

COMPATIBILITY AND COMPLEMENTARITY OF ALEWIFE (ALOSA
PSEUDOHARENGUS) AND GIZZARD SHAD
(DOROSOMA CEPEDIANUM) AS FORAGE FISH IN SMITH MOUNTAIN LAKE,
VIRGINIA

by

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(ABSTRACT)

The attributes of alewife and gizzard shad as coexistent forage fishes for striped bass (Morone saxatilis), walleye (Stizostedion vitreum vitreum) and largemouth bass (Micropterus salmoides) were evaluated in Smith Mountain Lake, an 8,337 ha hydro-electric impoundment in south-central Virginia. Alewife and gizzard shad larvae exhibited strong spatial segregation which minimized the potential for direct trophic competition and increased feeding opportunities for piscivores. Gizzard shad spawning peaked in June while alewife spawning peaked in July. Daily growth rate of age-0 gizzard shad was 37% greater than for age-0 alewives. Later spawning and slower growth enhanced temporal and morphological availability of alewives to piscivores and reduced the potential for exploitative competition between the clupeids.

Distributional analysis indicated that gizzard shad were primarily uplake and littoral while alewives were mostly downlake and pelagic. Alewives co-occurred with striped bass and walleye during the growing season and were crucial in providing forage for

these piscivores. Largemouth bass shared a common distribution with gizzard shad and were more trophically dependent than other piscivores on them.

Prey supply and predator demand were one year out of phase; gizzard shad and alewife production peaked in the first year of life while their predators' cohort production peaked in the second year. Cohort production analysis indicated that over their lifespan, striped bass prey demand (per 1000 fish) would exceed that of walleye and largemouth bass by 17% and 166%, respectively. Lifespan cohort production patterns and ingestibility limitations on prey assured that most predation pressure in Smith Mountain Lake came from piscivores ages 0-2 and was constrained to alewives ages 0 and 1 and young-of-the-year gizzard shad. Prediction of patterns of consumption of alewife and gizzard shad by piscivores was derived from analyses of morphological and distributional availabilities; these agreed closely with actual diets for most predator-prey location, season and age combinations. The alewife appears to be both compatible with, and complementary to, the gizzard shad as a forage species in Smith Mountain Lake. Suitability of alewives for introductions into other reservoirs will vary with the morphometry and management objectives for those waters.

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INTRODUCTION

Availability of prey is often the principal factor limiting sportfish production in reservoirs (Jenkins 1979; Noble 1981). Realization that prey supply is a finite and often limiting resource has focused increasing attention on the importance of efficient energy transfers to production of fishes at higher trophic levels (Ney 1981; Stewart et al. 1981). As a consequence, attempts to augment growth and production of sport fishes through expansion of the forage base have become commonplace (Noble 1981; Kircheis and Stanley 1981). Non-native forage fishes are often introduced to expand the existing forage base without full consideration of ecological implications (Kohler et al. 1986). Introductions of forage species to develop a polyspecific forage base may not produce the desired results due to competitive or predatory interactions with the resident species complex or ineffective utilization by intended predators. However, the pressure to introduce forage species is often intense, particularly in reservoirs.

Forage Fish in Southeastern Reservoirs

The importance of an adequate forage base to a reservoir fishery cannot be over-emphasized. Indigenous riverine forage species (e.g., cyprinids, catostomids, cottids, percids, centrarchids) are often unable to expand in new lacustrine habitat (Kimsey 1957; Shields 1957; Fitz 1968). Introduction of potential forage species into reservoirs has

consequently become common practice in fisheries management (Kohler et al. 1986). Sport fish populations in the large, deep reservoirs which have been developed in the southeastern United States are heavily dependent on clupeid forage fishes. In this region, gizzard shad (Dorosoma cepedianum) and threadfin shad (D. pentenense) are the major indigenous forage-fish species, constituting an average of 45% of the biomass in large (> 500 ha) impoundments (Jenkins 1967). As adults, gizzard shad feed primarily on phytoplankton and detritus (Miller 1960; Becker 1983), while threadfin shad consume phytoplankton/detritus and zooplankton (Miller 1967; Baker and Schmitz 1971). This would appear to make them ideal forage-fish species because of their low positions on the trophic pyramid. Energy transfer should be highly efficient, and there should be a minimum amount of diet overlap with adult sport fishes which are principally piscivorous. However, both species possess traits that have made them problematic. The rapid growth of gizzard shad may quickly render the bulk of a particular cohort invulnerable as prey (Miller 1960; Bodola 1966; Scott and Crossman 1973). The threadfin shad, while not exceeding a size vulnerable to predation throughout its life cycle, is limited in its northern range due to an inability to withstand water temperatures below 9°C for prolonged periods (Strawn 1965). In addition, threadfin shad may compete with young sport fishes for available food (Davies et al. 1979; Noble 1981).

Presently, the alewife (Alosa pseudoharengus) is receiving widespread consideration as an alternative forage species in lakes and reservoirs because of the success of the Great Lakes salmonid fishery which depends upon the landlocked form of this anadromous clupeid (Smith 1968; Stewart et al. 1981; Eck and Brown 1985; Stewart and Binkowski 1986). Alewives are establishing abundant populations in an increasing number of southeastern reservoirs where its perceived attributes include small adult size and tolerance of the winter thermal regime (Ney et al. 1982). Alewives have been pur-

posely stocked in some systems to augment the pelagic forage base and have frequently migrated to downstream reservoirs (Ney 1981; Daniel 1984). The suitability of the alewife as a pelagic forage fish for southeastern reservoirs was evaluated by Kohler and Ney (1981) from a study of the species' trophic relationships in Claytor Lake, Virginia. This impoundment has no other pelagic prey species, but many of the systems in which alewives have or may become established also contain large populations of gizzard shad that are heavily utilized by piscivores. The extent to which alewives and gizzard shad are compatible as coexistent forage species is unknown. This species combination may be beneficial in expanding the overall trophic availability of the forage base by increasing total forage-fish production. However, total forage-fish production will be limited to the extent that the forage species compete between themselves.

Alewives and gizzard shad are most likely to be in direct competition for food during the larval stages. Gizzard shad larvae (< 35 mm TL) feed almost exclusively on zooplankton (Warner 1940; Kutkuhn 1957; Cramer and Marzolf 1970; Barger and Kilambi 1980), whereas alewives are zoo-planktivorous throughout their entire life (Odell 1934; Gross 1959; Morsell and Norden 1968; Lackey 1968; Hutchinson 1971; Rhodes 1971; Kohler 1980; Wells 1980; Ney et al. 1982). In Canandaigua Lake, New York, introduced alewives completely replaced rainbow smelt (Osmerus mordax) as the principal forage species (Eaton and Kardos 1972). Intense competition from (and perhaps predation on early life stages of other forage fishes by) alewives may have contributed to the drastic declines and extinctions of native planktivorous fishes that have occurred in some of the Great Lakes (Smith 1970; Crowder 1980, 1986). Gizzard shad appear to be susceptible to competition. In Lake Texoma, Oklahoma-Texas, where gizzard shad was the most abundant species, the clupeid population changed to over 60% threadfin shad (by number) one year after their inadvertent introduction; threadfin

shad are trophically similar to alewives (Riggs and Moore 1957). Similarly, in Bull Shoals Reservoir, Arkansas, threadfin shad comprised 80% of shad numbers five years after introduction (Bryant and Houser 1969). Barker and Schmitz (1971) suggest that threadfin shad predation on gizzard shad larvae may partially account for the displacement of gizzard shad observed in Bull Shoals Reservoir. In Lake Sinclair, Georgia, Ager (1978) also found a negative correlation between standing stocks of gizzard shad (declining) and threadfin shad.

Feeding opportunities for piscivores could be enhanced by complementary differences in the morphological and spatial availability of alewives and gizzard shad. Morphological availability (i.e., the presence of forage fish of a size which can be swallowed by a given predator) is a function of timing of reproduction and subsequent growth rates. In this context, the actual supply of a prey species available to meet predator demand will be the product of its total abundance multiplied by the fraction small enough to be eaten. A key problem in reservoir fisheries management is maintaining adequate stocks of prey within size ranges vulnerable to the predators of interest (Noble 1981). Forage species typically have shorter lifespans and reach their peak production (supply) earlier in life than when their predators achieve peak trophic demand (Stewart et al. 1981; Ney and Orth 1986). As a consequence of these inequalities, piscivore cohorts may experience early deficiencies in available prey and also depend for their ultimate success on the production of forage-fish year classes younger than themselves (Ney and Orth 1986). The problem of forage-fish availability can be immediate and acute for sport fish which become piscivorous at or soon after stocking or hatching, but are limited in their consumption to only very small forage fish, usually of the same cohort (year class). Mass starvation of juvenile piscivores due to a dearth of morphologically vulnerable prey is a very real possibility (Shelton et al. 1979). Mitzner

and McWilliams (1986) reported that young-of-the-year walleyes (Stizostedion vitreum vitreum) are often faced with near starvation in mid summer when gizzard shad outgrow the size they can feed upon in Lake Rathbun, Iowa. Young-of-the-year striped bass (Morone saxatilis) in Cherokee (Saul 1981; Humphreys 1983) and Norris (Richardson 1982) Reservoirs, Tennessee, which contain both gizzard shad and threadfin shad, appeared starved and in extremely poor condition in years when the threadfin shad population was low. Forage-fish availability may also be a life-long problem for stocked piscivores when the forage supply is variable and the demand is partitioned among various predators, including cohorts of the same species stocked in preceding and following years (Ney and Orth 1986).

Size relationships alone do not determine prey availability; predator and prey must co-occur in space and time for feeding encounters to be realized. Seasonal habitat differences in distribution of forage fishes and piscivores have real potential to minimize prey consumption independent of abundance. Coutant (1985) reported that striped bass became spatially segregated from gizzard shad during the summer months in Cherokee Reservoir, Tennessee, because shad preferred warmer water temperatures than striped bass. In Hoover Reservoir, Ohio, Momot et al. (1977) reported that walleyes also became thermally isolated from gizzard shad during the summer months. The alewife has a lower thermal preferendum than gizzard shad (Coutant 1977), and so might experience a summer distribution more congruent with coolwater piscivores.

Analysis of Prey Availability

A successful feeding encounter by a predator occurs when three conditions affecting prey availability have been met. First, predator and prey must occur at the same place and time (distributional availability). Then the predator must recognize the potential prey as food and be able to pursue and capture it (behavioral availability). Finally, the prey must be of a size and shape that can be swallowed (morphological availability). When any of these conditions of availability is missing, predators will go hungry, even when the actual abundance of potential prey is high.

However, analysis of prey availability as a factor influencing growth and survival of predatory fish is only now beginning to receive attention. Morphological availability has been studied most, perhaps because it is the easiest aspect to quantify. Most piscivorous fish swallow their prey whole, and prey body depth relative to predator throat diameter sets the limit on ingestibility. Jenkins and Morais (1978) quantified this relationship for a variety of reservoir predator and prey species. They developed a series of curvilinear equations to predict the maximum total length of a particular prey species of a given total length. These ingestibility limits were then applied to cove rotenone standing stock estimates to determine the prey biomass morphologically available to the cumulative biomass of successively larger predators (Jenkins and Morais 1978; Jenkins 1979). The graphical illustration of available prey to predator ratio (AP:P) has been widely used in southeastern reservoirs to identify sizes of predators that are experiencing prey deficiencies. As such, it offers a point in time "snapshot" of available prey supply versus predator food demand. However, the ingestibility limit equations of Jenkins and Morais (1978) can also be used without absolute abundance data to examine the pattern

of changing prey availability over time. This “movie” approach to analyzing morphological availability was used by Ney and Orth (1986) to identify periods in the lifespan of same-age predator and prey cohorts when the prey would be unavailable. Their approach can be elaborated to compare the morphological availability of alewives and gizzard shad to juvenile and other ages of predators. In this instance, it is important to know not only when prey will be available to predators but also how much of the prey supply will then be present to meet co-occurring predator demand. In the absence of absolute abundance estimates, the lifespan production patterns of prey and predators can be used to approximate supply and demand, respectively. Production, the amount of tissue elaborated per unit time regardless of its fate (Ricker 1946), can be patterned over the lifespan by starting with a cohort of any arbitrary size (e.g., 1000 individuals) and applying age-specific growth and mortality rates. Production will underestimate supply and demand to some extent for older fishes but provides a reasonable approximation for purposes of comparing morphological availability between prey species (Ney 1989, in press).

Distributional availability of reservoir predator and prey species can be expected to vary both by location and season. Introduced pelagic species should have limited interaction with resident littoral species (Kohler et al. 1986). Seasonally, differences in thermal preferences between predators and prey can result in predator starvation (Coutant 1985). The study of distributional availability therefore requires sampling of all habitats in all seasons.

Behavioral availability is extremely difficult to study in nature because it requires direct observation and control of confounding variables. Most studies of behavioral availability of prey have been rather narrow investigations of particular aspects (e.g.,

reaction distance, avoidance responses) in laboratory aquaria; their relevance to large systems is unproven. However, it is obvious from them that predators differ in their ability to locate various prey species, which themselves differ in their ability to escape (Stein 1979). The three major predator species in Smith Mountain Lake all consume both alewives and gizzard shad (Ney et al. 1988). Although the behavioral availability of alewives and gizzard shad to each of these predators might differ to some small extent, it is reasonable to assume that this effect will be overridden by morphological and distributional constraints on feeding success.

Smith Mountain Lake, Virginia, contains abundant populations of both alewives (introduced in 1965) and indigenous gizzard shad, as well as resident (black basses) and stocked (striped bass and walleye) piscivores. It therefore provides an excellent opportunity to evaluate the suitability of alewives and gizzard shad as a combined forage-fish resource for southeastern reservoirs. Throughout this text, the term "shad" will refer to gizzard shad unless otherwise stated.

Goals and Objectives

Many unfortunate forage fish introductions can be avoided if the effectiveness of particular combinations of predators and prey are fully evaluated in systems in which they have already become established. To that end, this study was undertaken to evaluate the compatibility and the complementarity of alewife and gizzard shad as forage species for striped bass, walleye, and largemouth bass, the major predators and principal sport species in Smith Mountain Lake. The study was designed also to provide a more

general evaluation of the utility of an alewife/gizzard shad combination in other reservoir systems. Specifically, objectives were to:

1. assess the potential for trophic competition by comparing larval distributions of alewife and gizzard shad;
2. analyze morphological availability of alewives and gizzard shad through analysis of forage-fish spawning periods and growth rates versus ingestibility limits of striped bass, walleye and largemouth bass;
3. identify lags between predator demand and prey supply by analysis of lifespan production patterns developed from growth and survival characteristics for both prey and predator;
4. evaluate complementarity between clupeid species in terms of distributional availability (time and space) from seasonal distribution and predator diet data.

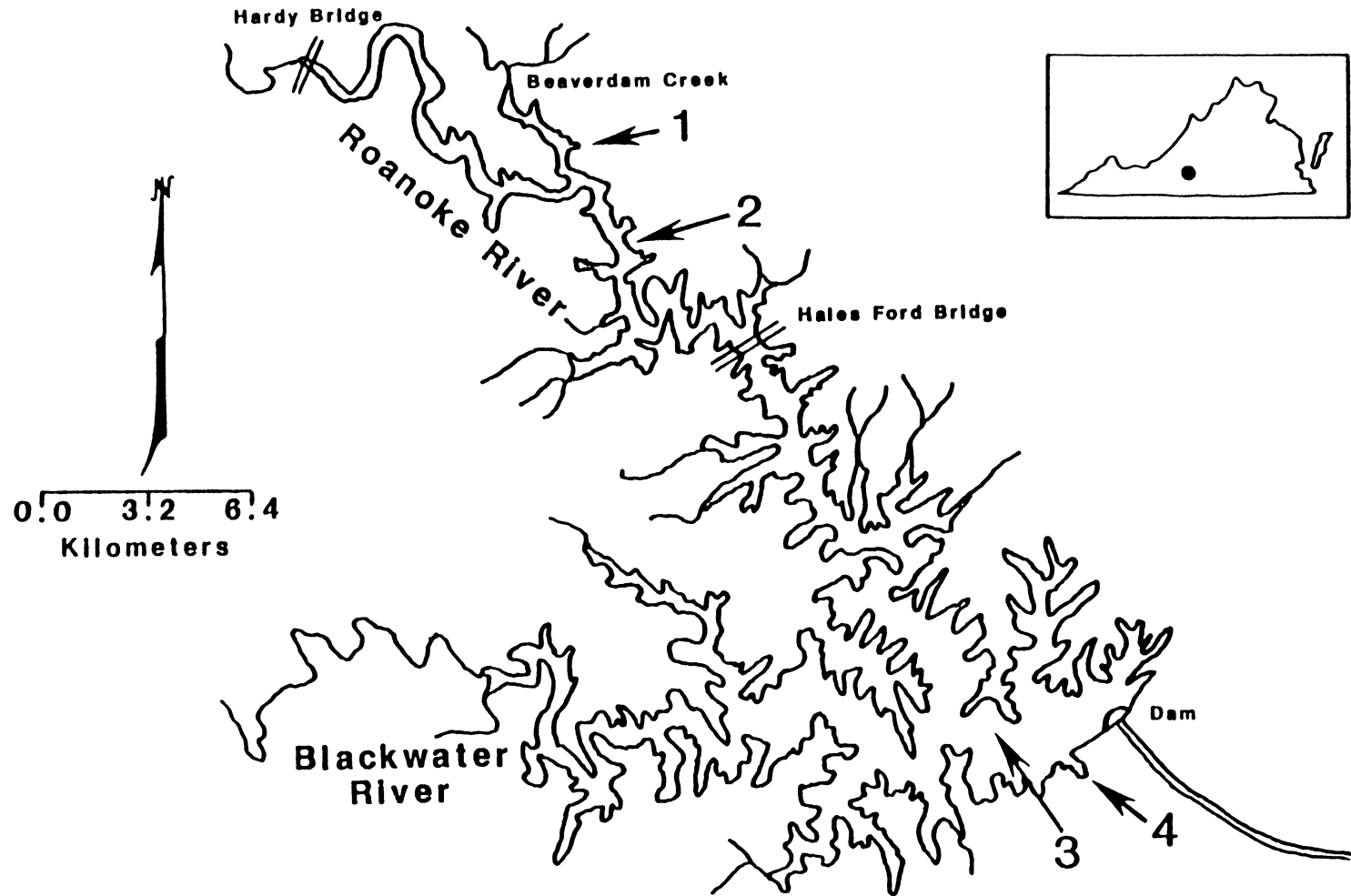
METHODS AND MATERIALS

Study Area

Smith Mountain Lake is an 8,337 ha (20,600 acre) impoundment of the Roanoke River in south-central Virginia. It was filled in 1965 and is operated by Appalachian Power Company as a combination hydroelectric and pump storage system in tandem with downstream Leesville Reservoir. The reservoir consists of two long, narrow tributary arms, the Roanoke River (65 km) and the Blackwater River (32 km) segments, and a broad and deep lower lake extending 10 km above the dam (Fig. 1). Smith Mountain Lake has approximately 805 km (500 miles) of shoreline. It has a maximum pool elevation of 242 m, a maximum depth of 61 m, and a mean depth of 17 m (Simmons and Neff 1969). The lower lake is mesotrophic (Benfield and Hendricks 1975) with oxygen concentrations in the cool hypolimnetic waters reduced to approximately 2-4 mg/l during the summer months (Ney et al. 1988). Littoral regions contain only sparse cover and grade steeply into the profundal zone. In contrast, the tributary arms are more eutrophic from domestic and industrial effluents (Cumming and Estes 1969; Benfield and Hendricks 1975). During summer months, these upper reservoir waters may be devoid of oxygen 5 m below the surface (Ney et al. 1988). Littoral regions contain more vegetation and other cover than the lower lake and slope more gradually into the main channel. Because of these distinct differences between the lower and upper lake (i.e.

