from a hydrodynamic refuge into higher velocity water to feed momentarily.

Distributional and seasonal movement studies on striped bass in southeastern reservoirs are widespread (Coutant and Carroll 1980; Combs and Peltz 1982; Summers 1982; Cheek et al. 1985; Siler et al. 1986; Hampton et al. 1988; Lamprecht and Shelton 1988; Braschler et al. 1989; Matthews et al. 1989; Poarch 1989; Zale et al. 1990; McDaniel et al. 1993; Wilkerson and Fisher 1997). Adult striped bass are often confined to areas where a combination of sufficient temperature (< 22 °C) and dissolved oxygen level (> 3mg/l) can be found in southeastern reservoirs during summer lake stratification (Matthews et al. 1989). Younger striped bass, as stated earlier, can tolerate much warmer temperatures (to 30 °C) and maintain good growth rates (Coutant 1985; Matthews et al. 1989; Hartman and Brandt 1995a). Coutant (1985) demonstrated convincingly the impact thermal requirements have on the ecology of striped bass in Cherokee Reservoir, Tennessee. Adult striped bass in this system were found densely packed into a thermal refuge during summer stratification. Although few prey existed in this area, the bass refused to enter warmer surface waters to feed on abundant shad and often starved as a result. McDaniel et al. (1993) presented a similar case for striped bass in the St. Johns River, Florida. Striped bass show less susceptibility to deleterious effects of the "summer-stratification squeeze" in reservoirs with an abundance of suitable summer habitat and the presence of prey species that have similar physiological preferences (e.g., alewife; Wilkerson and Fisher 1997).

These examples point to the importance of recognizing distributional availability of prey to predators. Any loss of prey biomass that occurs during periods when a given predator is segregated must not be considered available to that predator. Few quantitative attempts at this sort of adjustment have been attempted. However, telemetry and acoustic technology promise increased understanding of limnological habitat influences on fish distribution and more accurate measurement of the extent of spatial and temporal segregation of predator and prey (Ney 1990).

Behavior

Prey consumption by predators is still not guaranteed when prey are not spatially segregated from predators and can be found at small enough sizes to ingest. This is due to behavioral interactions of predator and prey. Adult largemouth bass, for example, rarely consume larval alewife and gizzard shad when these tiny prey fishes are plentiful in the early summer in SML. This choice might be based in optimal foraging strategy (Pyke et al. 1977; Townsend and Winfield 1985; Juanes 1994). The time taken to consume mass quantities of these larvae in order to derive sufficient nutrition might be better spent on one feeding attempt directed at a single, large prey fish. Predator and prey behavior can both reduce the size range of prey items eaten by predators more stringently than morphology would suggest. Gape width puts an upper bound on the size of prey items that can be consumed, but behavioral interactions keep predators from consuming tiny prey and from capturing larger but ingestible prey. Juanes (1994) reviewed over thirty studies that examined predator/prey size relationships among fishes and concluded that predators generally consumed smaller prey sizes than would be suggested on the basis of morphology alone. He primarily attributes this phenomenon to evidence that capture success declines with increasing prey size, but he also recognizes that encounter rates with various prey sizes can make a difference. Schooling fishes usually form congregations of similar-sized individuals (Major 1978; Pitcher et al. 1985; Theodorakis 1989). Small prey fishes are usually more abundant than larger prey fishes, so predators would encounter schools of small prey more often than schools of intermediate to large-sized prey. Einfalt and Wahl (1997) also determined that juvenile walleye ate smaller prey items than morphological limitation allowed, but they attributed the result to active prey selection by the predator rather than the passive hypotheses based on encounter rates and capture success (Juanes 1994). Dettmers and Stein (1996) argue that selectivity for smaller prey cannot be explained by reduced capture efficiency of predators attempting to ingest larger prey items. They propose that discrepancies in vulnerability can be attributed to differences in relative abundance, habitat preferences, schooling capabilities, and escape responses of prey fish of various sizes.

Behavioral availability is dependent upon the success of the predator in search, encounter, pursuit, capture, and handling of prey (Holling 1959; Juanes 1994). Many variables influence each component of this sequence, making behavioral availability a complex and difficult concept to quantify. The act of searching requires that the predator be hungry. Predators will often encounter prey when satiated, but they have no motivation to begin pursuit (Diana 1995). Encounter of prey also has much to do with the distributions of predator and prey as well as the behavior of each participant. Predators must recognize a prey item as exactly that once located. Investigators have shown the importance of search-image development in predators and how these images are cemented through repeated encounter (Dill 1983). These visual cues in some instances become so inflexible that predators will ignore abundant potential prey items when density of their accustomed prey has been drastically decreased. Stevens (1958) reported that striped bass starved when clupeid abundance decreased despite an abundance of cyprinids and centrarchids in Santee-Cooper Reservoir, South Carolina. Ney (1990) hypothesized that the same phenomenon might be responsible for failure of Pacific salmon in Lake Michigan to utilize other prey after alewife declines.

Pursuit and capture will depend on the habitat where the encounter takes place as well as morphology and physiology of predator and prey. Some predators attack using ambush techniques while others simply run prey down, with numerous variations evident (Hobson

1979; Diana 1995). Evasion responses by prey are also highly variable and species-specific (Stein 1979; Webb 1984). Many prey fishes use either cover (weeds, rocks) or schooling mechanisms to inhibit predation (Ney 1990) and some species are capable of either response depending on available habitat (Diana 1995). The influence of cover on predator-prey interactions between largemouth bass and bluegill (*Lepomis macrochirus*) has been investigated by Mittelbach (1981), Savino and Stein (1982), Wiley et al. (1984), Schramm and Zale (1985), and Gotceitas and Colgan (1987). These studies indicate that intermediate densities of vegetation produce the greatest standing stocks of largemouth bass. At low macrophyte density bass are too efficient and overcrop bluegill populations, while dense vegetation allows bluegill to evade predation entirely. Largemouth bass are most efficient predators when occupying edge-habitat in natural systems, where they hover just outside of vegetated areas waiting for prey to wander from cover (Savino and Stein 1982; Engel 1987; Smith 1993).

Behavioral interactions between predators and schooling prey have been investigated by Neill and Cullen (1974), Shaw (1978) and Partridge (1982). Schooling prey in general are much more susceptible to predation by schooling predators, while solitary predators succumb to anti-predator schooling behavior such as the "confusion" and "fountain" effects (Shaw 1978; Partridge 1982). Matthews et al. (1988) hypothesized that striped bass can starve after clupeid crashes because their evolutionary history has honed their skills to feed on schooling pelagic prey. This tactic, however, has left them under-prepared to efficiently feed on cover-oriented, non-schooling cyprinids and centrarchids.

This research clearly demonstrates that even when predator and prey overlap in space and time the inability of the predator to forage effectively could severely impact prey availability. Behavior of involved parties impacts capture efficiency, nutrient intake, and eventually growth and survival of predators (Ney 1990). Tomcko et al. (1984) showed that the inability of tiger muskellunge (*Esox masquinongy* X *Esox lucius*) to feed efficiently on centrarchid prey should preclude this predator from stocking consideration in centrarchid-dominated systems. Behavioral availability still remains a mysterious metric despite the obvious importance behavior has on predator-prey encounters. This complex interaction is not easily reduced to a measurable quantity that can be used to assess the behavioral availability of various prey items.

The first and oft-modified attempt to quantitatively assess behavioral aspects of predator-prey interactions stems from the work of Ivlev, beginning with his 1961 opus *Experimental Ecology of the Feeding of Fishes*. He developed an experimental protocol to measure the electivity of a predator for various prey items. This was accomplished by computing a function of the proportion of a prey item in the diet (r_i) and its proportional abundance in the environment (p_i):

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

Electivity in the field is a composite measure incorporating both preference and availability of prey items to the predator. Availability and preference can be distilled from electivity by measuring electivity for prey items in a laboratory setting where all prey are made equally available. Laboratory electivity thus measures only preference and availability can be determined as the difference between field and laboratory-determined electivity measures:

$$\text{Availability} = E_{\text{field}} - E_{\text{laboratory}}$$

The requirement of uniform availability demands imaginative and carefully planned experimental design in order to negate differences in prey motility and morphology. This is perhaps why no investigations concerning prey availability attempt to follow Ivlev’s protocol, despite its promise of a coherent, stepwise, practical, quantitative answer (Ney 1990). Diana (1995) argues that electivity is not a predictive quantity but rather an actual measure of performance for a predator in a specific system. E_{field} will not be applicable to the same species in another system. This, however, is only an indication of changes in availability of prey from system to system because preference ($E_{laboratory}$) for various prey items should be much less variable for a given predator species.

Defining the fraction of prey actually available for predator consumption is perhaps more critical than refining techniques for absolute assessment of prey densities. The former task has often been neglected in predator-prey studies (Ney 1990). Quantitatively incorporating morphological (Jenkins and Morais 1978), behavioral (Tomcko et al. 1984; Einfalt and Wahl 1997), and distributional (Crowder et al. 1981; Kohler and Ney 1981; Coutant 1985) aspects of prey availability will enhance the accuracy and efficacy of predator-prey studies. The cumulative effect of these three factors will likely be to greatly reduce the levels of prey available to the predator. The failure to incorporate prey invulnerability results in unwarranted optimism concerning the adequacy of the prey supply (Stewart et al. 1981; Brandt et al. 1992; LaBar 1993). Care must be taken, however, to insure that redundancy in correction for unavailability is avoided (Figure 3.1).

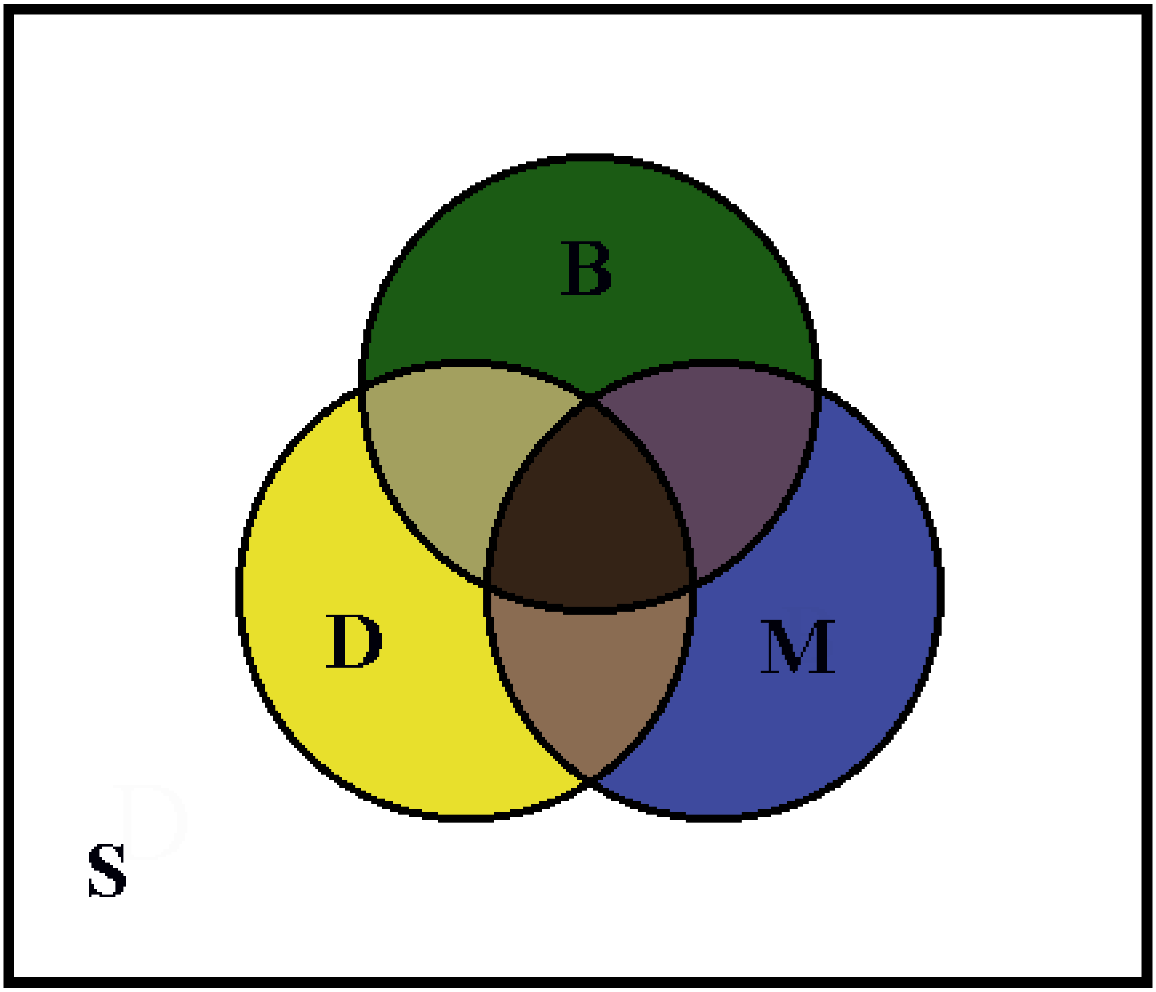

Figure 3.1. Schematic representation of prey availability. The large square labeled "S" represents total prey supply. The three shaded circles represent unavailable prey: "M" represents morphologically unavailable prey, "D" represents distributionally unavailable prey, and "B" represents behaviorally unavailable prey. Prey unavailable in multiple ways are depicted in the overlap of the three circles. One would use the following equation to estimate total available prey supply: Available Supply = S - (M + D + B) + MB + MD + DB - MDB. Here, MD represents the overlap of circles M and D, with similar definitions for MB and BD. MDB defines the darkest center region of overlap on all three availability axes.

METHODS

It is easier in practice to come to the same conclusions as those of Figure 3.1 by using another protocol (Figure 3.2). I first calculated the component of alewife and gizzard shad prey that was behaviorally unavailable to each cohort of largemouth bass and striped bass. I then determined the behaviorally available portion of each prey species that was morphologically unavailable to that cohort. Finally, I estimated that portion of prey that was behaviorally and morphologically available to that cohort, but not spatially available.

BEHAVIORAL AVAILABILITY

Two major behavioral components of prey availability were examined. These stemmed from multiple observations concerning the sizes of prey ingested by largemouth bass and striped bass. First, there were strong indications from stomach content analyses that larger predators consume prey only above a certain minimum size despite spatial and morphological access to larval and small juvenile prey fishes. Second, diet analyses showed that predators neglected shad over a certain size despite the morphological availability of these prey fish. Surplus production of prey fish at these unutilized sizes was determined and then subtracted from total surplus production to account for these various forms of behavioral neglect/unavailability.

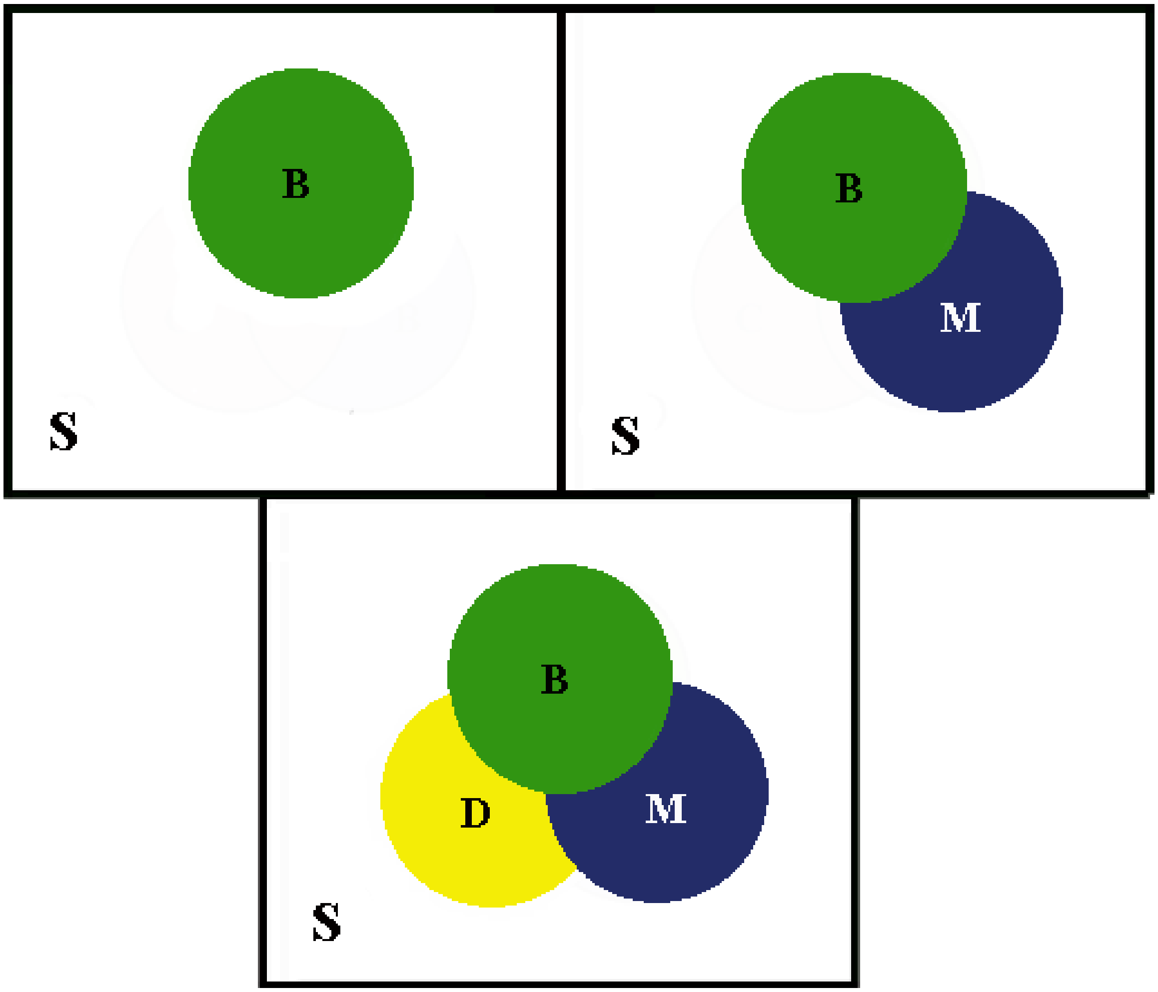

Figure 3.2. Schematic representation of the determination of prey availability. First the amount of behaviorally unavailable prey (B) is determined (top left square). Then prey that is behaviorally available but not morphologically available (M) is found (top right square). Finally prey that is behaviorally and morphologically available but not distributionally available (D) is determined (bottom square). This total is then subtracted from the total prey supply (S). This would be done on a cohort by cohort basis for each predator species.

Other behavioral prey refuges such as schooling behavior and cover usage were not examined. These were thought in general to play minor roles in the predator/prey interaction in SML. Quantification of their effects on prey availability also would have been difficult. Clupeids do not utilize cover, rather they adopt schooling behavior to protect them from predation. Striped bass also school, however, which to some extent negates this anti-predator tactic. Littoral predators generally feed on alewife when this prey fish is onshore and spawning and therefore not inclined to school or seek cover. For littoral predators and gizzard shad schooling behavior could serve as a behavioral constraint. This problem could be assuaged if littoral predators fed on gizzard shad mainly at dawn and dusk as prey schools disband and low light levels increase the probability of successful prey capture. There is evidence of crepuscular feeding patterns for littoral predators (Becker 1983; Collins and Hinch 1993).

MORPHOLOGICAL AVAILABILITY

Ingestibility equations (Jenkins and Morais 1978) were used to predict maximum sizes of prey that could be ingested by a given size of largemouth bass. These equations were based on a relation between prey total length (which is proportional to maximum body depth) and predator total length (which is proportional to throat diameter). The relationship for each clupeid prey species was:

Shad $Y = 0.014*X^2 + 0.17*X + 1.1$

Alewife $Y = 0.022*X^2 + 0.213*X + 1.1$

where Y is maximum ingestible length of prey and X is the total length of the largemouth bass (X and Y in inches). Alewife equations were derived from gizzard shad equations by multiplying the coefficients preceding X^2 and X by 1.25. This adjusted for the smaller body depth to total length ratio of alewife relative to gizzard shad (Nigro and Ney 1982). Jenkins and Morais (1978) also proposed adjustments to their equations for other predator species.

These were based on comparisons between the gape of the desired predator species and the gape of a largemouth bass. They determined, for example, that a 13-inch striped bass had the same gape as a 10-inch largemouth bass. Striped bass length therefore would first have to be divided by 1.3 to use the above equations to determine the prey size that a striped bass could ingest.

Moore (1988) found these relationships, while fairly accurate for largemouth bass, to be too conservative for striped bass even with corrections for differences in throat diameter between largemouth and striped bass. He noted that striped bass less than 300 mm TL ate clupeids significantly greater in length than the maximum ingestible size predicted by Jenkins and Morais (1978). Striped bass consumed clupeids up to 60% of their body length in the Abermarle Sound, North Carolina (Manooch 1973). I chose to use 60% of striped bass body length to determine maximum size of ingestible alewife and 50% for gizzard shad. The percentage was lower for gizzard shad to adjust for the deeper body morphology of gizzard shad as compared to alewife. These ingestibility limits were consonant with striped bass/clupeid prey size ratios found by Moore (1988).

Observed growth of alewife and gizzard shad in SML was plotted versus the predicted maximum ingestible size for a given size of predator as an indication of the severity of morphological constraints. Data on the variation of sizes within prey year-classes were garnered from Tisa (1988). He found the semi-quartile range for alewife to be approximately 25% of mean TL for age-0 and age-1 individuals, 15% for age-1 members, and 12% for age-2 fish. The semi-quartile range for gizzard shad ages 0,1, and 7 was about 14% of the mean TL, while for intermediate ages (2-6) it was approximately 20%. I chose to set the 25th and 75th percentile of prey length for all clupeid age-classes to ± 20% of the mean length-at-age based on these findings. Available prey supply for each predator cohort at this stage equaled the product of the behaviorally-available annual prey surplus production and the cumulative fraction of prey small enough to be eaten by a predator cohort.

DISTRIBUTIONAL AVAILABILITY

A number of inputs were used to estimate the distributional availability of clupeid prey to largemouth and striped bass. First, a common knowledge of the habitat preferences of predator and prey species was utilized. Largemouth bass can be assumed to be, for the most part, littoral predators (Carlander 1977). Striped bass are known to be more mobile, pelagic predators. Second, samples obtained from a variety of gear-types such as gill-nets, shoreline electrofishing, and rotenone indicated the presence and/or absence of certain species from certain zones of the reservoir in various seasons. Third, seasonal diet information (see Tables 2.10 and 2.11) gave additional evidence concerning the unavailability of prey to largemouth and striped bass due to spatial constraints. Finally, the water column at various stations throughout the reservoir was sampled during the final days of the summer stratification period in 1998 with a temperature/dissolved oxygen (DO) probe. The probe was lowered into the water at each station and temperature and DO measures were taken at various depths. The location of the thermocline became apparent with a sudden decrease in temperature and DO readings. Several more measures were taken at increasing depths in the hypolimnion to insure that the true thermocline and not some limnological aberration had been found. These measures were used to determine available habitat for adult striped bass based on findings that these predators prefer cool, oxygenated water (< 24 °C and > 3mg/l DO; Coutant 1985). Age-0 striped bass were found to prefer warmer waters as were age-0 alewife (Stewart and Binkowski 1986; Moore et al. 1993; Hartman and Brandt 1995a). I was able to formulate a description of seasonal availability of each clupeid prey item to largemouth and striped bass using these tools.

Not all forage-fish production that occurs while the prey is spatially disjunct from the predator is unavailable, however. Only production *that is lost* during this period, regardless of when it was created, cannot be consumed by the predator. Production during the period must be lessened by the difference in ending and starting biomass of the prey population to calculate this quantity, which is exactly equation 1 in Chapter One for surplus production.

For example, suppose that age-0 gizzard shad were unavailable to striped bass for three months of the growing season. There occurred 25 kg/ha of production from this shad cohort during this time period. Age-0 cohort biomass was 6 kg/ha at the beginning of the three months and was 12 kg/ha at the end of the period. Only 19 kg/ha [25 - (12-6)] of shad production was actually lost due to distributional unavailability in this situation. Some prey might also grow to a size that is invulnerable to a certain cohort of predators during a period of spatial segregation. This segment of the prey population was accounted for while investigating morphological availability.

RESULTS

BEHAVIORAL AVAILABILITY

<u>Responses to Small Prey</u>

There appeared to be a minimum size of clupeid prey consumed by both largemouth bass and striped bass. Stomach analyses indicated that clupeids are fed upon after reaching a size of 40 mm TL (Figures A.2 and A.2). Alewife surplus production of all individuals less than 40 mm TL was approximately 4.0 kg/ha annually. This amount was only 1.6 kg/ha annually for gizzard shad.

<u>Responses to Large Prey</u>

Evidence gathered by Moore (1988), Sutton (1997), and my own investigation indicated that both largemouth bass and striped bass in SML do not consume gizzard shad up to the maximum ingestible size as determined by the equations of Jenkins and Morais (1978) and Manooch (1973). Moore (1988) found that only two of 456 gizzard shad eaten by striped bass, and one of 115 shad eaten by largemouth bass, were greater than 160 mm TL. I found three clupeids over 160 mm TL in the stomachs of striped bass out of over three hundred clupeids consumed (Figure A.2). The largest clupeid eaten was 172 mm TL. I also did not find a single clupeid prey item over 160 mm TL in the stomachs of largemouth bass (Figure

A.3). The cause for this lack of utilization is not definitively known but perhaps larger clupeids are too fast for predators to have a reasonable hope of chasing them down. Juanes (1994) reviewed over thirty papers on predator-prey size ratios, concluding that capture success decreases and handling time increases with prey size. Many striped bass anglers have success using live shad larger than 200 mm TL to catch striped bass so obviously these partially-immobilized large shad are palatable and recognized as prey items. Moore (1988) found that alewife up to the maximum size seen in SML (approximately 160 mm TL) were eaten by both striped bass and largemouth bass. The numbers of alewife of this size seen in predator stomachs was low, but this was assumed to be more a reflection of the relative paucity of these large alewife when compared to the great numbers of their smaller brethren. Growth data from SML indicated that in late-August of their second growth season gizzard shad are approximately 160 mm TL, so surplus production after this time (60 kg/ha) was assumed to be behaviorally unavailable to predators. This amount was about 40% of the total annual surplus production of the shad population.

MORPHOLOGICAL AVAILABILITY

Morphological constraints can seriously affect prey availability to predators according to the equations of Jenkins and Morais (1978), the work of Manooch (1973), and the observed growth patterns of SML clupeids. This is especially true for trophic interactions between largemouth bass, which don't grow as large as striped bass, and gizzard shad, which grow quickly and reach large adult sizes (about 350-400 mm TL). A series of figures (Figures 3.3 - 3.8) depicts the morphological vulnerability of various age-classes of clupeid prey to specific cohorts of predators throughout their lifetime. The entire range of prey sizes is depicted but results from the previous section indicated that only clupeids between the sizes of 40-160 mm TL were behaviorally available.

These graphs can all be interpreted similarly in a straightforward manner. The ordinate axis is prey total length (mm) while the abscissa shows the age of a particular predator cohort.

The thin solid line in each graph indicates the size of prey predicted to be small enough to be eaten by the average-sized predator of the cohort. This line slopes upward from left to right as cohort members age and subsequently grow. There are multiple dashed lines on each graph. These represent the observed growth of the "average" individual in a particular age-class of clupeids relative to the predator. The dashed line with vertical bars, representing the 25th and 75th percentile of the prey length-at-age distribution, represents the growth trajectory of the cohort of clupeids born in the same year as this cohort of predators. The growth curves of other cohorts of clupeids were not given error bars to prevent clutter but some indication of the variation in prey sizes can be gained by examining the dashed line with error bars.

The vertical distance between any dashed line and the solid line is an indication of the relative strength of the morphological constraint on the predator. If a dashed line is far below the solid line, all but the most immense members of a prey cohort will be available to the predator. Only the tiniest members of that clupeid cohort could be consumed by the predator if the dashed line is far above the solid line. The "average" member of that prey cohort could be consumed by the average predator if the dashed line lies practically on the solid line. About 50% of the prey cohort in this case would be considered vulnerable to the predator cohort assuming a symmetric distribution of lengths about the mean size for the prey population. This would mean 50% of the annual surplus production of this cohort would be morphologically available for consumption, but this requires a further assumption concerning equal amounts of surplus production within subsets of the prey cohort. The information in these figures is quantitatively summarized in Tables 3.1-3.4, which give the percent of behaviorally-available surplus production of each clupeid cohort that is also morphologically available to the various predator age-classes.

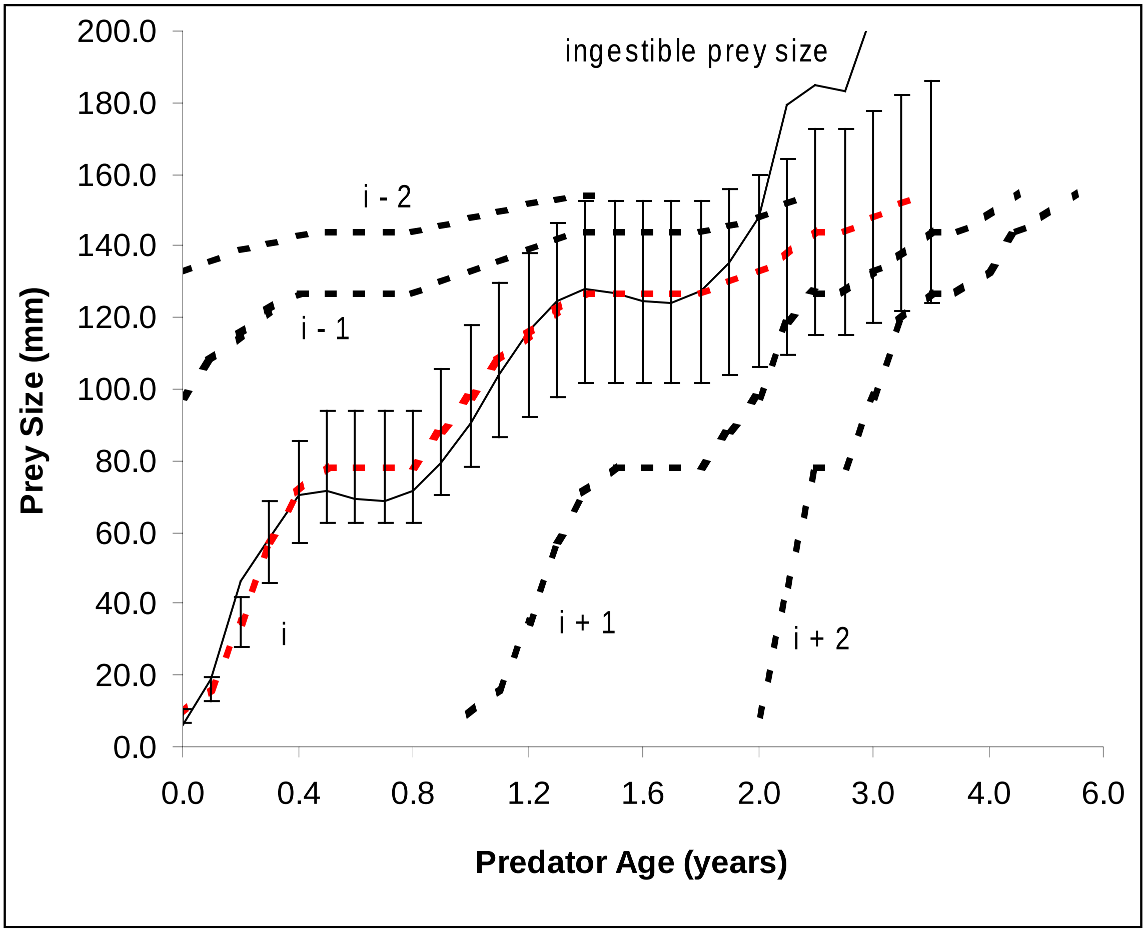

Figure 3.3. Lifespan morphological availability of various cohorts of alewife for a cohort of largemouth bass. Each dashed line represents the average individual growth for a cohort of prey. The number next to each dashed line gives the prey cohort's temporal relation to the predator cohort. For instance, i + 1 would indicate the growth of the prey cohort born one year after the predator cohort. The vertical bars on the ith prey cohort indicate the 25th and 75th percentiles of prey sizes seen within the cohort. The single solid line represents the maximum ingestible prey size by an average individual of the predator cohort.

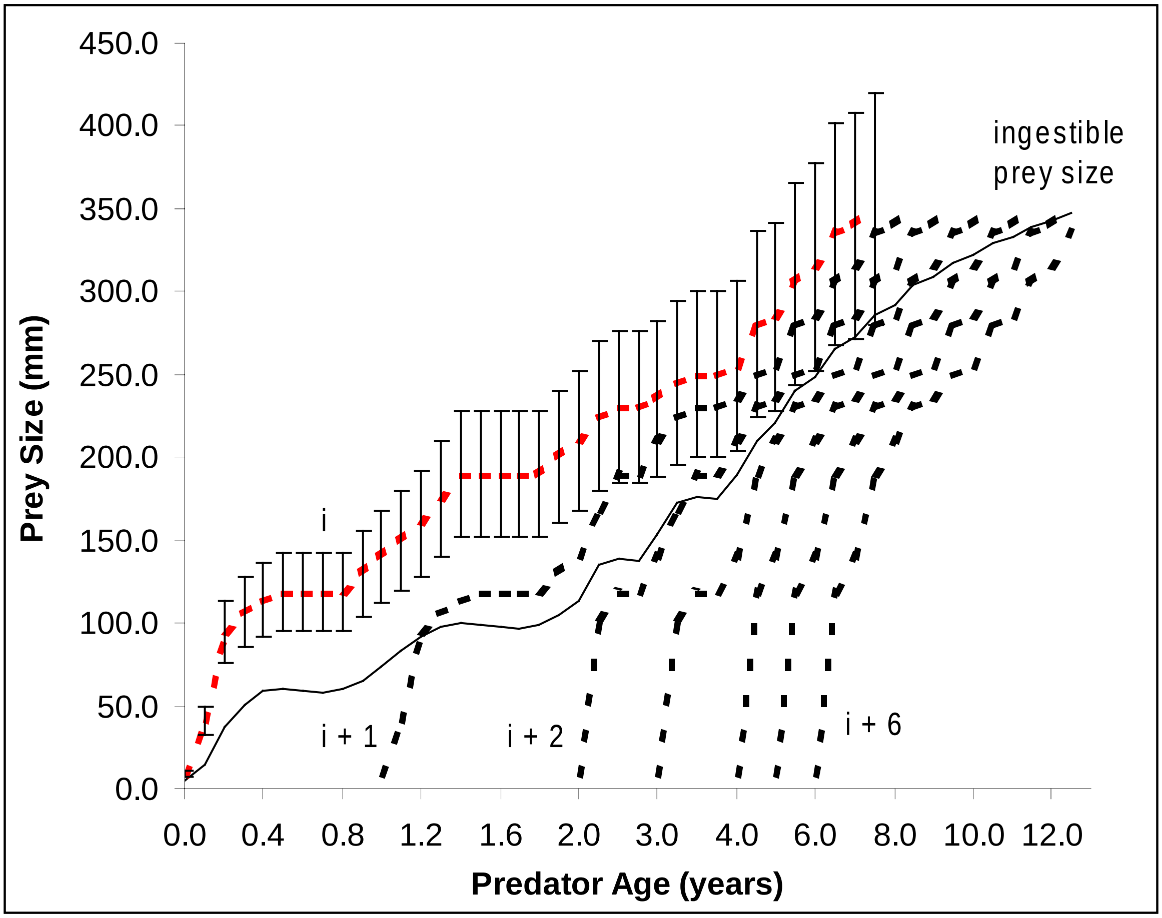

Figure 3.4. Lifespan morphological availability of various cohorts of gizzard shad for a cohort of largemouth bass. Each dashed line represents the average individual growth for a cohort of prey. The number next to each dashed line gives the prey cohort's temporal relation to the predator cohort. For instance, i + 1 would indicate the growth of the prey cohort born one year after the predator cohort. The vertical bars on the ith prey cohort indicate the 25th and 75th percentiles of prey sizes seen within the cohort. The single solid line represents the maximum ingestible prey size by an average individual of the predator cohort.