Figure 1. Map of Smith Mountain Lake with location of larval fish sampling sites: 1) Beaverdam Creek, 2) upper main channel, 3) lower lake main channel, and 4) cove site (lower lake).

SMITH MOUNTAIN LAKE



fertility, thermal regime, and habitat), the lake was divided into two sections for this study. The upper lake (Roanoke River arm) extended downstream to the Hales Ford Bridge, and the lower lake extended from the bridge to the dam (Fig. 1). The Blackwater River arm was not included in the sampling design because of time/effort constraints and because its physical and chemical characteristics are similar to those of the Roanoke River arm.

Field Collections

The study involved three years (1982-84) of field work. Most of the first year's effort consisted of preliminary work such as logistical arrangements, learning general patterns of fish distributions within the lake and developing a sampling design. The remaining two years were devoted entirely to research collections.

Larval Clupeids

Larval (<30 mm TL) gizzard shad and alewives were collected to determine the spawning periods of adults as well as early distribution, growth, and mortality rates of these species. Main channel (offshore) and cove (nearshore) sites in both the upper and lower lake (Fig. 1) were sampled on a weekly basis from late April through the end of August, 1983 and 1984. Linear length of each site was approximately 300 m. In the upper lake, R45 to R47 (R = Roanoke River Piling) was the location of the main

channel site and Beaverdam Creek, B4 to B7 (B = Beaverdam Creek Piling) was the cove site. In the lower lake, R8 to Saunder's Point was the main channel site, and a cove along the mountain to the right of the dam was the nearshore site. Selection of sampling sites was based on 1982 surveys, which included larval fish collections at more than 30 locations in both the upper and lower lake as well as visual observations of both spawning fish and larval fish aggregations.

Larval fish were collected with a 505-micron mesh conical net, 0.5 m in diameter at the opening and 1.8 m long. Sampling was conducted after dark to minimize net avoidance (Silliman 1943; Bridges 1956; Ehrlich 1975). Stratified hauls were made at depths of 1, 3, and 5 meters (two per depth) at each of the four sampling sites in 1983. Analysis of 1983 samples revealed few larvae of either species at 5 m, and therefore sampling was discontinued at that depth in 1984. Standardized hauls were made by towing at a constant speed of 1 m/s for 5 minutes. Kilch (1976) and Nigro (1980) also sampled larval gizzard shad and alewives, respectively, and found that towing at approximately 1 m/s was an effective speed for capturing these clupeids. A calibrated flow meter (General Oceanics Model No. 2030-R), positioned approximately one third the radial distance to the center of the net's mouth (Tranter and Smith 1968), was used to estimate the volume of water filtered. Surface temperature was measured at each site just prior to sampling. Larval fish were preserved in 4% buffered formalin immediately upon capture (Braum 1978).

Juvenile Clupeids

Periodic collections of young-of-the-year clupeids were made throughout the growing season to: 1) describe the remaining pattern of first-year growth; 2) estimate production; and 3) describe distribution. Midwater trawling for juvenile clupeids was conducted at night using an otter trawl in 1984 (headrope 8.5 m, bottomline 10.4 m, total net length 14 m). Trawling was conducted once in June at the Hales Ford Bridge and upper main channel, three times during July in the upper main channel and twice in the lower main channel, twice in August at both the upper and lower main channel locations, and once in September at the upper and lower main channel sites and at the Hales Ford Bridge (Fig. 1). A standard haul was made by pulling the trawl at a depth of 2 m for 15 minutes at 2 m/s. Bio-acoustic (Eagle Z-15 Computer Graph Recorder) transects conducted at night revealed that clupeids were abundant in the upper 5 m of the water column. While pulling the trawl, the boat's maximum speed (2m/s) was maintained to minimize net avoidance. I used bioacoustic equipment in conjunction with midwater trawling in September to better assess the distribution of clupeids. I conducted one bioacoustic transect during the day and one at night at the Hales Ford Bridge, as well as day and night transects at the upper and lower main channel sites. Bioacoustic transects were made by crossing from shore to shore and then directly down the middle of the channel over an approximately 500 m linear stretch of water. Trawling was done at night to minimize net avoidance and concurrently with bioacoustic transects to identify fish "marked" in acoustic recordings. Several attempts were made to collect clupeids located during daytime bioacoustic transects, but none were successful. Apparently, the black-colored trawl was easily avoided by clupeids in daylight. Shoreline electrofishing was also done approximately once a month (in the upper lake) during July, August, Sep-

tember, and November 1984 to collect juvenile gizzard shad. Attempts to collect juvenile alewives by electrofishing in the lower lake were unsuccessful. After sampling, all fish were measured to the nearest millimeter (TL) and weighed to the nearest 0.01 gram.

Adult Clupeids and Sport Fishes

Adult gizzard shad and alewife populations were also sampled to describe their distributions, growth, and mortality rates and to estimate production. Four experimental-mesh gill nets (60.8 m X 1.8 m), two each with four 15.2-m panels of bar-mesh sizes 38, 51, 64, and 76 mm and two with four 15.2-m panels of bar-mesh sizes 6, 13, 19, and 25 mm, were fished overnight once a week from April through August in 1983 and 1984 in both the upper and lower lake. Nets were primarily fished along the bottom during the spring. During the summer, nets were fished 2-3 meters below the surface in deeper water or along the bottom at sites < 5 m in depth. In September, October, and November 1983 and 1984, gill netting was done once a month in both ends of the lake. Electrofishing was also performed approximately twice a month (primarily in the upper lake) in April, May, June, November, and December, and approximately three times between July and September to supplement gill netting. Fish were measured to the nearest millimeter (TL) and weighed to the nearest gram upon completion of sampling. Scales were also taken for age and growth determinations. If nets contained large numbers (> 50) of gizzard shad and alewives, a random sub-sample of both species (20 each) was measured, with the remaining fish enumerated and discarded.

Striped bass, walleye, and largemouth bass were collected to describe their patterns of growth and mortality and to estimate cohort production over their lifespans. Gill netting and electrofishing were conducted on the same schedule and gear as previously described for adult gizzard shad and alewives. Sport fish were also measured and weighed to the nearest millimeter (TL) and gram, respectively. Scales were collected for age and growth determinations.

Data Analysis

Statistical Procedures

Parametric methods were used in all instances for linear regression analysis because they yielded more information (i.e. coefficient of determination, r^2) than non-parametric methods. Linear regression was used in developing weight-length relationships and in estimating growth and mortality rates. Non-parametric statistical methods were, however, applied to all other data sets throughout this dissertation because they require fewer assumptions (e.g., normality) than do parametric methods (Hollander and Wolfe 1973). Moreover, non-parametric procedures are only slightly less efficient than their normal theory counterparts under conditions of normality and can be much more efficient when conditions are not normal (Hollander and Wolfe 1973). Parametric methods can also lead to erroneous interpretation of research results when normal theory assumptions are violated (Pirie and Hubert 1977). All tests were two-sided, and probability of committing a Type I error was controlled at $P = 0.05$.

Measurement of Larval Clupeids

In the laboratory, fish larvae were separated from plankton and debris 24 to 48 h after collection and were then placed in small plastic vials containing 40% ethanol (Nigro 1980). Samples collected in 1983 remained in alcohol approximately one year, while 1984 samples remained in alcohol approximately five months. Individual specimens were then identified and measured for total length to the nearest millimeter, blotted dry with a damp towel in a manner described by Parker (1963) as heavy blotting, and weighed to the nearest 0.0001 g on a Mettler H45 analytical balance. Alewife and gizzard shad are quite similar in appearance throughout early development and growth. Identification of larval gizzard shad and alewife was accomplished with a phase-contrast microscope based on the characters described by previous investigators (Norden 1967a; Lippson and Moran 1974; Tin 1982). Essentially, alewife and gizzard shad larvae (< 20 mm TL) differ as follows: 1) preanal length as a percent of total length is greater for gizzard shad than alewife (80% to 89% versus 59% to 64%, respectively); 2) spines are absent on the gill rakers of gizzard shad; and 3) greater number of myomeres are present on gizzard shad compared to alewives (47 to 51 versus 33 to 42, respectively).

Total lengths of all larval fish were measured with a dissecting microscope equipped with an ocular micrometer; no difficulty was encountered in obtaining consistent results. A greater potential source of error was the blotting of each fish to remove excess moisture prior to weighing. Precision of weight measurements was evaluated by weighing a 10, 20, and 30 mm gizzard shad 10 times each. After each measurement, the fish was returned to the vial of ethanol, blotted dry again, and reweighed. The standard de-

viations calculated for 10, 20, and 30 mm gizzard shad were 2.5%, 1.6% and 1.6% of the mean weight, respectively.

There is considerable reported variation in the effects of preservation on the lengths and weights of fishes. When age-0 plaice (Pleuronectes platessa) were preserved in 4% neutral formalin, there was no significant change in length, but weight loss was in excess of 20% of the initial weight (Lockwood 1973). In contrast, Parker (1963) found that juvenile salmon (Oncorhynchus spp.) stored in a 3.8% solution of formalin shrank to 96% of original length in 30 days and increased by 10% in weight. Still another investigator observed that Sarotherodon mossambicus increased in length by 2% and increased in weight by 22% when preserved in 10% formalin (Billy 1982). He also found that after transfer to 37.5% isopropyl alcohol for 65 days, fish returned to live length and initial weight increase was reduced to 4% of the live value.

Information on the effects of preservation on length and weight changes in larval gizzard shad and alewife is nonexistent. Since no standardized fish preservation technique has been established, there are no standardized correction factors for determining live state measurements based on measurements of preserved fish. However, Leslie and Moore (1986) reported that changes in body measurements of freshwater larval fishes associated with fixatives (formalin and ethanol) were of little or no practical consequence for taxonomy and growth studies. Therefore, I assumed larval fish measurements in this study reflected approximate live-state conditions.

Fish Distribution

Concurrent distribution of juvenile and adult gizzard shad, alewives, and their predators were described to determine the degree to which differences in spatial availability of prey affected feeding opportunities for piscivores. Temporal distributions of larval gizzard shad and alewives were analyzed to characterize the spawning periods of the species.

Larval clupeids: Horizontal and vertical distributions were described for both larval gizzard shad and alewives. Horizontal distribution was examined in terms of upper lake verses lower lake, and nearshore verses offshore sites. The Kruskal-Wallis one-way layout procedure was used to test for differences in densities of larval fish among depths (3) in 1983. In 1984, densities between depths (2) were analyzed using the Wilcoxon rank sum test. Horizontal distributions (i.e., nearshore versus offshore) of larval clupeids were also analyzed using the Wilcoxon rank sum test.

Prolarvae (< 5 mm TL) of both species were not fully vulnerable to the sampling gear, as indicated by their lower density (number/m³) relative to that of 5-10 mm larvae, which was the most abundant of all size ranges collected. Therefore, relative abundance of 5-10 mm larvae was selected as the index of spawning periods and intensities because: 1) larvae of this size range were both abundant and vulnerable to sampling equipment; and 2) development to this size from fertilization is rapid, requiring only about one week at water temperatures recorded in Smith Mountain Lake (Scott and Crossman 1973). Durations of spawning periods were estimated by subtracting seven days from the

catch-date of 5-10 mm larvae. Data from the upper lake sites were combined to characterize the spawning periods of gizzard shad; alewife spawning was characterized by combining the lower lake sites.

Other fish: Description of horizontal and vertical distribution of juvenile clupeids was based on midwater trawling, electrofishing, and bioacoustic data. Horizontal distributions of adult clupeids and sport fishes (striped bass and walleye) were derived primarily from gillnet collections. I also used bioacoustic data to help determine use of pelagic habitat by predators. Largemouth and smallmouth bass were infrequently captured with gill nets; their distributions were derived from electrofishing data. Horizontal distributions (nearshore versus offshore) of adult clupeids and predators were analyzed using the Wilcoxon rank sum test.

Weight-Length Relationships

Weight-length relationships were described for gizzard shad and alewife and used to estimate mean weight over the growing season to calculate production estimates. Alewives ranging in size from 5-178 mm and gizzard shad 4-389 mm were used to develop weight-length relationships (Appendix Table 1). Weights from ten individual fish per millimeter length group were used for both species up to 35 mm (TL). Beyond 35 mm, nearly all of the remaining length groups (1 mm) were represented by at least one fish.

Weight-length relationships for major predators were described by Moore (1988) and used to estimate mean weight over the growing season to derive age-specific production.

Age Determination

Data from age analysis for clupeids and sport fishes were used to determine 25th, median, and 75th percentile length-at-age. Length-at-age is based only on the fish of the age caught (length at last annulus). All age data were combined for 1983 and 1984 because length-at-age for all species were not significantly different between years (Tables 1 and 2). Although scale samples were collected from both gizzard shad and alewife, I only analyzed alewife scales because the Virginia Department of Game and Inland Fisheries (VDGIF) had developed age-and-growth data on gizzard shad for 1983 and 1984. Alewife scales were mounted between two plastic slides and read using a Bausch and Lomb microprojector at 12X magnification. At least five scales from each individual were examined. The distance from the focus to each annulus (for each of the five scales) was recorded and the mean value used. Fish captured after January 1 were assumed to have completed their growth for the previous year (Jearld 1983), and were accordingly assigned an annulus mark to the anterior margin of the scale. Length of fish at formation of each annulus was calculated from linear regression equations (Appendix Table 2) generated by the VDGIF age and growth program (Marquess et al. 1982).

Annulus measurements for predators were determined by Moore (1988). Length-at-age was calculated using linear regression equations (Appendix Table 2) also generated by the VDGIF age and growth program.

Table 1. Median length-at-age for gizzard shad and alewife for 1983, 1984 and 1983-84 combined with semi-quartile range in parentheses for combined years. N = 1983/1984 sample sizes. P-value represents test for differences between years. Asterisk (*) indicates that only one year of data was available.

Age	N	Length-at-age (mm)			P-value
		1983	1984	Combined	
Gizzard shad					
1	23/43	130	137	134 (124-142)	0.391
2	20/11	209	174	186 (165-203)	0.072
3	10/32	217	231	224 (205-248)	0.107
4*	6/0	257	---	257 (233-281)	-----
5*	3/0	290	---	290 (260-314)	-----
6*	8/0	314	---	314 (280-338)	-----
7*	2/0	320	---	320 (296-344)	-----
Alewife					
1*	0/43	---	84	84 (74-95)	-----
2*	0/50	---	120	120 (111-129)	-----
3*	0/4	---	157	157 (148-167)	-----

Table 2. Median length-at-age for striped bass, walleye and largemouth bass for 1983, 1984 and 1983-84 combined with semi-quartile range in parentheses for combined years. N = 1983/1984 sample sizes. P-value represents test for differences between years. Asterisk (*) indicates sample sizes were too small to test for between year differences or only one year of data was available.

Age	N	Length-at-age (mm)			P-value
		1983	1984	Combined	
Striped bass					
1	71/225	205	214	213 (190-262)	0.280
2	64/53	402	423	406 (374-445)	0.167
3	35/20	517	541	524 (485-593)	0.083
4	27/14	587	617	598 (575-697)	0.110
5	18/19	684	706	690 (639-775)	0.093
6	7/19	745	758	752 (686-835)	0.332
7*	2/5	813	774	782 (716-880)	-----
8*	0/8	---	832	832 (738-910)	-----
9*	1/2	1017	847	856 (760-922)	-----
Walleye					
1	8/4	179	171	176 (149-217)	0.540
2	8/4	337	329	335 (296-384)	0.553
3	10/6	431	426	430 (393-479)	0.500
4	70/66	488	503	495 (456-544)	0.120
5	38/112	546	519	532 (501-578)	0.063
6	8/40	553	564	558 (529-601)	0.338
7*	0/11	---	574	574 (549-616)	-----
Largemouth bass					
1	73/35	140	151	144 (109-197)	0.240
2	31/136	273	256	263 (228-297)	0.134
3	28/43	320	327	325 (310-344)	0.355
4	14/16	390	365	375 (356-398)	0.130
5*	0/2	---	421	421 (392-441)	-----
6*	0/2	---	452	452 (415-476)	-----

Growth

Growth rates were derived for prey and predators for three main purposes: 1) to describe total length of each species throughout life; 2) to estimate maximum total length of ingestible prey from predator total length; and 3) to determine instantaneous growth rates to estimate production of forage fishes and piscivores.

Juvenile clupeids were not vulnerable to the sampling gear (gill netting and electrofishing) used in 1983. In 1984, however, I was able to collect juvenile clupeids using a midwater (otter) trawl; therefore, first-year growth rates were based only on 1984 data. Maximum total lengths of young-of-the-year gizzard shad and alewives collected on successive sampling dates were used to describe the pattern of first-year growth. Median total lengths could not be used because of the extended spawning season and the inability to collect fish of all sizes in proportion to their abundance. I proceeded on the assumptions of Nigro and Ney (1982) that: 1) the largest young-of-the-year collected on each date were members of the first cohort (products of initial spawning); 2) growth was continuous; and 3) all larvae grew at the same daily rates as the initial cohort.

A modified version of the von Bertalanffy growth equation was used to describe the pattern of growth (25th, median, and 75th percentile) for gizzard shad and alewife over their lifespan excluding first-season growth (Gaschutz et al. 1980, as cited in Moreau 1987). This modified version was used because it appears to describe more accurately the pattern of growth of fishes over their lifespan in temperate regions by taking into account the fluctuations in growth that occur over the course of a year. The equation

was modified by the addition of two new parameters, one of which regulates the magnitude of winter growth and a second which indicates the time period of most rapid growth. A sine function was also added to the equation which generated growth “stanzas” as regulated by the two new additional parameters. Length-at-capture data over the course of the growing season for most ages of gizzard shad and alewife were limited, so the equation was fitted to length-at-age data.

Colby (1973) found that Lake Michigan alewives ceased to grow during the winter months. Adams et al. (1982), investigating the bioenergetics of the largemouth bass in a Tennessee reservoir, found that energy storage and growth did not occur from December through March. Therefore assumed that zero growth occurred for all species in Smith Mountain Lake from December through March, inclusive.

The equation as modified was:

$$\text{Length} = L_{\infty}(1 - \exp(-K*(T - T_0) + A*\sin(2\pi*(T - Ts))))$$

where

L_{∞} = the mathematical asymptote of the curve, often referred to as the final or maximum size (mm).

K = a measure of the rate at which the growth curve approaches the asymptote (year^{-1}).

T = time of year

T_0 = a time scaler equivalent to the hypothetical starting time at which the fish would

have been zero-sized if they had always grown according to the model.

A = a parameter regulating the magnitude of growth during the winter period.

T_r = time of most rapid growth during the year.

Striped bass, walleye, and largemouth bass growth (25th, median, and 75th percentiles) was also described using the modified version of the von Bertalanffy growth model. Median lengths estimated monthly from length-at-capture data were used to describe “average” growth of striped bass and largemouth bass with back-calculated lengths of age groups (length-at-age) used to define the semi-quartile range in growth. Length-at-age data were used to describe walleye growth (25th, median, and 75th percentile) because of insufficient length-at-capture data for a number of age groups. One equation for each of the three percentile-length groups per each species was used to describe growth over the lifespan.

Mortality

Mortality estimates were derived to calculate annual production of forage fish and predator age groups. To estimate mortality of larval gizzard shad and alewives, length-frequency data from standardized plankton net hauls on each sampling date were converted to number of larvae/1000 m³ per millimeter length-class (Farris 1960; May 1974; Mansfield and Jude 1986). Starting with an initial length, estimated daily growth rates were used to project length of these larvae on successive sampling dates. The density of larvae of the projected length was then compared to the density of larvae of the initial

size the preceding week to estimate daily mortality rate. The procedure was followed until fish reached 30 mm, when they were no longer collected in proportion to their abundance. In this study, the following assumptions were made in estimating mortality rates of larval gizzard shad and alewives: 1) all size groups analyzed (5-30 mm TL) were equally vulnerable to the sampling gear (i.e. sampled in proportion to their abundance; and 2) growth rates were constant (linear) over the range of lengths considered. Mortality rates for larger age-0 clupeids were derived from the literature because I was unable to capture these sizes in proportion to their abundance.

Annual mortality, estimated as the slope of the descending limb of the catch curve (Ricker 1975), was derived for adult gizzard shad and alewives from VDGIF cove rotenone and my gillnet data based on the following assumptions: 1) survival rate was constant at all ages > 0 ; 2) all year-classes were recruited at the same abundance; and 3) all ages were equally vulnerable to the sampling apparatus. Mortality estimates for gizzard shad were derived primarily from cove rotenone data. Houser and Bryant (1967) reported that cove rotenone sampling provided a representative sample of the gizzard shad population in Beaver Reservoir, Arkansas. Alewives are a "hit or miss" situation when it comes to cove rotenone sampling because of their pelagic nature. Therefore, mortality estimates for alewives were derived from experimental gillnet data. Where data sets allowed, mortality estimates were derived by following the decline in catch-per-unit-effort over time for a single cohort. Annual mortality estimates for piscivores were derived by Moore (1988).

Ingestibility Limits

The effect of growth on morphological availability of young-of-the-year and adult gizzard shad and alewife as prey in Smith Mountain Lake was examined by the technique of Jenkins and Morais (1978). Based on the relationship of mouth diameter of largemouth bass to maximum body depth of gizzard shad, they derived a regression equation:

$$Y = 0.0141X^2 + 0.1668X + 1.0972$$

that estimated the maximum total length of gizzard shad (Y) in inches that was morphologically available to largemouth bass of a given length (X) in inches. They also calculated factors to convert other predators to largemouth bass total length equivalents including striped bass = 1.3 and walleye = 1.7 (e.g., a 13-inch striped bass has the same ingestibility limit as a 10 inch largemouth bass). I converted maximum total lengths of gizzard shad that can be swallowed by given size predators into alewife length equivalents by comparing ratios of gizzard shad versus alewife body depths. I used a median value ratio of 1.18 (semi-quartile range 1.09-1.21) based on 12 measurements (each species) of gizzard shad and alewife less than or equal to 65 mm (range 40-65 mm); and 1.25 (semi-quartile range 1.21-1.29) based on 23 measurements (each species) of gizzard shad and alewife greater than 65 mm (range 71-160 mm).

Ingestibility limits were applied to growth data for predators and prey to identify the periods during their lifespans when prey of a particular cohort could be consumed by the various age groups of predators. These periods were then transformed to determine:

1) the percent of a prey cohort's lifespan supply available to predator cohorts; and 2) the fraction of a predator cohort's total lifespan food demand which occurred during the period of availability. This was accomplished by using lifespan production patterns of prey and predators to simulate supply and demand, respectively. For a given predator and prey combination, the percent of prey supply available or predator demand co-occurring was estimated as the portion of lifespan production which happened during the period of morphological availability in which ingestibility limits were not exceeded.

Production

Production estimates for prey and predators were calculated on a per cohort basis to compare seasonal and lifespan patterns as an indication of available prey supply and concurrent predator food demand. Production was calculated as $P = G\bar{B}$, where G is the instantaneous growth rate and $\bar{B}$ is the mean biomass during the time interval (Ricker 1946). Extended spawning of gizzard shad and alewives resulted in a series of weekly sub-cohorts over the course of the spawning period. To develop temporal patterns of production for all species, I assumed that the initial size of each cohort was 1000 individuals. The number of gizzard shad or alewife in a weekly sub-cohort would be represented by that fraction of individuals spawned during the week. For example, if 12% of gizzard shad spawning occurs the week of June 1, the initial sub-cohort size for that week would be 120 individuals.

The estimated fraction of individuals spawned each week was based on the number of 5-10 mm fish collected each week with the catch-date adjusted back seven days (see Fish Distribution). Weekly production estimates were then derived for each of these

sub-cohorts over the first growing season based on daily growth and mortality estimates calculated for young-of-the-year gizzard shad and alewife. Sub-cohort production estimates were summed first to obtain total weekly and then first-year production.

To calculate the pattern of second and succeeding years' annual production for gizzard shad and alewife cohorts, I began with the number of survivors at the end of the first season of growth. The number of survivors, based on an initial cohort of 1000, was obtained from previous calculations used to derive first-year production estimates. It was assumed that no growth occurred between December and March, but that mortality was continuous and cohort numbers declined between as well as during the growing seasons. Production estimates were calculated using length-at-age data, weight-length relationships, and annual mortality estimates. It was assumed that the daily mortality rate for adults clupeids was constant over the year. Since length-at-capture data over the course of the growing season were limited for most of the older age classes, annual production estimates were based on end-point data (i.e. length-at-age data).

Production patterns of striped bass, walleye and largemouth bass cohorts in successive years were calculated in the same manner as was used for adult clupeids. Input data included growth rates, weights from weight-length relationships and annual mortality estimates.

RESULTS

Age-0 Forage Fish

Spatial and temporal distributions of age-0 gizzard shad and alewives were described to determine compatibility as well as spatial availability of these two forage fishes for young piscivores. In addition, patterns of available prey (supply) versus predator (demand) in terms of production were estimated based on morphological ingestibility limits.

Larval Distributions

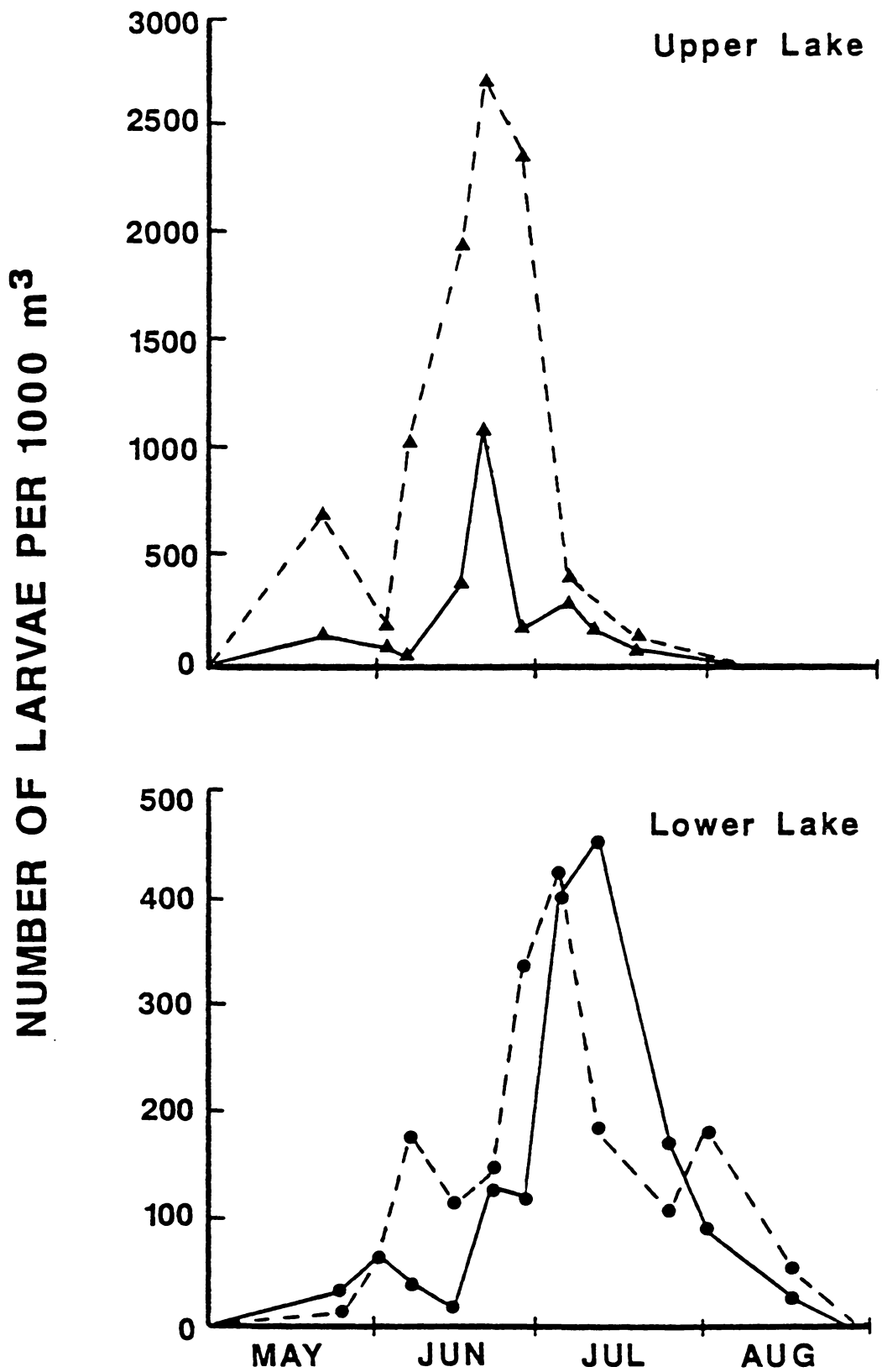
Gizzard shad and alewife larvae did not co-occur in any tow net samples in 1983. No alewife larvae were collected in the upper lake, and no gizzard shad larvae were taken in the lower lake over the 4.5-month sampling period (Table 3). Both species were concentrated in the upper 3 m of the water column. Median abundance at 1 m versus 3 m did not differ significantly at any site, but densities at 5 m were markedly lower ($P < 0.001$). Collections from 1 m and 3 m tows were pooled in subsequent analyses.

Gizzard shad larvae were significantly more abundant ($P < 0.001$) at the cove site in the upper lake than in the main channel in 1983 (Fig. 2). In contrast, there was no sig-

Table 3. Median densities (numbers/1000 m³) of alewife and gizzard shad larvae collected at sites in Smith Mountain Lake, Virginia 1983. Mean densities in parentheses.

<u>Depth (m)</u>	<u>Lower Lake</u>				<u>Upper Lake</u>			
	<u>cove</u>		<u>main channel</u>		<u>cove</u>		<u>main channel</u>	
	<u>Alewife</u>	<u>Shad</u>	<u>Alewife</u>	<u>Shad</u>	<u>Alewife</u>	<u>Shad</u>	<u>Alewife</u>	<u>Shad</u>
1	87(121)	0(0)	45(83)	0(0)	0(0)	385(877)	0(0)	166(317)
3	154(157)	0(0)	79(159)	0(0)	0(0)	434(1040)	0(0)	88(160)
5	6(40)	0(0)	0(9)	0(0)	0(0)	0(71)	0(0)	0(21)
1+3 (pooled)	110(139)	0(0)	65(121)	0(0)	0(0)	385(959)	0(0)	130(238)

Figure 2. Densities of larval clupeids in upper and lower lake collections in 1983. Dashed line = cove; solid line = main channel; triangles = gizzard shad; dots = alewives.



nificant difference ($P=0.141$) in the density of larval alewives between cove and main channel collection sites the lower lake (Fig. 2).

Median densities of larval gizzard shad over the 4.5-month sampling period at both sites in the upper lake in 1983 were several times as great as median densities of alewife larvae at the two down-lake sites (Table 3). The greatest densities of gizzard shad at both sites occurred on June 20 (3,057 and 640/1000 m³, cove and channel sites, respectively). Peak alewife densities were encountered at the cove site on July 5 (397/1000 m³) and in the channel on July 12 (351/1000 m³).

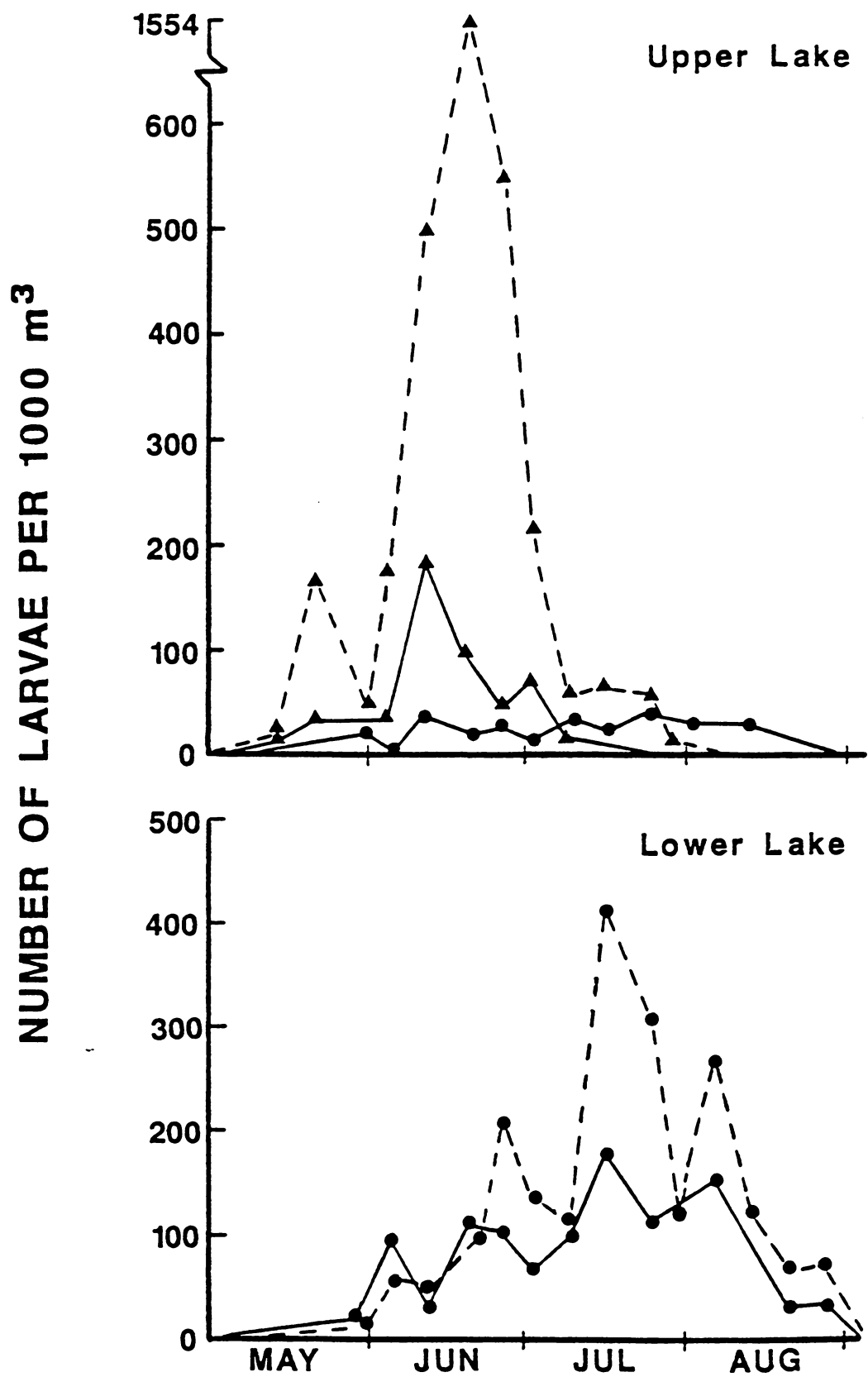
In 1984, as in 1983, only alewife larvae were collected in the lower lake, (Table 4). In the upper lake, only gizzard shad were taken at the cove site, but both gizzard shad and alewife larvae were found at the channel site (Table 4). Alewives represented 32% of the clupeids collected in the upper main channel location in 1984; however, these were only 6% of all alewife larvae collected for the entire lake that year. Vertical distributions of gizzard shad and alewife larvae were consistent with the previous year's findings. No significant difference occurred in relative abundance between 1 m and 3 m depths, with the exception of the main channel site in the lower lake where densities of larval alewives were significantly ($P=0.002$) greater at 3 m depth.