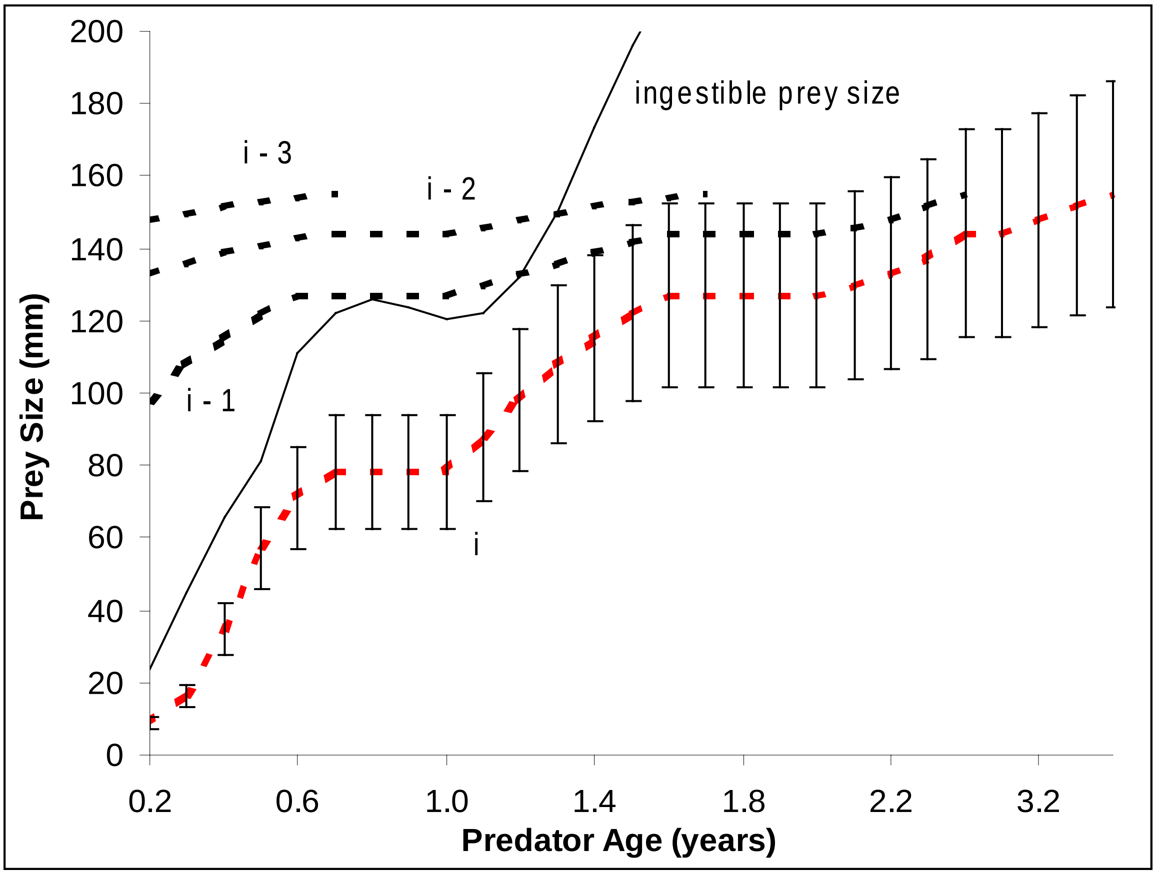

Figure 3.5. Lifespan morphological availability of various cohorts of alewife for a large-mode cohort of striped bass. Each dashed line represents the average individual growth for a cohort of prey. The number next to each dashed line gives the prey cohort's temporal relation to the predator cohort. For instance, i - 1 would indicate the growth of the prey cohort born one year before the predator cohort. The vertical bars on the ith prey cohort indicate the 25th and 75th percentiles of prey sizes seen within the cohort. The single solid line represents the maximum ingestible prey size by an average individual of the predator cohort.

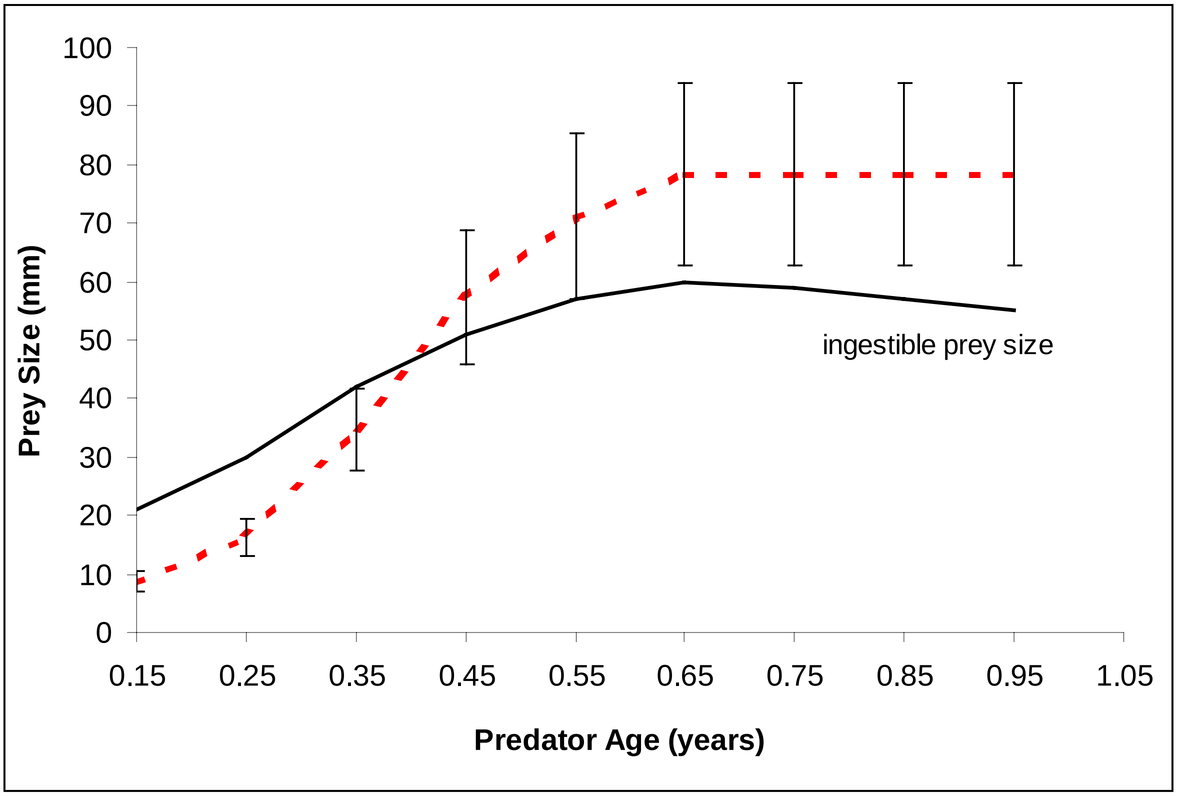

Figure 3.6. Lifespan morphological availability of a cohort of alewife for a same-age small-mode cohort of striped bass. The dashed line, with vertical bars that demarcate the 25th and 75th percentiles of prey sizes, is the growth curve of the average individual of the alewife cohort, while the solid line is the maximum ingestible prey size by the average individual of this small-mode cohort of striped bass.

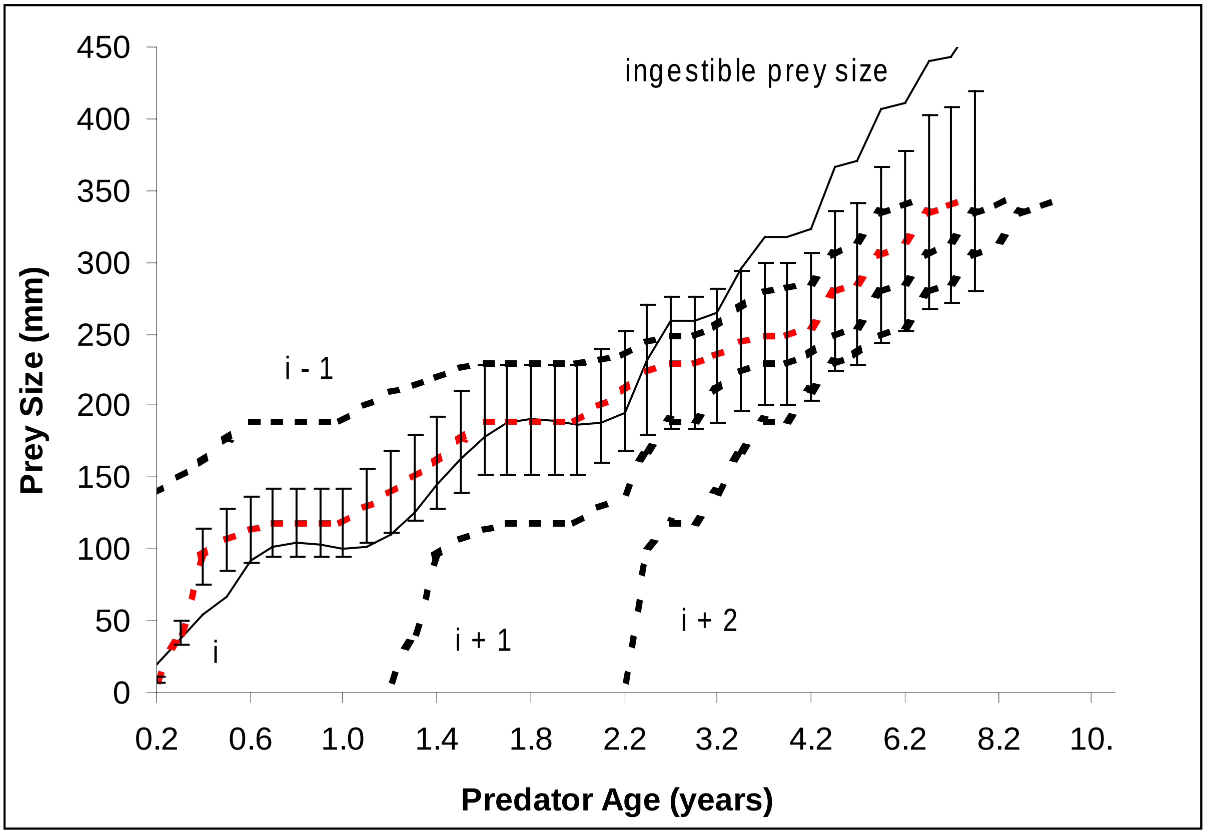

Figure 3.7. Lifespan morphological availability of various cohorts of gizzard shad for a cohort of large-mode striped bass. Each dashed line represents the average individual growth for a cohort of prey. The number next to each dashed line gives the prey cohort's temporal relation to the predator cohort. For instance, i - 1 would indicate the growth of the prey cohort born one year before the predator cohort. The vertical bars on the ith prey cohort indicate the 25th and 75th percentiles of prey sizes seen within the cohort. The single solid line represents the maximum ingestible prey size by an average individual of the predator cohort.

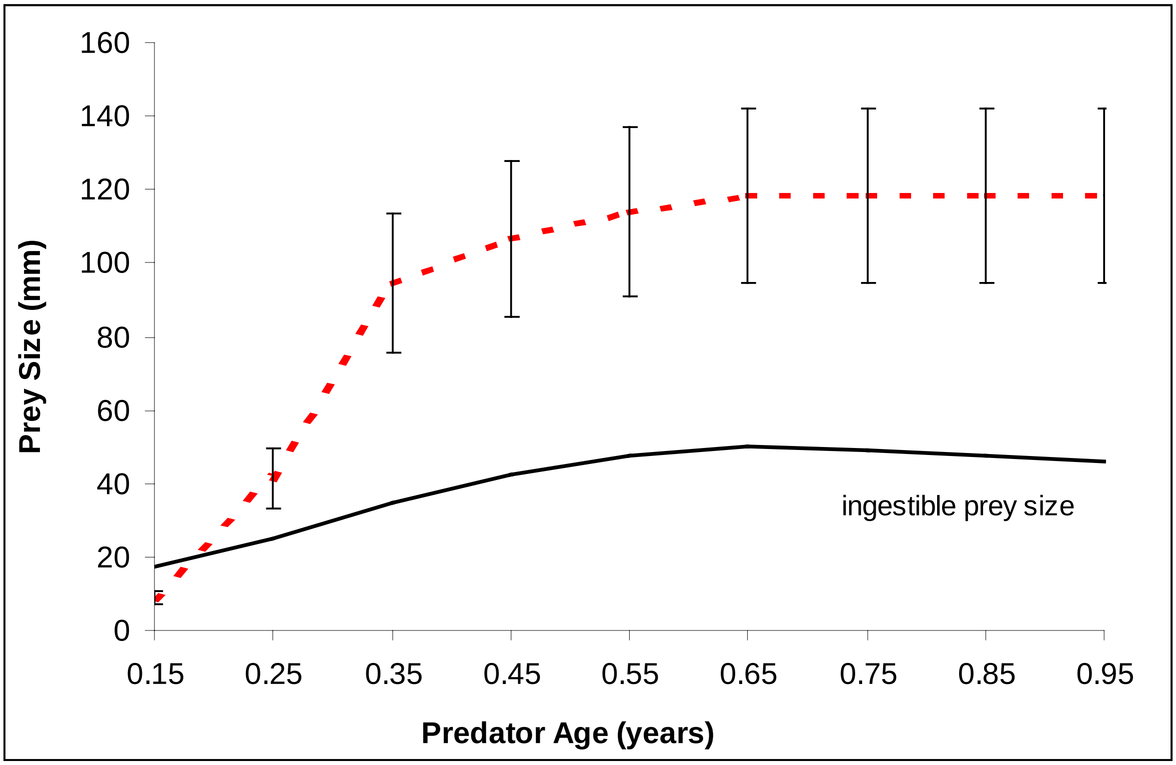

Figure 3.8. Lifespan morphological availability of a cohort of gizzard shad for a same-age small-mode age-0 striped bass. The dashed line, with vertical bars that demarcate the 25th and 75th percentiles of prey sizes, is the growth curve of the average gizzard shad in the cohort, while the solid line is the maximum ingestible prey size by the average individual of the cohort of striped bass.

Table 3.1. Percent of behaviorally-available annual surplus production of successive age-classes of alewife morphologically vulnerable to cohorts of largemouth bass. Values determined using Jenkins and Morais (1978) vulnerability equations and modeled growth of largemouth and alewife in Smith Mountain Lake. Variation in alewife length-at-age was considered, but not variation in largemouth bass length-at-age.

Largemouth	Alewife Age-Class			
Age-Class	YOY	1	2	3
YOY	45	0	0	0
1	100	50	30	20
2	100	100	75	30
3+	100	100	100	100

Table 3.2. Percent of behaviorally-available annual surplus production of successive age-classes of shad morphologically vulnerable to largemouth bass cohorts. Values determined using Jenkins and Morais (1978) vulnerability equations and modeled growth of largemouth and shad in Smith Mountain Lake. Variation in shad length-at-age was considered, but not variation in largemouth bass length-at-age.

Largemouth	Shad Age-Class	
Age-Class	YOY	1
YOY	5	0
1	50	0
2	75	50
3+	100	100

Table 3.3. Percent of behaviorally-available annual surplus production of successive age-classes of alewife morphologically vulnerable to striped bass cohorts. Values determined using Manooch (1973) vulnerability assumptions and modeled growth of striped bass and alewife in Smith Mountain Lake. Variation in alewife length-at-age was considered, but not variation in striped bass length-at-age.

Striped Bass	Alewife Age-Class			
Age-Class	YOY	1	2	3
Small YOY	25	0	0	0
Large YOY	100	30	15	0
1	100	100	90	80
2+	100	100	100	100

Table 3.4. Percent of behaviorally-available annual surplus production of successive age-classes of shad morphologically vulnerable to striped bass cohorts. Values determined using Manooch (1973) vulnerability assumptions and modeled growth of striped bass and shad in Smith Mountain Lake. Variation in shad length-at-age was considered, but not variation in striped bass length-at-age.

Striped Bass	Shad Age-Class	
Age-Class	YOY	1
Small YOY	0	0
Large YOY	25	0
1	90	30
2+	100	100

The average largemouth bass could not quite consume the average individual of the same-age cohort of alewife during their first or second growth season (Figure 3.3, Table 3.1). Largemouth bass began to outgrow these morphological constraints early in their third growth season. All but the largest individuals of the same-age cohort of alewife were available to them after this point. It appears from the graph that the majority of members from all subsequent cohorts of alewife were morphologically available to this largemouth bass cohort. Smaller members of alewife cohorts from the previous two years became available to largemouth bass in early summer of their second growth season. However, there was very little biomass and even less production of these older alewife (see Chapter One), so they would not provide much of a sustainable benefit to the bass population. All alewife surplus production in SML was morphologically available to bass entering their fourth growth season and beyond.

Gizzard shad were less morphologically available to largemouth bass than alewife (Figure 3.4, Table 3.2) due to the faster growth and greater adult size of gizzard shad. It was not until their fourth or perhaps even their fifth growth season that largemouth bass could consume even the smallest members of a same-age gizzard shad cohort if a very short initial time period immediately after hatching was ignored (during this time age-0 shad were behaviorally unavailable). Shad were well beyond 160 mm TL by this time, so the behavioral constraint discussed previously had taken effect. Many members of a shad cohort spawned one year later quickly became morphologically unavailable to a particular cohort of bass. The largest members of a shad cohort spawned three years after a largemouth bass cohort were too large for these bass to consume after the shad's initial growth season. Age-0 bass had virtually no shad surplus production available to them. Age-1 bass had about 50% of the behaviorally available age-0 shad surplus production morphologically available to them. Age-2 largemouth bass had morphologic access to approximately 75% and 50% of behaviorally available age-0 and age-1 shad surplus production, respectively. Age-3 and older largemouth bass were large enough to ingest all shad less than 160 mm TL.

Striped bass, due to their larger adult size, were not as severely affected by morphological constraints as largemouth bass, especially in regards to the relatively small alewife (Figure 3.5, 3.6, Table 3.3). All members of an alewife cohort (> 40 mm TL) spawned in the same year could be ingested by large-mode age-0 striped bass. An "average" age-0 alewife could be ingested by the small-mode age-0 striped bass only until mid-September, but until this time most alewife were less than 40 mm TL so behavioral constraints would arise (Figure 3.6, Table 3.3). Only the smallest of the alewife cohort could be utilized as prey by small age-0 striped bass after mid-September. Large YOY striped bass, in addition to complete morphological access to age-0 alewife, also had access to smaller members of the previous two years' alewife cohorts as the growth season continued. Striped bass were capable of swallowing most alewife in SML midway through their second growth season.

Gizzard shad presented more of a morphological challenge to striped bass (Figure 3.7, 3.8, Table 3.4). Only approximately 25% of behaviorally-available age-0 shad surplus production, and no surplus production of older shad cohorts, was morphologically available to large age-0 striped bass. Several months into the next growth season, however, the average age-1 striped bass could consume all shad under 160 mm TL. The average age-1 striped bass had morphological access to 90% of the behaviorally available age-0 shad and 30% of the behaviorally available age-1 shad during the growth season. Small age-0 striped bass had no behaviorally available surplus production of gizzard shad morphologically available to them.

DISTRIBUTIONAL AVAILABILITY

I determined the amount of prey that was behaviorally or morphologically unavailable to cohorts of largemouth bass and striped bass in the previous two sections. Next I calculated the component of remaining available prey that was spatially separated from each predator cohort. There was no indication that adult alewife were spatially unavailable to adult striped bass at any time during the year. The is also the case for gizzard shad distributional availability in regards to largemouth bass. Adult striped bass (but not age-0 striped bass) were spatially isolated from age-0 alewife and gizzard shad for a part of the year due to differences in thermal preference. It therefore is only the spatial relationships between largemouth bass and alewife, adult striped bass and age-0 alewife, and adult striped bass and gizzard shad that will be discussed further.

Largemouth Bass and Alewife

Largemouth bass are considered littoral predators. Alewife are primarily pelagic forage fish. Diet analyses (Michaelson 1996, this investigation) definitively show that in SML it is only during the protracted alewife spawn (late May through late August), as adults invade near-shore areas, when they are consequently available to largemouth bass in substantial quantities. Alewife < 40 mm TL were not found in the stomachs of any age-class of largemouth bass, possibly due to behavioral preferences for larger, more energetically-rich prey (Juanes 1994). The distribution of these alewife need not be discussed for this reason. Age-0 alewife > 40 mm TL were found by Tisa (1988) to be concentrated mainly offshore and thus are generally unavailable to most largemouth bass. Moore (1988) did find juvenile alewife in a few largemouth bass stomachs in late summer. These predators could have captured remnant littoral members of migrating juvenile alewife or this aberration could be due to offshore movements of some adult largemouth bass at this time of year (Hayne et al. 1967; Allan and Romero 1975; Axon and Summers 1980; Hightower et al. 1982).

I estimated spatially-unavailable surplus production of alewife to largemouth bass from these foundations. Approximately 24 kg/ha of surplus production from age-0 alewife > 40 mm TL occurred by late November. Forty-five percent of this quantity was morphologically available to age-0 largemouth bass (Table 3.1). Because these juvenile alewife were offshore, this percentage was lost to this predator cohort due to spatial constraints. The entire 24 kg/ha was lost to spatial constraints for all other largemouth bass age-classes because it was all morphologically available. There was 21 kg/ha of surplus production from 1 December through 25 August of the alewife cohort's second growth season. Diet analysis showed that largemouth bass feed on adult alewife from approximately 25 May to 25 August (the alewife spawning season). About 75% of the 21 kg/ha was lost (16 kg/ha) between 1 December and 25 May, assuming constant surplus production (no growth occurs in the winter but previous production dies). Fifty percent of this 16 kg/ha was already lost to morphological constraints for age-1 largemouth bass. The entire amount was lost to distributional unavailability for age-2 and older largemouth bass. Thirty eight kg/ha of alewife biomass died before 25 August of their second growth season. This loss occurred prior to largemouth bass having an opportunity to consume the members of a particular alewife cohort. There was 15.5 kg/ha of alewife surplus production between 25 August of their second growth season and the next 25 August. Largemouth had access to these clupeids for only three months during these 365 days (25% of the time). The total amount of inaccessible surplus production was therefore approximately 75% of 15.5, or 11.6 kg/ha. Seventy percent of the 11.6 kg/ha had already been lost to morphological constraints for age-1 largemouth bass. In the same way, 25% of this 11.6 kg/ha was morphologically unavailable to age-2 largemouth bass. The entire 11.6 kg/ha was lost to distributional factors for age-3 and older largemouth bass. Inaccessible alewife surplus production totaled 6 kg/ha for the period of 25 August during their third growth season to the 25 of August of their final growth season. Again, 75% of this (4.5 kg/ha) was unavailable to largemouth bass. The 1.4 kg/ha of alewife biomass remaining in late August of the cohort's fourth growth season was also soon lost while alewife were segregated from largemouth bass. Total alewife biomass spatially unavailable to largemouth bass is thus approximately 6 kg/ha (4.5 + 1.4 kg/ha) after

25 August of their third growth season. Only 20% of this amount was morphologically available to age-1 largemouth bass, and only 30% was morphologically available to age-2 largemouth bass. All 6 kg/ha was morphologically available to age-3 and older largemouth bass. Summing up inaccessible alewife surplus production during all of the periods examined, 57.5 kg/ha (24 + 16 + 11.6 + 4.5 + 1.4), or almost 80% of total surplus production, was distributionally unavailable to age-3 and older largemouth bass. Surplus production lost to distributional unavailability was only 12, 37, and 51 kg/ha, respectively, for age-0, age-1, and age-2 largemouth bass because some percentage of the 57.5 kg/ha was morphologically unavailable to each of these predator cohorts.

Striped Bass and Clupeid Distributions

Results of the temperature/dissolved oxygen readings performed on SML in early October of 1998 indicate that the survey year was a worst-case scenario for striped bass due to a summer drought (Table 3.1). The hypolimnion of SML becomes anoxic quickly in uplake regions, where the lake is much more productive/eutrophic, each year after the mid-June stratification (Ney et al. 1990). The longer the lake remains stratified, the further downlake this anoxic hypolimnion extends. A sufficiently oxygenated hypolimnion for striped bass (> 3.0 mg/l) was only found within a kilometer of the dam in early October of 1998, likely only a few days before fall turnover occurred. Surface waters, however, had already cooled to the point where striped bass could occupy them (< 22 °C). Striped bass were confined to the hypolimnion from stratification to the middle of September. Epilimnion temperatures were too warm for these predators during this period (over 24 °C). They could initially meet temperature and oxygen demands throughout much of the lake’s deep water (below about 8 meters). They were pushed far downlake by mid-September, however, based on the location of sufficiently oxygenated hypolimnion waters in early October. Surface temperatures in late October had already declined sufficiently to allow them access to the epilimnion. Striped bass would not be forced as far downlake in a more typical year but they would still be excluded from warm epilimnion waters from mid-June to mid-September.

Table 3.5. Results of the temperature/dissolved oxygen (DO) profiling done in October of 1998. The top table shows data for four stations on the Blackwater arm, moving downlake from left to right. The bottom table gives readings for two stations on the Roanoke arm (R28 and R17), and three stations below the confluence of the Blackwater and Roanoke arteries (Confluence, R2 and R1). An anoxic hypolimnion extended nearly all the way to the dam by the end this long, dry summer.

	B20		B19		B10		B9	
Depth	Temp	DO	Temp	DO	Temp	DO	Temp	DO
6	21.6	6.8						
7	21.7	6.7						
8	21.6	6.6	21.6	7.3	21.3	6.4	21.6	6.0
9	21.1	1.0						
10	20.3	0.5	20.3	0.6	19.0	1.4	20.3	1.5
12	19.5	0.3						
15	19.0	0.1						

	R28		R17		Confluence		R2		R1 (Dam)	
Depth	Temp	DO	Temp	DO	Temp	DO	Temp	DO	Temp	DO
1			21.8	6.9	21.3	7.3	21.0	6.6	20.9	6.3
4									20.4	5.0
5							20.7	5.7	20.1	4.3
6	21.8	5.8	21.5	6.9	21.3	7.2	20.1	3.0	20.0	4.6
8	20.4	0.2	21.4	5.9	21.3	7.1	19.4	2.0	19.7	4.3
10	19.5	0.2	19.6	1.6	19.5	1.5	19.3	1.8	19.5	4.0
15	18.9	0.2	19.0	1.0	19.0	0.9	18.9	1.3	19.4	3.4
20	18.6	0.1	18.7	0.4			18.7	0.9	18.9	3.3

During this three-month period of exclusion from the warm upper waters of SML, it was assumed that striped bass had little access to any biomass of gizzard shad or age-0 alewife that was lost. Any prey biomass that was still extant in the middle of September would be available to striped bass upon their return to the surface waters. Adult alewife retreat into the cooler hypolimnetic zone during the day after nocturnal spawning and feeding events, and thus are available to striped bass throughout the summer. These diet assertions were supported by striped bass stomach analyses of Moore (1988) and this investigation, which indicated that gizzard shad and age-0 alewife were less than 10% of the diet in the summer months, while adult alewife were 80% of the diet.

AGE-0 ALEWIFE AND ADULT STRIPED BASS. As discussed previously, age-0 alewife can tolerate warmer water than adult alewife (Stewart and Binkowski 1986) and are concentrated primarily in the upper 3-5 meters of the water column during summer in SML (Tisa 1988). Adult striped bass confined to the hypolimnion therefore have little access to these prey fishes. When large numbers of alewife reach the juvenile stage they move offshore (Tisa 1988), but generally do not encounter adult striped bass until the epilimnion cools sufficiently to allow adult striped bass back into the surface waters (mid-September). At this point the average age-0 alewife would be nearly 50 mm TL. This scenario is supported by Sutton (1997), Moore (1988), and this investigation. Alewife less than approximately 40 mm TL were not found in the hundreds of striped bass stomachs that were examined. Only surplus production of age-0 alewife > 40 mm TL before 15 September need be accounted for here because surplus production of alewife < 40 mm TL has already been subtracted out. I estimated this quantity to be 8.8 kg/ha from age-0 alewife cohort simulations.

AGE-0 ALEWIFE AND AGE-0 STRIPED BASS. Sutton (1997) found that age-0 striped bass begin dispersing to pelagic zones as they reach a size of 150 mm TL, which occurred as early as August in the fastest growing individuals. Small-mode age-0 striped bass remained in coves for basically the entire growth season. Large-mode age-0 striped bass that moved offshore may have had access to adult alewife but generally could not ingest them until very late in the growth season due to morphological constraints. Age-0 striped bass in littoral regions were large enough to consume age-0 alewife that had not yet moved offshore but instead fed on benthic invertebrates, centrarchids, and cyprinids (Sutton 1997). This lack of predation could have been due to behavioral interactions or possibly spatial segregation, but the matter has not been thoroughly investigated. Only upon reaching a size of 120 mm TL did age-0 striped bass begin consistently feeding on 40-60 mm alewife in SML (Sutton 1997). Striped bass in theory would have access to any littoral-dwelling age-0 alewife if the former reached 120 mm TL early in the growth season. Age-0 striped bass followed the waves of age-0 alewife moving to pelagic habitats after a few more weeks of growth. The slower-growing age-0 striped bass remained in the coves as juvenile alewife moved offshore and eventually were spatially separated from this prey species. As the growth season wore on, even if these smaller striped bass would have moved offshore, 75% of age-0 alewife had become morphologically-invulnerable (Figure 3.5). The critical period of initial growth is probably determined by site-specific variability in the quality and quantity of food items available to age-0 striped bass. In any case, behavior had already accounted for the lack of predation on alewife less than 40 mm TL. No additional surplus production of alewife was lost to this predator group because large-mode age-0 striped bass occupy the same habitat as age-0 alewife. For small age-0 striped bass, 25% of age-0 alewife surplus production occurring after mid-September (approximately 4 kg/ha) could be correctly identified as lost due to spatial separation between predator and prey.

GIZZARD SHAD AND STRIPED BASS. There had already been 24.5 kg/ha of age-0 shad surplus production when adult striped bass gained access to the epilimnion on 15 September (Table 1.4, Figure 1.2). However, approximately 1.5 kg/ha of this amount had already been deducted for behavioral reasons. This left 23 kg/ha of surplus production lost due to distributional factors. For age-1 striped bass, 10% of the 23 kg/ha was morphologically unavailable, so only 20.7 kg/ha was deducted. The entire 23 kg/ha was considered a distributional loss for all older striped bass. Surplus production of shad between 1 December and 25 August of their second growth season totaled 30 kg/ha. Assuming a constant loss, approximately 30% (9 kg/ha) occurred during a period when adult striped bass and shad did not spatially overlap (15 June to 25 August). The average age-1 shad reached 160 mm TL at this time. The amount of spatially-unavailable production of later shad cohorts did not need to be calculated after this date, as it had already been considered under behavioral availability. For age-1 striped bass, 70% of the previously-mentioned 9 kg/ha of lost biomass had already been subtracted out due to morphologic constraints. The entire 9 kg/ha was deducted and attributed to distributional constraints for age-2 and older striped bass. The grand total of lost shad biomass due to spatial segregation from adult striped bass was thus 32 kg/ha for age-2 and older striped bass, and 23.5 kg/ha for age-1 striped bass. Because a shad cohort had about 90 kg/ha of surplus production before 25 August of its second growth season, about 35% of this production was not available to age-2 and older striped bass due to habitat constraints. None of the 23 kg/ha of age-0 shad biomass lost prior to 15 September was deducted for large age-0 striped bass because this predator cohort was not spatially segregated from age-0 shad during this time period. Small age-0 striped bass were unable to feed on age-0 gizzard shad due to morphological and behavioral constraints, so no further deductions were necessary.

SYNTHESIS OF AVAILABILITY

I have described how the three components of availability reduce the amount of prey production that is capable of being eaten by various-sized predators. Tables 3.6 through 3.9 summarize these assorted constraints on each age-class of largemouth bass and striped bass in SML. The second column in each table is the total surplus production of the prey species in kg/ha. The third through the sixth columns are the kg/ha of this prey biomass that is unavailable to a given cohort of predator. In keeping with the methodology depicted in Figure 3.2, BUP is behaviorally-unavailable prey, MUP is behaviorally available but morphologically-unavailable prey, and DUP is behaviorally and morphologically-available prey that is distributionally unavailable. There are two forms of unavailability within BUP: neglect of small prey and disregard of large prey. The penultimate column is total prey surplus production minus all forms of unavailability. The final column is demand of the predator cohort from Chapter Two bioenergetic modeling.

The values in the "Available Surplus" column for each predator cohort are generally much greater than those numbers in the "Total Demand" column, leading one to think that there is a great surplus of prey in SML for these predators. However, the surplus production available to a certain cohort is also lost to competing sources of mortality, namely starvation, disease, senescence, and other predators (both of the same and different species). These factors will take some of the available production before individuals from the cohort in question can eat it. A very difficult task is to determine how much greater available production must be when compared to demand. This would depend on the intensity of the other forms of mortality on prey available to a given cohort and the efficiency with which the predator can find and consume its prey.