Gizzard shad were again significantly ($P<0.001$) more abundant in the nearshore (cove site) versus offshore (main channel) areas in 1984 (Fig. 3). In contrast to 1983, alewife densities were not equally abundant ($P=0.025$) in cove and main channel locations in 1984; the median densities of larvae in the cove were 1.6 times higher than the densities in the main channel (Fig. 3).

Table 4. Median densities (numbers/1000 m³) of alewife and gizzard shad larvae collected at sites in Smith Mountain Lake, Virginia 1984. Mean densities in parentheses.

<u>Depth (m)</u>	<u>Lower Lake</u>				<u>Upper Lake</u>			
	<u>cove</u>		<u>main channel</u>		<u>cove</u>		<u>main channel</u>	
	<u>Alewife</u>	<u>Shad</u>	<u>Alewife</u>	<u>Shad</u>	<u>Alewife</u>	<u>Shad</u>	<u>Alewife</u>	<u>Shad</u>
1	110(143)	0(0)	51(54)	0(0)	0(0)	93(334)	13(13)	28(66)
3	94(145)	0(0)	103(118)	0(0)	0(0)	78(231)	21(26)	16(32)
1+3 (pooled)	107(144)	0(0)	66(86)	0(0)	0(0)	80(283)	14(19)	25(49)

Figure 3. Densities of larval clupeids in upper and lower lake collections in 1984.
Dashed line = cove; solid lines = main channel; triangles = gizzard shad; dots
= alewives.



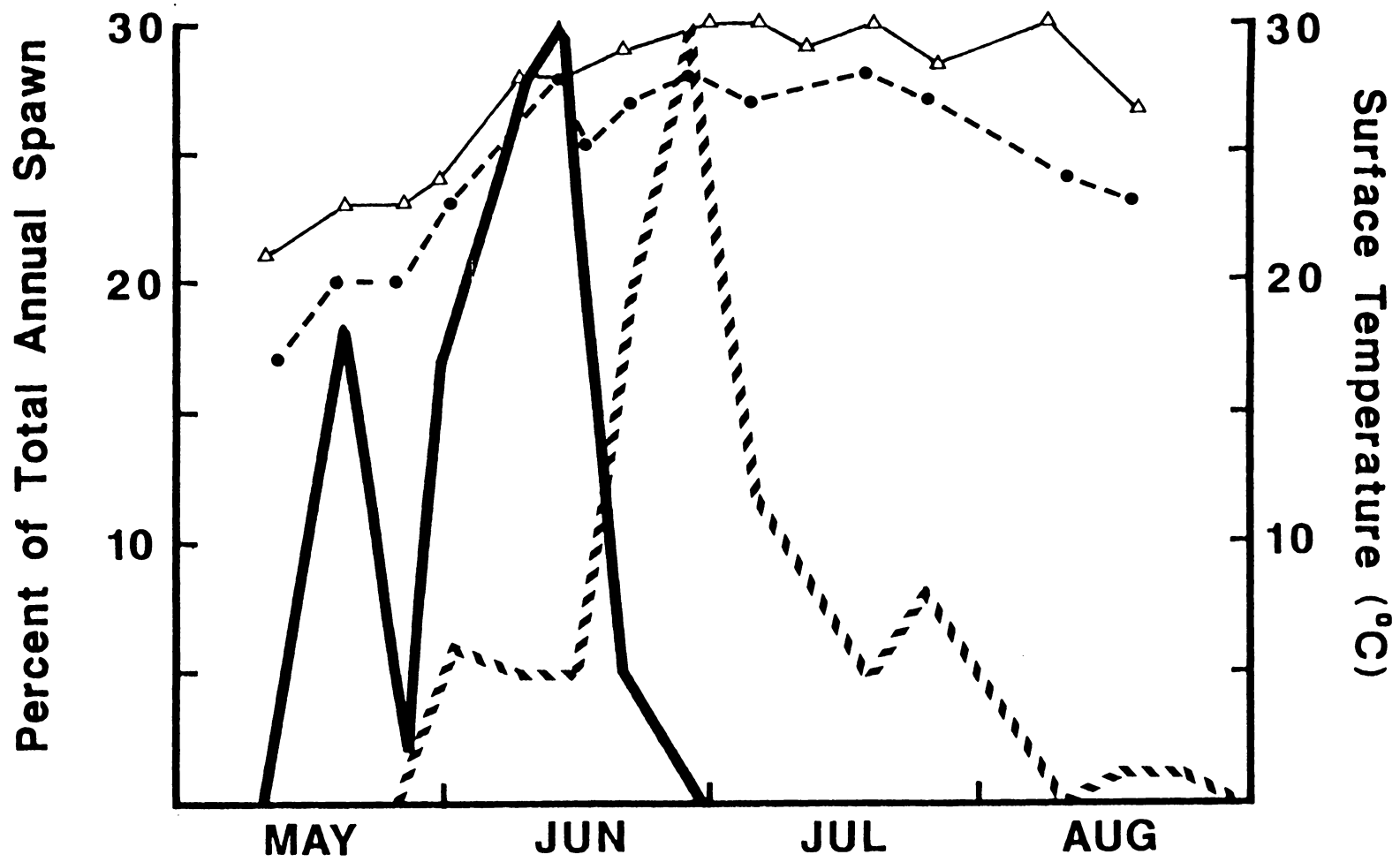
Densities of alewife larvae did not differ significantly between years in the cove ($P = 0.614$) or channel sites in the lower lake ($P = 0.649$). In the upper lake, larval gizzard shad densities were significantly different between years in the cove ($P = 0.003$) and main channel ($P = 0.001$) sites. Median densities of gizzard shad larvae at both the cove and channel sites in 1983 were more than four times greater than in 1984.

In contrast to 1983, median densities of larval alewives in 1984 at both sites in the lower lake were greater than the median densities of gizzard shad larvae at the two up-lake sites (Table 4). Peak densities of larval alewives at the cove ($450/1000 \text{ m}^3$) and channel ($164/1000 \text{ m}^3$) sites occurred on July 16. Gizzard shad larvae reached maximum densities in the cove ($1819/1000 \text{ m}^3$) and channel ($119/1000 \text{ m}^3$) sites on June 19.

Spawning Periods

In 1983, gizzard shad spawned in Smith Mountain Lake from mid May until late June at water temperatures between 22 and 29°C. Alewives had a considerably longer spawning period, lasting approximately 13 weeks. Beginning in late May, alewife spawning continued through the last week of August at water temperatures between 20 and 28°C. Peak spawning occurred later for alewives than gizzard shad in Smith Mountain Lake (Fig. 4). Gizzard shad had a minor peak at the start of their spawning period, with the major peak occurring around the middle of June. Peak spawning for alewives occurred near the first of July. Although peak spawning occurred for both species in different areas of the lake and at different times, the water temperature at which peak spawning occurred was identical (28°C) for both species (Fig. 4).

Figure 4. Temporal distribution of spawning by gizzard shad (heavy solid line) and alewife (slashed line) with corresponding surface temperatures in the upper (solid line/triangles) and lower (dashed line/dots) regions of Smith Mountain Lake 1983.



In 1984, gizzard shad spawned over an 11-week period beginning in early May and continuing through late July at surface temperatures ranging from 17-28°C. Alewives had a spawning period of approximately 12 weeks. Beginning in late May, alewife spawning continued through early August at water temperatures between 18 and 29°C. Although gizzard shad and alewives had similar spawning durations in 1984, 97% of gizzard shad spawning was completed within the first 6 weeks of their period (Fig. 5). Alewife spawning, however, was more evenly distributed over their 12-week period. In 1984, gizzard shad spawning also peaked in mid June at the same water temperature as in 1983. The major peak for alewives occurred around the beginning of the second week of July, approximately 2 weeks later than in 1983, with a minor peak in the last week of July (Fig. 5). Water temperature in which peak spawning occurred for alewives in 1984 was 26°C, 2°C cooler than the previous year.

Growth

First-year growth of both gizzard shad and alewife was examined over the entire growing season in 1984. Growth appeared to proceed in two linear phases for both species (Fig. 6). The regression of gizzard shad maximum total length versus time from hatching through the end of August was strongly linear ($r^2 = 0.96$) as was that for alewives ($r^2 = 0.97$). Over this period, gizzard shad grew at 1.33 mm/day (SE $\pm$ 0.09); alewives increased at 0.84 mm/day (SE $\pm$ 0.06). Growth decelerated in the September-November period, but still approximated a linear pattern ($r^2 = 0.89$ and 1.00 for gizzard shad and alewives, respectively). Over these three months, gizzard shad increased at 0.20 mm/day (SE $\pm$ 0.05) and alewives gained 0.30 mm/day (SE $\pm$ 0.00).

Figure 5. Temporal distribution of spawning by gizzard shad (heavy solid line) and alewife (slashed line) with corresponding surface temperatures in the upper (solid line/triangles) and lower (dashed line/dots) regions of Smith Mountain Lake 1984.

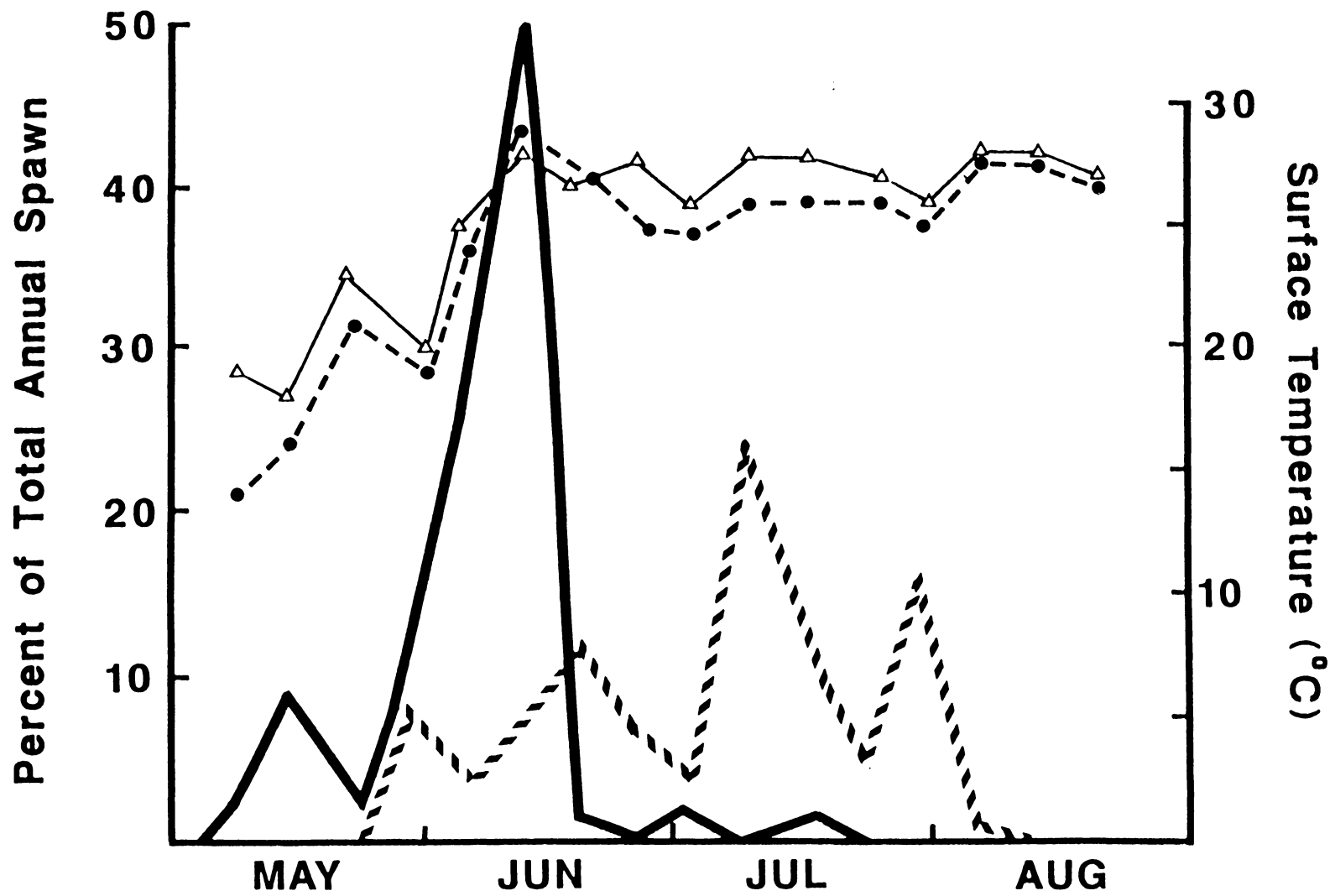
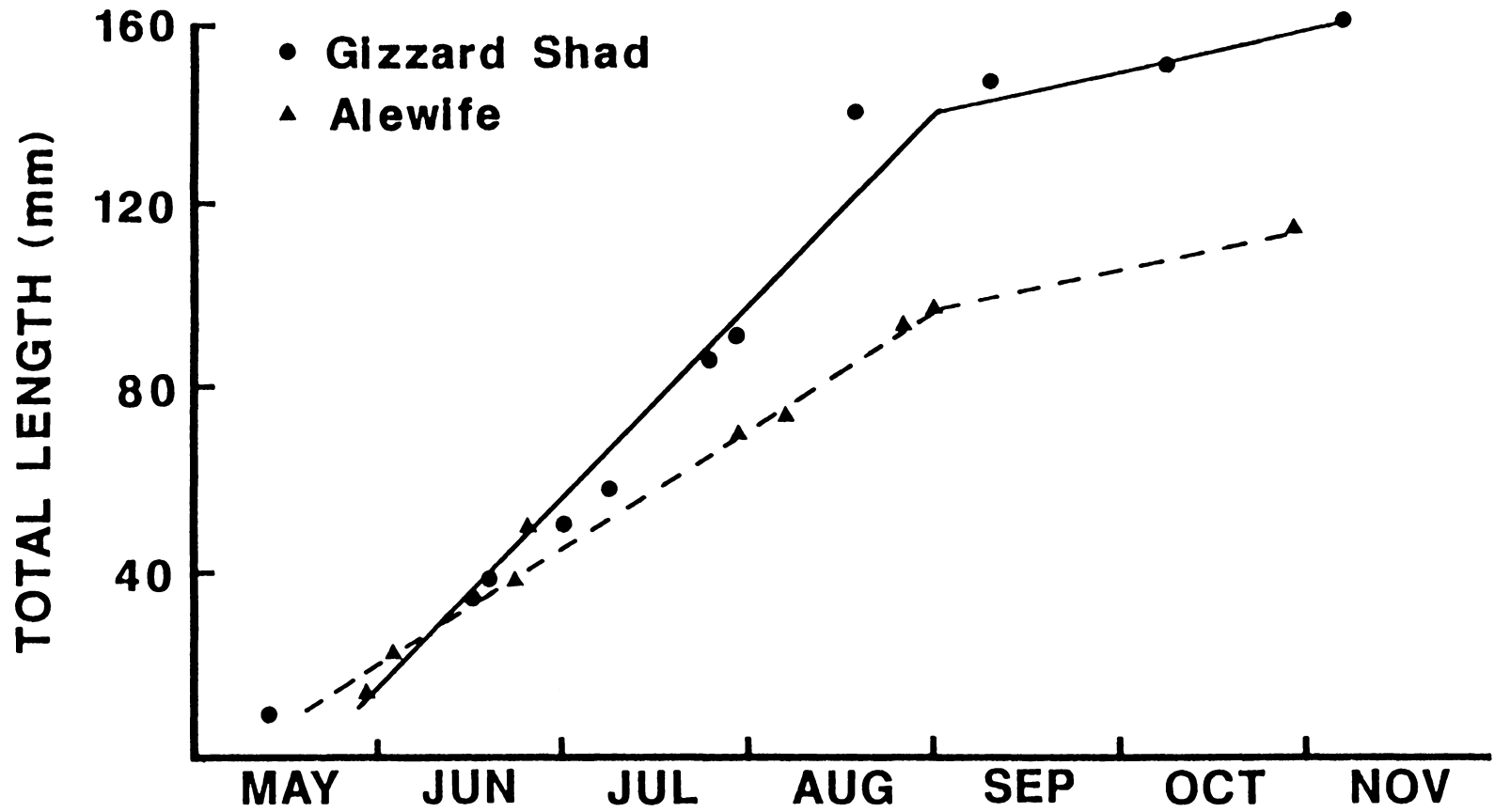


Figure 6. Patterns of first-year growth of alewife (dashed line/triangles) and gizzard shad (solid line/dots) in Smith Mountain Lake 1984. Length-at-capture (triangles/dots) are maxima and are assumed to represent first-spawned fish.



Mortality

Larval clupeids: Estimates of mortality rates for larval gizzard shad and alewives were derived for sizes ranging from 5-30 mm total length. The slope of the regression for length versus alewife daily mortality rate was not significantly different from zero ($P = 0.83$, $r^2 = 0.001$; Fig. 7). Therefore, the median value (7.1%/day, semi-quartile range 4.8% to 9.8%) was used as the estimate of daily mortality for alewives of 5 to 30 mm TL. In contrast to alewives, gizzard shad exhibited a significant ($P < 0.001$) negative linear relationship between length and mortality. However, the rate of decline did not appear to be continuous ($r^2 = 0.34$; Fig. 8). Daily mortality estimates were then divided into two length groups (5-17 mm and 18-30 mm) for further analysis, based on visual inspection of the graphed data. The daily mortality rate estimate for the 5-17 mm group were significantly ($P = 0.005$) higher than that estimated for the 18-30 mm group. Regression analysis revealed no significant relationship between length and mortality within either of the two length groups. The median value from each group, therefore, was used as the estimate of daily mortality. The daily mortality rate was 12.7% (semi-quartile range 7.8% to 14.0%) for gizzard shad 5-17 mm and 8.3% (semi-quartile range 6.2% to 9.2%) for gizzard shad 18-30 mm.

Juvenile clupeids: I was unable to capture juvenile clupeids (31-80 mm) in proportion to their abundance and consequently, could not derive their mortality rates. I could find no published mortality rates for juvenile gizzard shad and only one reported estimate for alewives in the literature. I was, however, able to derive mortality estimates for juvenile gizzard shad in Beaver Reservoir, Arkansas, using data presented by Houser and Netsch (1971) (Table 5). Because of the limited information pertaining to shad and alewives, I

Figure 7. Relationship between length and percent daily mortality rate of larval alewife in Smith Mountain Lake, Virginia.

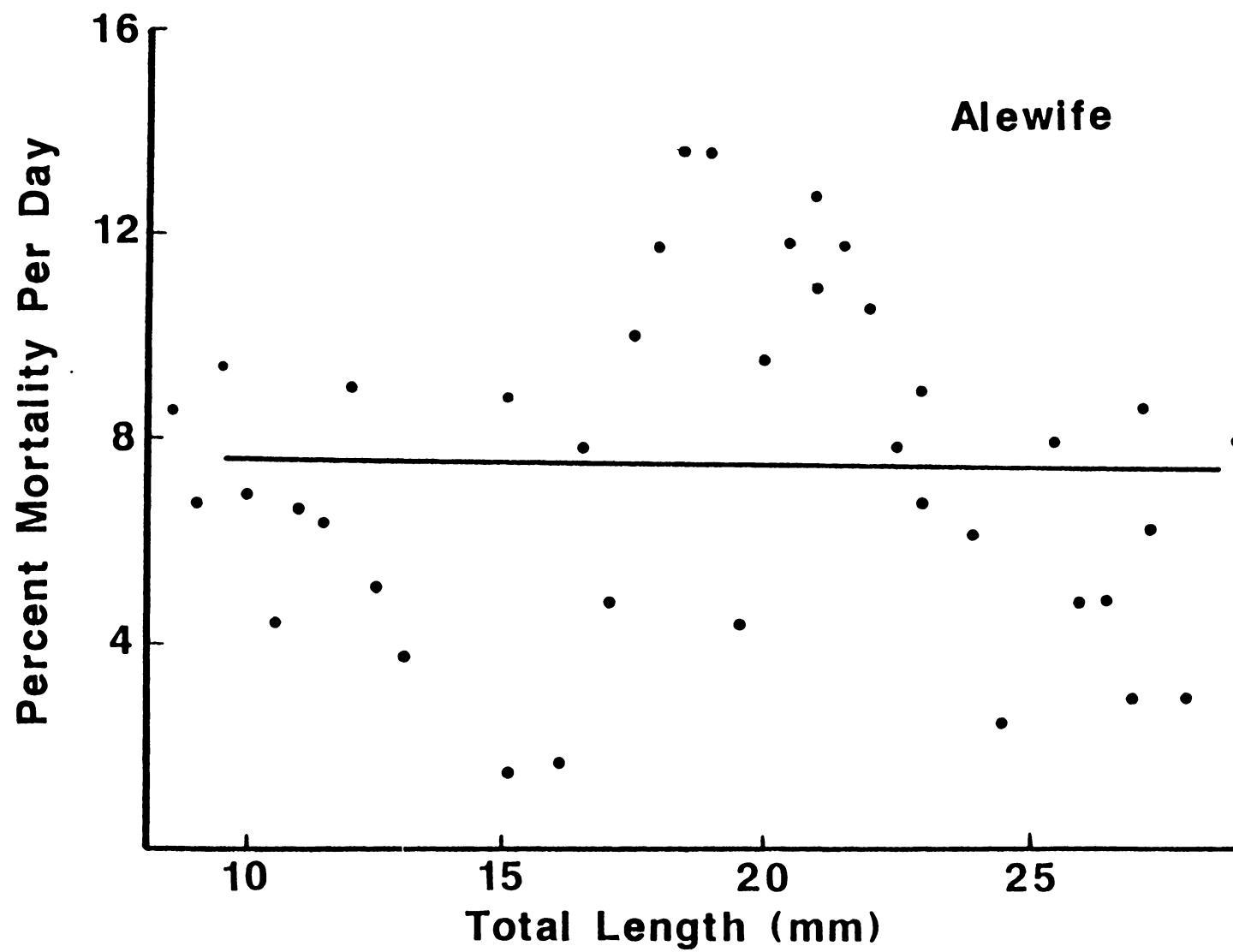


Figure 8. Relationship between length and percent daily mortality rate of larval gizzard shad in Smith Mountain Lake, Virginia.

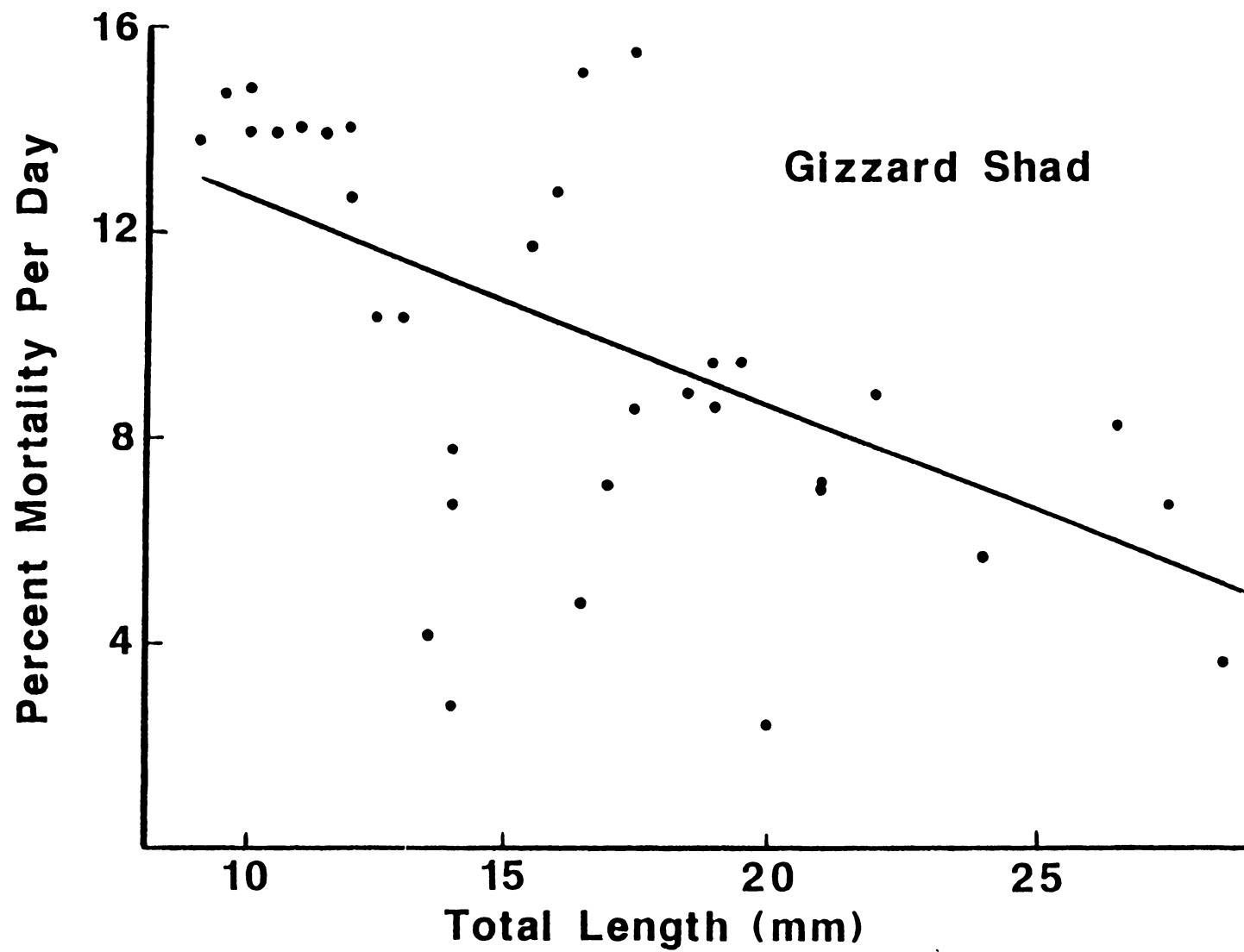


Table 5. Mortality rates for juvenile fishes reported in the literature.

Source	Species	Length (mm)	Method of calculation	Mortality rate (daily)
<u>CLUPEIDS</u>				
Mansfield and Jude (1986)	<u>Alosa pseudoharengus</u>	21-80	Length-frequency	2.1 - 2.5%
Houser and Netsch (1971)	<u>Dorosoma cepedianum</u>	30-80	Length-frequency	*1.0 - 3.0%
Crecco et al. (1983)	<u>Alosa sapidissima</u>	40-80	Catch curve	1.8 - 2.0%
<u>OTHER</u>				
Smith (1985)	<u>Engraulis mordax</u>	35-60	Postulated	1.0%
Smith (1985)	<u>Engraulis mordax</u>	60-85	Postulated	2.0%
Lockwood (1981)	<u>Pleuronectes platessa</u>	35-54	Population estimates	1.5%
Dey (1981)	<u>Morone saxatilis</u>	≥ 50	Catch curve	0.5%

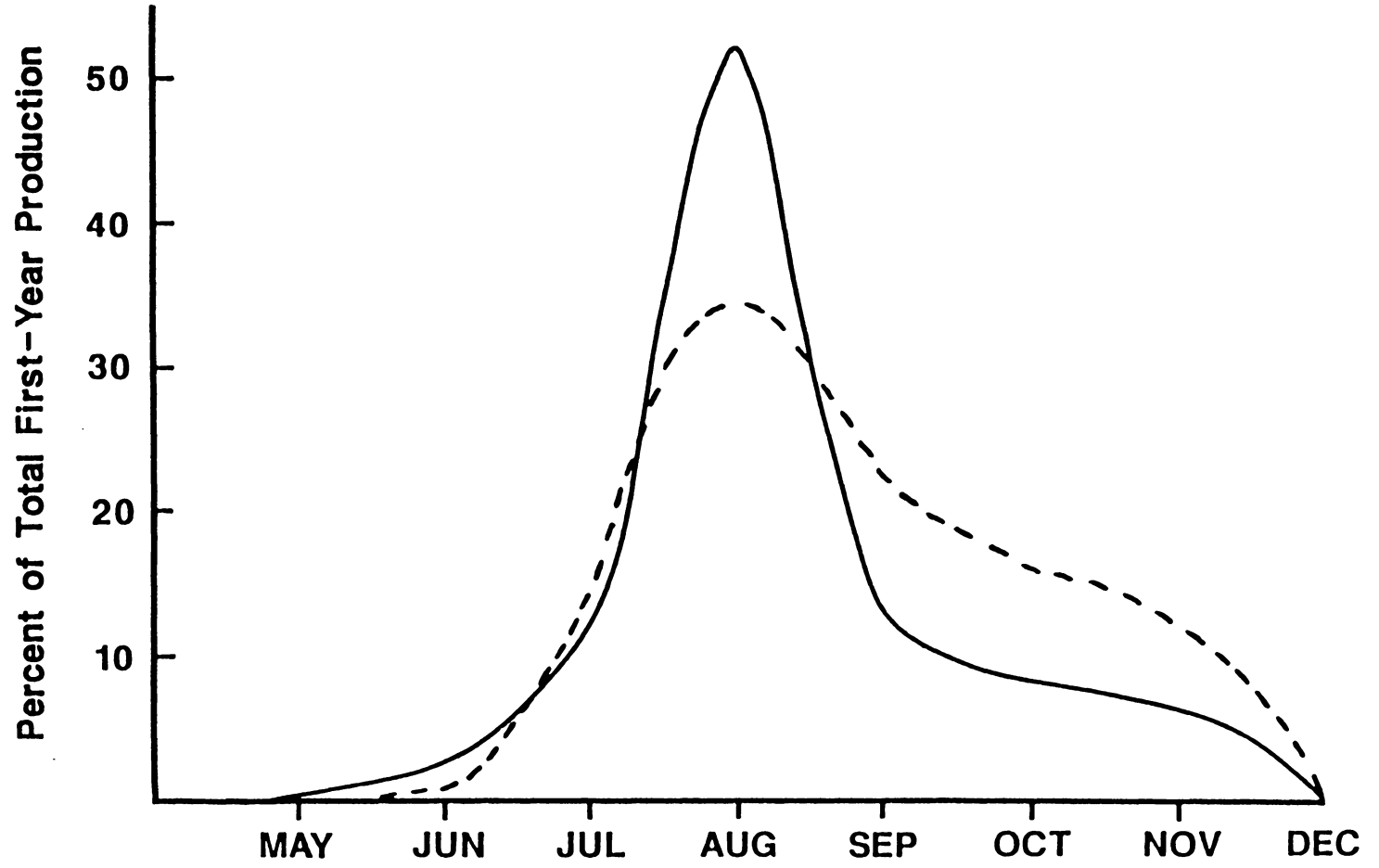
*Derived from data presented by Houser and Netsch (1971)

also focused on mortality rates for other clupeid and similar species in the literature (Table 5). Essentially, daily mortality rates appear to average approximately 2%/day in the earlier juvenile stages (30-60 mm) and 1%/day in the later stages. Therefore, I used a mortality rate of 2%/day for all clupeids between 31 and 60 mm TL and 1%/day for fish > 60 mm TL (through the end of their first season of growth). Mortality rates were assumed to be the same for alewives and gizzard shad because of the similarity between their reported estimates (Table 5), and lack of information to support an assumption to the contrary.

Age-0 Production Patterns

Age-0 gizzard shad and alewife production patterns are similar in that they both peak in late August and drop sharply thereafter (Fig. 9). They differ, however, in that nearly 50% of the alewife production still occurs after September 1 compared to only 25% for gizzard shad. The median weekly production estimate per initial cohort of 1000 larvae was more than three times as high for gizzard shad (28.0 g/wk, semi-quartile range 22.4 and 82.8) compared to alewives (8.0 g/wk, semi-quartile range 6.1 and 10.4). Total first-year production for gizzard shad was more than 6 times higher than for alewives based on an initial cohort of 1000 individuals per species (Appendix Tables 3 and 4, respectively). However, absolute abundances of alewives and shad could not be determined, and so relevance of first year production comparisons is limited to the temporal patterns.

Figure 9. Pattern of total first-year production of gizzard shad (solid line) and alewife (dashed line) cohorts in Smith Mountain Lake, Virginia 1984.



Availability of Young-of-the-Year Gizzard Shad and Alewife to Age-0 and -1 Predators

Striped bass and walleye are stocked annually around July 1 at approximately 50 mm total length (D.K. Whitehurst, VDGIF, personal communication) and become piscivorous at about 100 mm total length (Gomez 1970; Ney 1978), a size achieved by early August in Smith Mountain Lake (Ricci and Ney 1978). Largemouth bass become piscivorous at approximately 80 mm total length (Scott and Crossman 1973). In Smith Mountain Lake, largemouth bass spawned in May reach 80 mm in early August (Ricci and Ney 1978). Lacking data to the contrary, I assumed that variability in growth among age-0 individuals within their respective cohorts was negligible until they became piscivorous in early August. Length-at-age data were used to estimate subsequent variability of growth (median length with semi-quartile range) within a cohort as previously described.