Total cumulative demand of the largemouth bass population for alewife was about 9 kg/ha and total available production to age-3 and older largemouth bass equaled 12 kg/ha (Table 3.6). This led to an available supply/demand ratio (AS/D) of 1.3. Total largemouth bass demand for gizzard shad totaled 15 kg/ha and available gizzard shad production to age-3 and older largemouth bass was 85 kg/ha (Table 3.7). This led to a much higher AS/D of 5.7. From these ratios, it appears that alewife prey supply to largemouth bass is much more limited than gizzard shad prey supply. However, competition for 40-160 mm TL gizzard shad could be more intense than for that fraction of the adult alewife population that are eaten by largemouth bass. Largemouth bass only consumed adult alewife during the latter's three month onshore spawning period when the availability of the prey species was very high. The gizzard shad that were available to largemouth bass were also available to all other littoral predators at most times of the year, and during most months to pelagic striped bass as well.

Total demand of striped bass for alewife was 46 kg/ha and supply to adult striped bass was 60 kg/ha, for an AS/D of 1.3 (Table 3.8). Due to the pelagic nature of alewife and their similar thermal preferences to striped bass, this forage fish was generally much more available to striped bass than other predators. Competition among piscivores for alewife thus heavily favored striped bass, and a low AS/D would then be reasonable. Total demand of striped bass for gizzard shad equaled 27 kg/ha while availability of gizzard shad to adult striped bass was 53 kg/ha, for an AS/D of 2.0. The availability of this prey species to striped bass might be considered more limited than alewife availability considering that gizzard shad were more available to littoral predators than to striped bass from mid-June to mid-September. A higher AS/D would thus be necessary for striped bass to meet their demand for gizzard shad.

The amount of prey eaten by other predators up to this point has not been accounted for. For example, adult largemouth bass had 85 kg/ha of gizzard shad available to them. However, if I subtracted the 62 kg/ha of gizzard shad that I estimated to be consumed by other predator species, availability to adult largemouth bass would be 23 kg/ha. This was still 53% greater than the population demand of largemouth bass for gizzard shad (15 kg/ha). The problem with this approach is that prey availability is different for each predator species and even each cohort within that species. Adult largemouth bass, for example, had 12 kg/ha of alewife available to them. If I subtracted the amount of alewife eaten by other predator species (59 kg/ha), a negative number would result. However, 58 kg/ha of alewife was distributionally unavailable to adult largemouth bass. This amount could be eaten by other predators such as striped bass. Instead of subtracting 59 kg/ha, I subtracted 59 - 58 = 1 kg/ha, leaving 11 kg/ha of available alewife biomass for largemouth bass. This was 20% greater than the largemouth bass population demand of 9 kg/ha.

Continuing the calculations of the previous paragraph, availability of gizzard shad for adult striped bass totaled 53 kg/ha. Demand of all other predator species for gizzard shad was 50 kg/ha. Assuming gizzard shad surplus production that was distributionally unavailable to striped bass (32 kg/ha) was available to other predators, other predator demand was reduced from 50 kg/ha to 18 kg/ha. The resulting 35 kg/ha of gizzard shad supply (53 kg/ha - 18 kg/ha) remaining for striped bass still exceeded striped bass demand for gizzard shad (27 kg/ha) by 30%. Alewife availability to adult striped bass was 60 kg/ha. Demand of other predators for alewife was 21 kg/ha. I subtracted the 9 kg/ha of age-0 alewife that was distributionally unavailable to adult striped bass from this 21 kg/ha. That left 12 kg/ha of other predator demand, which was subtracted from 60 kg/ha to get 48 kg/ha of available supply. This was only 4% larger than the 46 kg/ha demand of the striped bass population.

Table 3.6. Summary of alewife availability and demand for each cohort of largemouth bass. All values are in kg/ha. See text for explanation of terms.

Age-Class	Total Alewife Surplus Production	BUP Too Small	BUP Too Large	MUP	DUP	Available Surplus	Total Demand
YOY	73	4	*	56	12	1	0.0
1	73	4	*	26	37	6	0.2
2	73	4	*	8	50	11	1.9
3	73	4	*	*	58	12	1.9
4	73	4	*	*	58	12	1.5
5	73	4	*	*	58	12	1.1
6	73	4	*	*	58	12	0.7
7	73	4	*	*	58	12	0.5
8	73	4	*	*	58	12	0.3
9	73	4	*	*	58	12	0.2
10	73	4	*	*	58	12	0.1

Table 3.7. Summary of gizzard shad availability and demand for each cohort of largemouth bass. All values are in kg/ha. See text for explanation of terms.

Age-Class	Total Shad Surplus Production	BUP Too Small	BUP Too Large	MUP	DUP	Available Surplus	Total Demand
YOY	146	2	60	82	*	3	0.4
1	146	2	60	58	*	27	4.8
2	146	2	60	29	*	56	2.4
3	146	2	60	*	*	85	2.2
4	146	2	60	*	*	85	1.7
5	146	2	60	*	*	85	1.2
6	146	2	60	*	*	85	0.8
7	146	2	60	*	*	85	0.5
8	146	2	60	*	*	85	0.3
9	146	2	60	*	*	85	0.2
10	146	2	60	*	*	85	0.1

Table 3.8. Summary of alewife availability and demand for each cohort of striped bass. All values are in kg/ha. See text for explanation of terms.

Age-Class	Total Alewife Surplus Production	BUP Too Small	BUP Too Large	MUP	DUP	Available Surplus	Total Demand
Small YOY	73	4	*	61	4	4	0.0
Large YOY	73	4	*	34	*	35	4.0
1	73	4	*	3	9	58	13.6
2	73	4	*	*	9	60	12.2
3	73	4	*	*	9	60	8.5
4	73	4	*	*	9	60	4.4
5	73	4	*	*	9	60	2.1
6	73	4	*	*	9	60	0.9
7	73	4	*	*	9	60	0.4
8	73	4	*	*	9	60	0.2
9	73	4	*	*	9	60	0.1
10	73	4	*	*	9	60	0.0

Table 3.9. Summary of gizzard shad availability and demand for each cohort of striped bass. All values are in kg/ha. See text for explanation of terms.

Age-Class	Total Shad Surplus Production	BUP Too Small	BUP Too Large	MUP	DUP	Available Surplus	Total Demand
Small YOY	146	2	60	85	*	0	0.0
Large YOY	146	2	60	71	*	14	0.0
1	146	2	60	26	24	35	5.8
2	146	2	60	*	32	53	9.7
3	146	2	60	*	32	53	6.2
4	146	2	60	*	32	53	3.0
5	146	2	60	*	32	53	1.4
6	146	2	60	*	32	53	0.6
7	146	2	60	*	32	53	0.3
8	146	2	60	*	32	53	0.1
9	146	2	60	*	32	53	0.0
10	146	2	60	*	32	53	0.0

DISCUSSION

BEHAVIORAL AVAILABILITY

While the reasons for neglect of very large prey fishes are debatable, the conclusions are the same. Diet analyses from this investigation and Moore (1988) indicate that adult largemouth bass and striped bass in SML rarely consume gizzard shad over 160 mm TL even if they have a gape width sufficient to do so. Production of shad after late August of their second growth season (when they are approximately 160 mm TL), therefore, can be considered generally unavailable to predator populations. About 40% of current SML gizzard shad surplus production is thus unavailable to predators.

This investigation, as well as Moore (1988), found no clupeids less than 40 mm TL in predator stomachs. Sutton (1997) found that age-0 striped bass over 120 mm TL did not consume alewife less than 50 mm TL in SML, but they did consume large quantities of age-0 cyprinids between 5-50 mm TL. The latter consumption of small cyprinids occurred when striped bass were between 40 and 120 mm TL, however. This indicates that age-0 striped bass consumption could be determined by a combination of distributional and behavioral foraging factors. Striped bass are littoral, benthic creatures after stocking and thus come into contact with age-0 cyprinids more often than larval alewife, which are primarily in the upper surface waters of the lake (Tisa 1988). Upon reaching approximately 120 mm TL, juvenile striped bass move up into the water column and at 150 mm TL travel offshore into pelagic habitats where they encounter schools of juvenile alewife (Sutton 1997). It would seem likely that given the opportunity to eat small alewife before they move offshore, young striped bass certainly would, but do not because of the small probability of encountering an alewife while hovering over the littoral sediments. Age-0 largemouth bass, which are large enough to consume age-0 alewife, also rarely do. Young largemouth bass usually stay close to littoral vegetation, which enables them to lessen their own risk of predation. The age-0 alewife are not associated with any littoral structure, instead preferring the upper surface waters where they can feed on zooplankton (Tisa 1988).

Clupeids under 40 mm TL were also not consumed by adult largemouth bass and striped bass in SML, possibly due to the failure of predators to notice them, noticing them but not recognizing them as prey, or recognizing them as prey but avoiding them due to minimal nutritional potential (optimal foraging strategy). Larval clupeids are less conspicuous than juveniles within the aquascape, especially for visual, particulate piscivores (Langsdale 1993). Batty (1989) proposes that larval fishes depend upon this transparency to conceal them from predators. As time passes, increases in size, activity levels, and pigmentation of larvae make them much more conspicuous, especially after body scales develop (Langsdale 1993). They must therefore abandon their sedentary lifestyle and adopt behavioral responses to predation, and primary among these is schooling (Gallego and Heath 1994). Gallego and Heath (1994) found that the Atlantic herring (*Clupea harengus*) initiated schooling between 35-40 mm TL and demonstrated well-established schooling behavior at 50-55 mm TL. Although Masuda and Tsukamoto (1998) point out that some other fish species begin schooling at much smaller sizes (12-16 mm TL), they note that nearly all schooling fishes demonstrate this behavior just prior to or shortly after metamorphosis from the larval to juvenile stage, in association with increased development of the retina and lateral line systems. This transition occurs between 30-35 mm TL for clupeid fishes (Gallego and Heath 1994). The unorganized larvae are not aggregated into a large, recognizable prey "unit" before this time Surplus production of clupeids prior to the formation of more visible aggregates (schools) was thus behaviorally-unavailable to predators.

Small clupeids (< 40 mm TL) have high mortality rates in SML despite the fact that largemouth bass and striped bass do not eat them (Tisa 1988). Starvation mortality of newly-hatched clupeid larvae can be great (Kashuba and Matthews 1984; Matthews 1984), but predation is hypothesized to play a larger role as larval clupeids grow and become more active and conspicuous (Noble 1981; Sissenwine et al. 1988; Storck 1986; Johnson et al.

1988a; Batty 1989; Michaletz 1997a, 1997b). Invertebrate predators that do not rely on vision for prey detection have been shown to feed on larval clupeids in other systems (Hartig et al. 1982; Hartig and Jude 1984). There is a plethora of other piscine predators who could concentrate on these small, super-abundant clupeids. Crappie, white bass, white perch, yellow perch, sunfishes, and even adult alewife would seem like ideal candidates, but could be restricted by visual difficulties in locating larval clupeids. Michaletz (1997b) found that the minimum size of gizzard shad prey in the stomachs of adult crappie and white bass was approximately 25 mm TL. The alewife has been shown to feed on fish larvae in some systems (Crowder 1980; Kohler and Ney 1980; Brandt et al. 1987; Krueger et al. 1995; Mason and Brandt 1996), although Tisa and Ney (1991) conclude that spatial segregation would limit adult alewife predation on gizzard shad larvae in SML. Further research is needed to determine what organisms, if any, feed on larval clupeids in SML and to what extent.

MORPHOLOGIC AVAILABILITY

As expected, alewife showed only minor morphological invulnerability to young predators in SML. Gizzard shad, however, demonstrated a proclivity for rapidly growing beyond predator ingestion capabilities. Age-0 largemouth bass were not large enough to feed on virtually any of the age-0 shad cohort. This result was supported by the recent diet work of Sutton (1997), who did not find a single age-0 gizzard shad in the stomachs of 1,350 age-0 largemouth bass from June to the following March in two sampling seasons. Michaletz (1997b) found that in gizzard-shad dominated Missouri reservoirs the size of age-0 gizzard shad was most important for growth of young predators, not shad production. Older predators grew better when gizzard shad production was higher, and growth of these predators was less dependent on the growth rates of age-0 shad. Very few age-0 predators utilized age-0 gizzard shad in SML, almost certainly due to high shad growth rates leading to morphological invulnerability. It would be more likely, therefore, that current growth rates of adult piscivores in SML are limited to some extent by shad production.

DISTRIBUTIONAL AVAILABILITY

Striped bass distribution during the summer, and thus their access to prey, was primarily affected by epilimnion water temperatures and dissolved oxygen concentrations. Adult striped bass prefer temperatures near 20 °C and must have oxygen levels of at least 2-3 mg/l of O_2 (Coutant 1985; Coutant and Benson 1990). Many investigators have noted striped bass movements within aquatic systems into refuges with sufficient temperature and oxygen profiles when surface waters warm considerably (Coutant and Carroll 1980; Schaich and Coutant 1980; Waddle et al. 1980; Wooley and Crateau 1983; Cheek et al. 1985; Matthews et al. 1989). These areas were found downlake in the main basin in some reservoirs (Combs and Peltz 1982; Matthews et al. 1985), and in other impoundments preferred habitat occurred in uplake riverine sections (Cheek et al. 1985; Moss 1985). Negative impacts on growth and survival have been documented when appropriate habitat was very limited within a system, forcing a large population into a small refuge (Coutant 1985; Coutant 1987). In addition to stress from overcrowding, increased competition for prey, and increased susceptibility to disease, concentrated angling effort on the aggregated bass population has been implicated (Schaich and Coutant 1980; Waddle et al. 1980). The volume of the cool-water refuge for striped bass during the summer has been hypothesized to determine the capacity of a system for a reservoir population of adult striped bass (Coutant 1983). This period in essence served as a bottleneck, reducing the population if too many adults tried to use the refuge, despite an overabundance of habitat during other periods of the year.

Data from SML indicated that beginning in mid-June temperatures in the epilimnion began to get uncomfortable for striped bass. At this point they likely retreated to hypolimnetic waters (assuming stratification had occurred). They did not have to move far downlake to find oxygen in the hypolimnion because stratification had recently occurred. However, in the warm and extremely dry summer of 1998, striped bass were likely confined farther and farther downlake until mid-September. Epilimnion temperatures at that time cooled sufficiently (below 24 °C) to allow re-entry. Feeding should not have been greatly hindered as long as alewife also moved with the striped bass. My data indicated that striped bass also utilized crayfish to some extent (10-15% of the diet) in the summer when confined to the hypolimnion. Kelso and Ney (1983) report that during the summer alewife moved into the warm upper surface waters at night in Claytor Lake, Virginia, to utilize upward-migrating zooplankton aggregations, and returned to the cool, oxygenated hypolimnion during the day. The price of increased metabolic demands in the warmer waters were likely paid by intensive feeding on an abundant prey resource. The alewife had to retreat to the cooler depths during the day to save energy, especially because zooplankton also migrate into deeper water at this time (Hall et al. 1979; Redfield and Goldman 1980; Fairchild 1981; Kelso and Ney 1983). In summer, then, striped bass should feed during the day on alewife, and possibly at night on crayfish.

Striped bass would be forced to endure temperatures much warmer than their preferred range in order to find clupeid prey (gizzard shad) in uplake regions without alewife in SML. The striped bass could not inhabit cooler, deeper water in uplake regions due to the lack of oxygen there, and thus would have to move far downlake to find sufficiently cool, oxygenated water after feeding. The energy expended in these daily foraging forays would likely exceed the amount gained by feeding. The lack of a cool-water clupeid in this type of system would lead to little consumption, subsequent weight loss, and deteriorating condition for striped bass during the summer. Striped bass would basically aestivate in the cool downlake depths, waiting for epilimnion temperatures to cool sufficiently and free them from their trophic prison. They could move uplake at that time to find juvenile gizzard shad, averaging approximately 100 mm TL, and begin to feed.

Largemouth bass and other littoral predators are even more spatially segregated from alewife than striped bass are from gizzard shad. As opposed to a three month feeding ban, alewife and near-shore predators have low encounter rates for a nine-month period. It is only during the protracted alewife spawn, running from late May through August (Tisa 1988), that these predators have access to adult alewife. Older largemouth bass are more often found the pelagic zone compared to younger individuals (Hayne et al. 1967; Summers and Axon 1980), and thus would have access to alewife more frequently than their littoral con-specifics. As stated previously, juvenile alewife move offshore and begin to school after reaching 30-40 mm TL. Few appear to be utilized as prey by young largemouth bass before this time. It is not surprising, then, that the only abundant and truly pelagic piscivore, the striped bass, should account for more than 70% of the biomass of alewife consumed by predators in SML.

ANNUAL VARIABILITY IN SUPPLY/DEMAND

Prey supply and predator demand are in a constant state of flux, both determined by the abundance and growth rates of the participants. It is well known that clupeid supply can be highly variable in reservoir systems (Adams et al. 1982a, 1982b; Storck 1986; Adams and DeAngelis 1987; Hale 1996; Michaletz 1997b). Although the possibility exists that heavy predation on age-0 clupeids is keeping population levels of these forage fishes low, variability in clupeid prey supply is more likely to dictate predator consumption in SML. Fluctuations in prey supply can be attributed to changes in larval survival of alewife and gizzard shad. Mortality in reservoir clupeids at this life stage is probably dictated more by food availability than predation (Matthews 1984; Kashuba and Matthews 1984; Welker et al. 1994; Michaletz 1997a, 1997b). Age-0 clupeid larvae either starve in years with little food or, if they can make it to the juvenile stage when predation mortality is paramount (Diana 1995; Michaletz 1997a), their reduced size increases their probability of death. Growth rates are crucial in determining survival of small fishes because both feeding efficiency and predator evasion skills increase with size (Juanes 1994; Diana 1995). Rotenone surveys indicate that the densities of age-0 gizzard shad varied by a factor of four in the 1990's in SML, but the size of age-0 clupeids appeared more consistent from year to year. This could be interpreted to mean that in years with a super-abundance of food more age-0 clupeids grow as needed to survive, while in years with low food abundance far fewer age-0 clupeids reach a size necessary for survival.

Predator demand changes from year to year in response to clupeid supply. This is accomplished through changes in predator growth rates and, to a lesser extent, changes in predator densities. The wealth of papers that investigate growth and survival of age-0 largemouth bass in direct response to age-0 shad availability (Noble 1981; Storck 1986; DeVries et al. 1991; Hambright et al. 1991; Stein et al. 1995; Olson 1996; Michaletz 1997b; Garvey and Stein 1998; Garvey et al. 1998) are not entirely relevant to SML predators. Sutton (1997) found that age-0 largemouth do not prey upon clupeids in SML, likely due to morphological and distributional limitations. It is also unlikely that the survival of other juvenile littoral predators (e.g., crappie, smallmouth bass, and catfish) is dependent on these prey fishes. Changes in clupeid supply for these species primarily result in alterations of adult growth rates (Ney et al. 1990; Hartman and Margraf 1992; Michaletz 1997b, 1998b). The growth of young predators in SML might be less responsive than older predators to changes in clupeid availability, which would be contrary to the conclusions of Michaletz (1998b).

Reductions in clupeid abundance could indirectly increase the survival of age-0 littoral predators. Decreased clupeid densities would mean less competition for zooplankton for both the larval stages of the predator species, as well as the ancillary prey species on which their first-year growth will later depend (Kirk et al. 1986; Kirk and Davies 1987; Guest et al. 1990; Dettmers and Stein 1992; DeVries and Stein 1992; Welker et al. 1994; Stein et al. 1995; Dettmers and Stein 1996). Increased food resources for young piscivores throughout their first growth season leads to augmented growth and survival (Storck 1986; DeVries et al. 1991; Bettoli et al. 1993; Stein et al. 1995; Olson 1996; Garvey and Stein 1998; Garvey et al. 1998). Increases in recruitment and subsequent population densities of the adult predator populations would then have ramifications on later cohorts of clupeid prey species. Because the effect of a single above-average predator year-class would be relatively minor, however, predator-prey dynamics would not be greatly affected unless this phenomenon was consistently seen over a period of three to five years.

Most adult predators can resort to other prey items such as cyprinids, lepomids, and crayfish to meet their caloric requirements in years with poor production of gizzard shad and/or alewife. The energetic content of clupeid prey surpasses these other forage items (Table 2.4), however, so more absolute biomass would have to be eaten to maintain the same predator growth rate. For a species such as striped bass, which has been shown to be nearly an obligate clupeid predator as an adult (Stevens 1958; Ware 1970; Combs 1978; Matthews and Hill 1982; Moore et al. 1985; Matthews et al. 1988), declines in clupeid abundance would be more serious. An adequate supply of age-0 alewife not only affects the survival of stocked age-0 striped bass but also adult growth rates (Sutton 1997). Age-0 striped bass feed on benthic invertebrates, cyprinids, and lepomids until they reach a size of approximately 120 mm TL. After this point age-0 alewife become critical to their growth in late summer and fall. Young striped bass cannot store sufficient energy reserves to avoid winter starvation if they do not prey upon age-0 alewife, but they would also grow poorly and remain in littoral coves throughout the growth season without adequate supplies of small lepomids, cyprinids, and invertebrates (Sutton 1997). Food resources at both life stages are critical for recruitment to age-1. Low alewife density could even affect the survival of adult striped bass. Adult striped bass, as stated previously, heavily depend on alewife as prey during the summer when the former are confined to the hypolimnion refuge.

SUMMARY

Despite the myriad of ways that prey are unavailable to all cohorts of predators, the fact remains that most prey are always available to some subset of the predatory assemblage. Largemouth bass, catfish, smallmouth bass, and crappie consume age-0 gizzard shad when striped bass are confined to the hypolimnion and unable to feed on this prey resource. When alewife were segregated from littoral predators they still contended with striped bass and token populations of white bass and walleye. It is not certain whether or not a predator will capture a prey item it engages, but if there are enough predators the prey can remain lucky only so many times. Judging by the total surplus production of behaviorally-available clupeid prey in SML (approximately 154 kg/ha) and the total predator demand for this class of forage fishes (approximately 145 kg/ha), clupeids that disappeared without having been eaten were in the minority. The exception to this paradigm was the adult gizzard shad. Very few ended up in the stomachs of piscivores once these forage fishes attained a size of approximately 160 mm TL.

The SML predator assemblage appeared capable of ingesting a large proportion of age-0 clupeid surplus production. Predators in other systems have been shown to consume only a relatively minor portion of total age-0 gizzard shad production (Carline et al. 1984; Johnson et al. 1988a; Stein et al. 1995; Michaletz 1998a). Age-0 shad biomass in SML at the end of the growth season was approximately 35 kg/ha. Total production of shad during their first growth season was 93 kg/ha. That means 62% of age-0 shad production disappeared. Given a total predator demand for shad of 77 kg/ha in SML, and knowing that nearly all of this demand was for shad 15 months and younger, it is obvious that predators took a significant portion of age-0 shad production. Doing these same calculations for alewife, I estimated that approximately 63% of age-0 alewife production died while 37% made it to age-1. The great majority of alewife were likely eaten by one predator or another because total predator demand for alewife was 93% of total alewife surplus production.

Based on the data presented at the end of the Results section, gizzard shad and alewife available supply exceeded the demand of largemouth bass by 53% and 20%, respectively. Gizzard shad available supply exceeded striped bass demand by 30%, but available alewife supply exceeded striped bass demand by only 4%. Alewife supply to striped bass thus appeared most limited in SML. As striped bass stockings are increased, changes in the trophic dynamics of the system are likely to occur. Predator growth and survival and/or prey dynamics could be altered significantly. If increased predation on clupeids leads to a decline in the biomass of these forage fishes, the effect on their surplus production would depend on the current biomass of clupeid populations in SML (Figure 3.9).

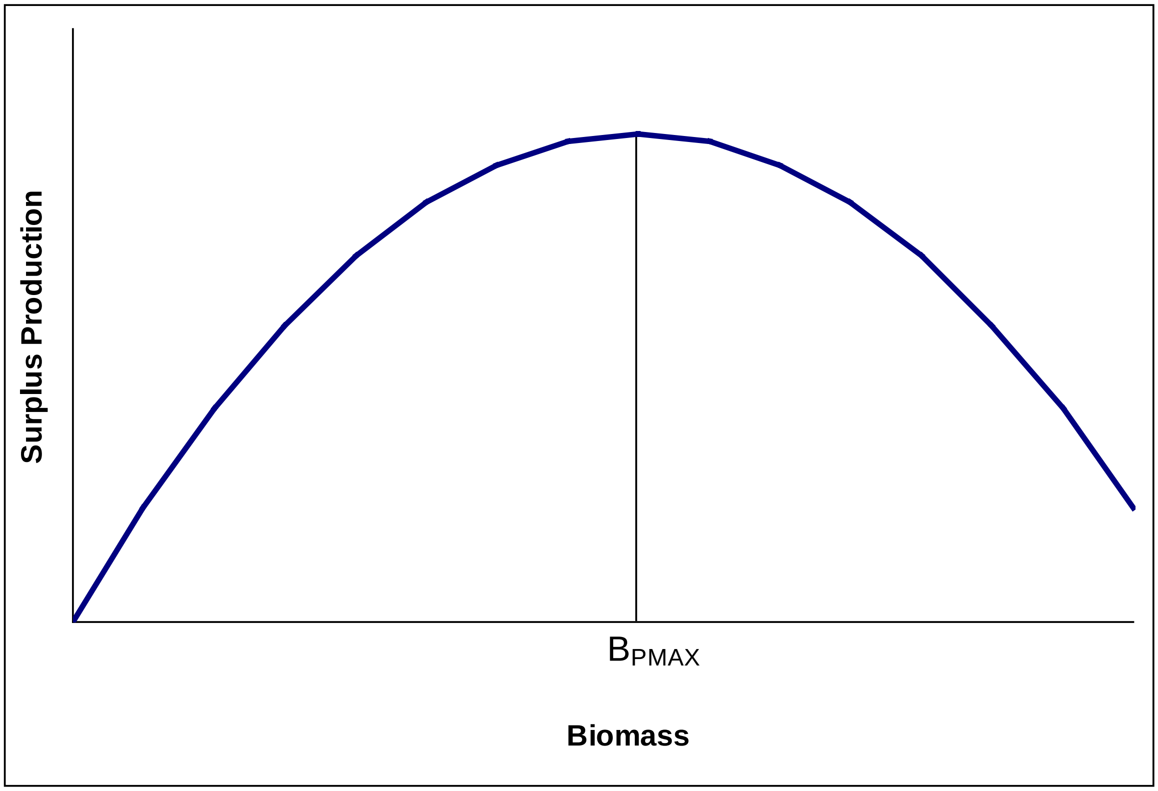

Figure 3.9. Relationship between biomass and surplus production, where B_{PMAX} is the biomass at which maximum production for the prey species occurs.

The relationship between biomass and production for a species is typically parabolic. Production is low at low biomass because there are few individuals. Production increases as population biomass increases, but declines as biomass increases past some point (B_{PMAX} in Figure 3.9). Growth rates of individuals at this biomass decline due to food limitation, as larger, older, less efficient individuals become more abundant. A decline in biomass therefore could either increase productivity or decrease productivity, depending on what side of B_{PMAX} the population currently resides. Evidence supports the assertion that clupeid biomass (especially alewife) in SML is located to the left of B_{PMAX}. The ecotrophic coefficient, discussed by Waters (1992), is the ratio of harvest to production for a given species. Waters concludes that a coefficient over 0.75 would indicate excessively high rates of removal. The ecotrophic coefficient for alewife in SML was 0.93, indicating intensive predation on this stock by predators. The average relative weights (indicative of condition compared to a species-specific standard, Wege and Anderson 1978) of striped bass and largemouth bass collected in SML from 1995 through 1998 were 86 and 90, respectively. These values are not indicative of a system with an overabundance of available prey (Murphy et al. 1991; Anderson and Neumann 1996). Stocking rates of striped bass in SML in the last decade were relatively high (36 per hectare compared to a median of 9 per hectare in nine southeastern states, Pritchard et al. 1978, and 16 per hectare in 53 southeastern reservoirs, Bailey 1975) and have been increased to 54 per hectare. The high P/B ratio calculated for alewife also suggests a young population with low biomass experiencing high mortality (Waters et al. 1990). The Chapter One discussion concerning the lower total fish biomass of SML compared to the predictions of Yurk and Ney (1989) is further evidence. Finally, the conclusions of Ney et al. (1988) concerning growth declines in SML predators and the decreasing trend in citation catches (Figure A.1) indicate an inadequacy of prey in the system. All of this information points to a higher probability of clupeid biomass being relatively low in SML (to the left of B_{PMAX}) than relatively high. This means reductions in forage fish biomass would lead to decreases in production, and could lead to prey shortages for the piscivores of SML. Chapter Four will explore the possible ramifications of increases in predator demand for clupeid prey in SML.

CHAPTER FOUR

CONSEQUENCES OF INCREASED STRIPED BASS STOCKINGS FOR THE SMITH MOUNTAIN LAKE FISHERY

INTRODUCTION

In my analysis in Chapter Three, I determined that over 94% of the available clupeid supply is utilized to meet predator demand in SML (145 of 154 kg/ha). This indicates a remarkable degree of predator efficiency, but it also implies a precarious trophic state: a substantial increase in predator demand or decrease in prey supply could have detrimental consequences to both predator and prey populations that would challenge effective management of the fishery.

All predator and prey populations in SML are reproductively self-sustaining except for striped bass. While abundances of these species can be expected to fluctuate annually within historic bounds, the density of piscivorous striped bass can be expected to increase in the near term. The Virginia Department of Game and Inland Fisheries, responding to angler demands, committed to increasing the annual striped bass stocking by 50% (to 450,000 fingerlings per year) for at least several consecutive years, beginning in 1998. Efforts to increase first-year survival of stocked striped bass in SML are also underway. These include spreading the stocked fingerlings among more sites and stocking earlier in the year and/or larger fingerlings (Sutton 1997). Anecdotal observations indicated an unusually high abundance of age-0 striped bass in the fall of 1998, although first-year survival will not be assessed until the fall of 1999. However, first-year survival rate of the 1997 year-class (300,000 stocked) was 58%, twice the long-term average (M.C. Duval, VDGIF, unpublished data). Thus two successive exceptional year-classes of striped bass are entering the piscivorous population and will increase predator demand on the clupeid forage resource, at least in the short term. More strong cohorts of juvenile striped bass may follow.

What will happen to both predator and prey populations if the striped bass density increases? Studies of landlocked striped bass in other systems and the Great Lakes experience with stocked salmonids provide some indication of potential responses. In Lakes Superior, Huron, Michigan, and Ontario, large populations of introduced Pacific salmonids contributed to the drastic decline in alewife populations (Stewart et al. 1981; Jude and Tesar 1985; Stewart and Binkowski 1986). After the decline, salmonid growth and survival decreased, to the detriment of local Great Lake economies that depended on the salmonid fishery. Researchers noted that the situation was exacerbated because salmonids were extremely efficient predators and consumed prey at rates more proportional to their own abundance than prey abundance, meaning that they could feed at near-normal rates even as prey populations declined (Negus 1995). Weak year-classes of prey were thus subjected to heavy predation, and the prey population as a whole became much more susceptible to a total collapse. Walleye in Lake Erie have also approached densities at which their consumption was above the capacity of prey fishes to support (Muth and Wolfert 1986). These predator-prey imbalances can lead to a shift in the prey assemblage, as when the decline of the introduced alewife allowed the recovery of native bloater, yellow perch, rainbow smelt, and deepwater sculpin (*Moxocephalus thompsoni*) to occur in Lake Michigan (Jude and Tesar 1985; Stewart and Binkowski 1986; Negus 1995).

A number of studies have linked increases in striped bass abundance to a decrease in clupeid abundance, and eventual declines in striped bass condition and growth rates (Bailey 1975; Morris and Follis 1978; Stevens 1979; Gustaveson et al. 1983). Decreased encounter rates between predator and prey would mean reduced growth for striped bass, due to increased activity costs to find prey schools. Radovich (1979) argues that the evolution of schooling behavior as a predator defense mechanism would lead to the maintenance of school size even as prey populations decreased. If clupeid populations in SML decline, this reasoning predicts that fewer and fewer schools of historical size, rather than a historic number of smaller schools, would be the result. Striped bass would therefore encounter an aggregation of prey much less frequently. This depends somewhat on striped bass feeding behavior. It could be possible that adult striped bass would simply follow schools of alewife and gizzard shad relentlessly, feeding whenever hungry.

If increased predation on clupeids led to a significant decline in clupeid standing stock and recruitment, striped bass would be affected more severely than predators who have more varied diets. Investigators have demonstrated that declines in clupeid abundance and striped bass growth can occur without any noticeable effects on other resident sport fishes (Bailey 1974; Combs 1980; Bettoli et al. 1995). Stewart and Ibarra (1991) found that native lake trout were better able to deal with reductions in the biomass of an important prey species when compared to introduced chinook salmon (*Oncorhyncus tshawytscha)* because lake trout had a more varied diet and could easily turn to other prey species to fill the void. This example parallels the situation in SML, where black bass, catfish, and crappie have a more diversified diet than striped bass.

If clupeid standing stock is depressed, clupeid growth rates might increase in SML as a result of decreased intra-specific competition. This phenomenon was found to occur in other systems (Buynak et al. 1992; Dicenzo et al. 1996). This would affect the morphological availability of prey, most importantly to those young piscivores that are most severely gape-limited (Storck 1986; Muoneke et al. 1992; Hale 1996; Garvey and Stein 1998). Many researchers have noted the importance of adequate numbers of sufficiently small prey fishes for the growth and survival of young sport fishes (Saul 1981; Ney and Orth 1986; Michaletz 1997b, 1998b; Garvey and Stein 1998). Sutton (1997) established the importance of a diet of alewife for young-of-the-year striped bass in SML to acquire enough energy reserves for over-winter survival. If reduced growth of young striped bass adversely affected their survival, this population might decline enough to reduce prey exploitation to tolerable levels. In essence, a negative feedback loop between the density of age-0 alewife and the survival of age-0 striped bass would exist. Even if this occurred, misallocation of Virginia's hatchery resources should be identified and resolved. If survival of age-0 striped bass were not adversely affected, an overabundance of small striped bass could lead to increased intra-specific competition for food, poor growth, and eventually a stunted population of adults, such as that reported in Lake Texoma and Lake Mead, both of which have naturally-reproducing striped bass populations (Moczygemba and Hysmith 1994; Paulson 1994). This would adversely affect fishing quality and angler satisfaction.

If predation mortality of clupeids increases rapidly, an insufficient spawning population leading to a clupeid population collapse is a possibility. Clupeid populations in SML nearly crashed in the late 1970's (Duval 1996). However, as clupeid populations declined, adult striped bass would have a harder time finding sufficient prey to maintain growth rates, and starvation mortality of age-0 striped bass would likely increase. This could result in a lessening of predation intensity, allowing clupeid populations to rebound. A difficult question concerns how much of a role the spawning stock of clupeids plays in determining clupeid recruitment, and how much larval and juvenile survival of clupeids is determined by environmental stochasticity such as the abundance of predators, food, and the length/intensity of winter. With current clupeid populations undergoing very heavy predation, adult stock size of clupeids is likely to be within a range where decreases in adult densities lead to linear declines in the number of larvae produced (Figure 4.1). Given the best of environmental circumstances, with a paucity of spawners, year-class strength would be low due to low numbers of larvae produced.