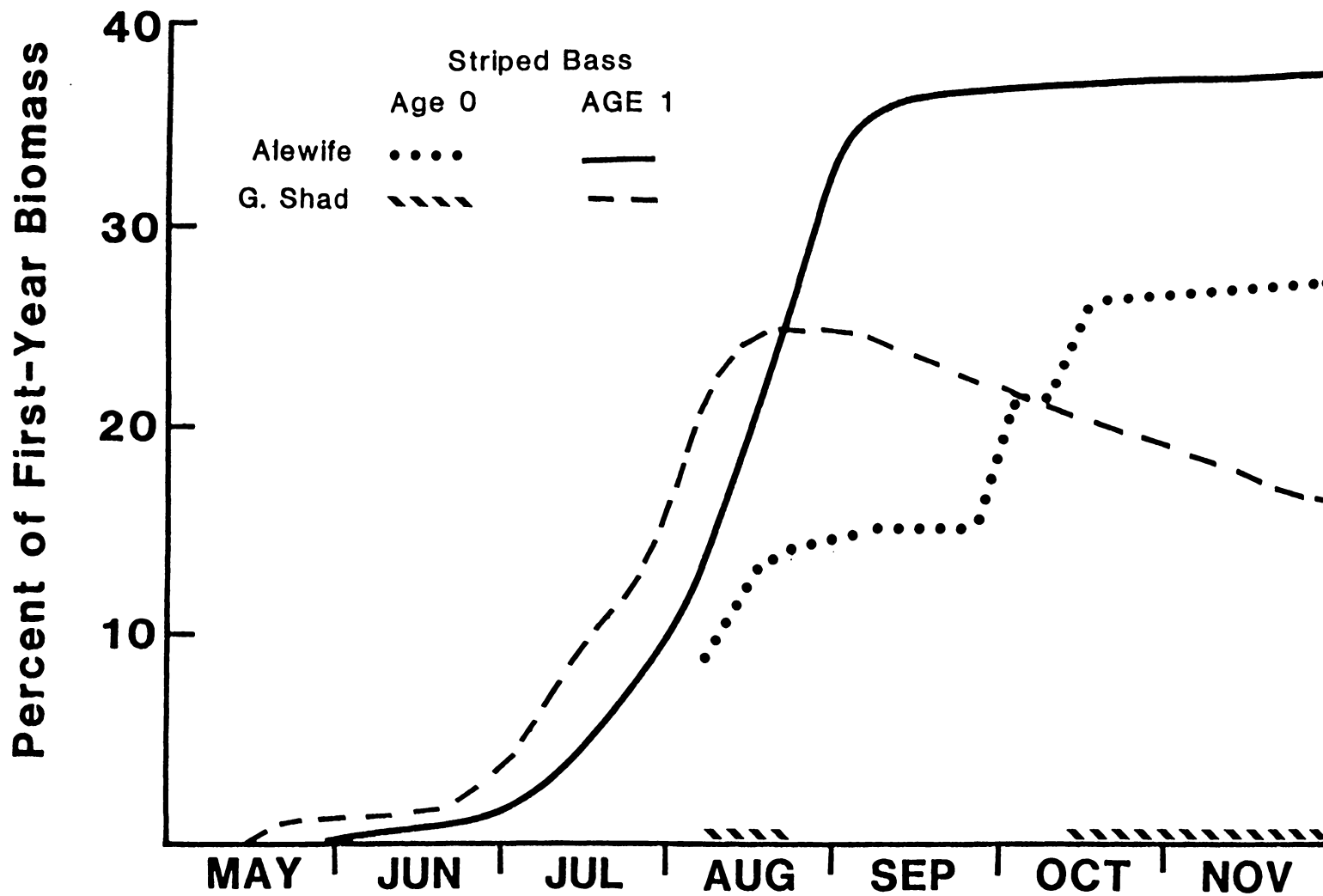
Two procedures were used to compare morphological availability of age-0 alewives and gizzard shad to juvenile piscivores. In-season patterns of availability were calculated as the amount of alewife or gizzard shad biomass extant and ingestible at weekly intervals. Biomass was determined for each subcohort (initial sum of subcohorts equals 1000 individuals) in the calculations of first-year production by subjecting it to daily growth and mortality rate functions. For each successive date, the maximum total length of gizzard shad or alewife ingestible by the predator was estimated by the method of Jenkins and Morais (1978). The biomass of all subcohorts less than or equal to this size was then summed to determine total available biomass (Appendix Tables 5-10). To directly compare alewife and gizzard shad availability patterns on the same scale, I divided

the actual biomass available by total first-year biomass produced by the 1000-fish cohort of each species. In the first year of life, total production is the sum of all cohort biomass made to date; there is no carry-over from previous years. The resulting graphical depictions, therefore, show the percentage of the biomass produced during the year which can be eaten at any particular time if it had not been eaten before. Substitution of production for biomass in these temporal comparisons would be incorrect because it is the amount of prey present (the result of earlier production) that defines the potential food supply at any point in time.

In the second procedure, I determined the cumulative percentage of first-year biomass produced by the clupeid cohorts that could be eaten over the course of the growing season by the various juvenile predators (Appendix Tables 11-16). The procedure was as for the in-season biomass analysis except that I summed weekly subcohort production ingestible rather than biomass and totaled weekly sums for the growing season. Biomass could not be used to compare total first-year morphological availabilities because it is not additive, whereas production is time-specific.

Striped bass: The patterns of age-0 alewife and gizzard shad availability to striped bass ages 0 and 1 are depicted in Figure 10. Age-0 striped bass of average (median) total length can consume only 0.14% of the first-year gizzard shad production (semi-quartile range 0.10 to 0.19% for 25th and 75th percentile-length striped bass). The smallest gizzard shad are morphologically available when striped bass become piscivorous in early August and again from mid October to late November. In contrast to gizzard shad, alewives provide a continuous supply of forage to age-0 striped bass from the time they become piscivorous through the end of the growing season (Fig. 10). Overall, 58%

Figure 10. Percent of first-year biomass of age-0 gizzard shad and alewife ingestible by median length striped bass ages 0 and 1 in Smith Mountain Lake 1984.



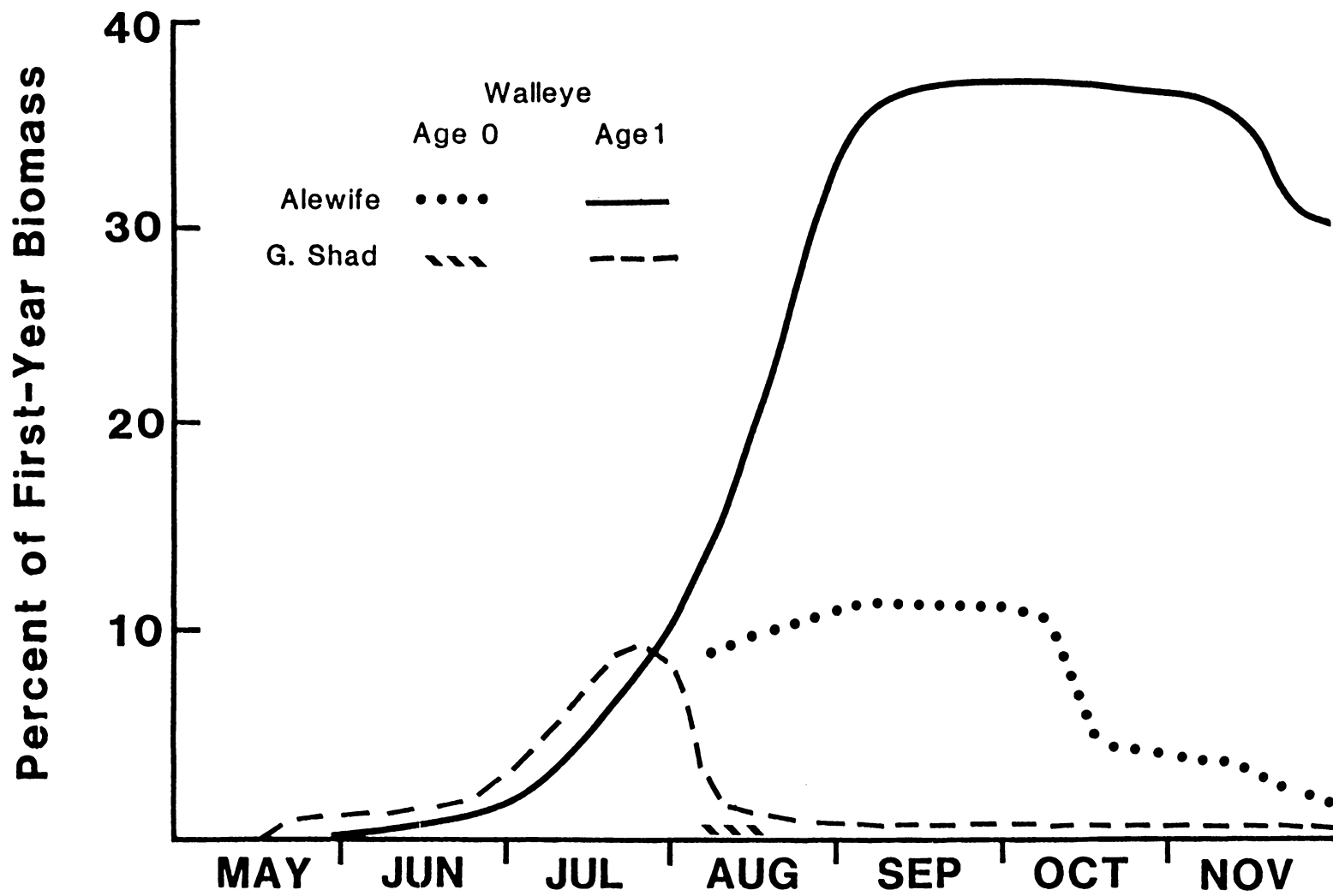
of the first-year alewife production is ingestible by median-length striped bass during their first season of growth (semi-quartile range 47% to 68%).

Age-1 striped bass can ingest all sizes of age-0 alewife throughout the growing season from the time of alewife hatch; all first-year alewife production is morphologically available to them (Fig. 10). However, young-of-the-year gizzard shad begin to outgrow the ingestibility limits of age-1 striped bass by early September, and the fraction of existing gizzard shad production that can be eaten progressively declines. For the year, 66% of the first-year shad production is available to age-1 striped bass of average total length (semi-quartile range 58 to 76%). Age-1 striped bass can also consume same-age alewives in the spring, a period when no age-1 gizzard shad are small enough to be eaten by them.

Walleye: The patterns of age-0 alewife and gizzard shad availability to ages 0 and 1 walleye are illustrated in Figure 11. Walleye are more sharply constrained in their consumption of gizzard shad than striped bass because of their smaller mouth gape. Age-0 walleye can eat only the smallest age-0 gizzard shad (latest spawned) for a few weeks in early August before the shad outgrow their ingestibility limits; available shad production constitute < 0.05% of the total first-year shad biomass produced.

Availability patterns indicate that age-0 alewives, unlike gizzard shad, provide a continuous and uninterrupted food supply until the end of the growing season for age-0 walleye (Fig. 11). Age-0 walleye of average length have about 36% (semi-quartile range 30 to 39%) of first-year alewife production morphologically available to them. Age-1 walleye can feed on some young-of-the-year gizzard shad until the end of the growing

Figure 11. Percent of first-year biomass of age-0 gizzard shad and alewife ingestible by median length walleye ages 0 and 1 in Smith Mountain Lake 1984.

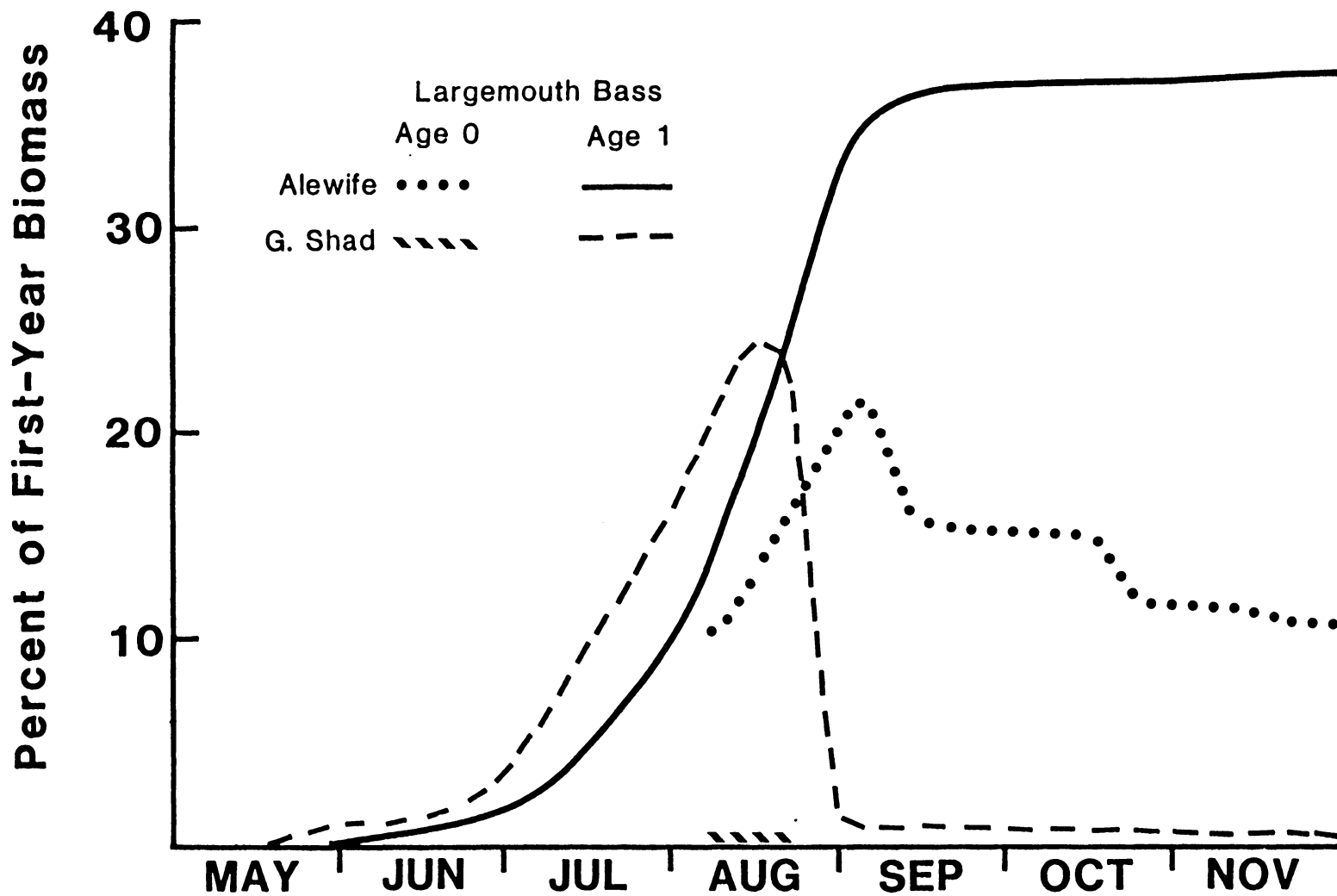


season, but this constitutes only 21% (semi-quartile range 19 to 28%) of the first-year shad biomass produced. Further, available shad production begins to drop sharply by late July (Fig. 11). The months of September, October and November account for only 0.10% of the total available shad supply (21%) to age-1 walleye. In contrast to age-0 gizzard shad, 99% (semi-quartile range 95 to 100%) of first-year alewife production is available to age-1 walleye, of this about 48% is available during the fall. Unlike striped bass, one-year old walleye cannot ingest age-1 alewives and thereby remediate a potential spring prey deficiency.

Largemouth bass: Prey availability patterns indicate that age-0 largemouth bass of median length can only feed on age-0 gizzard shad for about three weeks in August (Fig. 12); only 0.15% of first-year gizzard shad production is available to them (semi-quartile range 0.09 to 0.33% for 25th and 75th percentile-length bass). However, as for striped bass, alewives extend morphological availability of clupeid prey through the end of the growing season (Fig. 12); an estimated 52% of the first-year alewife production is available for median-length largemouth bass (semi-quartile range 38 to 78%).

Age-1 largemouth bass can consume some age-0 gizzard shad from the time of gizzard shad hatch through the end of the growing season (47% of the first-year shad production is morphologically available to them; semi-quartile range 26 to 68%). By late August, the available supply of age-0 gizzard shad for age-1 largemouth bass has diminished sharply with more than one-third the growing season still remaining (Fig. 12). However, like striped bass, age-1 largemouth bass can ingest all sizes of age-0 alewives throughout the growing season from the time of alewife hatch; all first-year alewife production is morphologically available to them (Fig. 12). During the fall, 49%

Figure 12. Percent of first-year biomass of age-0 gizzard shad and alewife ingestible by median length largemouth bass ages 0 and 1 in Smith Mountain Lake 1984.



of first-year alewife production is still available to age-1 largemouth bass and could mitigate low availability of gizzard shad during this same period. Age-1 gizzard shad are not morphologically available to same-age largemouth bass; however, some same-age alewives are available which provides an alternative to a potential spring prey deficiency resulting from the absence of morphologically vulnerable shad.

In summary, prey availability patterns indicate that age-0 gizzard shad are virtually invulnerable to same-age piscivores except in August and in the late fall; in both periods only a small fraction of shad biomass produced can be eaten. In contrast to gizzard shad, age-0 alewives extend prey availability for age-0 sport fish from the time they become piscivorous in August until the end of the growing season. Age-0 gizzard shad also begin to outgrow the ingestibility limits of age-1 walleye in July, largemouth bass in August and striped bass in September. However, all three of these piscivores have almost all first-year alewife production available to them. Unlike walleye, age-1 striped bass and largemouth bass can also eat same-age alewives in the spring, a period when no gizzard shad are morphologically available to age-1 piscivores and neither clupeid has produced a new cohort of young.

Lifespan Supply and Demand Relationships

This analysis examines availability of cohorts (age groups) of alewife and gizzard shad over their lifespans to successive cohorts of striped bass, walleye, and largemouth bass. Its purpose is to identify later periods in the lives of these predators when the supply of either forage species might be inadequate to meet their trophic demands and

to assess the degree to which the combined availability of alewife and gizzard shad resolves the deficiency.