It thus appears that the greatest immediate challenge to predator-prey interactions and the status of the SML fishery is posed by the increase in striped bass abundance. My objective in this chapter is to explore the responses of the striped bass and alewife populations to a heightened predator food demand. To meet this objective, I developed a predator-prey simulation model based on the current state of knowledge concerning the population ecology and dynamics of these species. I chose to only examine the effect of increased demand of striped bass on alewife because: 1) age-0 striped bass survival is tightly coupled to the availability of age-0 alewife (Sutton 1997); 2) adult striped bass must primarily utilize alewife during the summer when the former is restricted to downlake hypolimnetic waters; 3) alewife compose about 60% of the annual diet, by weight, of adult striped bass; 4) alewife appear nearer to overexploitation by piscivores in SML than gizzard shad (Chapter Three); and 5) available supply of alewife exceeds demand of striped bass by only 4%.

I did not include effects on other predators (largemouth bass in particular) because: 1) other predators have more diverse diets (rely less on clupeids for nutritional requirements) and therefore would be more resistant to clupeid declines; 2) there are no indications that densities of other predators in the system will change significantly in the coming years; and 3) the current supply of either clupeid species to largemouth bass exceeded demand by more than 20%, indicating that clupeid availability to largemouth bass could decrease that amount without significantly affecting largemouth bass dynamics.

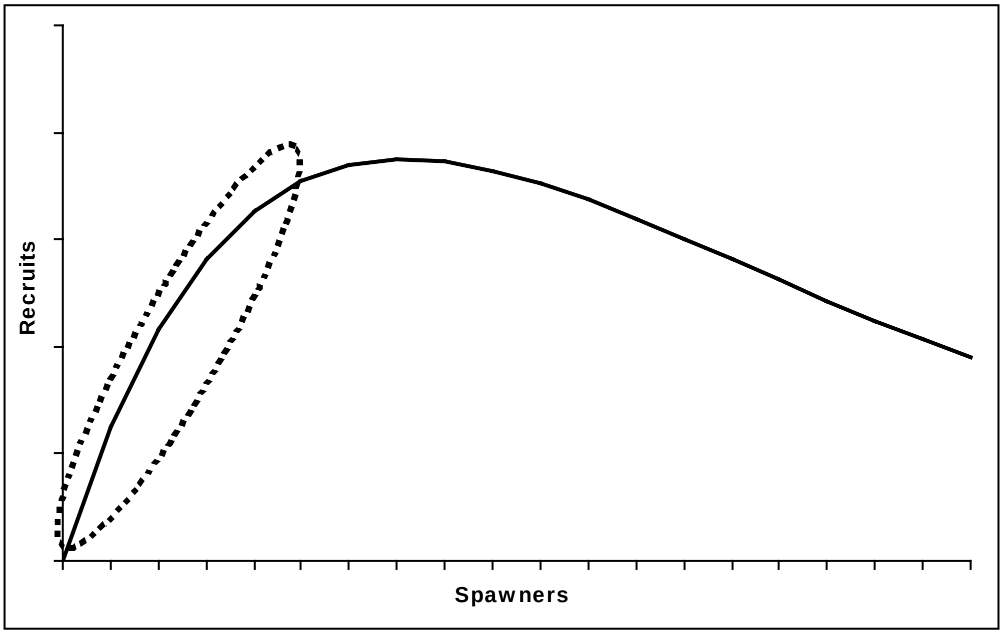

Figure 4.1. A general Ricker stock-recruitment relationship. The dashed ellipse encompasses the region of near-linearity within which the clupeid populations of SML are assumed to reside.

METHODS

I utilized STELLA software (Peterson and Richmond 1994) to construct a trophic model that would allow me to investigate consequences of increased predator demand on the striped bass and alewife populations of SML. This package provides a visual modeling environment that aids in the development and comprehension of the mathematics that drive the simulation. The biological foundation of this model was that increased abundance of striped bass would lead to increased mortality of alewife, and this would in turn affect growth of adult striped bass and survival of age-0 striped bass. Primary among the model assumptions was that any increase in striped bass abundance would lead to declines in striped bass growth if alewife abundance was constant. This assumption was based on the findings of previous chapters that showed almost no surplus production of alewife went unutilized by the predator population of SML. If this were not the case, i.e., significant amounts of surplus production of alewife were currently available to striped bass, the model would have to be changed. A flow chart of the model is depicted in Figure 4.2 and definitions and values for all model variables and parameters are given in Table 4.1.

The connections in Figure 4.2 are representative of the following interactions:

1) the abundance of alewife larvae, age-0 striped bass, and age-1+ striped bass all affect the survival of age-0 striped bass
2) numbers of age-0 and age-1+ striped bass affect the survival of age-0 alewife
3) numbers of age-1+ striped bass affect the survival of alewife cohorts beyond the end of the latter’s first growth season
4) the abundance of age-1 and older alewife partially determines the number of alewife larvae produced
5) the abundance of age-0 to age-3 alewife affects the weight-at-age of striped bass (dashed lines in Figure 4.2).

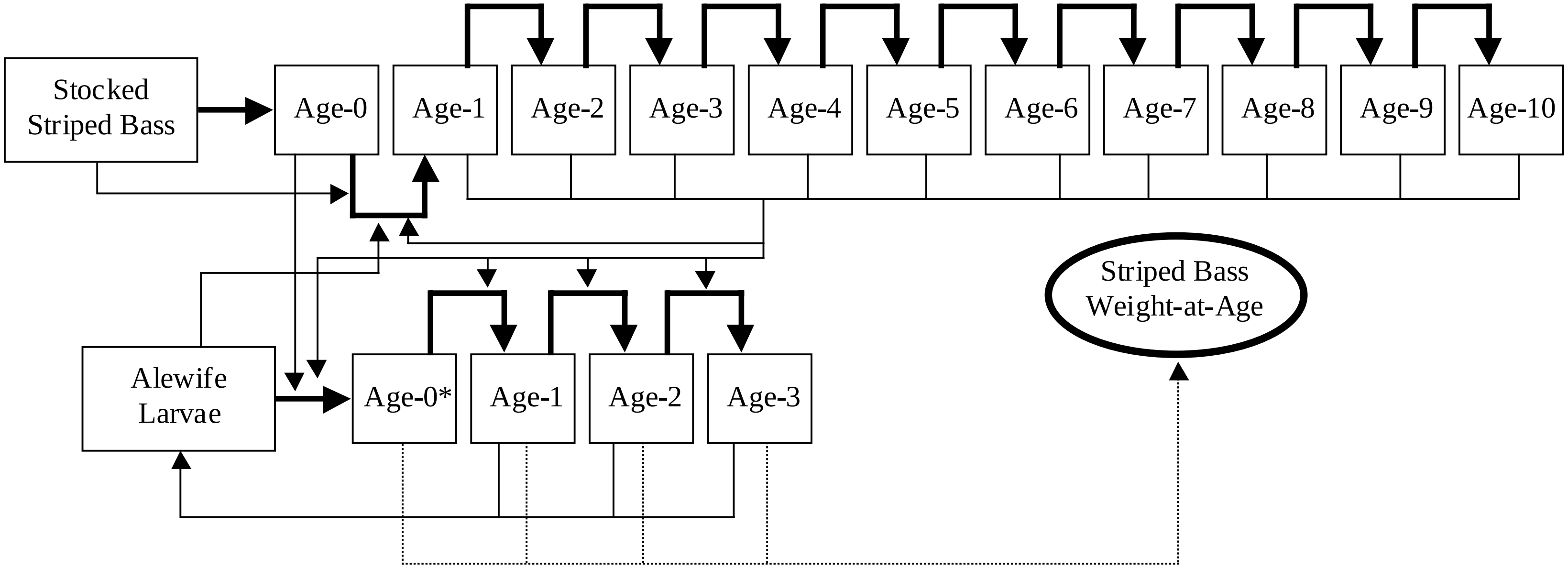

Figure 4.2. The trophic model flow chart. Thick lines with terminal arrows indicate the flow of survivors from one cohort to the next. Thin lines with terminal arrows indicate that the component from which the line originates affects the survival rate of the cohort. See text for the mathematical relationships that were used to model these interactions.

* This is the number of age-0 alewife remaining in late November. Numbers of individuals in older alewife cohorts were estimated in late August.

Table 4.1. Parameters and variables used in the trophic model. Initial values of N_A and CW_A (also the initial values of W_A) for striped bass, and initial numbers of alewife in each cohort are given in "Simulation Specifics."

Variable	Definition	Current Mean Estimate
AA	Number of age-1+ alewife in late August	13.8 million
AL	Number of alewife larvae	2 billion
AP	Number of age-1+ alewife in late August plus number of age-0 alewife at the end of first growth season	51 million
N_A	Number of striped bass in cohort A	Dependent on A
SN	Total number of age-1+ striped bass	182,000
ST	Annual number of stocked striped bass	Variable
W_A	Mean weight (kg) of member of striped bass cohort A	Dependent on A

Parameter	Definition	Value
α	Normally-distributed random variable	Mean=0, StDev=0.13
CW_A	Current mean weight of member of striped bass cohort A	Initial values of W_A
M_1	Mortality constant for age-0 striped bass	0.97
M_2	Mortality constant for age-0 striped bass	0.57
M_3	Mortality constant for age-0 striped bass	5850
M_4	Mortality constant for age-0 alewife	0.89806
M_5	Mortality constant for age-0 alewife	0.04
M_6	Mortality constant for age-0 alewife	0.0000126
M_7	Mortality constant for age-0 alewife	0.055
M_8	Mortality constant for age-0 alewife	0.0000156
M_9	Mortality constant for age-1 alewife	0.55
M_{10}	Mortality constant for age-1 alewife	0.45
M_{11}	Mortality constant for age-1 alewife	0.0000065
M_{12}	Mortality constant for age-2 alewife	0.65
M_{13}	Mortality constant for age-2 alewife	0.35
M_{14}	Mortality constant for age-2 alewife	0.0000077
P_1	Weight-at-age coefficient for adult striped bass	0.6
P_2	Weight-at-age coefficient for adult striped bass	0.7
P_3	Weight-at-age coefficient for adult striped bass	125
SR_1	Ricker stock-recruitment coefficient	5.48
SR_2	Ricker stock-recruitment coefficient	150 million

STRIPED BASS DYNAMICS

The inflow of age-0 striped bass at the beginning of each time period was equal to a constant, representing the number of fingerlings stocked annually. Annual outflow (mortality) of this cohort was modeled as a exponentially-decreasing function of the ratio of the number of alewife larvae produced (AL) to the number of striped bass stocked annually (ST) and the number of adult striped bass in SML (SN):

$$\text{Mortality} = M_1 - M_2 * (1 - \text{EXP} (- (AL / (SN + ST)) / M_3))$$

where M_1, M_2, and M_3 are constants set equal to 0.97, 0.57, and 5850, respectively. These values were chosen to precisely simulate the estimated age-0 striped bass mortality in SML. If AL, SN, and ST were at their current mean estimates (2 billion, 182,000, and 300,000, respectively) mortality of age-0 striped bass from June stocking to the next March was 68%. This mortality rate was exactly the rate determined from empirically-based population dynamics of striped bass investigated in Chapter Two. As the ratio of age-0 alewife larvae to striped bass declined, age-0 striped bass mortality rose towards M_1 (Figure 4.3). The value for M_1 (97%) was chosen because age-0 striped bass that did not consume alewife during their first growth season had near-complete over-winter mortality (Sutton 1997). M_1 was made slightly less than 100% to allow for the possibility of a small percentage of age-0 striped bass survivors without access to age-0 alewife. M_1 - M_2 (40%) defines the lowest possible mortality rate for age-0 striped bass. Sutton (1997) found that 60% was approximately the highest survival rate of any age-0 striped bass cohort in SML since 1973.

The number of surviving age-0 striped bass then served as inflow to the age-1 striped bass cohort in the next time period. Annual mortality rates of age-1 and older cohorts were set to constant values because changes in alewife availability would not greatly affect the survival of these larger piscivores (much greater somatic energy reserves as compared to age-0 striped bass). Based on data discussed in Chapter Two annual mortality of age-1 and age-2 striped bass was set to 50% and annual mortality of age-3 and older striped bass equaled 63%.

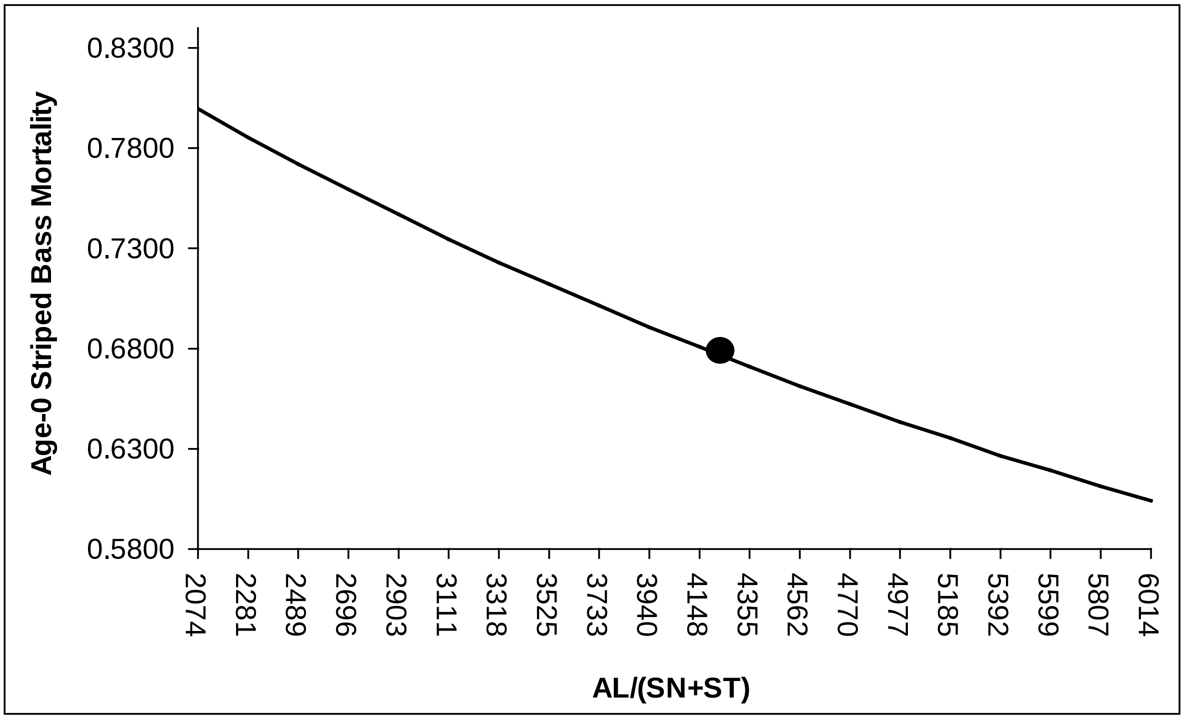

Figure 4.3. Modeled relationship between age-0 striped bass mortality and the relative abundance of alewife larvae. AL is the number of alewife larvae produced, SN is the total number of age-1+ striped bass, and ST is the number of striped bass fingerlings stocked into SML. The circle on the curve marks this location of estimated current conditions in SML..

Mean weight-at-age-A (W_A) of age-1+ striped bass was modeled as an exponentially-increasing function of the ratio of the abundance of alewife to total striped bass abundance:

$$W_A = CW_A * (P_1 + P_2 * (1 - EXP (- (AP / (SN + ST)) / P_3)))$$

where CW_A represents the initial (and current estimate of) mean weight-at-age of a member of cohort A (e.g., 3.8 kg for a striped bass beginning its sixth growth season), P_1, P_2, and P_3 are constants, SN and ST are as defined previously, and AP is the sum of age-0 alewife at the end of the growth season (currently 37.3 million) and the number of adult alewife in SML in late August (currently 13.8 million). The values of P_1 and P_2 were used to model changes in striped bass growth as relative alewife densities changed. W_A would become P_1*CW_A as (AP/(SN+ST)) approached zero. Alewife are approximately 60% of the annual diet of adult striped bass in SML, so one possible choice for P_1 would be 0.4. With this value for P_1, drastic reductions in relative alewife abundance in SML would reduce mean weight-at-age of striped bass to 40% of current mean weight-at-age. I assumed that as alewife relative abundance declined, however, striped bass would partially compensate by eating additional amounts of other prey items (e.g., crayfish and gizzard shad). I set P_1 to 0.6 to adjust for this compensation. A 40% reduction in mean weight-at-age would put striped bass in SML well below the average size-at-age of striped bass in Virginia reservoirs (Carlander 1997). As alewife relative abundance increased towards infinity, W_A would rise to (P_1 + P_2)*CW_A (Figure 4.4). I set P_2 = 0.7, meaning that W_A at most could reach 130% of CW_A. A 30% increase in mean weight-at-age would put SML striped bass far above other populations of Virginia striped bass (Carlander 1997). Research beyond the scope of this study would be needed to more accurately estimate P_1 and P_2. P_3 was set equal to 125, and like M_3, is merely a calibration constant that makes W_A equal to CW_A if AP were equal to the current mean (51.1 million). Weight-at-age-0 was not modeled because the age-0 mortality function shown earlier had implicit growth rate assumptions, i.e., I assumed that any surviving age-0 striped bass would have reached a minimum size in order to survive its first winter (Sutton 1997).

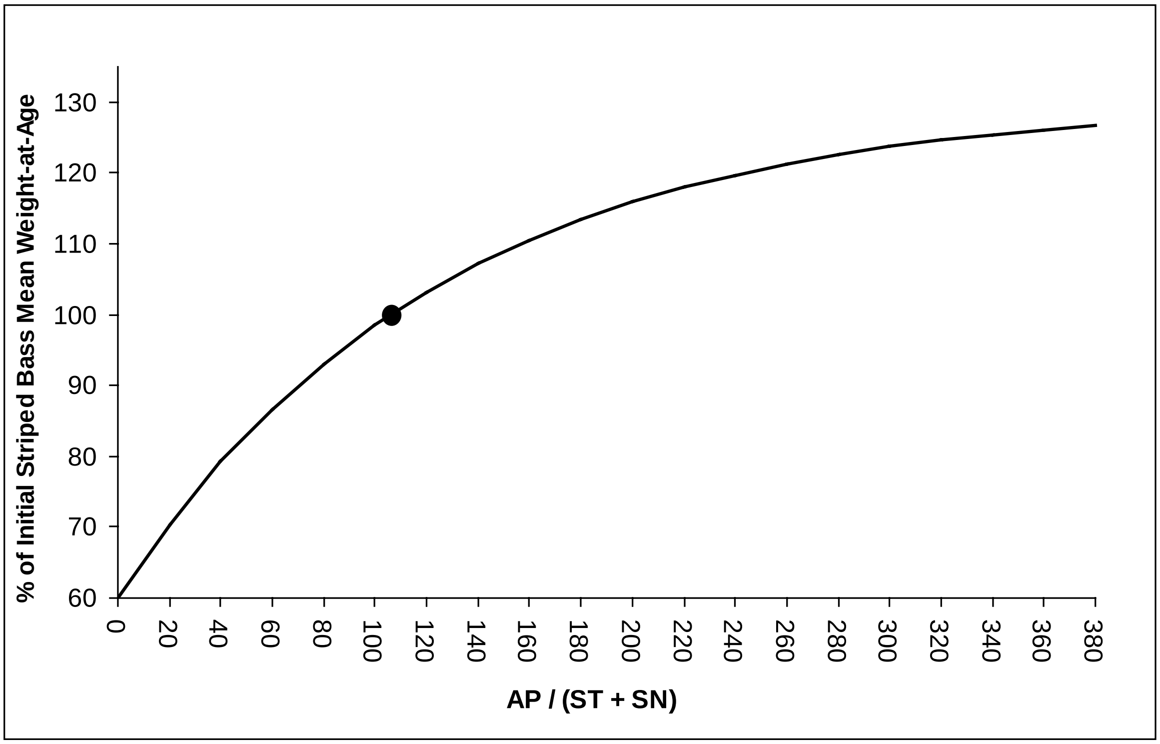

Figure 4.4. Modeled relationship between striped bass mean weight-at-age and the relative abundance of alewife in SML. AP is the number of alewife beyond the end of their first growth season, ST is the number of stocked striped bass fingerlings, and SN is the number of age-1+ striped bass. The circle represents the estimated current conditions in SML.

ALEWIFE DYNAMICS

The number of alewife larvae produced each year served as the annual inflow to the age-0 alewife cohort. Larval numbers were modeled using a Ricker stock-recruitment relationship:

$$\text{Number of Larvae} = AA * EXP\ (\ SR_1 * (1 - AA / SR_2)\ )$$

where AA is the number of adult alewife and SR_1 and SR_2 are parameters that describe the shape of the stock-recruitment curve. Values for SR_1 (5.48) and SR_2 (150 million) were derived from assuming: 1) intensive predation on alewife keeps adult stock size at the lower end of a typical stock-recruitment model (Figures 4.1 and 4.5); and 2) 2 billion larvae are produced when adult stock size is 13.8 million (the mean annual estimates derived in Chapter One). These values for SR_1 and SR_2 produced a curve that had the desired shape/location and passed through the desired point (13.8 million spawners and 2 billion recruits). The above relationship is entirely deterministic. This is an unrealistic outcome due to random environmental factors that affect the survival of alewife larvae. Stochasticity was incorporated into the determination of alewife larval density using the following formula:

$$\text{Number of Larvae} = AA * EXP(\ SR_1 * (1 - AA / SR_2)\ ) * EXP(\alpha)$$

where AA, SR_1, and SR_2 are as defined previously, and α is a Gaussian random variable with a mean of 0 and a standard deviation of 0.13. The variance of this random variable was approximated by determining the number of larvae needed to produce the high and low alewife biomass seen in five years of acoustic estimates (approximately between 1-3 billion larvae, see Chapter One). This equation resulted in a lognormal distribution (bell-shaped but right-skewed compared to a normal distribution) of alewife larvae produced annually. Quantities that arise as the product of a number of independent environmental factors most often are lognormally distributed (Ott 1995). The effect of this stochastic component on the alewife stock-recruitment relationship can be seen in Figure 4.5.

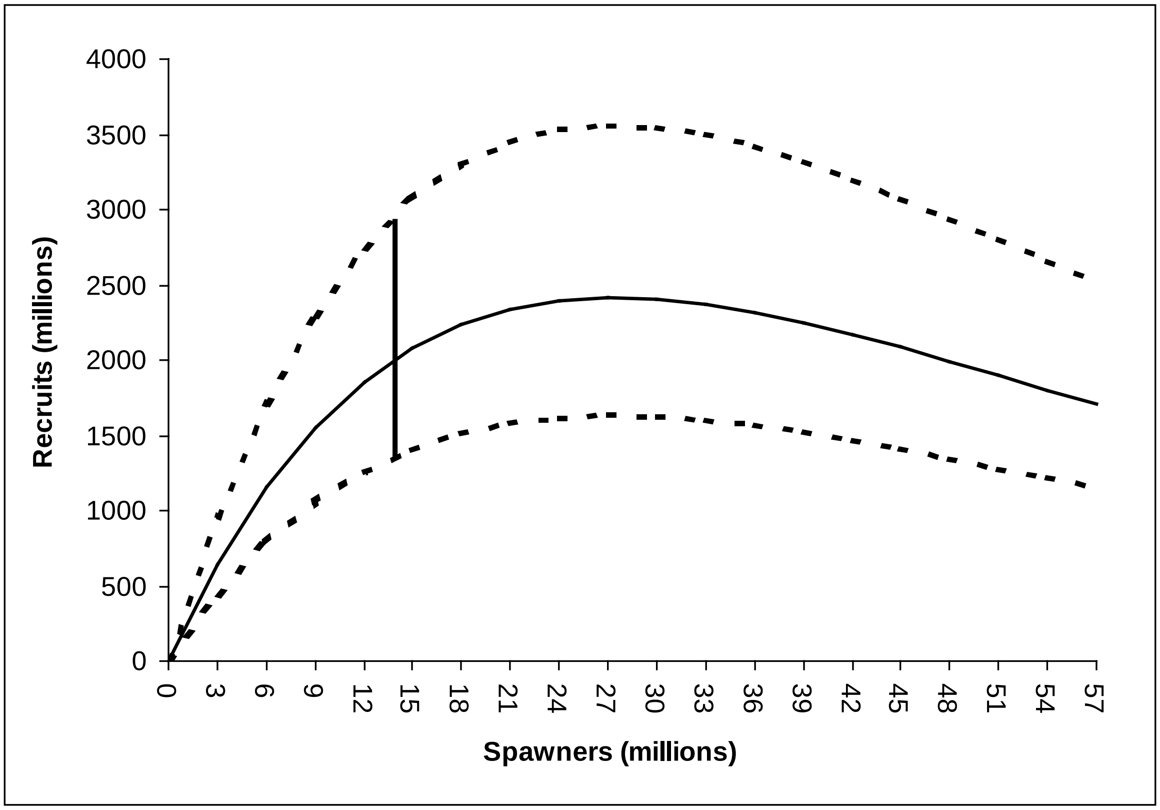

Figure 4.5. Modeled relationship between the number of alewife spawners and the number of larvae produced. The solid line is the deterministic relationship and the dashed lines form the bounds where 99% of the number of recruits resulting from a given stock size would occur. The vertical line represents the estimated range of larvae produced given current mean alewife densities in SML.

As with striped bass, the number of alewife of any cohort surviving an annual period served as the influx to the next cohort. Because both age-0 and adult striped bass consume age-0 alewife, the mortality rate of this prey cohort during its first growth season (from hatching to 30 November) was a function of the abundance of both age-0 striped bass fingerlings and age-1+ striped bass:

$$\text{Mortality} = M_4 + M_5 * (1 - \text{EXP}(- M_6 * \text{ST}))^3 + M_7 * (1 - \text{EXP} (- M_8 * \text{SN}))^3$$

where M_4 through M_8 are mortality constants, and SN and ST are as defined previously. The values of M_4 through M_8 were 0.89806, 0.04, 0.0000126, 0.055, and 0.0000156, respectively. If ST and SN were at the current annual means (300,000 and 182,000), mortality of age-0 alewife over the growth season was 98.135% (the current value, determined in Chapter One). Mortality of age-0 alewife increased as SN and ST increased (Figure 4.6). I determined that if ST increased by 50%, from 300,000 to 450,000, and growth of these age-0 striped bass did not change, an additional 4.5 million age-0 alewife would be eaten. This would lead to an increase of 0.225% in the mortality of age-0 alewife during the growth season. Mortality in the above equation rises by 0.00225 if ST is increased from 300,000 to 450,000 while holding SN constant. I determined that if the abundance of age-1+ striped bass increased by 50% with no change in their growth rate, an additional 13.5 million age-0 alewife would be consumed. This would increase mortality of age-0 alewife by 0.675%. If SN is increased to 273,000 (50% greater than 182,000) while holding ST constant, mortality increases by 0.00675. If ST is 450,000 and SN is 273,000, mortality of age-0 alewife during the growth season would rise from 98.135% to 99.035%. The values of M_4 through M_8 therefore were carefully chosen to precisely simulate the effects (estimated from data presented in previous chapters) of changes in striped bass densities on the mortality of age-0 alewife, i.e., to insure that this curve passed through the points where mortality was estimated using previous data.

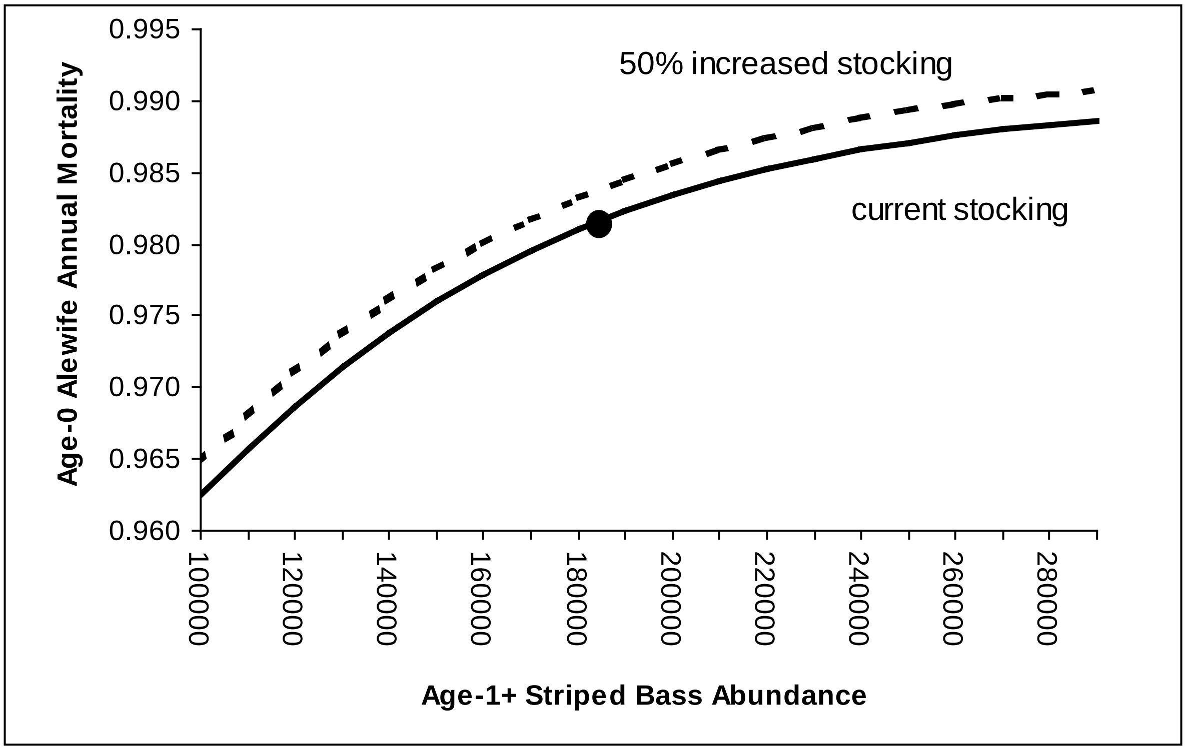

Figure 4.6. Modeled relationship between age-0 alewife mortality over the growth season and the number of stocked and age-1+ striped bass in SML. The dashed line represents age-0 alewife mortality when 450,000 striped bass are stocked annually and the solid line is age-0 alewife mortality when 300,000 striped bass are stocked annually. The circle represents the estimated current conditions in SML.

Mortality of age-1 and older alewife was modeled similarly, but equations were less complex because only adult striped bass consume these prey. To model alewife mortality during the nine months from end of their first growth season to late the next August, the equation was:

$$\text{Mortality} = M_9 + M_{10} * (1 - \text{EXP}(- M_{11} * \text{SN}))^3$$

where M_9, M_{10}, and M_{11} are constants and SN is as defined previously. M_9, M_{10}, and M_{11} were set equal to 0.55, 0.45, and 0.0000065, respectively. If SN equals the current annual mean abundance of age-1+ striped bass (182,000), mortality of alewife during this period would be 70% (the current estimate determined from empirical data). I calculated that if SN rose by 50% with no change in growth rates, additional numbers of alewife eaten would increase alewife mortality during this period by approximately 10%. If SN in the above equation is increased to 273,000, mortality rises from 70% to 80% (Figure 4.7). The values of M_9, M_{10}, and M_{11} also were specified so that the curve passed through the point where mortality was estimated from ancillary data.

Annual mortality of alewife after late August of their second growth season was modeled using the following equation:

$$\text{Mortality} = M_{12} + M_{13} * (1 - \text{EXP}(- M_{14} * \text{SN}))^3$$

where M_{12}, M_{13}, and M_{14} are mortality constants and SN is as defined previously. M_{12}, M_{13}, and M_{14} were set equal to 0.65, 0.35, and 0.0000077, respectively. If SN equals the current annual mean, mortality of alewife during this period would be 80% (the current estimate determined from empirical data). I calculated that if SN rose by 50% with no change in growth rates, additional numbers of alewife eaten would increase alewife mortality during this period by approximately 10%. If SN in the above equation is increased to 273,000, mortality rises from 80% to 90% (Figure 4.7). Similar to all other mortality constants in the model, the values of M_{12}, M_{13}, and M_{14} were specified so that the curve contained the point where mortality was estimated from other data.

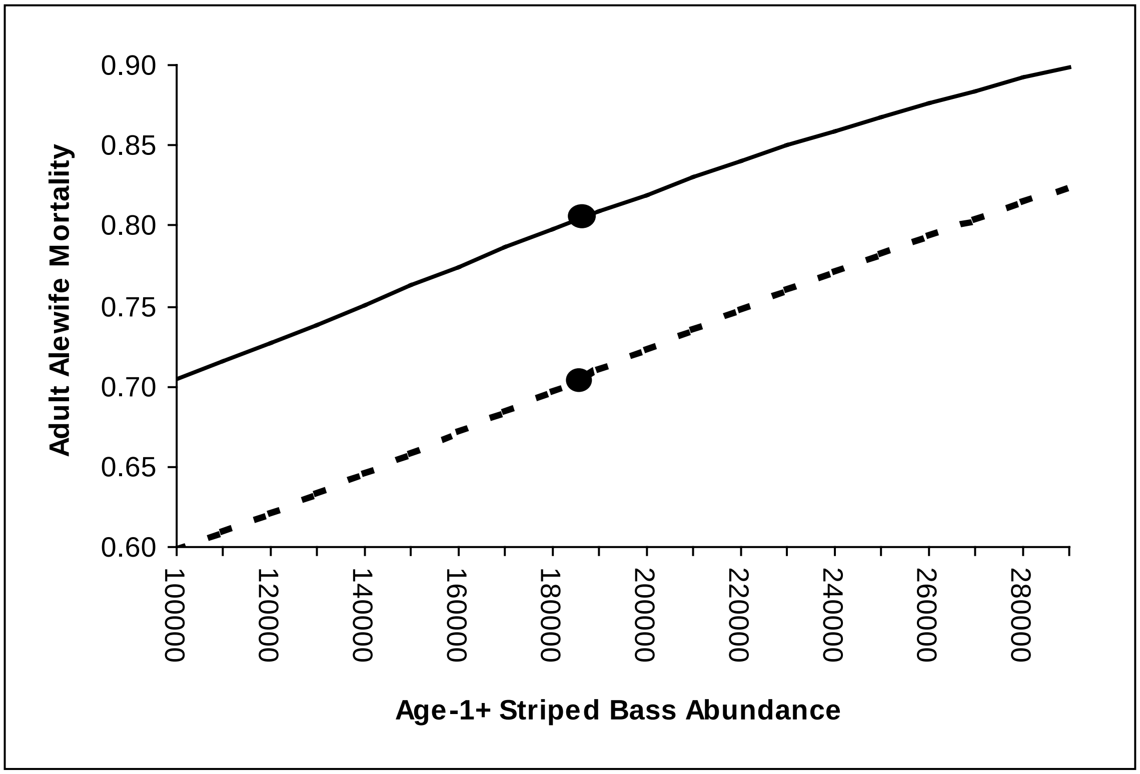

Figure 4.7. Modeled relationship between adult alewife mortality and the numbers of age-1+ striped bass in SML. The dashed line represents mortality of alewife from the end of the first growth season to late the next August. The solid line represents annual mortality of alewife after late August of their second growth season. The circles mark the estimated current conditions in SML.

SIMULATION SPECIFICS

I investigated five annual stocking densities of striped bass:

(1) 50,000 (2) 150,000 (3) 300,000 (4) 450,000 (5) 600,000.

These numbers (1 through 5) will later refer to results generated by each stocking density. Numbers of alewife in each cohort and numbers and weight of striped bass in each cohort at time zero had to be input. I used means (based on 300,000 stocking density and long-term mean survival and growth rates) for these initial values. For striped bass cohorts 0-10, initial numbers were 300000, 96065, 48033, 24016, 8886, 3288, 1216, 450, 167, 62, and 23, respectively. Initial weight-at-age for striped bass cohorts 1-10 was 0.63, 1.49, 2.59, 3.80, 5.04, 6.23, 7.34, 8.35, 9.24, and 10.03 kg, respectively. Initial numbers of alewife cohorts 0-3 were 37.3 million, 11.2 million, 2.2 million, and 445 thousand, respectively. Each simulation was run for a modeling period of 10 years. Unpredictable occurrences (ecological, scientific, and social) would make the usefulness of model output beyond this time minimal. Simulations were run for each stocking regime until the coefficient of variation of the examined metrics stabilized. I focused on the density of alewife and the number and weight of striped bass at each age in each scenario. Two Gaussian probability functions, which estimated the cumulative percentage over time of striped bass that attained legal (> 508 mm TL) and citation size (> 9075 g), were combined with model output on striped bass number and weight-at-age. Each Gaussian variable had a mean equal to the size that the fish would be legal or citation size and a standard deviation set to some percentage of the mean. Variation in mean weight-at-age for older fish should be higher that the variance in length-at-age for younger fish. The standard deviation for citation fish therefore was set to 25% of the mean and the standard deviation for legal striped bass was set to 15% of the mean. The magnitude of variation was consonant with the findings of Moore (1988). Using this methodology, the percentage of individuals reaching these milestones was near-zero for fish three standard deviations below the appropriate size, increased according to the Gaussian cumulative distribution function to 50% when the average individual was exactly legal or citation size, then rose to approximately 100% when the average individual was three standard deviations above the appropriate size. Due to the uncertainty associated with parameter values, I did not focus on the absolute quantification of the investigated metrics, but rather on qualitative comparisons between scenarios and the probability under any given scenario of seeing a decline of a given magnitude in a metric.

RESULTS

Exploratory analysis showed that 100 simulations for each stocking scenario were sufficient to stabilize the coefficient of variation in the measured metrics (Figure 4.8). To give a general indication of what occurred after several years under each stocking program, values recorded in years 5 through 8 (400 observations for each stocking scenario) were summarized using histograms. Alewife abundance declined as striped bass stocking density increased from 50,000 to 600,000 (Figure 4.9). In scenario 1, a large spread in alewife densities was seen. This was a result of an increasing alewife density from year 5 to year 8. Other stocking scenarios had more tightly grouped observations over the four-year period, indicating model output was similar from year to year Over the four-year span, stocking scenarios 4 and 5 produced similar alewife densities, and these were lower than those seen under stocking scenario 3. Stocking scenario 2 produced much greater alewife densities than scenario 3.

Mean weight-at-age of striped bass increased as stocking densities decreased (Figure 4.10). The upper limit of mean weight-at-age was reached quickly in scenario 1, i.e., mean weight at each age was 130% of the initial mean weight after five years of the low stocking levels. In stocking scenario 2 striped bass were slightly lighter than in scenario 1, but nevertheless also approached the maximum growth limit. The variation in mean weight-at-age in scenario 3 was centered around CW_A. Mean weight-at-age for scenarios 4 and 5 were much lower than for the other scenarios. The distribution of values in these scenarios showed no overlap with the distribution of values for other stocking scenarios.

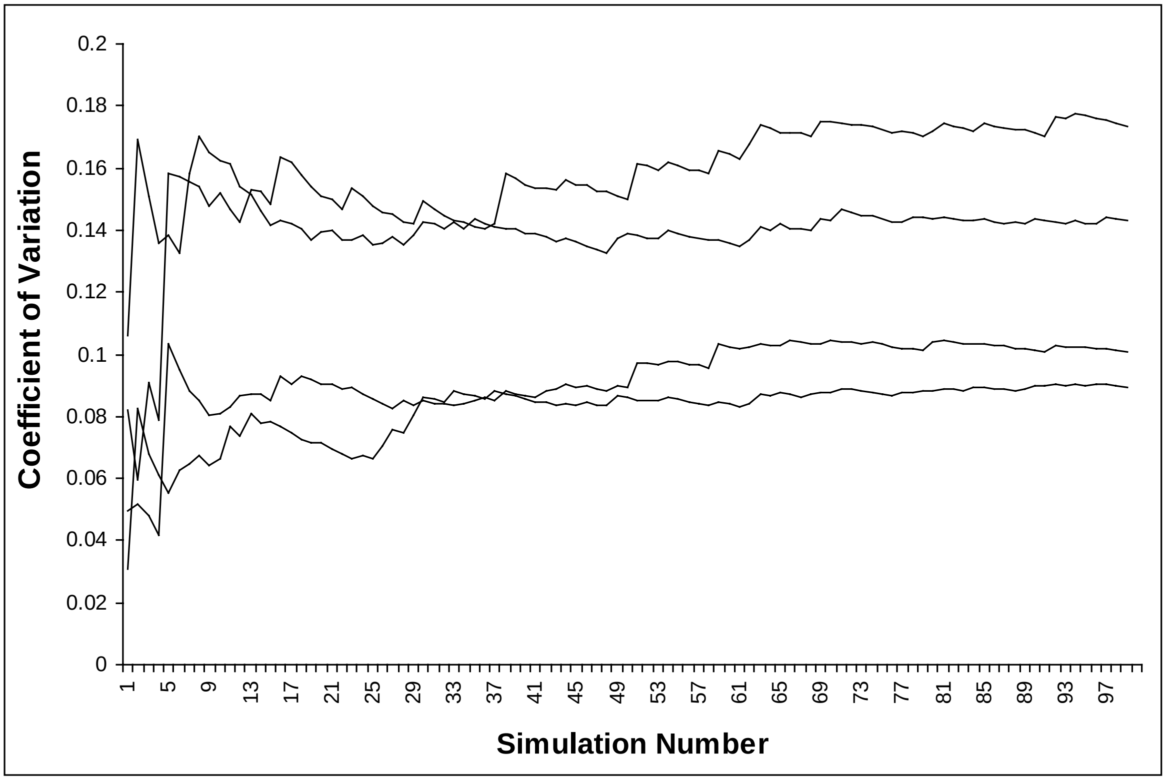

Figure 4.8. Changes in the coefficient of variation (CV) for four arbitrary metrics as the number of simulations was increased from 1 to 100. One hundred simulations appeared to be adequate to stabilize the CV in each case.

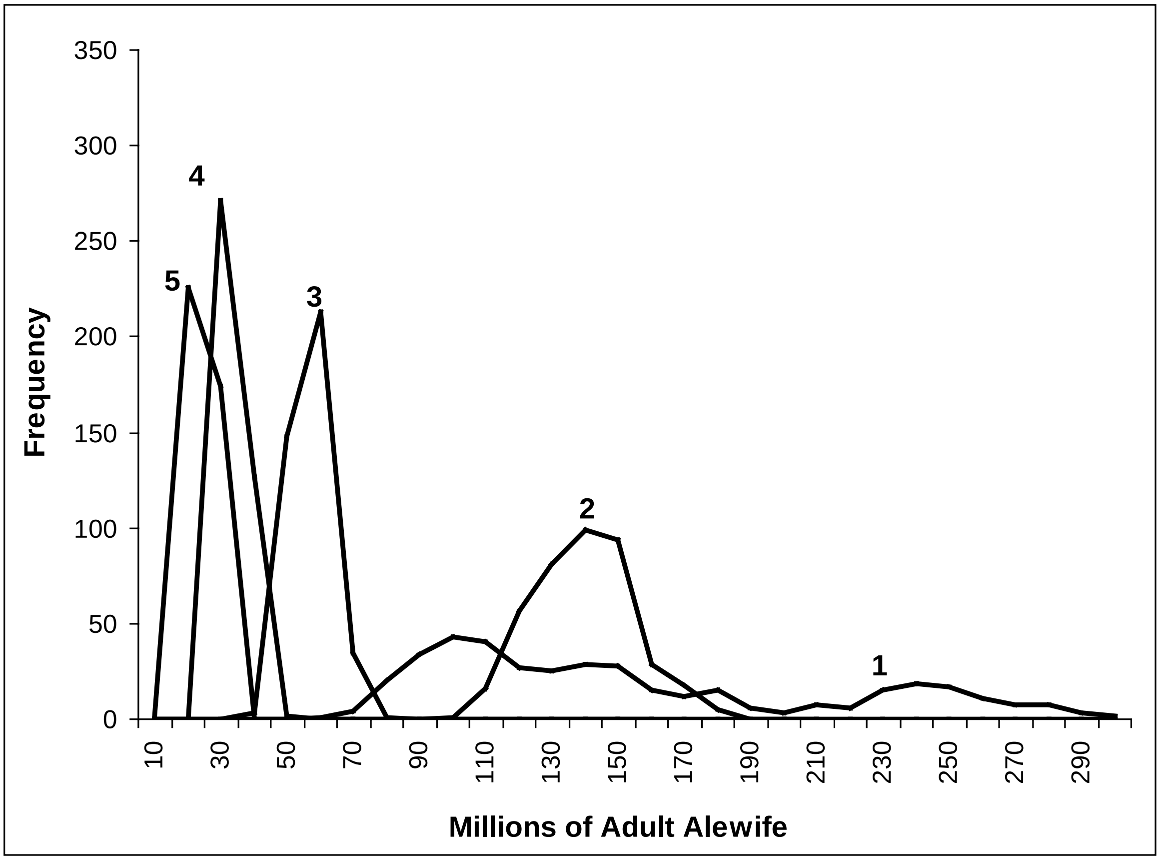

Figure 4.9. The distribution of alewife abundance under each stocking scenario. Four hundred values (representing observations in year 5 through year 8) are plotted for each scenario. Scenarios 1 through 5 represent stocking levels of 50,000, 150,000, 300,000, 450,000, and 600,000, respectively.

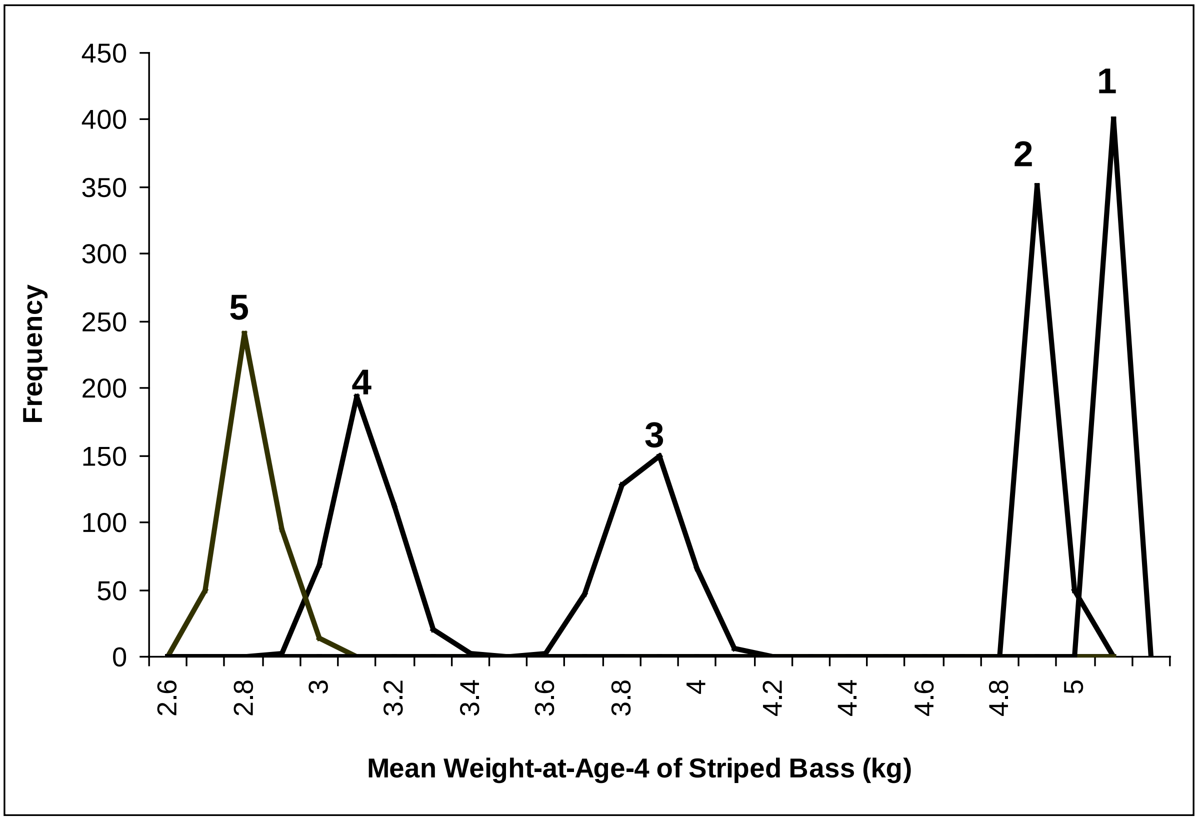

Figure 4.10. The distribution of mean weight-at-age-4 for striped bass under each stocking scenario. Distributions for other ages were similar. Four hundred values (representing observations in year 5 through year 8) are plotted for each scenario. Scenarios 1 through 5 represent stocking levels of 50,000, 150,000, 300,000, 450,000, and 600,000, respectively.

A quantitative method to determine how similarly each stocking strategy performed involves calculating the overlap in values from each stocking scenario (Figure 4.11). Total number of age-1+ striped bass under scenarios 1 and 2 had 0% overlap when compared to other scenarios (Figure 4.12). Scenario 1 produced the lowest numbers and scenario 2 generated the next-lowest number of age-1+ striped bass. Stocking regimes 3, 4, and 5 generated similar numbers of age-1+ striped bass. The overlap between scenarios 3 and 4 was 75%, and this was also the overlap for scenarios 4 and 5. The overlap for scenarios 3 and 5 was 57%. In addition to high overlap, the spread of values increased with increasing stocking density.

Stocking scenario 1 produced much lower numbers of legal fish than the other four stocking regimes (0% overlap with any other scenario, Figure 4.13). Scenario 3 generated the largest numbers of legal striped bass (i.e., distribution of values located furthest to the right). Overlap between scenarios 2 and 3, 2 and 4, 2 and 5, 3 and 4, 3 and 5, and 4 and 5 were 32%, 46%, 23%, 19%, 7%, and 76%, respectively. It is clear that scenarios 4 and 5 produced similar values as did scenarios 2 and 4 (overlap near 50%). The distribution of values under scenario 2, however, was shifted to the right of the distribution for scenario 4 (larger numbers of legal striped bass generally produced under scenario 2).

As was the case for alewife densities under scenario 1, the number of citation striped bass in this scenario changed (decreased) between year 5 and year 8 (causing the multiple "humps" or modes for this scenario seen in Figure 4.14). This phenomenon was also seen in stocking scenario 2, although the annual changes in the number of citation fish were not as great (i.e., the modes were closer together). Numbers of citation fish in year 8 under scenario 2 (which were lower than in the previous three years) were greater than those produced by scenarios 3, 4, and 5, i.e., scenario 2 was most successful in maximizing the number of citation striped bass. Numbers of citation fish under scenario 3 were greater than any values seen in scenarios 4 and 5 (0% overlap). Scenario 4 generally produced more citation fish than scenario 5, but some overlap of values was evident (28%).

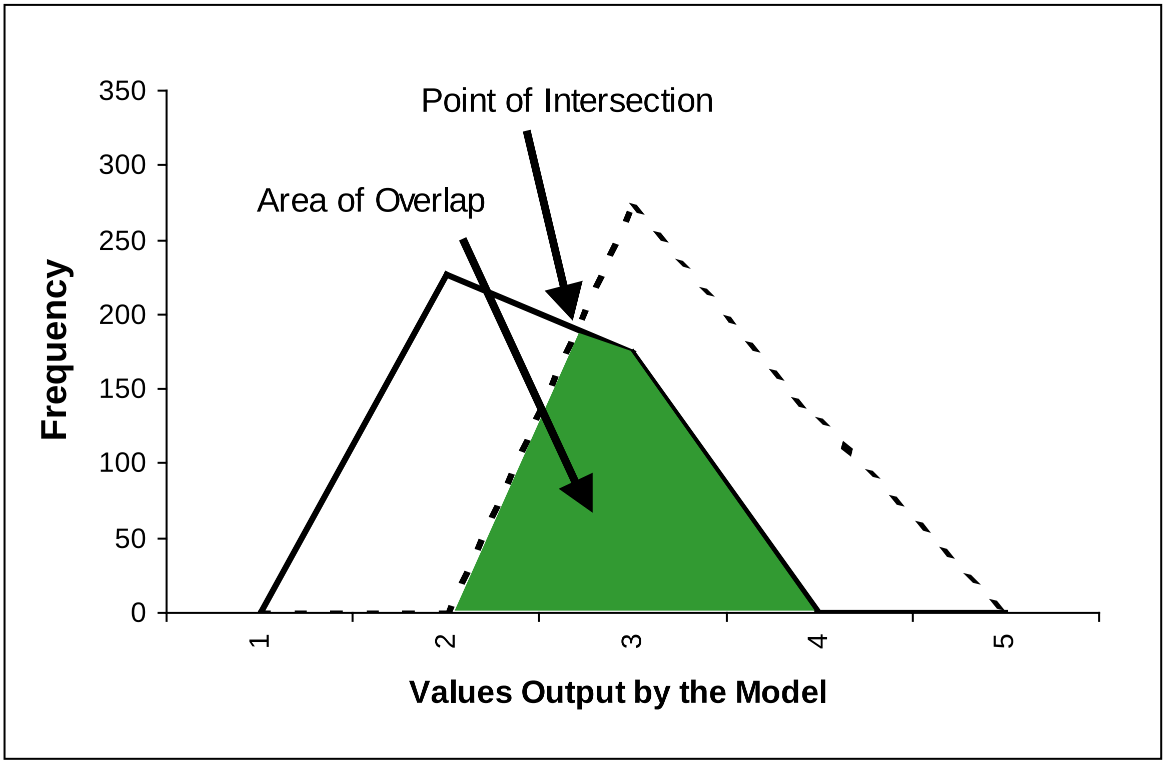

Figure 4.11. Depiction of overlap (the green area) in values generated by two stocking regimes. Percent overlap is found by summing the frequencies (y-values) for the dashed-line scenario to the left of the point of intersection and the frequencies for the solid-line scenario to the right of the point of intersection, and then dividing this sum by the total number of observations in either scenario (assuming total observations are equal for both scenarios).

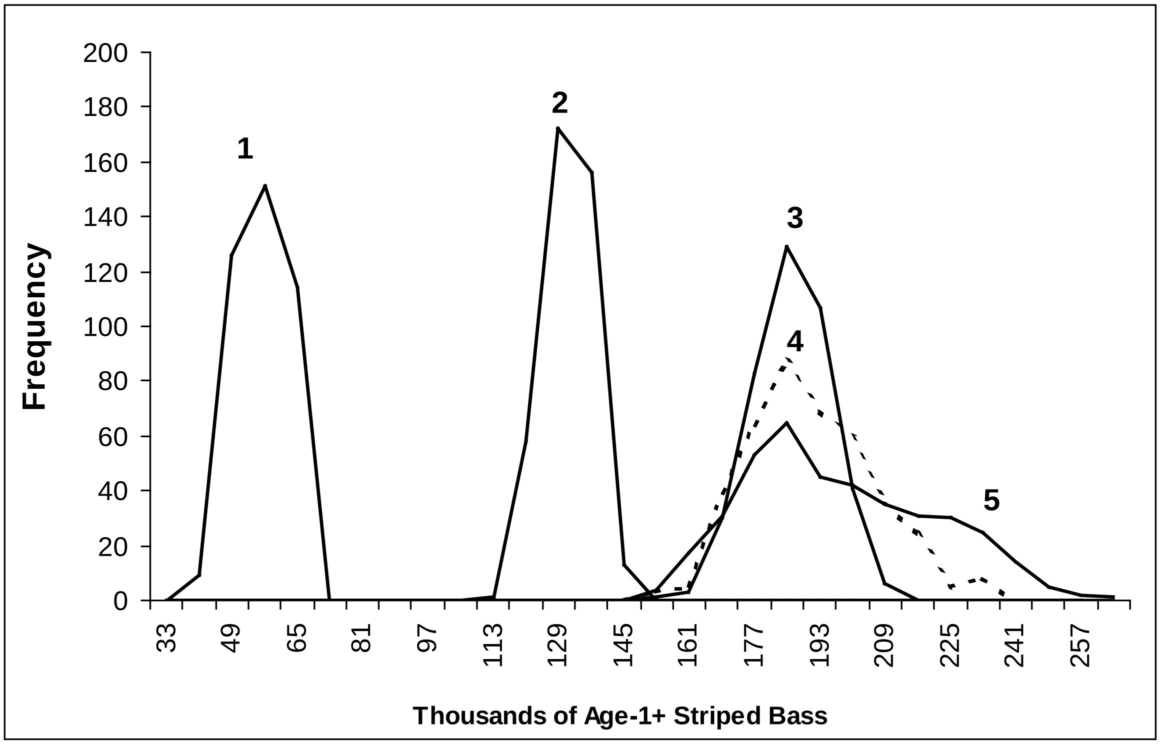

Figure 4.12. The distribution of total number of age-1+ striped bass under each stocking scenario. Four hundred values (representing observations in year 5 through year 8) are plotted for each scenario. Scenarios 1 through 5 represent stocking levels of 50,000, 150,000, 300,000, 450,000, and 600,000, respectively. The line for scenario 4 is dashed only to assist in distinguishing it from other scenarios.

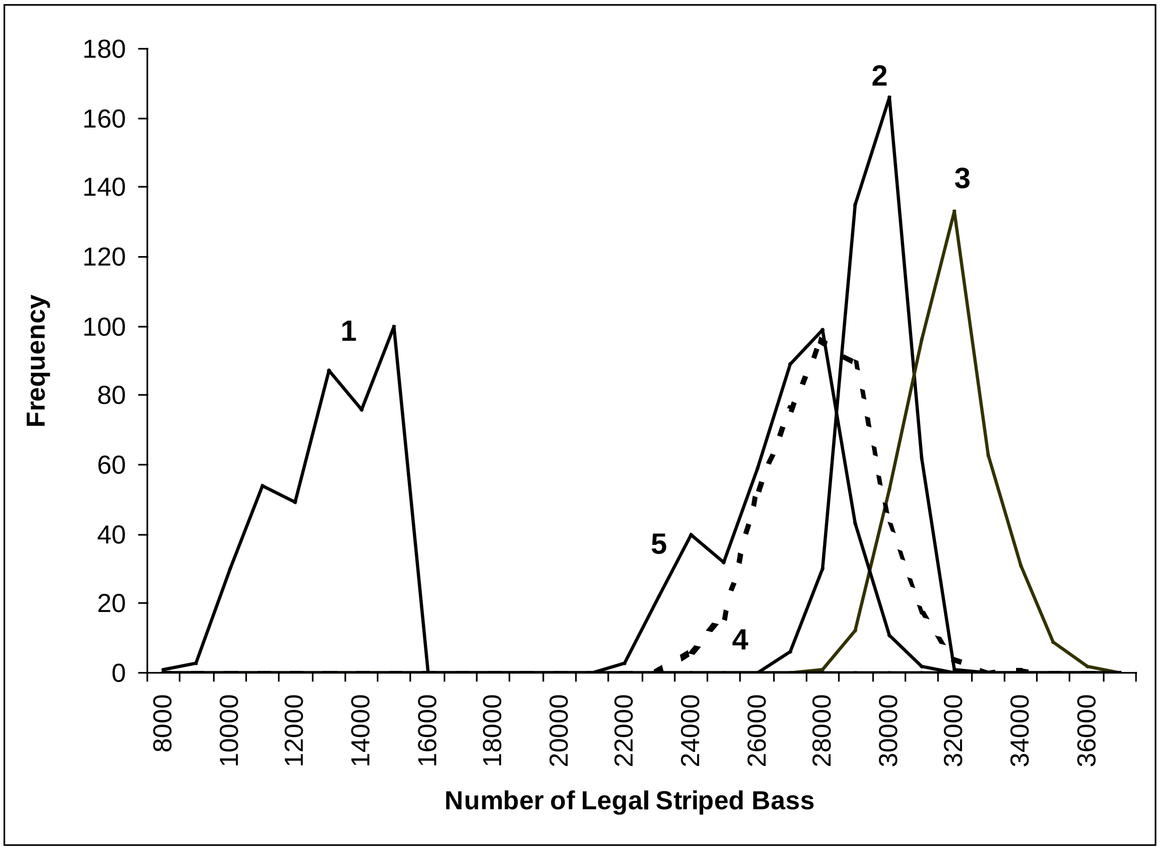

Figure 4.13. The distribution of number of legal striped bass under each stocking scenario. Four hundred values (representing observations in year 5 through year 8) are plotted for each scenario. Scenarios 1 through 5 represent stocking levels of 50,000, 150,000, 300,000, 450,000, and 600,000, respectively. The line for scenario 4 is dashed only to assist in distinguishing it from other scenarios. The multiple modes for scenario 1 indicate that numbers of legal striped bass were changing between year 5 and year 8.

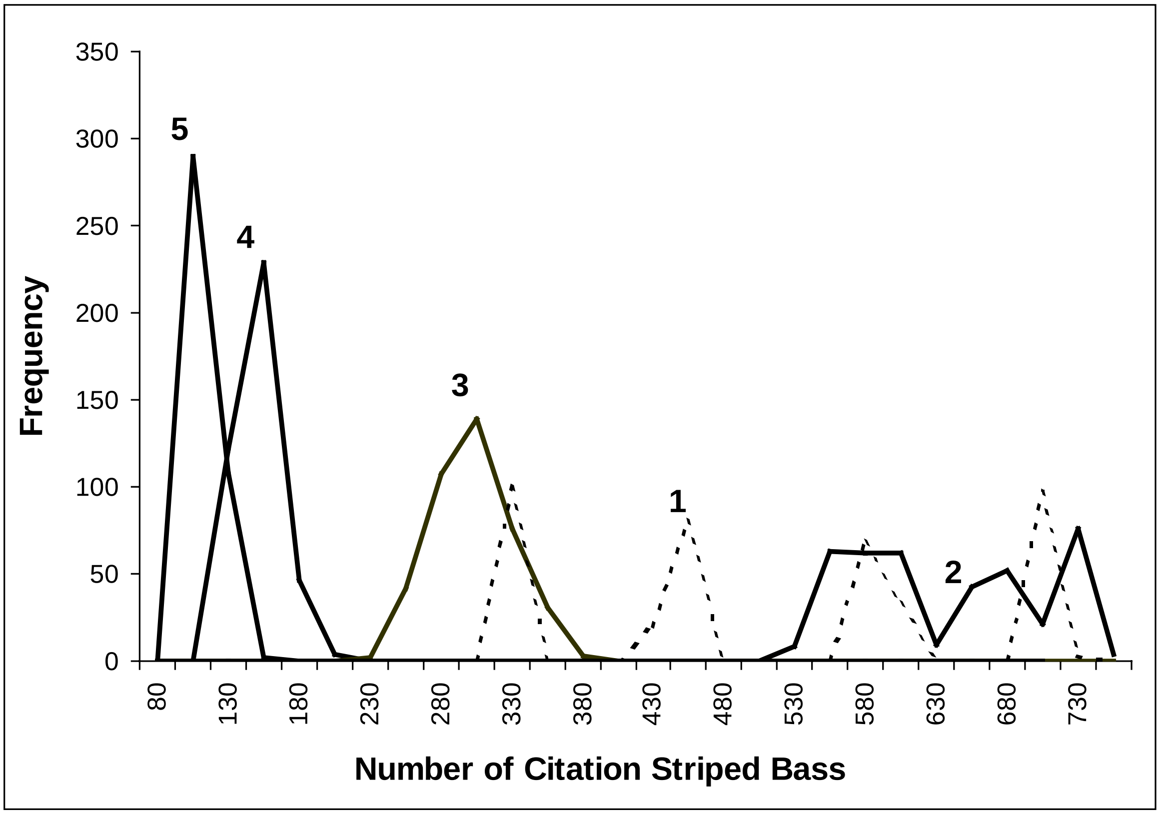

Figure 4.14. The distribution of number of citation striped bass under each stocking scenario. Four hundred values (representing observations in year 5 through year 8) are plotted for each scenario. Scenarios 1 through 5 represent stocking levels of 50,000, 150,000, 300,000, 450,000, and 600,000, respectively. The line for scenario 1 is dashed only to assist in distinguishing it from other scenarios. The multiple modes for scenario 1 and scenario 2 indicate that numbers of citation striped bass were changing between year 5 and year 8.

A cumulative probability plot is another way to display the distributional information of values produced under each stocking regime. Due to the importance of model output concerning the number of legal and citation striped bass in SML, I created cumulative probability plots for these metrics (Figures 4.15 and 4.16). The number of legal or citation striped bass under each scenario is given on the abscissa (x-axis). Probabilities are given on the ordinate (y-axis). A line was plotted for each stocking density. These lines begin at the left where the y-value is zero and slope upward toward a y-value of 1.00 as x-values increase. To determine the probability of producing a number of citation or legal striped bass equal to or less than a certain value, find that value on the x-axis and draw a line, parallel to the ordinate axis, from it to the curve of the scenario of interest. The y-value at that point of intersection is the correct probability. The reverse of this process can, of course, be used to find the x-value corresponding to a given probability.

Scenario 3 consistently output the highest number of legal striped bass, and scenario 1 performed the worst. Scenario 2 had better results than scenarios 4 and 5 (Figure 4.15). Fifty percent of the legal striped bass values produced under scenario 3 were greater than 31,200. Very few values were above 31,000 for scenarios 1, 2, 4, and 5. Fifty-percent values for scenarios 1, 2, 4, and 5 were 12,700, 29,100, 27,600, and 26,550, respectively. Ninety-seven percent of the values for scenario 3 were over 29,000, but only 57%, 16%, 3%, and 0% of the values were above this level in scenarios 2, 4, 5, and 1, respectively.

Scenario 2 was far and away most successful at producing citation striped bass; 53% of the numbers of citation fish were greater than 600 (Figure 4.16). For scenario 1 (not depicted in Figure 4.16), 25% of the numbers of citation striped bass were over 600, but all of these occurred in year 5. Under this light stocking regime, numbers of citations were much lower (about 320) by year 8. No citation magnitudes above 400 were seen in scenario 3, and no values above 200 were seen in scenarios 4 or 5. Fifty-percent values for scenarios 1 through 5 were 575, 616, 290, 137, and 99, respectively. The upper 10% values for scenarios 1 through 5 were 703, 716, 328, 157, and 113, respectively.

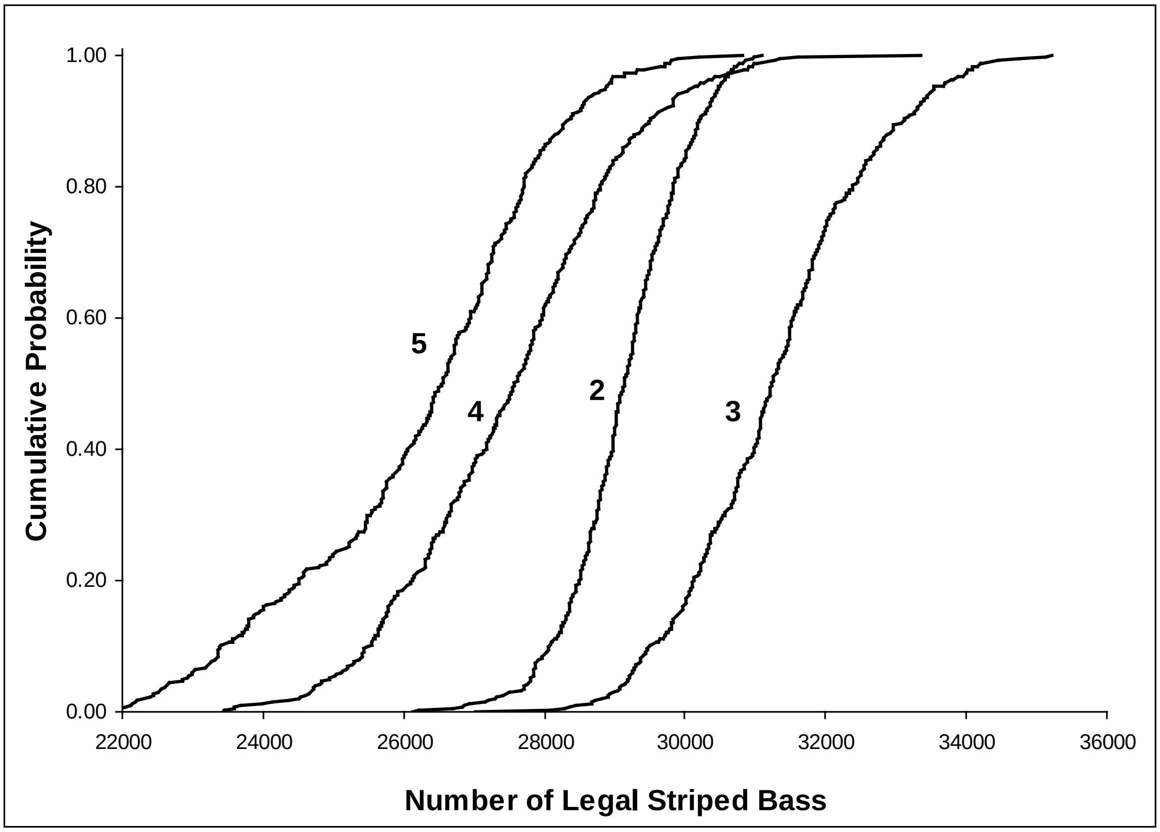

Figure 4.15. Cumulative probability plots for the number of legal striped bass produced under various stocking regimes. Four hundred values (representing observations in year 5 through year 8) are plotted for each scenario. Scenarios 2 through 5 represent stocking levels of 150,000, 300,000, 450,000, and 600,000, respectively. Stocking scenario 1 was not included because the plotting of its low values inhibited the clarity of the graph.