The analysis proceeds for each piscivore in three phases. First, ingestibility limits on alewives and gizzard shad for the various age groups of the piscivore are estimated using the modified version of the von Bertalanffy growth model to simulate total length of each species throughout its life, and the Jenkins-Morais equations to transform piscivore total length to maximum total length of ingestible prey. Second, patterns of age-specific cohort supply (forage fish) and demand (piscivore) in terms of production are calculated over each species' lifespan. Calculations assume each cohort initially consists of 1000 individuals and further assume that production is an accurate index of both supply and demand. Production estimates calculated in the previous section for young-of-the-year gizzard shad and alewife are expanded here to describe cohort lifespan production patterns. Adult prey and predator production estimates are derived from annual mortality estimates and length-at-age data. Third, ingestibility limits on each forage species for a particular piscivore are applied to the corresponding cohort production data to derive age-specific and cohort-specific available forage supply and the piscivore demand on it. The analysis first examines the vulnerability of a specific prey cohort to successive age groups of the coexisting predator cohorts over their concurrent lifespans and then, reversing the perspective, the availability of all prey cohorts to each age group of the predator in the system. Supply-and-demand comparisons are made in terms of the percentage of lifetime production available or required. Comparison of weight data would misrepresent supply-demand relationships (it is intuitively obvious that a cohort of striped bass will consume more than 1000 gizzard shad over its lifetime) unless absolute abundance of predators and prey form the basis of this comparison. Estimations of

absolute abundance of these species in Smith Mountain Lake was beyond the scope of this work.

Growth and Mortality

Alewives and gizzard shad achieved 54% and 42% of their maximum length during their first season of growth, respectively. (Table 1). Variability in total length at age would be expected to be high in these clupeids given their extended spawning seasons. The semi-quartile range for gizzard shad was 13%-15% of the median total length at ages 1 and 7 versus approximately 20% for the intermediate age-groups (2-6). In contrast to gizzard shad, semi-quartile variability in total length for alewives was highest for age-1 fish (25%) and progressively declined to 15% and 12% at ages 2 and 3, respectively.

Age-1 sport fish exhibited the greatest variability in total length; the semi-quartile range represented 34% (striped bass), 39% (walleye) and 65% (largemouth bass) of their respective median total length at age (Table 2). Variability decreased dramatically for older sport fish ($\geq$ age 2) and ranged from 10% to 21% based on their semi-quartile range as percent of median total length. The modified version of the von Bertalanffy growth function was used to describe median and semi-quartile growth for all age groups of prey (except first-year growth of gizzard shad and alewife) and piscivores. Estimates for von Bertalanffy growth parameters are presented in Table 6 for both prey and sportfish species; growth equations are graphically depicted in Figures 13 (gizzard shad), 14 (alewife), 15 (striped bass), 16 (walleye) and 17 (largemouth bass).

Table 6. Estimates of the von Bertalanffy growth parameters for clupeids and sport fish in Smith Mountain Lake.

Species (Percentile)	Growth Parameters				
	LINF TL(mm)	K (year ⁻¹)	T ₀ (April 1)	A	T _∞ (years)
Striped Bass (25th)	795	0.3400	0.0060	0.0612	0.8177
Striped Bass (median)	915	0.2781	-0.2000	0.0658	0.9503
Striped Bass (75th)	1025	0.2800	-0.1185	0.0599	1.0000
Walleye (25th)	580	0.4207	0.0515	0.0858	0.7535
Walleye (median)	600	0.4599	0.0293	0.0868	0.7853
Walleye (75th)	640	0.4941	0.0000	0.0896	0.8355
Largemouth Bass (25th)	456	0.4238	0.1887	0.0771	0.8334
Largemouth Bass (median)	548	0.2958	-0.3000	0.0717	0.7784
Largemouth Bass (75th)	629	0.2076	-1.0000	0.0380	0.8149
Gizzard Shad (25th)	375	0.1943	-1.0000	0.0578	1.0000
Gizzard Shad (median)	390	0.2278	-0.9979	0.0415	0.8335
Gizzard Shad (75th)	400	0.2674	-0.8010	0.0487	0.8335
Alewife (25th)	2805	0.0137	-1.1111	0.0025	0.8332
Alewife (median)	3100	0.0123	-1.4000	0.0022	0.8352
Alewife (75th)	3624	0.0102	-1.7987	0.0020	0.7999

Figure 13. Predicted median (solid line) and semi-quartile (dashed lines) seasonal growth of gizzard shad in Smith Mountain Lake. Growth curves were derived from a modified von Bertalanffy growth function fit to 25th (open stars), median (dots) and 75th (closed stars) percentile length-at-age data.

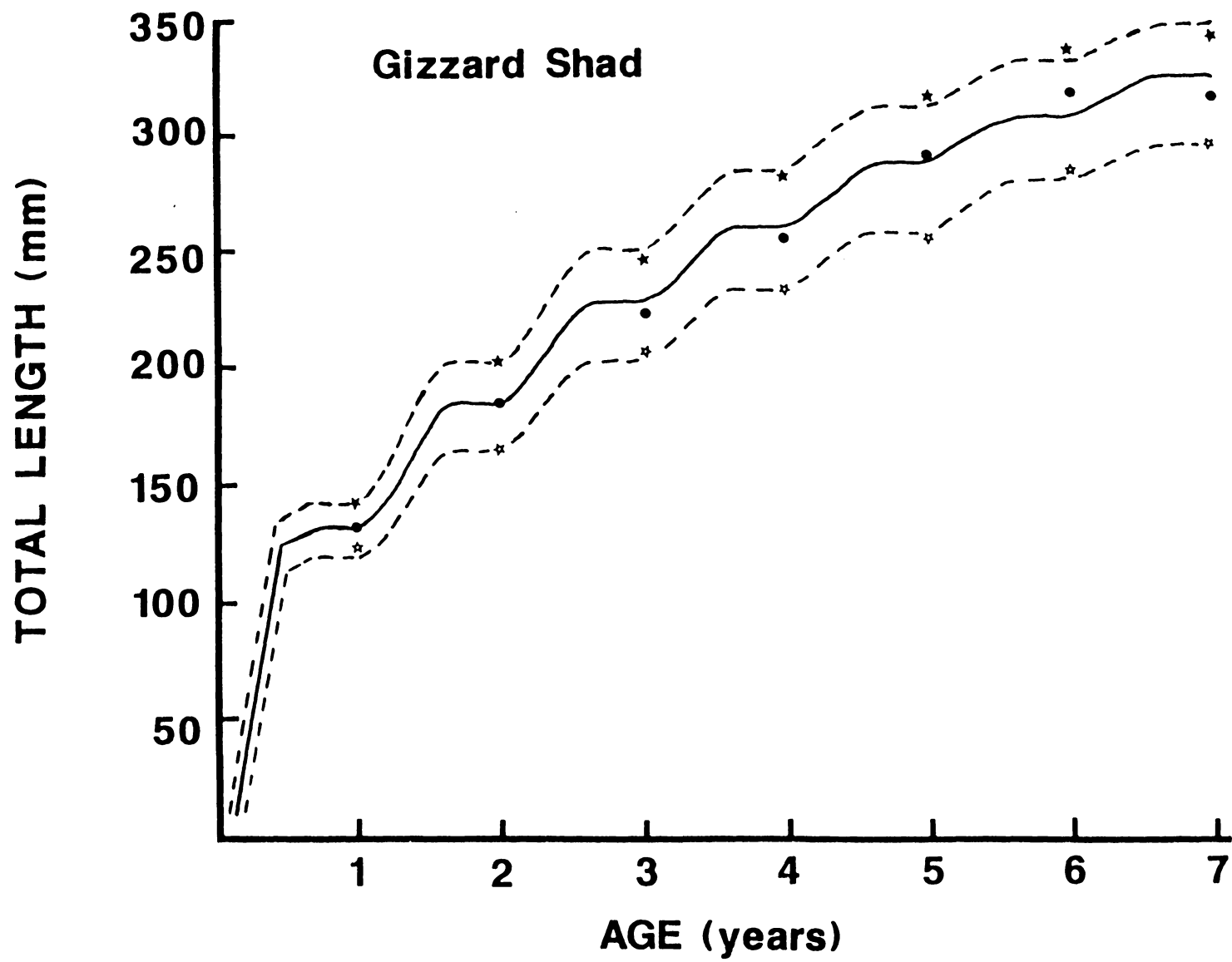


Figure 14. Predicted median (solid line) and semi-quartile (dashed lines) seasonal growth of alewife in Smith Mountain Lake. Growth curves were derived from a modified von Bertalanffy growth function fit to 25th (open stars), median (dots) and 75th (closed stars) percentile length-at-age data.

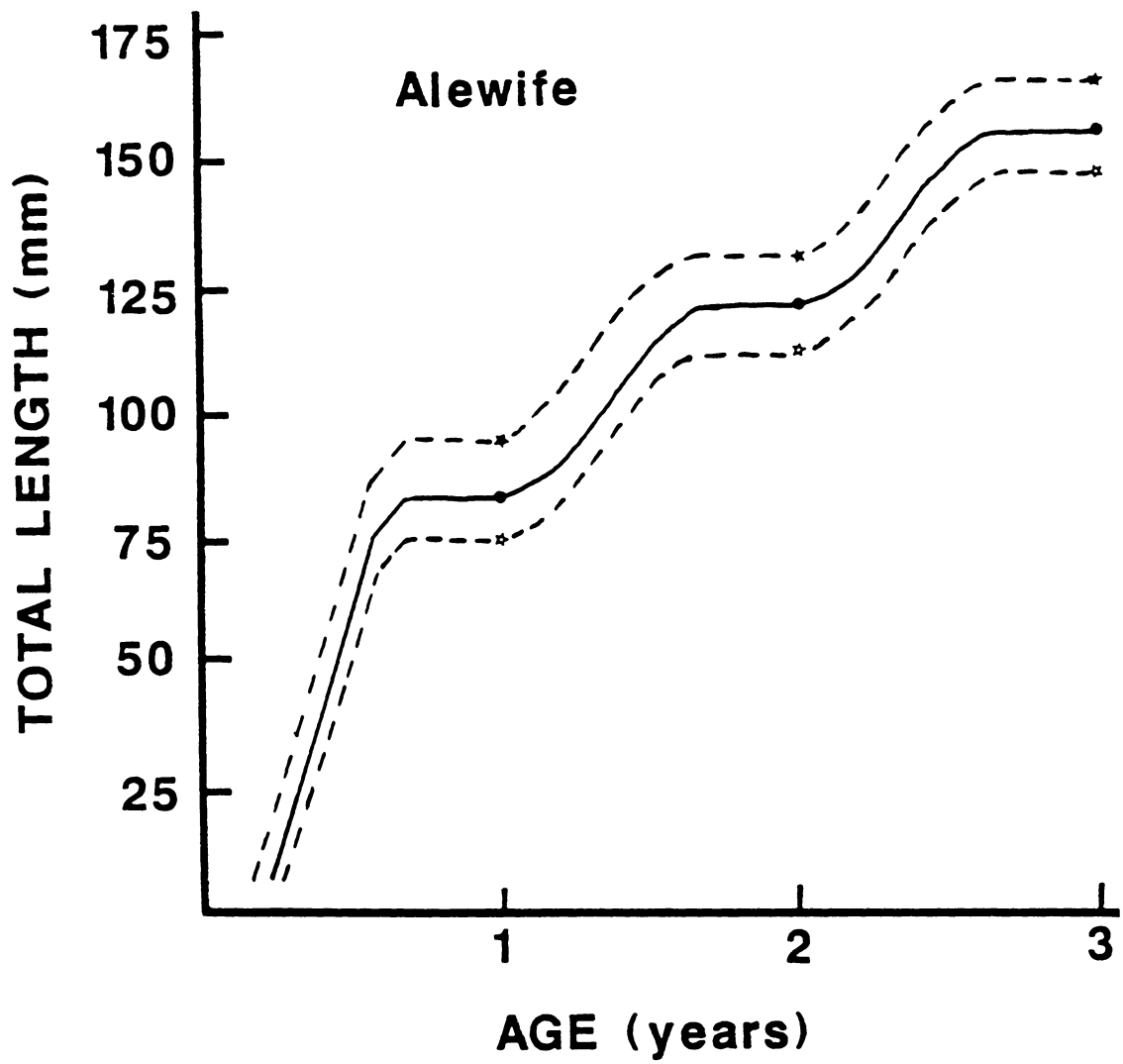


Figure 15. Predicted median (solid line) and semi-quartile (dashed lines) seasonal growth of striped bass in Smith Mountain Lake. Growth curves were derived from a modified von Bertalanffy growth function fit to monthly median lengths (dots) and length-at-age data for 25th (open stars) and 75th (closed stars) percentile growth.

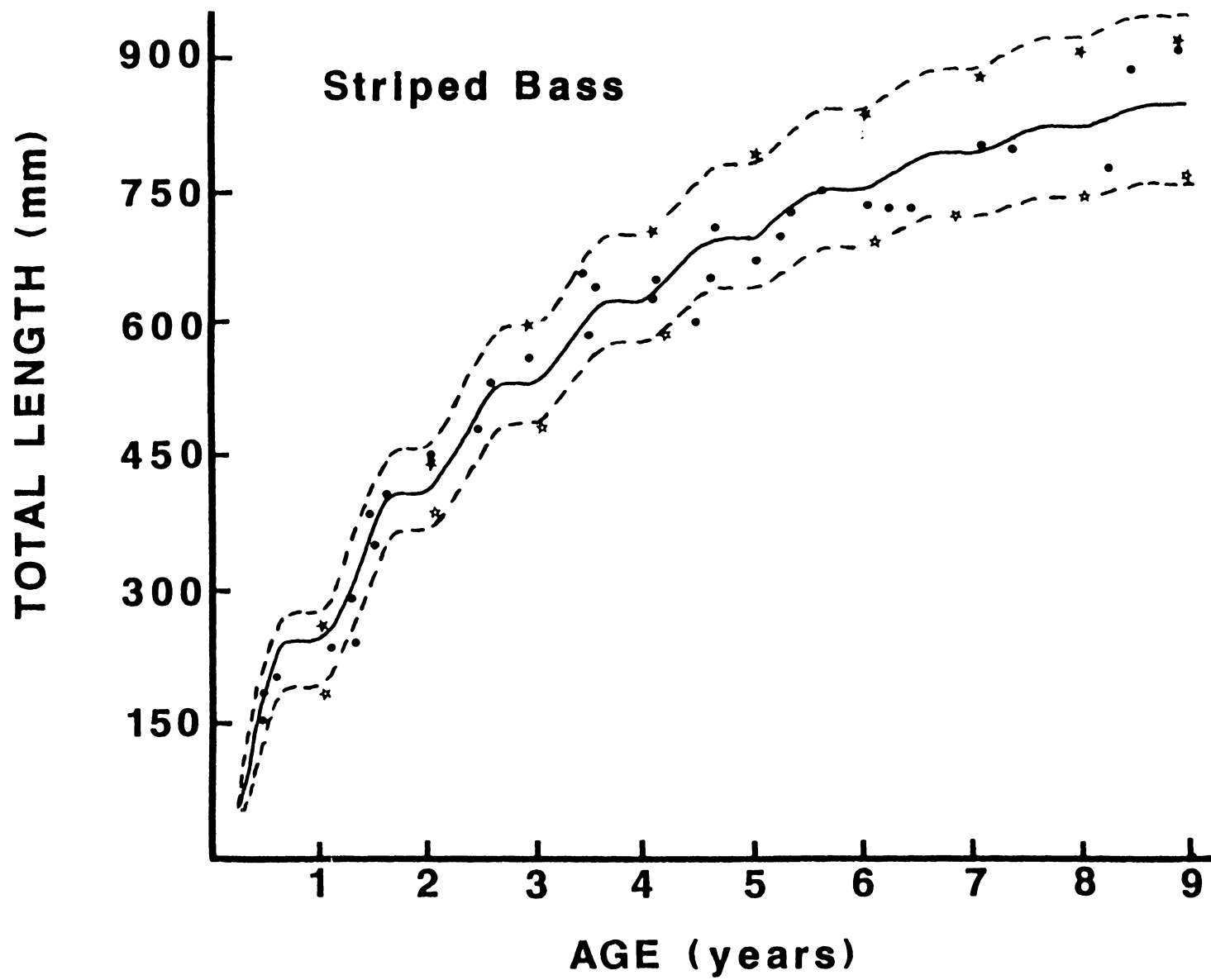


Figure 16. Predicted median (solid line) and semi-quartile (dashed lines) seasonal growth of walleye in Smith Mountain Lake. Growth curves were derived from a modified von Bertalanffy growth function fit to 25th (open stars), median (dots) and 75th (closed stars) percentile length-at-age data.