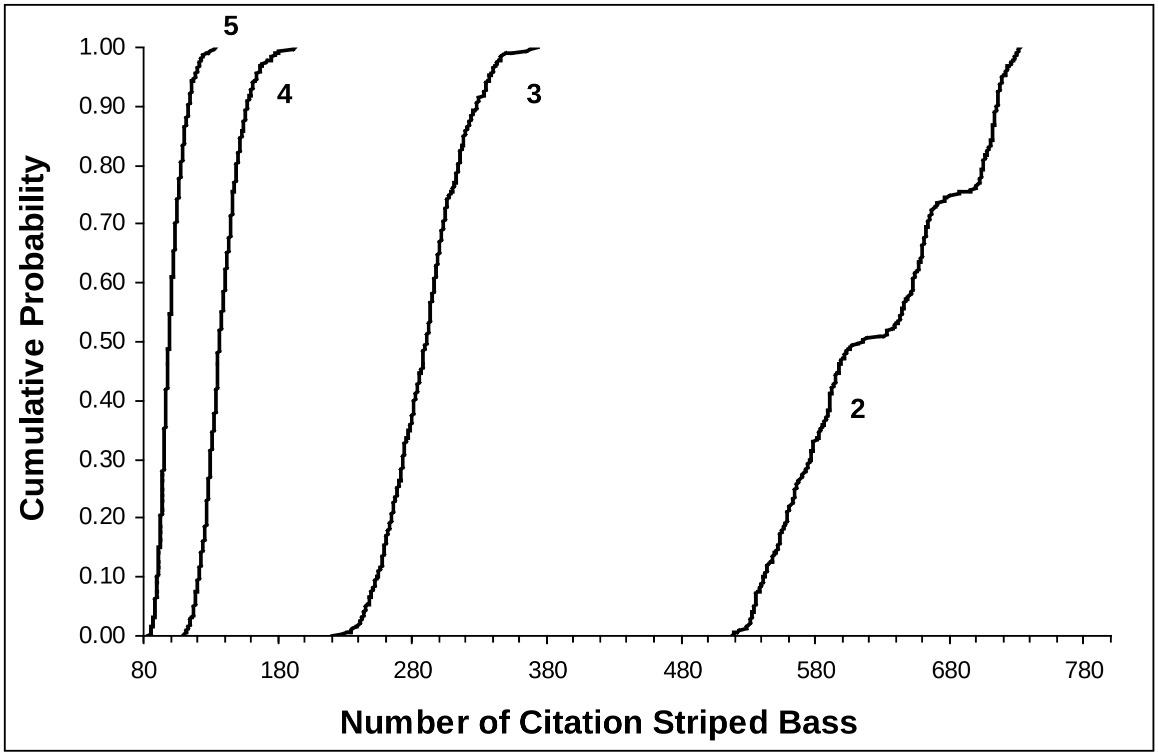

Figure 4.16. Cumulative probability plots for the number of citation striped bass produced under various stocking regimes. Four hundred values (representing observations in year 5 through year 8) are plotted for each scenario. Scenarios 2 through 5 represent stocking levels of 150,000, 300,000, 450,000, and 600,000, respectively. Stocking scenario 1 was not included because the plotting of its step-like trend (indicating much different numbers of citation fish from year to year) inhibited the clarity of the graph. A much less pronounced step-trend can be seen in the line for stocking scenario 2.

DISCUSSION

Based on these model results, increasing the number of striped bass fingerlings stocked into SML to 450,000 or 600,000 had a primarily negative effect on the number of legal and citation-sized striped bass remaining in the system 5-8 years later. A reduction in stocking to 150,000 greatly increased the number of citation striped bass beyond all other stocking regimes and did not lead to as great a decline in the number of legal striped bass as stocking 50,000, 450,000 and 600,000 striped bass did. Stocking 300,000 striped bass per year produced the greatest number of legal fish in the system.

In calculating the numbers of legal striped bass, however, I assumed that the condition of these fish would stay constant, i.e., the length-weight relationship would be unaltered. Increased or decreased competition for alewife could cause striped bass of a certain length to be lighter or heavier. Weight-at-age declined in scenarios 4 and 5. If length-at-age did not decline, these scenarios would produce a larger number of legal fish than reported earlier. In the opposite manner, weight-at-age increased in scenarios 1 and 2. If length-at-age did not increase, the numbers of legal striped bass reported for these scenarios would be too high. If length-at-age was not affected by weight-at-age (fish at a given size merely were either fatter or thinner), the mean numbers of legal fish in years 5 through 8 were 9,700, 22,300, 31,200, 35,700, and 39,100 for scenarios 1 through 5, respectively. In this case, increased stocking on average would lead to a larger number of legal fish in the system. At the higher stocking densities, however, legal fish would be 20-30% lighter than the recent mean weight-at-age. At the lower stocking densities, fish would be 20-30% heavier than is currently seen. Based on the limited amount of unutilized surplus alewife production in SML, any hope of maintaining current weight-based growth with an increase in stocking appears to be unrealistic. However, there do exist uncertainties that could influence the actual consequences of increased striped bass stocking in SML.

Declines in alewife availability, caused by increased striped bass demand, could lead predators to consume larger quantities of age-0 gizzard shad, which are relatively more available to other predators than to striped bass. In this case, gizzard shad could eventually limit growth of striped bass in SML. If a paucity of age-0 gizzard shad becomes common as adult striped bass emerge from the hypolimnion in late summer, their fall growth rates could decline. There appeared to be about 15 kg/ha of behaviorally-available gizzard shad surplus production that was not currently utilized by predators. However, I estimated that the predatory impact of catfish and crappie populations on gizzard shad was rather low (Table 2.7). Due to the great uncertainty in quantifying the demand and diets of these predator species in SML, it is possible that catfish and crappie could already be consuming the bulk of this apparent surplus. It is unlikely to expect striped bass to rely on any non-clupeid prey species for more than a minor portion of their diet (Stevens 1958; Bailey 1975; Combs 1978; Morris and Follis 1978; Matthews et al. 1988). If clupeid populations decline, the predator species that suffer the least will possess the greatest ability to switch between abundant prey items, and have prey most behaviorally, morphologically, and distributionally available to them.

The functional form of the equations used to derive age-0 striped bass mortality from relative age-0 alewife abundance, weight of adult striped bass from relative alewife abundance, and alewife mortality from striped bass abundance was assumed to be exponential. The use of other mathematical forms, such as linear or polynomial functions, for these associations could influence model results. The general slopes of these equations determine the "responsiveness" of the predator and prey populations to changes in the system. If the slopes of these relationships are increased, a change in conditions brings about rapid and relatively large changes in the components it affects. If the slope of these relationships were decreased, population variables would have to change far greater in order have noticeable consequences on associated model components. Population metrics would be less variable with very "responsive" relationships (i.e., greater slopes; any move away from current conditions would be quickly counteracted), but would fluctuate much more freely if the coupling link between model components was relaxed (i.e., slopes were lessened).

I explored the use of equations in which age-0 striped bass survival and weight-at-age-1+ of striped bass were dependent on absolute alewife abundance, rather than relative abundance (i.e., the number of alewife per striped bass). Increases in stocking levels in this model led to increases in the number of legal striped bass produced, but still resulted in much fewer citation striped bass. I chose to report results based on relative alewife abundance because this situation held more ecological appeal, i.e., the model using absolute abundance assumed no competition for alewife among striped bass. Regardless of which model I tested, mortality and growth equations were modeled deterministically. I did not attempt to incorporate stochasticity into all equations in order to limit model complexity. Random events which act very early life history of a population, however, when numbers of individuals are the highest, often have the greatest effect on later population size (Diana 1995). Perhaps a more important unresolved issue is the degree to which alewife recruitment is affected by adult stock size, i.e., the shape of the stock-recruitment relationship. It is unlikely that production of alewife larvae is completely independent of adult stock size. Judging by investigations in other systems (Brown 1972; Kashuba and Matthews 1984; Willis 1987; Bunyak et al. 1992; Welker et al. 1994; Michaletz 1997a; Sammons et al. 1998), however, a stochastic element likely plays a role in clupeid recruitment in SML. Environmental stochasticity was incorporated into the estimated Ricker stock-recruitment relationship through the addition of a lognormal error term. The relative effect of stochastic environmental occurrences (e.g., temperature, floods, water level fluctuations, turbidity, density of competitors, food availability) and alewife stock size in determining number of alewife larvae was estimated based on the range of alewife abundance seen in acoustic surveys.

Researchers have noted that at low clupeid stock size, reduced intraspecific and interspecific competition increased the condition of adult spawners, leading to better larval survival and increased numbers of age-0 clupeids (Swingle 1950; Sammons et al. 1998). If this compensation is great enough to offset augmented predation by striped bass, the outcome might be more favorable for the SML fishery. I determined that total predator demand for alewife and gizzard shad, with a 50% increase in striped consumption and no decline in predator growth rates, would be 91 kg/ha for each species. For total behaviorally-available (> 40 mm TL and < 160 mm TL) surplus production of alewife to just meet these levels, initial cohort size of alewife had to be approximately 2.75 billion, an increase of 38% over current levels. An initial shad cohort of 765 million (a 7% increase over current levels) had a total of 91 kg/ha of behaviorally-available surplus production. In theory this barely would be enough to meet increased predator demand. All behaviorally-available clupeid biomass that died under these circumstances would have to be eaten by some predator. This is an overly optimistic outcome. Mean annual alewife and gizzard shad cohort size would more reasonably have to increase by 45% and 15%, respectively, for predators to maintain their current growth rates. This is not a drastic increase for gizzard shad but is a much greater, and thus less likely, augmentation of alewife cohort size.

As posited in the Introduction, decreased abundance of clupeids in SML could lead to changes in their growth rates. This would affect their morphologic vulnerability, especially to young predators that are more gape-limited. Increased growth rates of age-0 gizzard shad would constrain predators more than increased growth of age-0 alewife. The former forage species has the capability to reach sizes that are invulnerable to the majority of predators (Noble 1981; Adams and DeAngelis 1987; DeVries and Stein 1990; DiCenzo et al. 1996; Michaletz 1997b, 1998b). Regardless of how fast age-0 alewife reach their asymptotic size, they will still be generally ingestible by most adult predators. The effect of increased age-0 alewife growth on age-0 striped bass would be less clear. It appears from Chapter Three as if large-mode age-0 striped bass have morphological access to all age-0 alewife. If age-0 alewife growth increased, however, these age-0 striped bass could become more morphologically constrained and this could have negative consequences on their growth and survival. Faster growth of age-0 alewife, however, would mean these prey fish would reach a behaviorally-available size (40 mm TL) sooner in the growth season and this could have a beneficial effect on age-0 striped bass growth and survival. For largemouth bass, increased growth of age-0 gizzard shad would have its largest effect on growth rates of age-1 individuals. This cohort of largemouth bass depends on small age-0 shad for about 65% of their diet (Moore 1988). If faster shad growth led to lower prey availability, this predator cohort would have to utilize more sunfishes, cyprinids, or crayfish for nutritional requirements. These items contain less calories per unit of mass, so bass would either have to eat more food, requiring more energy to conduct foraging activities, or suffer declines in growth.

One further issue should be discussed. It involves the relatively recent arrival of the threadfin shad into SML. This small forage fish is believed to have been introduced in the early 1990's via the bait buckets of zealous anglers. It is morphologically similar to the alewife and also inhabits limnetic waters but prefers warmer surface waters, like the gizzard shad (Ney et al. 1982; Siler 1986; Schael and Rice 1995). Threadfin are intolerant of cold water, making them extremely susceptible to winter kills in southern reservoirs (Noble 1982; Adams et al. 1982b; Sammons et al. 1998). Threadfin were initially noticed in appreciable numbers in SML in 1993. Rotenone data indicate that threadfin density was approximately 4 kg/ha in 1993 and 7 kg/ha in 1995. They were also detected in 1994 rotenone coves, although biomass averaged only 0.4 kg/ha. Few were seen in rotenone coves in 1997, but abundance was thought to increase somewhat in 1998 (M.C. Duval, VDGIF, personal communication). Because Hayne et al. (1967) found densities of threadfin in open water were similar to cove habitats during the day, whole-lake abundance of threadfin shad in each of these years is not expected to have been much greater than rotenone data suggest. Assuming these rotenone samples represent primarily age-0 fish, these quantities of threadfin are not massive considering an average age-0 alewife cohort would have an August biomass of 15 kg/ha.

Threadfin shad have been shown to reduce gizzard shad populations when abundant, the hypothesized mechanism being exploitative competition for food resources (Noble 1981; Guest et al. 1990; Sammons et al. 1998). Their effects on alewife populations are unknown.

It is debatable if threadfin were abundant enough in 1993 and 1995 to be a serious competitor in the system. This is not to say that they could not be in the future. Swingle (1970) depicts threadfin as prolific spawners with a vast production potential. Bryant and Houser (1968) documented the rise of the threadfin shad in Bull Shoals Reservoir, Arkansas. Threadfin composed 80% of clupeid biomass in a system previously dominated by gizzard shad five years after introduction. Ager (1978) and Riggs and Moore (1957) also document displacement of gizzard shad by threadfin shad in other reservoir systems. Cold winters and a large piscivore population are likely contributing to preventing threadfin shad from gaining more than a foothold in SML. In years with high threadfin abundance, SML predators would likely grow well because of the added prey resource that remains morphologically available throughout its first growth season, indeed its entire life. If this increase in abundance occurs at the expense of the gizzard shad, pelagic predators would not suffer (littoral predators might), for a prey species with a capacity to outgrow predator gapes would be replaced with one that cannot.

SUMMARY

This modeling exercise indicates that increased stockings of striped bass will do little to improve the fishery in Smith Mountain Lake. The number of citation fish will most certainly decline, and the number of legal striped bass is also not likely to be improved a great deal, if at all. The latter outcome will be determined by whether or not the condition of striped bass declines. My model indicated that up to a point, reduced stocking would lead to improvements in the fishery, especially from the standpoint of the number of citation striped bass produced. I have assumed no change in alewife recruitment processes, stable populations of other predators in SML, and a similar diet for striped bass before and after the stocking increase. These results stem from the fact that current alewife surplus production is almost entirely utilized by the predator assemblage of Smith Mountain Lake.

SUMMARY

1. The general goal of this dissertation was to conduct a thorough analysis of prey supply and predator demand in Smith Mountain Lake. Specific objectives, investigated sequentially in successive chapters, were as follows:

A. Derive the maximum sustainable supply of alewife and gizzard shad.
B. Calculate annual consumption of clupeids by all major piscivores.
C. Determine the behavioral, morphological, and distributional availability of each clupeid species for each cohort of largemouth bass and striped bass.
D. Make predictions of the consequences of changes in striped bass stocking densities on predator growth and survival, as well as clupeid population dynamics.

2. Mean alewife biomass, as determined by hydroacoustic surveys in 1993, 1994, 1995, 1997, and 1998, was approximately 37 ± 4.5 kg/ha in late August. Cove rotenone biomass of gizzard shad, which was assumed to be representative of whole-lake abundance, averaged 112 ± 18.5 kg/ha in 1990 through 1997 in SML. The lowest acoustic biomass of alewife was 28 kg/ha, in 1994 and 1997, and the highest was 52 kg/ha, in 1998. The highest biomass of shad seen in rotenone coves during 1990-1997 was 231 kg/ha, in 1990. The lowest value was 62 kg/ha, in 1997.

3. To calculate August biomass estimates of alewife identical to those found using hydroacoustics, initial cohort size was set at 2 billion individuals. For gizzard shad, an initial cohort size of 715 million led to August biomass estimates identical to that seen in cove rotenone surveys. At these initial abundances, total mortality of alewife over their first growth season was 98.1% and age-0 gizzard shad had a total mortality of 97.5%. At the end

of their first growth season, the average alewife was 78 mm TL, and the average shad was 118 mm TL.

4. At the above cohort sizes, total annual population production of alewife was an estimated 73 kg/ha. Total annual mean production of gizzard shad was estimated at 146.5 kg/ha. Using the range of biomass estimates seen in acoustic and rotenone surveys for both species, total annual production ranged from 55 to 102 kg/ha for alewife and 82 to 307 kg/ha for gizzard shad. The annual P/B ratio for alewife was 2.0 and for gizzard shad it was 1.3.

5. Surplus production, which is the amount of biomass that dies during a given period, regardless of when the biomass was produced, was defined as the maximum sustainable supply of clupeids for piscivore consumption. Surplus production across all cohorts equals the total annual production of a prey species. Mean annual surplus production of age-0, age-1, age-2, and age-3 alewife was 31.1, 28.4, 10.7, and 3.0 kg/ha, respectively. Surplus production of consecutive shad cohorts was 56.6, 44.7, 23.3, 12.3, 5.6, 2.4, 1.1, and 0.4 kg/ha.

6. Bioenergetic modeling was used to determine individual consumption by largemouth bass and striped bass, the primary piscivores in SML. Diet composition and growth rates were crucial inputs for this procedure. Adult largemouth bass diet was more varied than striped bass, but in late summer through late spring was primarily gizzard shad and crayfish. Alewife made up a large component of the largemouth bass diet during most of the summer, as adult alewife came onshore to spawn. The diet of adult striped bass was primarily alewife from early spring to early fall, then gizzard shad in fall and winter.

7. The average largemouth bass was found to reach a legal size (356 mm TL) during its fourth growth season, while average striped bass reached legal size (508 mm TL) near the end of their third growth season. The average striped bass reached citation size (9.1 kg) in its tenth growth season. In keeping with the findings of Sutton (1997), age-0 striped bass were divided into two growth groups, a "small" mode and a "large" mode. Virtually none of the small-mode striped bass survived their first winter.

8. Individual annual consumption for both largemouth bass and striped bass increased from cohort to cohort. For largemouth bass, age-0 individuals consumed about 60 grams of food during their first year, while age-10 individuals consumed almost 4 kilograms of food across the year. Small age-0- striped bass individuals consumed only 100 grams of food during their first year, while large age-0 striped bass ingested about 380 grams. An age-10 striped bass was estimated to consume over 25 kilograms of prey during a year.

9. In order to determine population consumption by largemouth bass and striped bass, estimates of their population size needed to be determined. The number of age-0 largemouth bass present in November in SML was estimated to be almost 840,000. Numbers of age-1 striped bass in March, just prior to their second growth season, were estimated at approximately 96,000 individuals. Annual mortality of sub-legal striped bass was estimated to be about 50%, and increased to 63% for harvestable fish. Adult largemouth bass annual mortality was estimated to be 40%. For age-0 largemouth bass, annual mortality was calculated to be approximately 92%. I estimated that, on average, approximately 244,000 largemouth bass over 200 mm TL were present in SML, resulting in a total largemouth bass standing stock of 18 kg/ha. Annual mean numbers of legal striped bass were estimated to be about 31,200 fish, with an mean of 285 citation fish (> 9.1 kg). Mean standing stock of striped bass was estimated to be 15 kg/ha.

10. When population sizes were coupled with estimates of individual consumption, the largemouth bass population ingested approximately 50 kg/ha of prey each year in SML, including 8.5 kg/ha of alewife and 14.8 kg/ha of gizzard shad. The bulk of consumption was done by age-1 through age-4 largemouth bass; fish over age-6 contributed very little to total population consumption. The striped bass population ate a total of 84 kg/ha of food annually, with a total alewife consumption of 46.5 kg/ha and a total gizzard shad consumption of 27 kg/ha. Age-1 through age-3 striped bass were responsible for 75% of the population's consumption. These three age-classes combined ate over 510,000 kg of food annually. The age-0 and age-4 cohorts ingested about 60,000 kg each. All other cohorts combined to consume about 50,000 kg.

11. Gross food conversion efficiency was determined for both largemouth bass and striped bass. For both species, food conversion decreased as fish aged. Age-0 largemouth bass had an annual

conversion efficiency of over 40%. For age-1 largemouth bass, this value was approximately 28%. After age-1, annual food conversion efficiency declined linearly, reaching a nadir at 8% for age-10 individuals. Large age-0 striped bass had a annual food conversion efficiency of 30%, age-1 striped bass converted food into body mass at 20% efficiency for the year, and annual food conversion efficiency of age-10 fish was lowest, at 3%. The average annual food conversion efficiency of age-1 and older largemouth bass was 23%; for striped bass it was approximately 17%.

12. Annual prey consumption by ancillary predators in SML was estimated to be approximately 163 kg/ha annually. Of this amount, ingested alewife biomass was 13 kg/ha and consumption of gizzard shad was 35 kg/ha. Within this predator conglomerate, catfish (white, channel, and flathead) and crappie combined for over 97% of consumption. Smallmouth bass, walleye and muskellunge consumption was basically negligible due to their small population sizes. For all piscivores, annual food consumption was 295 kg/ha. Total annual alewife biomass eaten was 68 kg/ha and biomass of shad consumed was 77 kg/ha annually.

13. Behavior availability of gizzard shad was reduced due the predator avoidance of shad over 160 mm TL. In addition, largemouth bass and striped bass neglected clupeids less than 40 mm TL. From a morphologic standpoint, young predator cohorts were more severely constrained that older predators, due to gape-width limitations, especially in regards to consumption of gizzard shad. Age-0 largemouth bass could not feed on age-0 gizzard shad, and large age-0 striped bass could only consume the smallest 25% of this prey cohort. Adult largemouth bass only had distributional access to adult alewife during the latter's spawning season, running from late May to late August. This habitat segregation reduced overall availability of alewife to largemouth bass by 80%. Striped bass were spatially disjunct from gizzard shad for approximately three months of the year, from mid-June to mid-September, when epilimnion temperatures became too warm for the predators. This isolation meant that over 20% of surplus production of gizzard shad was spatially unavailable to striped bass.

14. After correction for all forms of availability and the consumption of other predators, total available supply of alewife and total available supply of gizzard shad exceeded the demand of the largemouth bass population by 20% and 53%, respectively. For the striped

bass population, available gizzard shad supply exceeded demand by 30%, while available alewife supply exceeded demand by only 4%.

15. Total available production of alewife and gizzard shad was 69 kg/ha and 85 kg/ha, respectively. Despite subsets of this prey production being morphologically or distributionally unavailable to specific cohorts of a predator species, all of this prey production would be theoretically available to at least some predator cohorts. Thus, 145 of 154 kg/ha of behaviorally-available annual clupeid production in SML was currently being utilized by members of the predator assemblage.

16. A simulation model was constructed based on the ecological assumptions that relative abundance of age-0 alewife affects age-0 striped bass survival, abundance of adult striped bass affects alewife mortality, and relative abundance of alewife affects weight-at-age of adult striped bass. This model predicted that increasing striped bass stockings to 450,000 annually would likely lead to declines in the number of legal striped bass, and most certainly to declines in the number of citation striped bass in Smith Mountain Lake. A stocking rate of 300,000 had the highest probability of producing the largest numbers of legal striped bass, and a stocking rate of 150,000 produced the greatest numbers of citation striped bass.

CONCLUSIONS AND MANAGEMENT RECOMMENDATIONS

I determined that over 94% of the available clupeid supply is utilized to meet predator demand in SML (145 of 154 kg/ha). Total available supply of alewife to striped bass only exceeded striped bass population demand by only 4%. I have predicted that increased stocking of striped bass will cause growth of adult striped bass to decline. This stocking increase could likely lead to declines in the number of legal and citation striped bass in SML. None of the quantities in this investigation, however, were measured free of error. Prey supply could have been underestimated and/or predator demand for clupeids in SML overestimated. In either instance, increasing the number of striped bass stocked would have a greater chance of producing more legal and citation-sized striped bass, an improved fishery, and satisfied anglers. My findings, based on data-driven modeling using the best available information on clupeid and predator populations, portend a less optimistic future.

The prudent course based on this forecast would be to closely monitor striped bass harvested by anglers, or caught during the fall gillnet assessment, for signs of poor growth and declining condition. Statistical comparisons to previous size-at-age should be performed. The cooperative fishing-diary program recently undertaken by the VDGIF and the SML Striped Bass Club should facilitate gathering of useful information. If young cohorts of striped bass (age-0 through age-3) show a trend of increasing abundance and declining growth/condition, it would be wise to retreat to previous stocking levels, and/or to decrease the minimum legal size of striped bass from 508 to 356 mm TL (from 20 to 14 inches). The purpose of the latter regulation would be to thin out the ranks of overabundant young striped bass. More information is needed to determine whether or not anglers would perceive a 14-inch striped bass as a desirable fish to harvest. Increasing striped bass abundance alone is not a cause for concern; indeed, that was the primary objective of increasing their stocking densities. A genuine warning signal would be long-term declines in growth and condition of striped bass. In addition, other predators, most importantly largemouth bass, should be monitored for signs of a decrease in growth and/or abundance. Because rotenone surveys are no longer conducted, standardized shoreline electrofishing surveys could lend information on annual trends in littoral fish abundance and well-being. It is unlikely that survival of other predators would be greatly affected by declines in clupeid abundance, because current information indicated that the age-0 members of other predator species, which are most susceptible to starvation, do not heavily rely on clupeid prey.

Almost 40 kg/ha of combined catfish and crappie biomass were found in rotenone coves in the 1990's in SML. Due to the important role each might play in determining total clupeid demand, more detailed information on their diet, growth and mortality rates, and abundance in SML would be required to complete the supply-demand analysis. My demand estimates could be off in either direction depending on the extent that these predators utilize clupeids. If they rarely feed on clupeids, striped bass might not suffer significant growth declines as striped bass abundance rises. If crappie and catfish do utilize clupeids for a large portion of their diet, however, current clupeid populations would be at the brink of overexploitation by the predator assemblage of SML. Increases in striped bass densities thus would likely lead only to poorer growth and survival for piscivores.

This investigation indicated that alewife were closer to being overexploited by the predator population than gizzard shad. The latter species has a predator refuge in the large size that it attains, while the former has no such trophic sanctuary. I recommend that gillnets with smaller mesh sizes be added to the annual sampling protocol so that the relative abundance of age-0 alewife (and threadfin shad) can be tracked from year to year. This gear would also aid in producing a more accurate partitioning of clupeid biomass for analysis of acoustic data, allow information on clupeid growth and mortality in SML to be updated, permit refinement of the models presented here, and make comparisons to pre-increase clupeid populations possible.

Due to the striped bass stocking increase, clupeid densities must be examined annually. This can be accomplished through hydroacoustic assessment and the gillnets deployed concurrent with acoustic sampling endeavors. Because rotenone surveys are no longer performed on

SML, acoustic surveys have become that much more important, as they are now the only means of clupeid assessment for the system. Any improvement in acoustic methodology will thus lead to better management of the forage base of SML. Based on a comparison of acoustic to rotenone data in the same year, and assuming the latter method accurately represents whole-lake gizzard shad biomass, it appears as if the former technique slightly underestimated whole-lake gizzard shad biomass. Acoustic estimates of gizzard shad biomass in 1993, 1994, 1995, and 1997 averaged 69 kg/ha, while gizzard shad biomass in rotenone coves in these four years averaged 76 kg/ha. Thus, with a possible adjustment to correct for this underestimation, acoustic methodology could be used to develop estimates of annual gizzard shad standing stock in SML.

If the clupeid population shows a three-to-five year decline in abundance, a reduction in striped bass stocking would also be wise. Abundance of clupeid populations in most aquatic systems tend to be highly variable, however, so year-to-year variation is not necessarily indicative of predation impact. Because clupeids are prolific spawners, they normally could recuperate quickly from a major decline, especially if the hypotheses of Sammons et al. (1998) regarding competition-mediated control of clupeid recruitment are correct. With an overabundance of striped bass in SML, however, clupeid populations could be depressed for four or more years before predator intensity would decline sufficiently to allow for good forage-fish year-classes to arise.

Finally, consequences of threadfin shad presence in SML should be investigated. A shift in the clupeid composition of the forage base of SML might actually benefit the predator population in the long term, but an increase in threadfin shad at the expense of gizzard shad might have short-term deleterious effects on predator growth and survival. Due to the increased susceptibility of threadfin shad to winterkill, this prey resource would be more unstable and could lead to large deficits in prey supply in the spring following cold winters.

LITERATURE CITED

Adams, S.M., R.B. McLean and J.A. Parrotta. 1982a. Energy partitioning in largemouth bass under conditions of seasonally fluctuating prey availability. Transactions of the American Fisheries Society 111: 549-558.

Adams, S.M., R.B. McLean and M.M. Huffman. 1982b. Structuring of a predator population through temperature-mediated effects on prey availability. Canadian Journal of Fisheries and Aquatic Sciences 39: 1175-1184.

Adams, S.M. and D.L. DeAngelis. 1987. Indirect effects of early bass-shad interactions on predator population structure and food web dynamics. Pages 103-117 *in* C.W. Kerfoot and A. Sih, editors. Predation: direct and indirect impacts on aquatic communities. University Press of New England, Hanover, New Hampshire.

Ager, L.A. 1976. Monthly food habits of various size groups of black crappie in Lake Okochobee. Proceedings of the Annual Conference of the Southeastern Association of Game and Fish Commissions 29: 337-342.

Ager, L.M. 1978. Exploitation and mortality of largemouth bass in Lake Tobesofkee, Georgia. Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies 32: 429-436.

Aggus, L.R. and G.V. Elliot. 1975. Effects of cover and food on year-class strength of largemouth bass. Pages 317-322 *in* H. Clepper, editor. Black bass biology and management. Sport Fishing Institute, Washington, D.C.

Aggus, L.R. and W.C. Rainwater. 1975. Estimating largemouth bass populations in reservoirs from catches in angling tournaments. Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies 29: 106-114.

Allan, R.C. and J. Romero. 1975. Underwater observations of largemouth bass spawning and survival in Lake Mead. Pages 104-112 *in* H. Clepper, editor. Black bass biology and management. Sport Fishing Institute, Washington, D.C.

Anderson, R.O. and R.M. Neumann. Length, weight, and associated structural indeces. Pages 447-481 in B.R. Murphy and D.W. Willis, editors. Fisheries techniques, 2nd edition. American Fisheries Society, Bethesda, Maryland.

Annett, C., J. Hunt and E.D. Dibble. 1996. The compleat bass: habitat use patterns of all stages of the life cycle of largemouth bass. Pages 306-314 *in* L.E. Miranda and D.R. DeVries, editors. Multidimensional approaches to reservoir fisheries management. American Fisheries Society Symposium 16, Bethesda, Maryland.

Axon, J.R. and D.K. Whitehurst. 1985. Striped bass management in lakes with emphasis on management problems. Transactions of the American Fisheries Society 114: 8-11.

Bailey, W.M. 1975. An evaluation of striped bass introductions in the southeastern United States. Proceedings of the Annual Conference of the Southeastern Association of Game and Fish Commissions 28: 54-68.

Ball, R.L. and R.V. Kilambi. 1973. The feeding ecology of the black and white crappies in Beaver Reservoir, Arkansas, and its effect on the relative abundance of the crappie species. Proceedings of the Annual Conference of the Southeastern Association of Game and Fish Commissions 26: 577-590.

Banach, M.J. 1989. Age and growth of Virginia's freshwater fishes. Virginia Polytechnic Institute and State University, Blacksburg.

Bartell, S.M, J.E. Breck, R.H. Gardner and A.L. Brenkert. 1986. Individual parameter perturbation and error analysis of fish bioenergetics models. Canadian Journal of Fisheries and Aquatic Sciences 43: 160-168.

Batty, R.S. 1989. Escape responses of herring larvae to visual stimuli. Journal of the Marine Biological Association of the United Kingdom 48: 17-28.

Beauchamp, D.A., C. Luecke, W.A. Wurtsbaugh, H.G. Gross, P.E. Budy, S. Spaulding, R. Dillenger and C.P. Gubala. 1997. Hydroacoustic assessment of abundance and diel distribution of sockeye salmon and kokanee in the Sawtooth Valley Lakes, Idaho. North American Journal of Fisheries Management 17: 253-267.

Becker, G.C. 1983. Fishes of Wisconsin. University of Wisconsin, Madison.

Benfield, E.F. and A.C. Hendricks. 1975. Eutrophic gradient in Smith Mountain Lake, Virginia. Virginia Journal of Science 26: 20-26.

Bettoli, P.W. and M.J. Maceina. 1996. Sampling with toxicants. Pages 303-333 *in* B.R. Murphy and D.W. Willis, editors. Fisheries techniques, 2nd edition. American Fisheries Society, Bethesda, Maryland.

Bettoli, P.W., M.J. Maceina, R.L. Noble and R.K. Betsill. 1993. Response of a reservoir fish community to aquatic vegetation removal. North American Journal of Fisheries Management 13: 110-124.

Bettoli, P.W., R. Osborne and S. Owens. 1995. A review of the literature pertaining to the effects of striped bass on other fish populations. Report submitted to the Tennessee Wildlife Resources Agency.

Bevelhimer, M.S., R.A. Stein and R.F. Carline. 1985. Assessing significance of physiological differences among three esocids with a bioenergetics model. Canadian Journal of Fisheries and Aquatic Sciences 42: 57-69.

Boxrucker, J., P. Michaletz, M.J. Van Den Avyle and B. Vondracek. 1995. Overview of gear evaluation study for sampling gizzard shad and threadfin shad populations in reservoirs. North American Journal of Fisheries Management 15: 885-890.

Brandt, S.B. 1996. Acoustic assessment of fish abundance and distribution. Pages 385-432 *in* B.R. Murphy and D.W. Willis, editors. Fisheries techniques, 2nd edition. American Fisheries Society, Bethesda, MD.

Brandt, S.B., D.M. Mason, D.B. MacNeill, T. Coates and J.E. Gannon. 1987. Predation by alewife on larvae of yellow perch in Lake Ontario. Transactions of the American Fisheries Society 116: 641-645.

Brandt, S.B., D.M. Mason, E.V. Patrick, R.L. Argyle, L. Wells, P.A. Unger and D.J. Stewart. 1991. Acoustic measures of the abundance and size of pelagic planktivores in Lake Michigan. Canadian Journal of Fisheries and Aquatic Sciences 48: 894-908.

Brandt, S.B., D.M. Mason and E.V. Patrick. 1992. Spatially explicit models of fish growth rate. Fisheries 17: 23-35.

Brandt, S.B. and J. Kirsch. 1993. Spatially explicit models of striped bass growth potential in Chesapeake Bay. Transactions of the American Fisheries Society 122: 845-869.

Brandt, S.B. and K.J. Hartman. 1993. Innovative approaches with bioenergetics models - future applications to fish ecology and management. Transactions of the American Fisheries Society 122: 731-735.

Braschler, D.W., M.G. White and J.W. Foltz. 1989. Movements and habitat selection of striped bass in the Santee-Cooper Reservoir. Proceedings of the Annual Conference of Southeastern Fish and Wildlife Agencies 42: 27-34.

Brett, J.R. and T.D.D. Groves. 1979. Physiological energetics. Pages 279-352 *in* W.S. Hoar, D.J. Randall, and J.R. Brett, editors. Fish physiology, volume 8. Academic Press, New York.

Brouha, P. 1974. Evaluation of two reef materials and point or cove locations for construction of artificial reefs in Smith Mountain Lake, Virginia. M.S. Thesis. Virginia Polytechnic Institute and State University, Blacksburg.

Brown, E.H. Jr. 1972. Population biology of alewife in Lake Michigan. Journal of the Fisheries Research Board of Canada 29: 477-500.

Bryant, H.E. and A. Houser. 1968. Growth of threadfin shad in Bull Shoals Reservoir. Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies 22: 275-283.

Bryant, H.E. and A. Houser. 1971. Population estimate and growth of largemouth bass in Beaver and Bull Shoals Reservoirs. American Fisheries Society Special Publication 8: 349-357.

Bulak, J.S., D.S. Wethey and M.G. White III. 1995. Evaluation of management options for a reproducing striped bass population in the Santee-Cooper System, South Carolina. North American Journal of Fisheries Management 15: 84-94.

Bunyak, G.L., R.S. Hale, and B. Mitchell. 1992. Differential growth of young-of-the-year gizzard shad in several Kentucky reservoirs. North American Journal of Fisheries Mangement 12: 656-662.

Carlander, K.D. 1968. Handbook of freshwater fishery biology, volume I. Iowa State University Press, Ames, Iowa.

Carlander, K.D. 1977. Handbook of freshwater fishery biology, volume II. Iowa State University Press, Ames, Iowa.

Carlander, K.D. 1997. Handbook of freshwater fishery biology, volume III. Iowa State University Press, Ames, Iowa.

Carline, R.F., B.L. Johnson and T.J. Hall. 1984. Estimation and interpretation of proportional stock density for fish populations in Ohio impoundments. North American Journal of Fisheries Management 4: 139-154.

Cheek, T.E., J.M. Van Den Avyle and C.C. Coutant. 1985. Influences of water quality on distribution of striped bass in a Tennessee River impoundment. Transactions of the American Fisheries Society 114: 67-76.

Chevalier, J.R. 1973. Cannibalism as a factor in first-year survival of walleye in Oneida Lake. Transactions of the American Fisheries Society 102: 739-744.

Cochran, P.A. and J.A. Rice. 1981. A comparison of bioenergetics and direct field estimates of cumulative seasonal food consumption by largemouth bass. Pages 88-96 *in* G.M. Cailliet and C.A. Simenstad, editors. Fish food habit studies. Washington Sea Grant, University of Washington, Seattle.

Collins, N.C. and S.G. Hinch. 1993. Diel and seasonal variation in foraging activities of pumpkinseeds in an Ontario pond. Transactions of the American Fisheries Society 122: 357-365.

Combs, D.L. 1978. Food habits of adult striped bass from Keystone Reservoir and its tailwaters. Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies 32: 571-575.

Combs, D.L. 1980. Fish population changes in Keystone Reservoir fourteen years after striped bass introductions. Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies 34: 194-199.

Combs, D.L. and L.R. Peltz. 1982. Seasonal distribution of striped bass in Keystone Reservoir, Oklahoma. North American Journal of Fisheries Management 2: 66-73.

Coutant, C.C. 1975. Responses of bass to natural and artificial temperature regimes. Pages 272-285 *in* R.H. Stroud and H. Clepper, editors. Black bass biology and management. Sport Fish Institute, Washington, D.C.

Coutant, C.C. 1983. Striped bass and the management of cooling lakes. Pages 386-396 *in* S. Sengupta and S.S. Lee, editors. Waste heat utilization and management. Hemisphere, Washington, D.C.

Coutant, C.C. 1985. Striped bass, temperature, and dissolved oxygen: a speculative hypothesis for environmental risk. Transactions of the American Fisheries Society 114: 31-61.

Coutant, C.C. 1987. Poor reproductive success of striped bass from a reservoir with reduced summer habitat. Transactions of the American Fisheries Society 116: 154-160.

Coutant, C.C. 1990. Temperature-oxygen habitat for freshwater and coastal striped bass in a changing climate. Transactions of the American Fisheries Society 119: 240-253.

Coutant, C.C. and D.S. Carroll. 1980. Temperature occupied by ten ultrasonic-tagged striped bass in freshwater lakes. Transactions of the American Fisheries Society 109: 195-202.

Coutant, C.C. and D.L. Benson. 1990. Summer habitat suitability for striped bass in Chesapeake Bay: reflections on a population decline. Transactions of the American Fisheries Society 119: 757-778.

Crecco, V.T., T. Savoy and L. Gunn. 1983. Daily mortality rates of larval and juvenile American shad in the Connecticut River with changes in year-class strength. Canadian Journal of Fisheries and Aquatic Sciences 40: 1719-1728.

Crowder, L.B. 1980. Alewife, rainbow smelt, and native fishes in Lake Michigan: competition or predation? Environmental Biology of Fishes 5: 225-233.

Crowder, L.B., J.J. Magnuson and S.B. Brandt. 1981. Complementarity in the use of food and thermal habitat by Lake Michigan fishes. Canadian Journal of Fisheries and Aquatic Sciences 38: 662-668.

Cumming, K.B. and R.D. Estes. 1969. Some water quality aspects of the upper Roanoke River basin with special reference to temperature. Virginia Water Resources Center, Bulletin 23.

Dalton, P.D. 1987. Ecology of bay anchovy eggs and larvae in the mid-Chesapeake Bay. M.S. Thesis. University of Maryland, College Park.

Davies, W.D. and W.L. Shelton. 1983. Sampling with toxicants. Pages 199-214 *in* L.A. Nielson and D.L. Johnson, editors. Fisheries techniques. American Fisheries Society, Bethesda, Md.

Degan, D.J. and W. Wilson. 1995. Comparison of four hydroacoustic frequencies for sampling pelagic fish populations in Lake Texoma. North American Journal of Fisheries Management 15: 924-932.

Dendy, J.S. 1946. Food of several species of fish, Norris Reservoir, Tennessee. Journal of the Tennessee Academy of Science 21: 105-127.

Dent, R.J. Jr. 1986. Methods and parameters used in evaluating bass length limits on Pomme de Terre Lake, Missouri. Pages 65-72 *in* G.E. Hall and M.J. Van Den Avyle, editors. Reservoir fisheries management: strategies for the 80's. Reservoir Committee, Southern Division American Fisheries Society, Bethesda, Maryland.

Dettmers, J.M. and R.A. Stein. 1992. Food consumption by larval gizzard shad: zooplankton effects and implications for reservoir communities. Transactions of the American Fisheries Society 121: 494-507.

Dettmers, J.M. and R.A. Stein. 1996. Quantifying linkages among gizzard shad, zooplankton, and phytoplankton in reservoirs. Transactions of the American Fisheries Society 125: 27-41.

DeVries, D.R., R.A. Stein, J.G. Miner and G.G. Mittelbach. 1991. Stocking threadfin shad : consequences for young-of-year fishes. Transactions of the American Fisheries Society 120: 368-381.

DeVries, D.R. and R.A. Stein. 1990. Manipulating shad to enhance sport fisheries in North America: an assessment. North American Journal of Fisheries Management 10: 209-223.

DeVries, D.R. and R.A. Stein. 1992. Complex interactions between fish and zooplankton: quantifying the role of an open-water planktivore. Canadian Journal of Fisheries and Aquatic Sciences 49: 1212-1227.

Dewey, M.R. and T.E. Moen. 1981. Population dynamics of largemouth bass in DeGray Lake, Arkansas, 1975-1979. Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies 35: 430-437.

Diana, J.S. 1995. Biology and ecology of fishes. Cooper Publishing, Carmel, Indiana.

DiCenzo, V.J., M.J. Maceina and M.R. Stimpert. 1996. Relations between reservoir trophic state and gizzard shad population characteristics in Alabama reservoirs. North American Journal of Fisheries Management 16: 888-895.

Dill, L.M. 1983. Adaptive flexibility in the foraging behavior of fishes. Canadian Journal of Fisheries and Aquatic Sciences 40: 398-408.

Duval, M.C. 1996. Smith Mountain Lake Management Report, 1993-1995. Virginia Department of Game and Inland Fisheries, Lynchburg.

Eck, G.W. and E.H. Brown Jr. 1985. Lake Michigan's capacity to support lake trout and other salmonids: an estimate based on the status of prey populations in the 1970's. Canadian Journal of Fisheries and Aquatic Sciences 42: 449-454.

Einfalt, L.M. and D.H. Wahl. 1997. Prey selection by juvenile walleye as influenced by prey morphology and behavior. Canadian Journal of Fisheries and Aquatic Sciences 54: 2618-2626.

Elliott, J.M. 1976. The energetics of feeding, metabolism and growth of brown trout in relation to body weight, water temperature, and ration size. Journal of Animal Ecology 45: 923-948.

Engel, S. 1987. Impact of submerged macrophytes on largemouth bass and bluegills. Lake Reservoir Management 3: 227-234.

Fairchild, G.W. 1981. Movement and microdistribution of *Sida crystallina* and other littoral microcrustaceans. Ecology 62: 1341-1352.

Farman, R.S., L.A. Nielsen and M.D. Norman. 1982. Estimating largemouth bass abundance using creel census and tournament data in the fishing-success method. North American Journal of Fisheries Management 2: 249-256.

Fleischer, G.W., R. L. Argyle and G.L. Curtis. 1997. In situ relations of target strength to fish size for Great Lakes pelagic planktivores. Transactions of the American Fisheries Society 126: 786-794.

Foote, K.G. 1987. Fish target strengths for use in echo integrator surveys. Journal of the Acoustical Society of America 73: 688-700.

Forney, J.L. 1976. Year-class formation in the walleye population of Oneida Lake, New York, 1966-73. Journal of the Fisheries Research Board of Canada 33: 783-792.

Fry, F.E.J. 1947. Effects of the environment on animal activity. University of Toronto Studies, Biological Series 55 (Publication of the Ontario Fisheries Research Laboratory 68: 1-62).

Gallego, A. and M.R. Heath. 1994. The development of schooling behavior in Atlantic herring. Journal of Fish Biology 45: 569-588.

Garvey, J.E. and R.A. Stein. 1998. Linking bluegill and gizzard shad prey assemblages to growth of age-0 largemouth bass in reservoirs. Transactions of the American Fisheries Society 127: 70-83.

Garvey, J.E., N.A. Dingledine, N.S. Donovan and R.A. Stein. 1998. Exploring spatial and temporal variation within reservoir food webs: predictions for fish assemblages. Ecological Applications 8: 104-120.

Gotceitas, V. and P. Colgan. 1987. Selection between densities of artificial vegetation by young bluegills avoiding predation. Transactions of the American Fisheries Society 116: 40-49.

Guest, W.C., R.W. Drenner, S.T. Threlkeld, F.D. Martin and J.D. Smith. 1990. Effects of gizzard shad and threadfin shad on zooplankton and young-of-the-year white crappie production. Transactions of the American Fisheries Society 119: 529-536.

Gunderson, D.R. 1993. Surveys of fisheries resources. Wiley and Sons, New York.

Gutreuter, S.J. and R.O. Anderson. 1985. Importance of body size to the recruitment process in largemouth bass populations. Transactions of the American Fisheries Society 111: 317-327.

Hale, R.S. 1996. Threadfin shad use as supplemental prey in reservoir white crappie fisheries in Kentucky. North American Journal of Fisheries Management 16: 619-632.

Hall, D.J., E.E. Werner, J.F. Gilliam, G.G. Mittelbach, D. Howard, C.G. Doner, J.A. Dickerman and A.J. Stewart. 1979. Diel foraging behavior and prey selection in the golden shiner. Journal of the Fisheries Research Board of Canada 36: 1029-1039.

Hambright, K.D. 1991. Experimental analysis of prey selection by largemouth bass: role of predator mouth widths and prey body depth. Transactions of the American Fisheries Society 120: 500-508.

Hambright, K.D., R.W. Drenner, S.R. McComas, and N.G. Hairston, Jr. 1991. Gape-limited piscivores, planktivore size refuges, and the trophic cascade hypothesis. Hydrobiologie Archive 121: 389-404.

Hammond, T. 1997. A Bayesian interpretation of target strength data from the Grand Banks. Canadian Journal of Fisheries and Aquatic Sciences 54: 2323-2333.

Hampton, K.E., T.L. Wenke and B.A. Zamrzla. 1988. Movements of adult striped bass tracked in Wilson Reservoir, Kansas. Prairie Naturalist 20: 113-125.

Hansen, M.J., D. Boisclair, S.B. Brandt and S.W. Hewett. 1993. Applications of bioenergetics models to fish ecology and management - where do we go from here. Transactions of the American Fisheries Society 122: 1019-1030.

Hanson, W.D. 1962. Dynamics of the largemouth bass population in Bull Shoals Reservoir, Missouri. Proceedings of the Annual Conference of Southeastern Fish and Wildlife Agencies 16: 398-404.

Hanson, J.M. and W.C. Leggett. 1982. Empirical prediction of fish biomass and yield. Canadian Journal of Fisheries and Aquatic Sciences 43: 1640-1648.

Hanson, P.C., T.B. Johnson, D.E. Schindler and J.F. Kitchell. 1997. Fish bioenergetics 3.0 for Windows. Software Manual, Sea Grant Institute, University of Wisconsin, Madison.

Harrell, R.M. 1988. Catch and release mortality of striped bass caught with artificial lures and baits. Proceedings of the Annual Conference of Southeastern Association of Fish and Wildlife Agencies 41: 70-75.

Harris, F.A., L.M. Ager and E. Hayes. 1979. Comparison of various mark-recapture techniques for estimating abundance of largemouth bass in Barkley Lake, Kentucky. Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies 33: 703-709.

Hart, L.G. 1978. Smith Mountain Lake research study. Virginia Dingell-Johnson Project F-30-R. Virginia Department of Game and Inland Fisheries, Richmond.

Hartig, J.H. and D.J. Jude. 1984. Opportunistic cyclopoid predation on fish larvae. Canadian Journal of Fisheries and Aquatic Sciences 41: 526-532.

Hartig, J.H., D.J. Jude and M.S. Evans. 1982. Cyclopoid predation on Lake Michigan fish larvae. Canadian Journal of Fisheries and Aquatic Sciences 39: 1563-1568.

Hartman, K.J. and F.J. Margraf. 1992. Effects of prey and predator abundances on prey consumption and growth of walleye in western Lake Erie. Transactions of the American Fisheries Society 121: 245-260.

Hartman, K.J and S.B. Brandt. 1995a. Comparative energetics and the development of bioenergetics models for sympatric estuarine piscivores. Canadian Journal of Fisheries and Aquatic Sciences 52: 1647-1666.

Hartman, K.J and S.B. Brandt. 1995b. Predatory demand and impact of striped bass, bluefish, and weakfish in the Chesapeake Bay: applications of bioenergetics models. Canadian Journal of Fisheries and Aquatic Sciences 52: 1667-1687.

Hayne, D.W., G.E. Hall and H.M. Nichols. 1967. An estimation of cove sampling of fish populations in Douglas Reservoir, Tennessee. Reservoir Fishery Resources Symposium. Reservoir Committee, Southern Division American Fisheries Society, Bethesda, Maryland.

Heidinger, R.C. 1993. Stocking for sport fisheries enhancement. Pages 309-333 *in* C.C. Kohler and W.A. Hubert, editors. Inland fisheries management in North America. American Fisheries Society, Bethesda, Maryland.

Henderson, P.A., R.H.A. Holmes and R.N. Bamber. 1988. Size-selective overwintering mortality in the sand smelt, and its role in population regulation. Journal of Fish Biology 33: 221-233.

Hewett, S.J. and B.L. Johnson. 1987. A generalized bioenergetics model of fish growth for microcomputers. University of Wisconsin Sea Grant Institute Publication. WIS-SG-87-245.

Hickman, G.D. and K.W. Hevel. 1975. Comparison of population estimates of largemouth bass in Forrest Lake, Missouri, utilizing a bass tournament and an electroshocker for collection of recaptures. Proceedings of the Annual Conference of the Southeastern Association of Game and Fish Commissions 29: 102-114.

Hightower, J.E., R.J. Gilbert and T.B. Hess. 1982. Shoreline and cove sampling to estimate survival of young largemouth bass in Lake Oconee, Georgia. North American Journal of Fisheries Management 2: 257-261.

Hobson, E.S. 1979. Interactions between piscivores fishes and their prey. Pages 231-242 *in* H. Clepper, editor. Predator-prey systems in fisheries management. Sport Fishing Institute, Washington, DC.

Holling, C.S. 1959. The components of predation as revealed by a study of small-mammal predation of the European pine sawfly. The Canadian Entomologist 91: 293-320.

Huish, M.T. 1957. Food habits of three Centrarchidae in Lake George, Florida. Proceedings of the Southeastern Association of Game and Fish Commissions 11: 293-302.

Isely, J.J. and J.R. Tomasso. 1998. Estimating fish abundance in a large reservoir by mark-recapture. North American Journal of Fisheries Management 18: 269-273.

Ivlev, V.S. 1961. Experimental ecology of the feeding of fishes. Yale University Press, New Haven, Connecticut.

Jenkins, R.M. 1967. The influence of some environmental factors on standing crop and harvest of fish in U.S. reservoirs. Pages 298-321 *in* Reservoir Fishery Resources Symposium. Reservoir Committee, American Fisheries Society, Bethesda, Maryland.

Jenkins, R.M. 1975. Black bass crops and species associations in reservoirs. Pages 114-124 *in* R.H. Stroud and H. Clepper, editors. Black bass biology and management. Sport Fish Institute, Washington, D.C.

Jenkins, R.M. 1982. The morphoedaphic index and reservoir fish production. Transactions of the American Fisheries Society 111: 133-140.

Jenkins, R.M. and D. Morais. 1978. Predator-prey relations in predator-stocking-evaluation reservoirs. Pages 123-134 *in* R.H. Stroud and H. Clepper, editors. Predator-prey systems in fisheries management. Sport Fishing Institute, Washington, DC.

Johnson, T.B. and D.O. Evans. 1996. Temperature constraints on overwinter survival of age-0 white perch. Transactions of the American Fisheries Society 125: 466-471.

Johnson, B.M., R.A. Stein and R.F. Carline. 1988a. Use of a quadrat rotenone technique and bioenergetics modeling to evaluate prey availability to stocked piscivores. Transactions of the American Fisheries Society 117: 127-141.

Johnson, B.M., D.L. Smith and R.F. Carline. 1988b. Habitat preferences, survival, growth, foods, and harvests of walleyes and walleye X sauger hybrids. North American Journal of Fisheries Management 8: 292-304.

Juanes, F. 1994. What determines prey size selectivity in piscivorous fishes? Pages 79-100 *in* D.J. Stouder, K.L. Fresh, and R.J. Feller, editors. Theory and application in fish feeding ecology. Belle W. Baruch Library in Marine Science Number 18. University of South Carolina Press.

Jude, D.J. and F.J. Tesar. 1985. Recent changes in the inshore forage fish of Lake Michigan. Canadian Journal of Fisheries and Aquatic Sciences 42: 1154-1157.

Kashuba, S.A. and W.J. Matthews. 1984. Physical condition of larval shad during spring-summer in a southwestern reservoir. Transactions of the American Fisheries Society 113: 119-204.

Keast, A. and J. Eadie. 1985. Growth depensation in year-0 largemouth bass: the influence of diet. Transactions of the American Fisheries Society 114: 204-213.

Keith, W.E. 1986. A review of introduction and maintenance stocking in reservoir fisheries management. Pages 144-148 *in* G.E. Hall and M.J. Van Den Avyle, editors. Reservoir fisheries management: strategies for the 80's. Reservoir Committee, Southern Division American Fisheries Society, Bethesda, Maryland.

Kelso, W.E. and J.J. Ney. 1983. Nocturnal foraging by alewife in reservoir coves. Proceedings of the Southeastern Association of Fish and Wildlife Agencies 36: 125-134.

Kerr, S.R. 1980. Niche theory in fisheries ecology. Transactions of the American Fisheries Society 109: 254-257.

Kimura, K.K. and N.A. Lemberg. 1981. Variability of line intercept density estimates (a simulation study of the variance of hydroacoustic biomass estimates). Canadian Journal of Fisheries and Aquatic Sciences 38: 1141-1152.

Kirk, J.P. and W.D. Davies. 1987. Competitive influences of gizzard shad on largemouth bass and bluegill in small impoundments. Proceedings of the Annual Conference of Southeastern Associations of Fish and Wildlife Agencies 39: 116-124.

Kirk, J.P., W.D. Davies and K. Park. 1986. Response of some members of the fish community to gizzard shad removal from Chambers County Public Fishing Lake, Alabama. North American Journal of Fisheries Management 6: 252-255.

Kitchell, J.F., D.J. Stewart and D. Weininger. 1977. Applications of a bioenergetics model to yellow perch and walleye. Journal of the Fisheries Research Board of Canada 34: 1922-1935.

Kohler, C.C. and J.J. Ney. 1980. Piscivory in a land-locked alewife population. Canadian Journal of Fisheries and Aquatic Sciences 37: 1314-1317.

Kohler, C.C. and J.J. Ney. 1981. Suitability of alewife as a pelagic forage fish for southeastern reservoirs. Proceedings of the Annual Conference of Southeastern Fish and Wildlife Agencies 34: 272-286.

Kohler, C.C. and J.G. Stanley. 1984. A suggested protocol for evaluating proposed exotic fish introductions in the United States. Pages 387-406 *in* W.R. Courtenay, Jr. and J.R. Stauffer, Jr., editors. Distribution, biology, and management of exotic fishes. Johns Hopkins University Press, Baltimore, Maryland.

Kohler, C.C., J.J. Ney and W.E. Kelso. 1986. Filling the void: establishment of a pelagic fishery and its consequences to littoral fishes in a Virginia mainstream reservoir. Pages 166-177 *in* G.E. Hall and M.J. Van Den Avyle, editors. Reservoir fisheries management: strategies for the 80's. American Fisheries Society, Southern Division, Reservoir Committee, Bethesda, Maryland.

Krueger, C.C., D.L. Perkins, E.L. Mills and J.E. Marsden. 1995. Predation by alewife on lake trout fry in Lake Ontario: role of an exotic species in preventing restoration of a native species. Journal of Great Lakes Research 21 (Supplement 1): 458-469.

LaBar, G.W. 1993. Use of bioenergetics models to predict the effects of increased lake trout production on rainbow smelt following sea lamprey control. Transactions of the American Fisheries Society 122: 942-950.

Lamprecht, S.D. and W.L. Shelton. 1988. Spatial and temporal movements of striped bass in the upper Alabama River. Proceedings of the Annual Conference of Southeastern Fish and Wildlife Agencies 40: 266-274.

Lane, E.D., M.C.S. Kingsley and D.E. Thornton. 1979. Daily feeding and food conversion efficiency of the diamond turbot: an analysis based on field data. Transactions of the American Fisheries Society 108: 530-535.

Langsdale, J.R.M. 1993. Developmental changes in the opacity of larval herring and their implications for vulnerability to predation. Journal of the Marine Biological Association of the United Kingdom 73: 225-232.

LaRoche, A.L. III. 1981. Region II reservoir investigations, Smith Mountain Lake. Virginia Department of Game and Inland Fisheries, Dingell-Johnson Project F-39.

LaRoche, A.L. III and M. Duval. 1993. 1992 Smith Mountain Lake Creel Survey. Virginia Department of Game and Inland Fisheries, Lynchburg.

Lawrence, J.M. 1958. Estimated sizes of various forage fishes largemouth bass can swallow. Proceedings of the Annual Conference of Southeastern Game and Fish Commissions 11: 220-225.

Levy, D.A. 1990. Sensory mechanism and selective advantage for diel vertical migration behavior in juvenile sockeye salmon. Canadian Journal of Fisheries and Aquatic Sciences 47: 1796-1802.

Love, R.H. 1977. Target strength of an individual fish at any aspect. Journal of the Acoustic Society of America 62: 1397-1403.

Luecke, C.W. and W.A. Wurstbaugh. 1993. Effects of moonlight and daylight on hydroacoustic estimates of pelagic fish abundance. Transactions of the American Fisheries Society 122: 112-120.

Lyons, J. and J.J. Magnuson. 1987. Effects of walleye predation on the population dynamics of small littoral-zone fishes in a northern Wisconsin lake. Transactions of the American Fisheries Society 116: 29-39.

MacLennan, D.N. 1990. Acoustical measurement of fish abundance. Journal of the Acoustical Society of America 87: 1-15.

MacLennan, D.N. and E.J. Simmonds. 1992. Fisheries acoustics. Chapman and Hall, London.

Madenjian, C.P., B.M. Johnson and S.R. Carpenter. 1991. Stocking strategies for fingerling walleyes: an individual-based model approach. Ecological Applications 1: 280-288.

Magnuson, J.J., L.B. Crowder and P.A. Medvick. 1979. Temperature as an ecological resource. American Zoologist 19: 331-343.

Major, P.F. 1978. Predator-prey interactions in two schooling fishes. Animal Behavior 26: 760-777.

Maloney, J.E. and F.H. Johnson. 1957. Life histories and inter-relationships of walleye and yellow perch, especially during their first summer, in two Minnesota lakes. Transactions of the American Fisheries Society 85: 191-202.

Manooch, C.S., III. 1973. Food habits of yearling and adult striped bass from Albermarle Sound, North Carolina. Chesapeake Scientist 14: 73-86.

Mason, D.M. and S.B. Brandt. 1996. Effect of alewife predation on survival of larval yellow perch in an embayment of Lake Ontario. Canadian Journal of Fisheries and Aquatic Sciences 53: 1609-1617.

Masuda, R. and K. Tsukamoto. 1998. The ontogeny of schooling behavior in the striped jack. Journal of Fish Biology 52: 483-493.

Matthews, W.J. 1984. Influence of turbid inflows on vertical distribution of larval shad and freshwater drum. Transactions of the American Fisheries Society 113: 192-198.

Matthews, W.J. and L.G. Hill. 1982. Preliminary monitoring of interactions among striped bass, forage fish species, and zooplankton in Lake Texoma, Oklahoma-Texas. US Department of the Interior, Fish and Wildlife Service Project MON-RA-81-106.

Matthews, W.J., L.G. Hill and S.M. Schellhaass. 1985. Depth distribution of striped bass and other fish in Lake Texoma during summer stratification. Transactions of the American Fisheries Society 114: 84-91.

Matthews, W.J., L.G. Hill, D.R. Edds, J.J. Hoover and T.G. Heger. 1988. Trophic ecology of striped bass in a freshwater reservoir. Journal of Fish Biology 33: 273-288.

Matthews, W.J., L.G. Hill, D.R. Edds and F.P. Gelwick. 1989. Influences of water quality and season on habitat use by striped bass in a large southwestern reservoir. Transactions of the American Fisheries Society 118: 243-250.

McClatchie, S., J. Alsop and R.F. Coombs. 1996. A re-evaluation of relationships between fish size, acoustic frequency, and target strength. ICES Journal of Marine Science 53: 780-791.

McDaniel, C.K., L.E. Snyder and L.L. Connor. 1993. Impacts of thermal stress on the condition of striped bass. Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies 45: 361-369.

Michaelson, D.M. 1996. The impacts of stocking stress and largemouth bass predation on the survivorship of stocked juvenile striped bass in Smith Mountain Lake, Virginia. M.S. Thesis. Virginia Polytechnic Institute and State University, Blacksburg.

Michaletz, P.H., J. Boxrucker, S. Hale and J.R. Jackson. 1995. Comparison of four trawls for sampling juvenile shad. North American Journal of Fisheries Management 15: 918-923.

Michaletz, P.H. 1997a. Factors affecting abundance, growth, and survival of age-0 gizzard shad. Transactions of the American Fisheries Society 126: 84-100.

Michaletz, P.H. 1997b. Influence of abundance and size of age-0 gizzard shad on predator diets, diet overlap, and growth. Transactions of the American Fisheries Society 126: 101-111.

Michaletz, P.H. 1998a. Population characteristics of gizzard shad in Missouri reservoirs and their relation to reservoir productivity, mean depth, and sport fish growth. North American Journal of Fisheries Management 18: 114-123.

Michaletz, P.H. 1998b. Effects on sport fish growth of spatial and temporal variation in age-0 gizzard shad availability. North American Journal of Fisheries Management 18: 616-624.

Minckley, W.L. and J.E. Deacon. 1959. Biology of the flathead catfish in Kansas. Transactions of the American Fisheries Society 88: 344-355.

Minton, J.W. and R.B. McLean. 1982. Measurement of growth and consumption of sauger: implications for fish energetics studies. Canadian Journal of Fisheries and Aquatic Sciences 39: 1396-1403.

Miranda, L.E. and W.D. Hubbard. 1994. Winter survival of age-0 largemouth bass relative to size, predators, and shelter. North American Journal of Fisheries Management 14: 790-796.

Miranda, L.E., M.T. Driscoll and S.W. Raborn. 1998. Competitive interactions between striped bass and other freshwater predators. Mississippi Cooperative Fish and Wildlife Research Unit Final Report to the Tennessee Wildlife Resources Agency. Mississippi State, Mississippi.

Mittelbach, G.G. 1981. Foraging efficiency and body size: a study of optimal diet and habitat use by bluegills. Ecology 62: 1370-1386.

Moczygemba, J.H. and B.T. Hysmith. 1994. Evaluation of reduced striped bass bag limit, Lake Texoma, Texas and Oklahoma. Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies 48: 433-440.

Moore, C.M. 1988. Food habits, population dynamics, and bioenergetics of four predatory fish species in Smith Mountain Lake, Virginia. Doctoral Dissertation. Virginia Polytechnic Institute and State University. Blacksburg, Virginia.

Moore, C.M. R.J. Neves, J.J. Ney and D.K. Whitehurst. 1985. Utilization of alewife and gizzard shad by striped bass in Smith Mountain Lake, Virginia. Proceedings of the Annual Conference of the Southeastern Association of Fish and Wildlife Agencies 39: 108-115.

Moore, C.M., R.J. Neves and J.J. Ney. 1991. Survival and abundance of stocked striped bass in Smith Mountain Lake, Virginia. North American Journal of Fisheries Management 11: 393-399.

Moore, C.M., J.J. Ney and R.J. Neves. 1993. Parameter valuation of a bioenergetics model for striped bass. Virginia Sea Grant College Program Publication Number VSG-93-02, Blacksburg, Virginia.

Morris, D.J. and B.J. Follis. 1978. Effects of striped bass predation upon shad in Lake E.V. Spence, Texas. Proceedings of the Annual Conference Southeastern Association of Fish and Wildlife Agencies 32: 697-702.

Moss, J.L. 1985. Summer selection of thermal refuges by striped bass in Alabama reservoirs and tailwaters. Transactions of the American Fisheries Society 114: 77-83.

Muoneke, M.I., C.C. Henry and O.E. Maughan. 1992. Population structure and food habits of white crappie in a turbid Oklahoma reservoir. Journal of Fish Biology 41: 647-654.

Murphy, B.R., D.W. Willis, and T.A. Springer. 1991. The relative weight index in fisheries management: status and needs. Fisheries 16: 30-38.

Muth, K.M. and D.R. Wolfert. 1986. Changes in growth and maturity of walleye associated with stock rehabilitation in western Lake Erie, 1964-1983. North American Journal of Fisheries Management 6: 168-175.

Negus, M.T. 1995. Bioenergetics modeling as a salmonine management tool applied to Minnesota waters of Lake Superior. North American Journal of Fisheries Management 15: 60-78.

Neill, S.R.J. and J.M. Cullen. 1974. Experiments on whether schooling by their prey affects the hunting behavior of cephalopods and fish predators. Journal of Zoology 172: 549-569.

Nelson, K.L. 1998. Catch and release mortality of striped bass in the Roanoke River, North Carolina. North American Journal of Fisheries Management 18: 25-30.

Nero, R.W., J.J. Magnuson, S.B. Brandt, T.K. Stanton and J.M. Jech. 1990. Finescale biological patchiness of 70 kHz acoustic scattering at the edge of the Gulf Stream-Echofront 85. Deep Sea Research 37: 999-1016.

Ney, J.J. 1981. Evolution of forage-fish management in lakes and reservoirs. Transactions of the American Fisheries Society 110: 725-728.

Ney, J.J. 1990. Trophic economics in fisheries: assessment of demand-supply relationships between predators and prey. Reviews in Aquatic Sciences 2: 55-81.

Ney, J.J. 1993. Bioenergetics modeling today: growing pains on the cutting edge. Transactions of the American Fisheries Society 122: 736-748.

Ney, J.J. 1996. Oligotrophication and its discontents: effects of reduced nutrient loading on reservoir fisheries. American Fisheries Society Symposium 16: 285-295.

Ney, J.J., C.C. Kohler and A.A. Nigro. 1982. Landlocked alewife in Claytor Lake, Virginia. Evaluation as a forage species for inland waters. Management Report 4, Department of Fisheries and Wildlife Sciences, Virginia Polytechnic and State University, Blacksburg.

Ney, J.J. and D.J. Orth. 1986. Coping with future shock: matching predator stocking programs to prey abundance. Pages 81-92 *in* R.H. Stroud, editor. Fish culture in fisheries management. American Fisheries Society, Bethesda, Maryland.

Ney, J.J., C.M. Moore, R.J. Neves, M.S. Tisa and J.J. Yurk. 1988. The Smith Mountain Lake fishery: factors affecting major sport and forage fish populations. Department of Fisheries and Wildlife Sciences, Virginia Polytechnic and State University, Blacksburg.

Ney, J.J., C.M. Moore, M.S. Tisa, J.J. Yurk and R.J. Neves. 1990. Factors affecting the sport fishery in a multiple-use Virginia reservoir. Lake and Reservoir Management 6: 21-32.

Nielsen, L.A. 1980. Effect of walleye predation on juvenile mortality and recruitment of yellow perch in Oneida Lake, New York. Canadian Journal of Fisheries and Aquatic Sciences 37: 11-19.

Nigro, A.A. and J.J. Ney. 1982. Reproduction and early life history accommodations of landlocked alewife to a southern range extension. Transactions of the American Fisheries Society 111: 559-569.

Noble, R.L. 1981. Management of forage fishes in impoundments of the southern United States. Transactions of the American Fisheries Society 110: 738-750.

O'Gorman, R. and C.P. Schneider. 1986. Dynamics of alewife in Lake Ontario following a mass mortality. Transactions of the American Fisheries Society 115: 1-14.

Obenschain, N.A. and D.M. McLeod. 1981. Phosphorus control in the Smith Mountain Lake drainage basin. Virginia State Water Control Board Report, Roanoke.

Ogelsby, R.T. 1977. Relationships of fish yield to lake phytoplankton standing crop, production and morphological factors. Journal of the Fisheries Research Board of Canada 34: 2271-2274.

Olson, M.H. 1996. Ontogenetic niche shifts in largemouth bass: variability and consequences for first-year growth. Ecology 77: 179-190.

Ott, W.R. 1995. Environmental statistics and data analysis. Lewis Publishers, Boca Raton, Florida.

Partridge, B.L. 1982. The structure and function of fish schools. Scientific American 246: 114-123.

Pauly, D. 1986. A simple method for estimating the food consumption of fish populations from growth data and food conversion experiments. Fisheries Bulletin 84: 827-839.

Paulson, L.J. 1994. Effects of water diversions in the Virgin River on the sport fisheries in the Overton arm of Lake Mead. National Park Service Report, Boulder City, Nevada.

Penczak, T.E., E. Kusto, D. Kryzanowska and E. Suszycka. 1984. Food consumption and energy transformation by fish populations in two small lowland rivers in Poland. Hydrobiologia 108: 135-144.

Penczak, T.E. 1985. A method of estimating total food consumed by fish populations. Hydrobiologia 123: 241-244.

Peterson, S. and B. Richmond. 1994. STELLA II, technical documentation. High Performance Systems, Hanover, New Hampshire.

Pitcher, T.J., A.E. Magurran and J.I. Edwards. 1985. Schooling mackerel and herring choose neighbors of similar size. Marine Biology 86: 319-322.

Ploskey, G.R. and R.M. Jenkins. 1982. Biomass model of reservoir fish and fish-food interactions, with implications for management. North American Journal of Fisheries Management 2: 105-121.

Poarch, S.M. 1989. A biotelemetry study of striped bass in Old Hickory Reservoir, Cumberland River, Tennessee. M.S. Thesis. Tennessee Technological University, Cookeville.

Post, J.R. and A.B. Prankevicius. 1987. Size-selective mortality in young-of-the-year yellow perch: laboratory, in situ enclosure, and field experiments. Canadian Journal of Fisheries and Aquatic Sciences 44: 1840-1847.

Prince, E.D. 1976. The biological effects of artificial reefs in Smith Mountain Lake, Virginia. Doctoral Dissertation. Virginia Polytechnic Institute and State University, Blacksburg.

Pritchard, D.L., O.D. May, Jr. and L. Rider. 1978. Stocking of predators in the predator-stocking-evaluation reservoirs. Proceedings of the Annual Conference Southeastern Association of Fish and Wildlife Agencies 30: 108-113.

Prus, T. 1975. Measurements of caloric value using the Phillipson microbomb calorimeter. Pages 149-160 *in* W. Grodzinski, editor. IBP handbook 24. Blackwell Scientific Publications, Oxford, England.

Pyke, G.H., H.R. Pullman and E.L. Charnov. 1977. Optimal foraging: a selective review of theory and tests. Quarterly Review of Biology 52: 137-154.

Radonski, G.C. and L.C. Miller. 1986. Keynote address - fish culture is a tool, not a panacea. Pages 7-13 *in* R.H. Stroud, editor. Fish culture in fisheries management. American Fisheries Society, Bethesda, Maryland.

Radovich, J. 1979. Managing pelagic schooling prey species. Pages 365-376 *in* R.H. Stroud and H. Clepper, editors. Predator-prey systems in fisheries management. Sport Fishing Institute, Washington, DC.

Rainwater, W.C. and A. Houser. 1982. Species composition and biomass of fish in selected coves in Beaver Lake, Arkansas, during the first 18 years of impoundment (1963-1980). North American Journal of Fisheries Management 4: 316-325.

Redfield, G.W. and C.R. Goldman. 1980. Diel vertical migration by males, females, copepodids, and nauplii in a limnetic population of *Diaptomus*. Hydrobiologia 74: 241-248.

Rice, J.A., J.E. Breck, S.M. Bartell and J.F. Kitchell. 1983. Evaluating the constraints of temperature, activity, and consumption on growth of largemouth bass. Environmental Biology of Fishes 9: 263-275.

Rice, J.A. and P.A. Cochran. 1984. Independent evaluation of a bioenergetics model for largemouth bass. Ecology 65: 732-739.

Rottiers, D.V. and R.M. Tucker. 1982. Proximate composition and caloric content of eight Lake Michigan fishes. U.S. Fish and Wildlife Service Technical Paper 108.

Rudstam, L.G., F.P. Binkowski and M.A. Miller. 1994. A bioenergetics model for analysis of food consumption patterns of bloater in Lake Michigan. Transactions of the American Fisheries Society 123: 344-357.

Rudstam, L.G., P.E. Peppard, T.W. Fratt, R.E. Bruesewitz, D.W. Coble, F.A. Copes and J.F. Kitchell. 1995. Prey consumption by the burbot population in Green Bay, Lake Michigan, based on a bioenergetics model. Canadian Journal of Fisheries and Aquatic Sciences 52: 1074-1082.

Sammons, S.M., P.W. Bettoli and F.C. Fiss. 1998. Effect of threadfin shad density on production of threadfin shad and gizzard shad larvae in a Tennessee reservoir. Environmental Biology of Fishes 53: 65-73.

Saul, B.M. 1981. Food habits and growth of young-of-the-year striped bass in Cherokee Reservoir, Tennessee. M.S. Thesis. University of Tennessee, Knoxville.

Savino, J.F. and R.A. Stein. 1982. Predator-prey interaction between largemouth bass and bluegills as influenced by simulated, submersed vegetation. Transactions of the American Fisheries Society 111: 255-266.

Schaich, B.A. and C.C. Coutant. 1980. A biotelemetry study of spring and summer habitat selection by striped bass in Cherokee Reservoir, Tennessee, 1978. Oak Ridge National Laboratory, ORNL/TM-7127.

Schramm, H.L. and A.V. Zale. 1985. Effects of cover and prey sizes on preferences of juvenile largemouth bass for blue tilapias and bluegills in tanks. Transactions of the American Fisheries Society 114: 725-731.

Scott, W.B. and E.J. Crossman. 1973. Freshwater fishes of Canada. Fisheries Research Board of Canada, Bulletin 184, Ottowa.

Shaw, E. 1978. Schooling fishes. Scientific American 66: 165-175.

Shelton, W.L., W.D. Davies, T.A. King and T.J. Timmons. 1979. Variation in the growth of the initial year class of largemouth bass in West Point Reservoir, Alabama and Georgia. Transactions of the American Fisheries Society 108: 142-149.

Shuter, B.J., J.A. MacLean, F.E.J. Fry and H.A. Regier. 1980. Stochastic simulation of temperature effects on first-year survival of smallmouth bass. Transactions of the American Fisheries Society 109: 1-34.

Siler, J.R. 1986. Comparison of rotenone and trawling methodology for estimating threadfin shad populations. Pages 73-78 *in* G.E. Hall and M.J. Van Den Avyle, editors. Reservoir fisheries management: strategies for the 80's. Reservoir Committee, Southern Division American Fisheries Society, Bethesda, Maryland.

Siler, J.R., W.J. Foris and M.C. McInerny. 1986. Spatial heterogeneity in fish parameters within a reservoir. Pages 122-136 *in* G.E. Hall and M.J. Van Den Avyle, editors. Reservoir Fisheries Management: Strategies for the 80's. Reservoir Committee, Southern Division American Fisheries Society, Bethesda, Maryland.

Simmons, G.M. Jr. and S.E. Neff. 1969. The effect of pumpback storage reservoir operation on biological productivity and water quality. Virginia Water Resources Research Center Bulletin 21.

Sissenwine, M.P., M.J. Fogerty and W.J. Overholtz. 1988. Some fisheries management implications of recruitment variability. Pages 129-152 *in* J.A. Gulland, editor. Fish population dynamics. Wiley, Chichester, United Kingdom.

Smith, P. and J. Kauffman. 1982. Age and growth of Virginia's freshwater fishes. Virginia Department of Game and Inland Fisheries, Richmond.

Smith, K.D. 1993. Vegetation-open water interface and the predator-prey interaction between largemouth bass and bluegills. Doctoral Dissertation. University of Michigan, Ann Arbor.

Soofiani, N.M. and A.D. Hawkins. 1985. Field studies of energy budgets. Pages 283-307 *in* P. Tyler and P. Calow, editors. Fish energetics: new perspectives. John Hopkins University Press, Baltimore, Maryland.

Soule, M., M. Baranage and I. Hampton. 1995. Evidence of bias in estimates of target strength obtained with a split beam echosounder. ICES Journal of Marine Science 52: 139-144.

Stein, R.A. 1979. Behavioral responses of prey to fish predators. Pages 343-354 *in* Stroud, R.H. and H.E. Clepper, editors. Predator-prey systems in fisheries management. Sport Fishing Institute, Washington, DC.

Stein, R.A., D.R. DeVries and J.M. Dettmers. 1995. Food web regulation by a planktivore: exploring the generality of the trophic cascade hypothesis. Canadian Journal of Fisheries and Aquatic Sciences 52: 2518-2526.

Stevens, R.E. 1958. The striped bass of the Santee-Cooper Reservoir. Proceedings of the Annual Conference of the Southeastern Association of Game and Fish Commissions 11: 253-264.

Stevens, R.E. 1960. The white and channel catfishes of the Santee-Cooper Reservoir and tailrace sanctuary. Proceedings of the Annual Conference of the Southeastern Association of Game and Fish Commissions 13: 203-219.

Stevens, R.E. 1979. Comments in the fourth session discussion. Page 231 *in* Stroud, R.H. and H.E. Clepper, editors. Predator-prey systems in fisheries management. Sport Fishing Institute, Washington, DC.

Stewart, D.J. and F.P. Binkowski. 1986. Dynamics of consumption and food conversion by Lake Michigan alewife: an energetics-modeling synthesis. Transactions of the American Fisheries Society 115: 643-661.

Stewart, D.J. and M. Ibarra. 1991. Predation and production by salmonine fishes in Lake Michigan, 1978-88. Canadian Journal of Fisheries and Aquatic Sciences 48: 909-922.

Stewart, D.J., J.F. Kitchell and L.C. Crowder. 1981. Forage fishes and their salmonid predators in Lake Michigan. Transactions of the American Fisheries Society 110: 751-763.

Stewart, D.J., D. Weininger, D.V. Rottiers and T.A. Edsall. 1983. An energetics model for lake trout: application to the Lake Michigan population. Canadian Journal of Fisheries and Aquatic Sciences 40: 681-698.

Storck, T.W. 1986. Importance of gizzard shad in the diet of largemouth bass in Lake Shelbyville, Illinois. Transactions of the American Fisheries Society 115: 21-27.

Summerfelt, R.C. 1986. Summarization of the symposium. Pages 314-327 *in* G.E. Hall and M.J. Van Den Avyle, editors. Reservoir fisheries management: strategies for the 80's. Reservoir Committee, Southern Division American Fisheries Society, Bethesda, Maryland.

Summers, G.L. and J.R. Axon. 1980. History and organization of the Barkley Lake rotenone study. Proceedings of the Annual Conference Southeastern Association of Fish and Wildlife Agencies 33: 673-679.

Summers, G.L. 1982. Texoma striped bass biotelemetry. Oklahoma Department of Wildlife Conservation, Federal Aid in Sport Fish Restoration, Project F-29-R, Final Report, Oklahoma City.

Sutton, T.M. 1997. Early life history dynamics of a stocked, landlocked striped bass population and assessment of strategies for improving fingerling striped bass stocking success in Smith Mountain Lake, Virginia. Doctoral Dissertation. Virginia Polytechnic Institute and State University, Blacksburg.

Swingle, H.A. 1950. Relationships and dynamics of balanced and unbalanced fish populations. Bulletin 274, Alabama Agricultural Experiment Station, Auburn University.

Swingle, H.A. 1970. Production of the threadfin shad. Proceedings of the Annual Conference of the Southeastern Association of Game and Fish Commissioners 23: 407-421.

Theodorakis, C.W. 1989. Size segregation and the effects of oddity on predation risk in minnow schools. Animal Behavior 38: 496-502.

Thorne, R.E. 1983. Hydroacoustics. Pages 239-259 *in* L.A. Nielson and D.L. Johnson, editors. Fisheries techniques. American Fisheries Society, Bethesda, Maryland.

Timmons, T.J., W.L. Shelton and W.D. Davies. 1980. Differential growth of largemouth bass in West Point Reservoir, Alabama-Georgia. Transactions of the American Fisheries Society 109: 176-186.

Tisa, M.S. 1988. Compatibility and complementarity of alewife and gizzard shad as forage fish in Smith Mountain Lake, Virginia. Doctoral Dissertation. Virginia Polytechnic Institute and State University, Blacksburg.

Tisa, M.S. and J.J. Ney. 1991. Compatibility of alewife and gizzard shad as reservoir forage fish. Transactions of the American Fisheries Society 120: 157-165.

Tomcko, C.M., R.A. Stein and R.F. Carline. 1984. Predation by tiger muskellunge on bluegill: effects of predator experience, vegetation, and prey density. Transactions of the American Fisheries Society 113: 588-594.

Townsend, C.R. and I.J. Winfield. 1985. The application of optimal foraging theory to feeding behavior in fish. Pages 67-98 *in* P. Tyler and P. Calow, editors. Fish energetics: new perspectives. Johns Hopkins University Press, Baltimore, Maryland.

Unger, P.A. et al. 1987. Factors affecting acoustic assessments of fish stocks in small lakes: influence of seasonal and diel variations in distributions of fish and *Chaoborus*. Pages 112-124 *in* W.A. Karp, editor. Developments in fisheries acoustics. International Council for the Exploration of the Sea, Publication 189, Copenhagen, Denmark.

Ursin, E. 1979. Principles of growth in fishes. Symposia of the Zoological Society of London 44: 63-87.

Ursin, E. 1982. Multispecies fish stock and yield assessment in ICES. Special Publication of the Canadian Journal of Fisheries and Aquatic Sciences 59: 39-47.

Van Den Avyle, M.J. and B.J. Higginbotham. 1980. Growth, survival, and distribution of striped bass stocked into Watts Bar Reservoir, Tennessee. Proceedings of the Annual Conference Southeastern Association of Fish and Wildlife Agencies 33: 361-370.

Van Den Avyle, M.J. and J.E. Roussel. 1980. Evaluation of a simple method for removing food items from live black bass. Progressive Fish Culturist 42: 222-223.

Van Den Avyle, M.J., G.R. Ploskey and P.W. Bettoli. 1995a. Evaluation of gill-net sampling for estimating abundance and length frequency of reservoir shad populations. North American Journal of Fisheries Management 15: 898-917.

Van Den Avyle, M.J., J. Boxrucker, P. Michaletz, B. Vondracek and G.R. Ploskey. 1995b. Comparison of catch rate, length distribution, and precision of six gears used to sample reservoir shad populations. North American Journal of Fisheries Management 15: 940-955.

Vondracek, B. and D.J. Degan. 1995. Among and within-transect variability in estimates of shad abundance made with hydroacoustics. North American Journal of Fisheries Management 15: 933-939.

Waddle, H.R., C.C. Coutant and J.L. Wilson. 1980. Summer habitat selection by striped bass in Cherokee Reservoir, Tennessee, 1977. Oak Ridge National Laboratory, ORNL/TM-6927, Oak Ridge, Tennessee, USA.

Wahl, D.H. and R.A. Stein. 1988. Selective predation by three esocids: the role of prey behavior and morphology. Transactions of the American Fisheries Society 117: 142-151.

Wahl, D.H. and R.A. Stein. 1991. Food consumption and growth of three esocids: field tests of a bioenergetic model. Transactions of the American Fisheries Society 120: 230-246.

Ware, F.J. 1970. Some early life history of Florida's inland striped bass. Proceedings of the Annual Conference of Southeastern Associations of Game and Fisheries Commissions 24: 439-447.

Waters, T.F. 1992. Annual production, production/biomass ratio, and the ecotrophic coefficient for management of trout in streams. North American Journal of Fisheries Management 12: 34-39.

Waters, T.F., M.T. Doherty and C.C. Krueger. 1990. Annual production and production:biomass ratios for three species of stream trout in Lake Superior tributaries. Transactions of the American Fisheries Society 119: 470-474.

Waters, T.F., J.P. Kaehler, T.J. Polomis and T.J. Kwak. 1993. Production dynamics of smallmouth bass in a small Minnesota stream. Transactions of the American Fisheries Society 122: 588-598.

Webb, P.W. 1978. Partitioning of energy into metabolism and growth. Pages 184-214 *in* S.D. Gerking, editor. Ecology of freshwater fish production. John Wiley and Sons, New York.

Webb, P.W. 1984. Body and fin form and strike tactics of four teleost predators attacking fathead minnow prey. Canadian Journal of Fisheries and Aquatic Sciences 41: 157-165.

Wege, G.J. and R.O. Anderson. 1978. Relative weight (Wr): a new index of condition for largemouth bass. Pages 79-91 *in* G.D. Novinger and J.G. Dillard, editors. New approaches to the management of small impoundments. American Fisheries Society, North Central Division, Special Publication 5, Bethesda, Maryland.

Welker, M.T., C.L. Pierce and D.H. Wahl. 1994. Growth and survival of larval fishes: roles of competition and zooplankton abundance. Transactions of the American Fisheries Society 123: 703-717.

Whitehurst, D.K. 1984. Smith Mountain Lake, Annual Report, 1 April 1983 - 31 March 1984. Virginia Department of Game and Inland Fisheries, Lynchburg.

Whitledge, G.W. and R.S. Hayward. 1997. Laboratory evaluation of a bioenergetics model for largemouth bass at two temperatures and feeding levels. Transactions of the American Fisheries Society 126: 1030-1035.

Wiley, M.J., R.W. Gorden, S.W. Waite and T. Powless. 1984. The relationship between aquatic macrophytes and sportfish production in Illinois ponds: a simple model. North American Journal of Fisheries Management 4: 111-119.

Wilkerson, M.L. and W.L. Fisher. 1997. Striped bass distribution, movements, and site fidelity in Robert S. Kerr Reservoir, Oklahoma. North American Journal of Fisheries Management 17: 677-686.

Willis, D.W. 1987. Reproduction and recruitment of gizzard shad in Kansas reservoirs. North American Journal of Fisheries Management 7: 71-80.

Winberg, G.G. 1956. Rate of metabolism and food requirements of fishes. Byelorussian University, Minsk. (Translated from Russian by the Fisheries Research Board of Canada. Translation Series 194, 1960).

Wooley, C.M. and E.J. Crateau. 1983. Biology, population estimates, and movement of native and introduced striped bass, Apalachicola River, Florida. North American Journal of Fisheries Management 3: 383-394.

Yeager, D.M. and M.J. Van Den Avyle. 1978. Rates of angler exploitation of largemouth, smallmouth, and spotted bass in Center Hill Reservoir, Tennessee. Proceedings of the Annual Conference of the Southeastern Association of Game and Fish Commissions 31: 449-458.

Yurk, J.J. and J.J. Ney. 1989. Phosphorus-fish community biomass relationships in southern Appalachian reservoirs: can lakes be too clean for fish? Lake and Reservoir Management 5: 83-90.

Zale, A.V., J.D. Wiechman, R.L. Lochmiller and J. Burroughs. 1990. Limnological conditions associated with summer mortality of striped bass in Keystone Reservoir, Oklahoma. Transactions of the American Fisheries Society 119: 72-76.

APPENDICES

Figure A.1. Time series of citation striped bass (> 9.1 kg) harvested by anglers in Smith Mountain Lake. The vertical line indicates the year when a four dollar citation fee was initiated by the Virginia Department of Game and Inland Fisheries (1995).

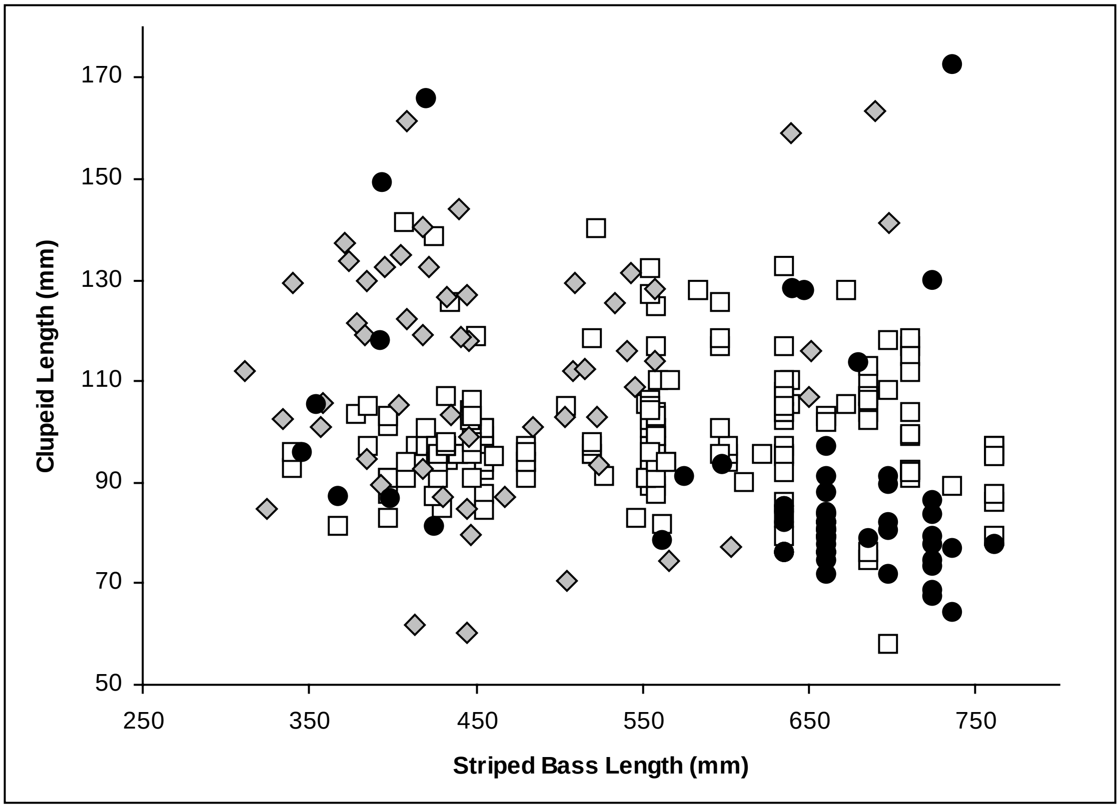

Figure A.2. Ranges of clupeid prey consumed by striped bass in Smith Mountain Lake. Striped bass were collected in 1995 through 1998 by gillnetting and angling. Open squares represent ingested alewife, filled circles are gizzard shad, and grey diamonds are unidentified clupeids.

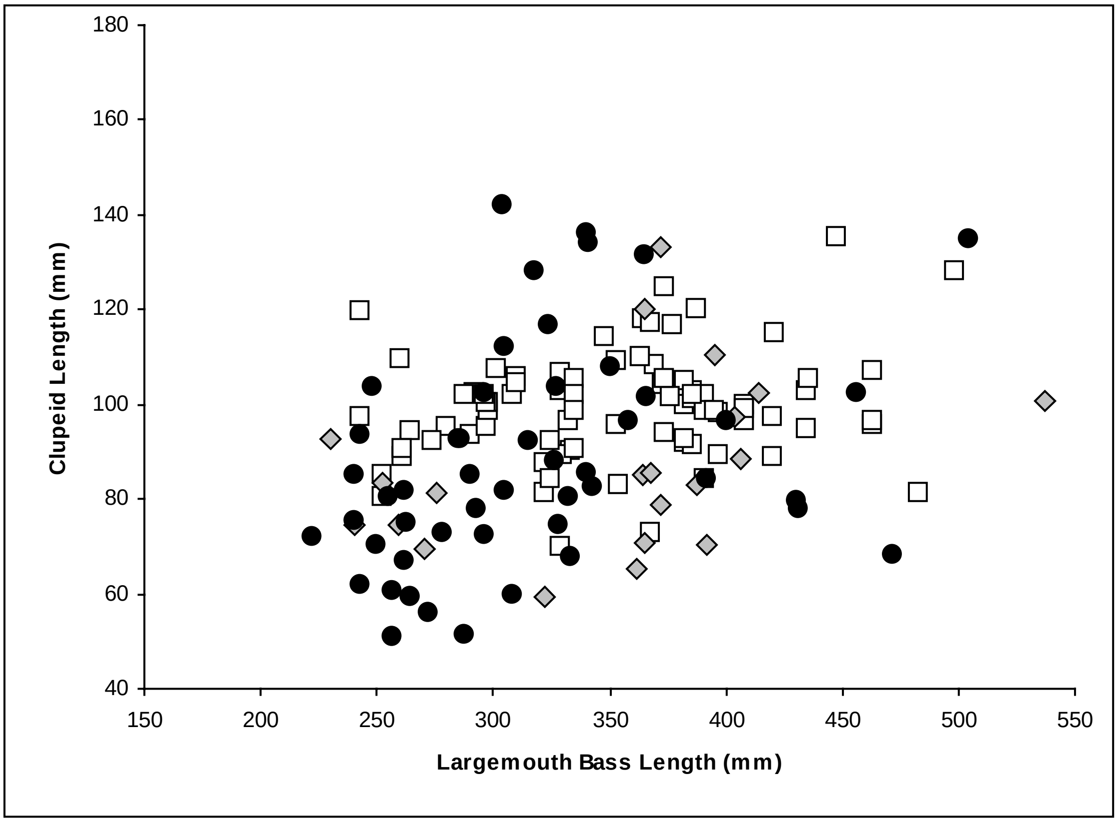

Figure A.3. Ranges of clupeid prey consumed by largemouth bass in Smith Mountain Lake. Largemouth bass were collected in 1995 through 1997 by shoreline electrofishing. Open squares represent ingested alewife, filled circles are gizzard shad, and grey diamonds are unidentified clupeids.

Table A.1. Annual estimates of standing stock (kg/ha) in littoral coves sampled using rotenone application from 1990-1997 by the Virginia Department of Game and Inland Fisheries. SEM is the standard error of the mean.

Species	1990	1991	1992	1993	1994	1995	1996	1997	Mean	SEM
Largemouth Bass	13.3	14.9	16.8	14.3	25.1	12.6	21.7	13.3	16.5	1.5
Smallmouth Bass	0.1	1.5	0.2	0.2	0.2	0.1	0.7	0.3	0.4	0.2
Black Crappie	2.8	6.4	7.5	8.7	6.5	33.7	13.4	4.9	10.5	3.3
Whte Crappie	0.2	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.1	0.0
Striped Bass	0.0	0.2	0.1	0.0	0.1	2.8	0.0	0.0	0.4	0.3
Walleye	0.0	0.0	0.1	0.0	0.0	0.1	0.0	0.0	0.0	0.0
Channel Catfish	10.9	8.7	10.2	8.1	11.7	20.0	12.9	11.4	11.7	1.2
White Catfish	3.6	1.6	3.5	2.0	1.9	2.4	0.6	0.4	2.0	0.4
Flathead Catfish	3.2	3.4	14.7	25.2	12.1	10.9	6.4	10.6	10.8	2.4
Bluegill	38.2	53.8	35.0	29.0	43.8	45.6	73.2	43.9	45.3	4.5
Redbreast Sunfish	4.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.5	0.5
Green Sunfish	0.3	0.1	0.0	0.2	0.1	0.3	0.1	0.0	0.1	0.0
Yellow Perch	2.7	2.0	1.8	2.7	4.6	3.2	3.4	4.4	3.1	0.3
Minnow	0.3	0.9	0.3	0.9	0.5	0.4	0.8	0.5	0.6	0.1
Alewife	3.6	0.4	1.7	4.0	1.8	0.9	6.6	1.3	2.9	0.7
Gizzard Shad	231.2	151.7	119.4	70.7	82.8	88.4	88.0	62.3	111.8	18.5
Threadfin Shad	0.0	0.0	0.0	4.7	0.4	7.0	0.0	0.0	1.5	0.9
Carp	40.2	50.9	46.1	61.6	74.3	74.6	80.1	67.6	61.9	4.9
Quillback	1.8	1.2	1.6	4.5	3.5	4.0	2.4	1.9	2.6	0.4
Redhorse	54.0	51.5	36.0	39.8	42.5	36.6	45.1	22.2	40.9	3.3
Yellow Bullhead	0.7	2.1	0.0	0.0	0.6	0.4	0.0	0.0	0.5	0.2
Brown Bullhead	1.0	0.0	1.5	0.6	0.0	0.0	1.1	0.7	0.6	0.2

Table A.2. Comparisons of individual annual consumption by largemouth and striped bass using multiple and a single growth period for a 365 day cycle.

	Largemouth Bass Annual Individual Consumption (g)	
Cohort	Multiple Periods	Single Period
YOY	59.0	50.8
1	511.0	509.3
2	1156.1	1185.9
3	1780.5	1874.2
4	2332.3	2471.5
5	2787.4	2935.9
6	3063.0	3296.2
7	3334.9	3576.3
8	3547.2	3784.1
9	3821.1	3942.2
10	3951.8	4061.4
Total	26344.2	27687.7

	Striped Bass Annual Individual Consumption (g)	
Cohort	Multiple Periods	Single Period
Small YOY	100.7	94.6
Large YOY	382.7	378.9
1	2563.6	2640.5
2	5740.5	6085.0
3	8711.2	9233.9
4	11926.1	12641.7
5	14919.5	15814.7
6	17611.0	18667.7
7	19979.0	21177.8
8	22032.8	23354.8
9	23791.8	25219.3
10	25289.9	26807.3
Total	153049.0	162116.2

Table A.3. Abundance and growth data used to model consumption by the Smith Mountain Lake largemouth bass population. Numbers of age-0, age-1, age-2, and age-3 bass in mid-August were derived from cove rotenone data. The initial number of larvae on 15 June was estimated assuming 33% survival from this date to 15 August.

Age	Date	Simulation Day	Number Remaining	Weight (g)
0.00	15-Jun	1	4650000	0.004
0.17	15-Aug	62	1534589	1.2
0.80	1-Apr	291	291163	24
1.38	1-Nov	505	97884	165
1.84	15-Apr	670	77700	157
2.38	1-Nov	870	58730	447
2.84	15-Apr	1035	46620	434
3.38	1-Nov	1235	35238	839
3.84	15-Apr	1400	27972	823
4.38	1-Nov	1600	21143	1292
4.84	15-Apr	1765	16783	1275
5.38	1-Nov	1965	12686	1762
5.84	15-Apr	2130	10070	1745
6.38	1-Nov	2330	7611	2217
6.84	15-Apr	2495	6042	2201
7.38	1-Nov	2695	4567	2638
7.84	15-Apr	2860	3625	2622
8.38	1-Nov	3060	2740	3013
8.84	15-Apr	3225	2175	3000
9.38	1-Nov	3425	1644	3340
9.84	15-Apr	3590	1305	3329
10.38	1-Nov	3790	986	3621
10.84	15-Apr	3955	783	3611

Table A.4. Abundance and growth data used to estimate consumption by the Smith Mountain Lake striped bass population. The two numbers given in the top four rows of the columns marked "Number Remaining" and "Weight" indicate the separate values used to model small and large members of the age-0 striped bass cohort.

Age	Date	Simulation Day	Number Remaining	Weight (g)
0.15	15-Jun	1	200000 / 100000	3.4
0.49	15-Oct	123	143903 / 56920	51 / 9.3
0.65	15-Dec	184	122228 / 43042	121 / 17
0.90	15-Mar	274	96065 / 1	121 / 12.8
1.11	1-Jun	352	82840	218
1.49	15-Oct	488	63985	373
1.65	15-Dec	549	56986	628
1.90	15-Mar	639	48033	627
2.11	1-Jun	717	41420	830
2.49	15-Oct	853	31992	1103
2.65	15-Dec	914	28493	1491
2.90	15-Mar	1004	24017	1489
3.11	1-Jun	1082	19419	1770
3.49	15-Oct	1218	13407	2122
3.65	15-Dec	1279	11355	2589
3.90	15-Mar	1369	8886	2588
4.11	1-Jun	1447	7185	2910
4.49	15-Oct	1583	4961	3302
4.65	15-Dec	1644	4201	3803
4.90	15-Mar	1734	3288	3802
5.11	1-Jun	1812	2659	4139
5.49	15-Oct	1948	1835	4538
5.65	15-Dec	2009	1554	5039
5.90	15-Mar	2099	1217	5038
6.11	1-Jun	2177	984	5368
6.49	15-Oct	2313	679	5755
6.65	15-Dec	2374	575	6232
6.90	15-Mar	2464	450	6231
7.11	1-Jun	2542	364	6542
7.49	15-Oct	2678	251	6902
7.65	15-Dec	2739	213	7343
7.90	15-Mar	2829	167	7341
8.11	1-Jun	2907	135	7625
8.49	15-Oct	3043	93	7953
8.65	15-Dec	3104	79	8349
8.90	15-Mar	3194	62	8348
9.11	1-Jun	3272	50	8602
9.49	15-Oct	3408	34	8893
9.65	15-Dec	3469	29	9244
9.90	15-Mar	3559	23	9243
10.11	1-Jun	3637	18	9467
10.49	15-Oct	3773	13	9722
10.65	15-Dec	3834	11	10028
10.90	15-Mar	3924	8	10027

VITA

Michael John Cyterski came into this world on December 28, 1969, on the shores of Lake Erie, in the Pennsylvania town sharing this Great Lake's name. At a very young age he showed an insatiable interest in organisms of all types but reserved a special place in his palms for creatures of the aquatic realm. He attended Cathedral Preparatory School and graduated as valedictorian in June of 1988. He went on to Harvard University where he graduated cum laude while earning a Bachelors of Arts degree in biology in June of 1992. He also found time to letter two years on the Crimson varsity football team. He was not able to enjoy the outdoors as frequently in urban Cambridge but returned to a more rustic location after accepting the John Dobie Memorial Fellowship from the Department of Fisheries and Wildlife at the University of Minnesota in St. Paul. He enjoyed his time there immensely, learning to fly fish and investigating a commercially-exploited population of walleye on the huge Red Lakes in northern Minnesota. After receiving a Master of Science degree in Fisheries in June of 1995 he headed south to the Virginia Polytechnic Institute and State University located in the Blue Ridge Mountains of western Virginia. He was lured by the Cunningham Fellowship and entered the doctoral program in the Department of Fisheries and Wildlife Sciences. His research focused on prey supply and predator demand in the popular recreational fishery of Smith Mountain Lake. He enjoyed fly-fishing the New River for smallmouth bass while at Tech and fulfilled professional obligations by serving as president of the Virginia Tech Chapter of the American Fisheries Society, secretary-treasurer for the Student Subsection of AFS, and editor of the AFS Southern Division newsletter. He took advantage of a bit of free time upon completion of his fisheries coursework to acquire an M.S. in statistics. His personal life took an unprecedented and welcome turn in November of 1998, when he married the lovely and intelligent Trina Paige Doran, who was enrolled in the doctoral program in psychology at Virginia Tech. Soon after completing his doctoral requirements in June of 1999, he moved to Athens, Georgia, where he timidly took his first prolonged look into the strange world beyond academia at the Ecosystems Research Division of the Environmental Protection Agency.