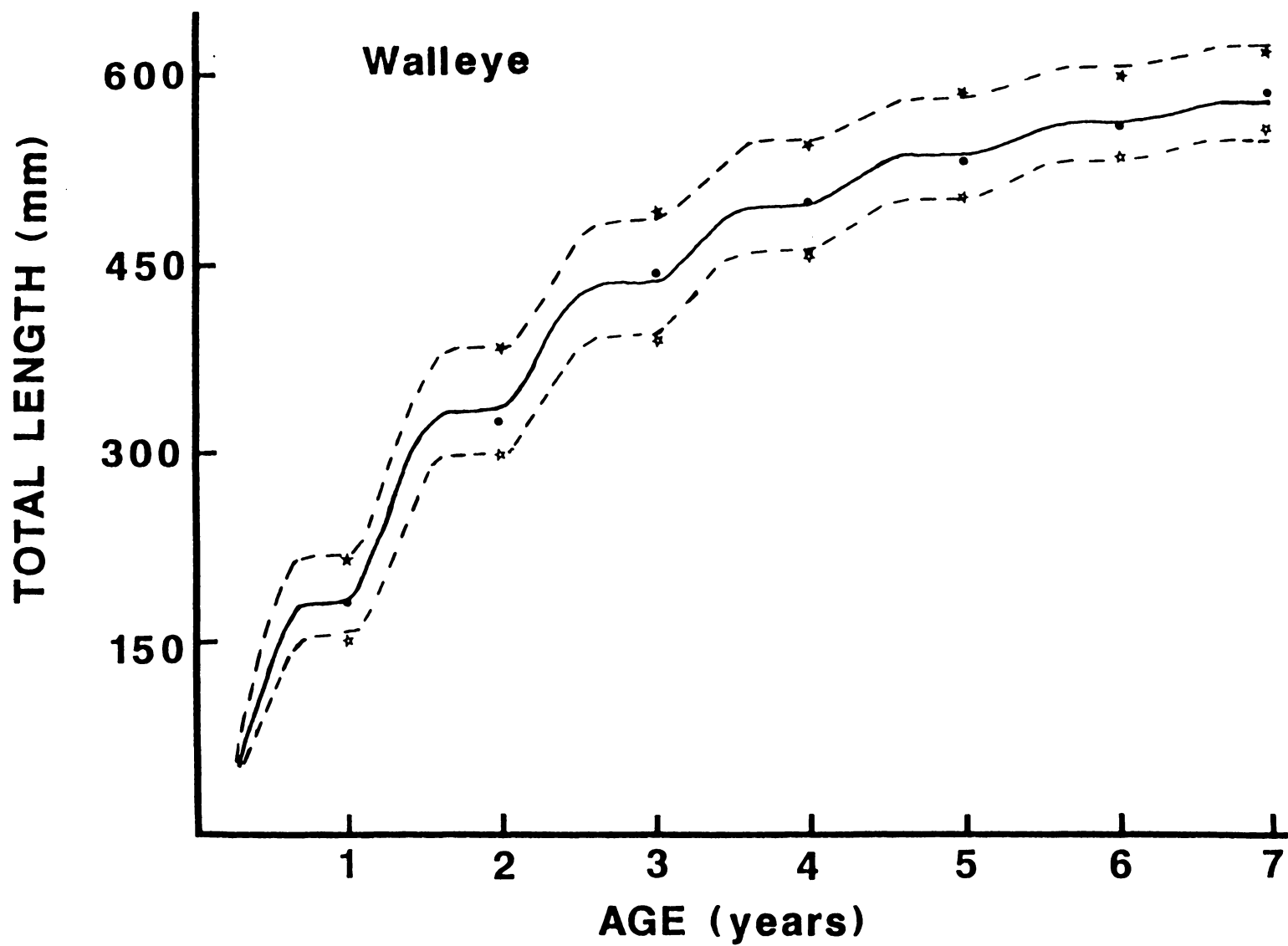
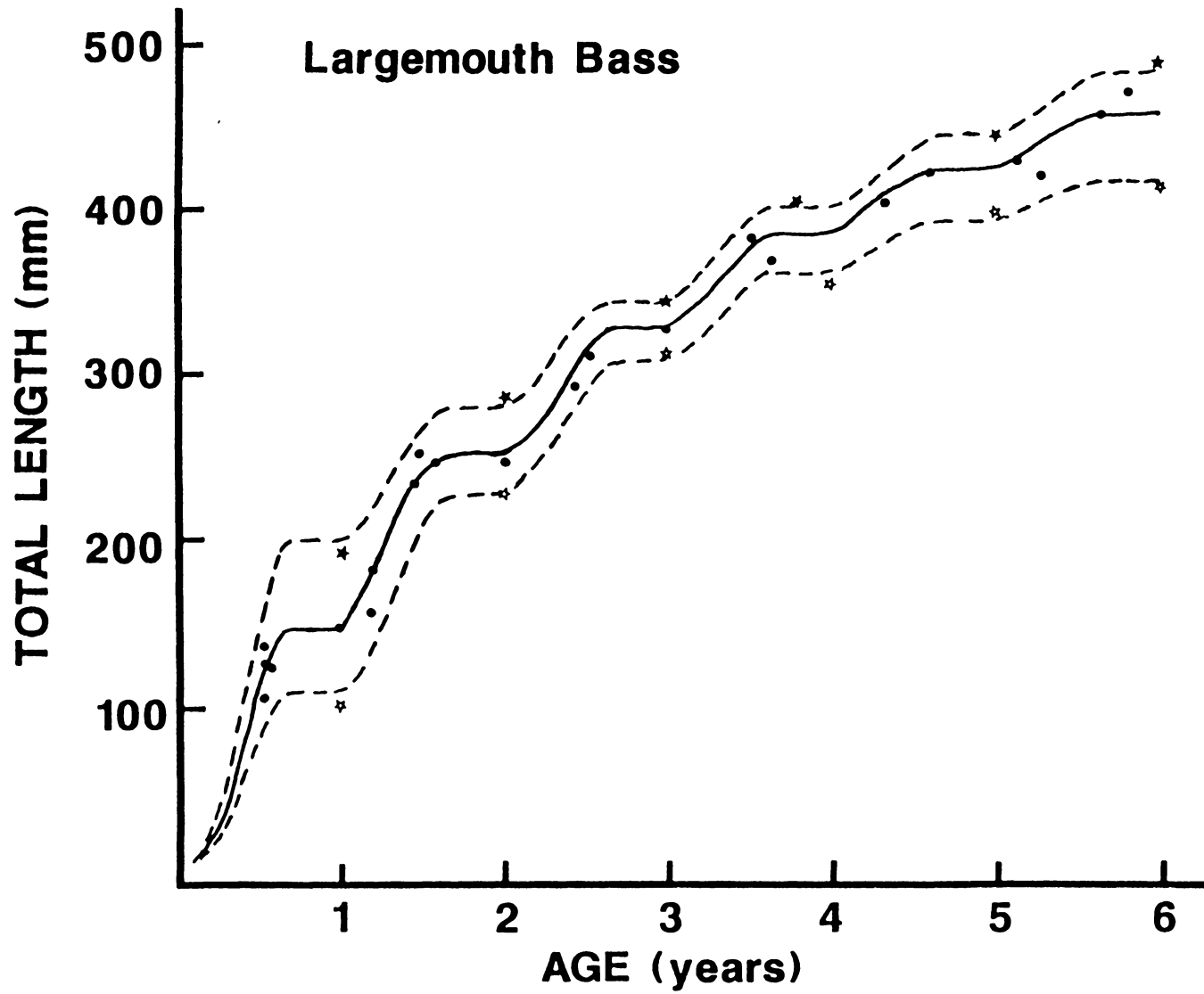


Figure 17. Predicted median (solid line) and semi-quartile (dashed lines) seasonal growth of largemouth bass in Smith Mountain Lake. Growth curves were derived from a modified von Bertalanffy growth function fit to monthly median lengths (dots) and length-at-age data for 25th (open stars) and 75th (closed stars) percentile growth.



Annual mortality estimates for adult gizzard shad were derived using the catch curve method (Ricker 1975) on cove rotenone data from Smith Mountain Lake (Table 7). Based on those estimates, I selected 70% as a representative annual mortality for gizzard shad (starting January 1 after their first season of growth) in Smith Mountain Lake. Annual mortality estimates for alewives were derived from cove rotenone and from gillnet CPUE data (Table 7). Given the close agreement between the two estimates, I assumed an annual mortality rate of 80% for adult alewives (starting January 1 after their first season of growth).

Annual mortality rates for predators were estimated by Moore (1988). First-year mortality of striped bass and walleye was estimated at 79%, with subsequent years at 60% and 41%, respectively. Estimated annual mortality of largemouth bass was 47% for age-0 fish, 71% for age 1, and 62% for bass $\geq$ age 2.

Ingestibility Limits

This analysis considers the variability in total length of predator and prey over their concurrent lifespans to assess when the former can consume the latter. In the previous section, all weekly subcohorts of prey were considered when assessing first-year prey availability to age-0 and 1 predators. In this section, the analysis centers on the use of median, 25th, and 75th percentile length-groups for both predator and prey to illustrate the variability within any age group of the availability of prey to predators. Throughout the text, I use the terms small or smaller, average, and large or larger as synonyms for 25th, median, and 75th percentile length-groups, respectively, of prey and predators. In addition the term “catch up”, such as “striped bass catch up to gizzard shad in their fifth

Table 7. Annual mortality estimates (mean value with range in parentheses) for adult gizzard shad and alewife derived using the catch curve method on cove rotenone and gillnet data from Smith Mountain Lake.

Species	Data Set	Number of Estimates	Source	Annual Mortality
Gizzard shad	1973-77 VCGIF cove rotenone data	4	Hart 1978	.70 (.58 - .95)
Gizzard shad	1979-80 VCGIF cove rotenone data	3	LaRoache 1981	.67 (.62 - .74)
Gizzard shad	1981-83 VCGIF cove rotenone data	3	Whitehurst 1984	.75 (.74 - .76)
Alewife	1974-76 VCGIF cove rotenone data	3	Hart 1978	.81 (.64 - .98)
Alewife	1983-84 gillnet data	4	This Study	.79 (.77 - .84)

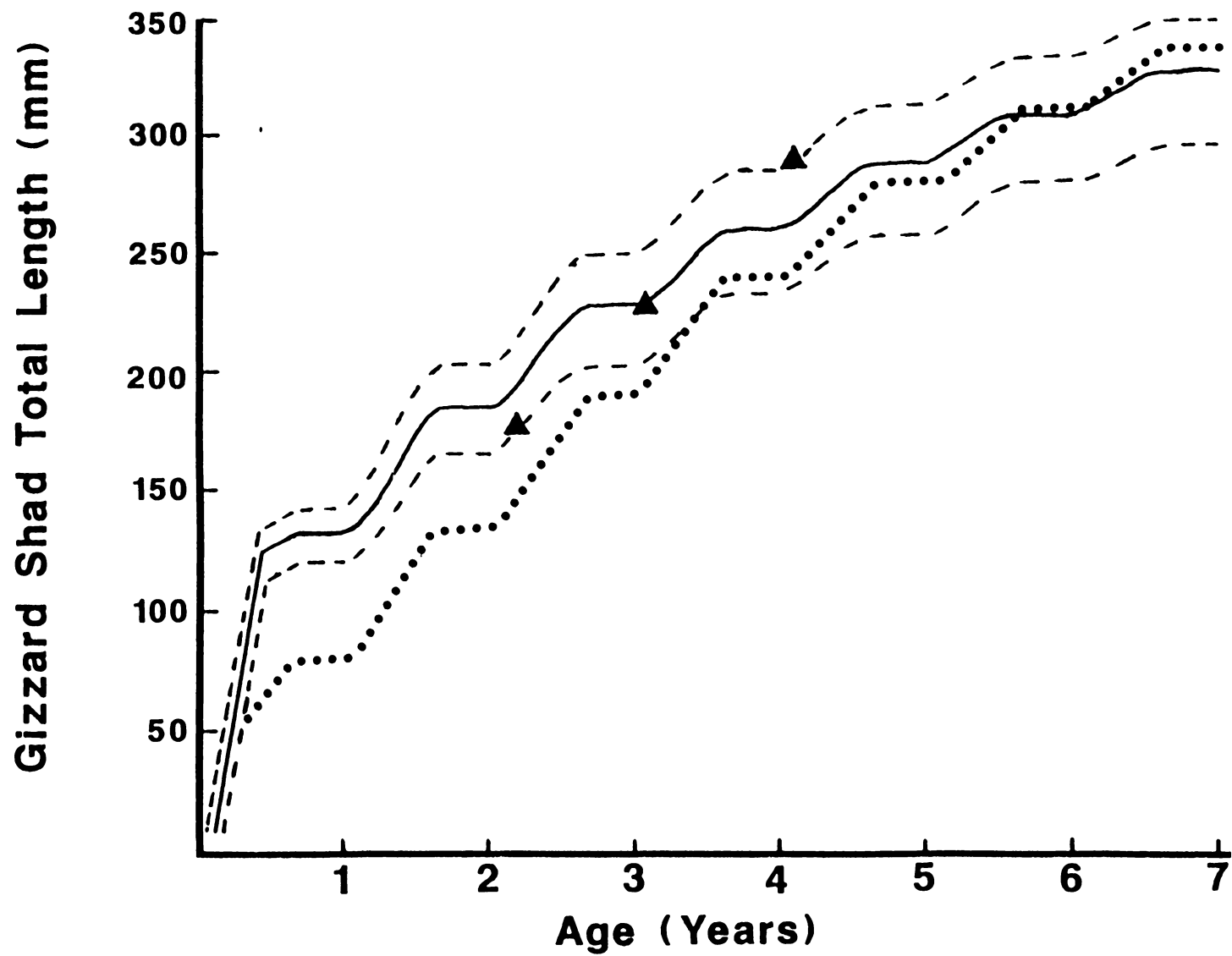
year”, refers to when the predator can begin eating the prey based on the morphological ingestibility limits of the predator.

The analyses of the supply-and-demand relationships, which follow after this treatment of ingestibility limits describe median length of predators and prey because the complexities of describing all possible combinations of availability of 25th, 75th, and median-length predators renders the task intractable.

Striped bass: Median, 25th, and 75th percentile length-groups of striped bass can consume some gizzard shad of the same cohort at age-0 (as detailed in previous section), but gizzard shad outgrow their maximum ingestibility limits by the end of their first season of growth. Striped bass in the 25th percentile length-group are never again able to consume even the smaller members of a gizzard shad cohort once they lose them in August of their first year. Median-length striped bass overtake the smaller gizzard shad by August during their fourth year of life (Fig. 18). They also eventually catch up with the median-length gizzard shad in mid-November in their sixth year, but the larger gizzard shad remain invulnerable to them their entire life (Fig. 18). The larger striped bass can begin feeding on the smaller gizzard shad as early as mid-June of their second year and can consume both the average and larger gizzard shad of the same age by May of their third and fourth year of life, respectively (Fig. 18).

Older striped bass cohorts are more able to capitalize on a gizzard shad cohort throughout its life. Median, 25th, and 75th percentile length-groups of striped bass one year older ($n+1$) than a gizzard shad cohort (n) can feed on age-0 gizzard shad to varying degrees which is described in detail in the preceding section. The smaller mem-

Figure 18. Growth of gizzard shad (median total length = solid line with semi-quartile range represented by dashed lines) versus the maximum total lengths of gizzard shad ingestible by same-age striped bass (median total length = dotted line) in Smith Mountain Lake, Virginia. Triangles indicate points in time where 75th percentile-length striped bass catch up to same-age gizzard shad. Slower growing (25th percentile) striped bass never catch up to same-age shad.



bers of the $n + 1$ striped bass cohort can resume consumption of the smaller-size gizzard shad (which initially outgrew them in September of the shad's first year of life) by the end of November of that second year. However, median and 75th percentile length-groups of gizzard shad are never again vulnerable to them. Age-1 striped bass of average size have the smaller gizzard shad morphologically vulnerable to them from the time the gizzard shad cohort is hatched. While they can begin to resume consumption of the median-length gizzard shad by late November of their (striped bass) second year, the larger gizzard shad remain morphologically invulnerable to them until mid September of their (striped bass) seventh year. The larger age-1 striped bass have the 25th, median, and 75th percentile length-groups of gizzard shad continuously available to them from the time the gizzard shad cohort hatches.

Median and 75th percentile length-groups of striped bass two years older ($n + 2$) than a cohort of gizzard shad (n), have the small, average, and large members of that cohort vulnerable to them from the time of emergence (hatching) through the remainder of their mutual lifespans. Smaller striped bass in the $n + 2$ cohort can feed on gizzard shad in the 25th percentile length-group throughout the lifespan of that gizzard shad cohort (n). They can also eat median-length gizzard shad through mid July of their eighth year of life, when the gizzard shad cohort is virtually extinguished. The larger gizzard shad are available to be taken by the smaller members of the $n + 2$ striped bass cohort through mid-August of the fifth year of life of the striped bass. A gizzard shad cohort is completely morphologically vulnerable to all striped bass $\geq n + 3$ throughout its lifespan with a single exception: striped bass ($n + 3$) in the 25th percentile length-group can no longer consume gizzard shad in the 75th percentile length-group in May of their (striped bass) eighth year.

Striped bass catch up to alewives much earlier in life and can consume most alewives of the same cohort at age-0 (see preceding section). Slower growing striped bass (25th percentile) have the smaller alewives of the same cohort morphologically vulnerable to them from the time they become piscivorous until the alewife cohort is extinguished at age 3. Striped bass in the 25th percentile length-group, however, can not begin consuming median and 75th percentile-length alewife until mid April and mid July of their second year, respectively (Fig. 19). Average-size striped bass can ingest median and 75th percentile-length alewives in early September and late October, respectively, during their first year of life (Fig. 19). Larger members of the striped bass cohort have average-size alewives available to them by late August and the larger alewives available in early October, both in their first year of life. The alewife cohort (n) is morphologically vulnerable to striped bass one year older ($n + 1$) throughout its three-year life span.

Walleye: Walleye (25th, median, and 75th percentile length-groups) are never able to consume gizzard shad of the same cohort except at age-0 during the early part of August as described in the preceding section. After this time, gizzard shad remain morphologically invulnerable to same-age walleye for the remainder of their concurrent lifespans (Fig. 20). In contrast to striped bass, walleye one year older ($n + 1$) than a gizzard shad cohort also never catch up to it (they can consume some young-of-the-year shad until late November in the walleye's second year of life). Ingestibility analysis indicates that walleye two years older ($n + 2$) than gizzard shad do not fare much better. Median and 25th percentile length-groups of walleye can never resume feeding on gizzard shad two years younger than themselves after gizzard shad, as young-of-the-year, outgrow their ingestibility limits in November. The larger walleye ($n + 2$) are capable of ingesting the smaller gizzard shad, but for less than one year. The scenario is similar for

Figure 19. Growth of alewife (median total length = solid line with semi-quartile range represented by dashed lines) versus the maximum total lengths of alewife ingestible by same-age striped bass (median total length = dotted line) in Smith Mountain Lake, Virginia. Squares and triangles indicate points in time where 25th and 75th percentile-length striped bass catch up to same-age alewives, respectively.

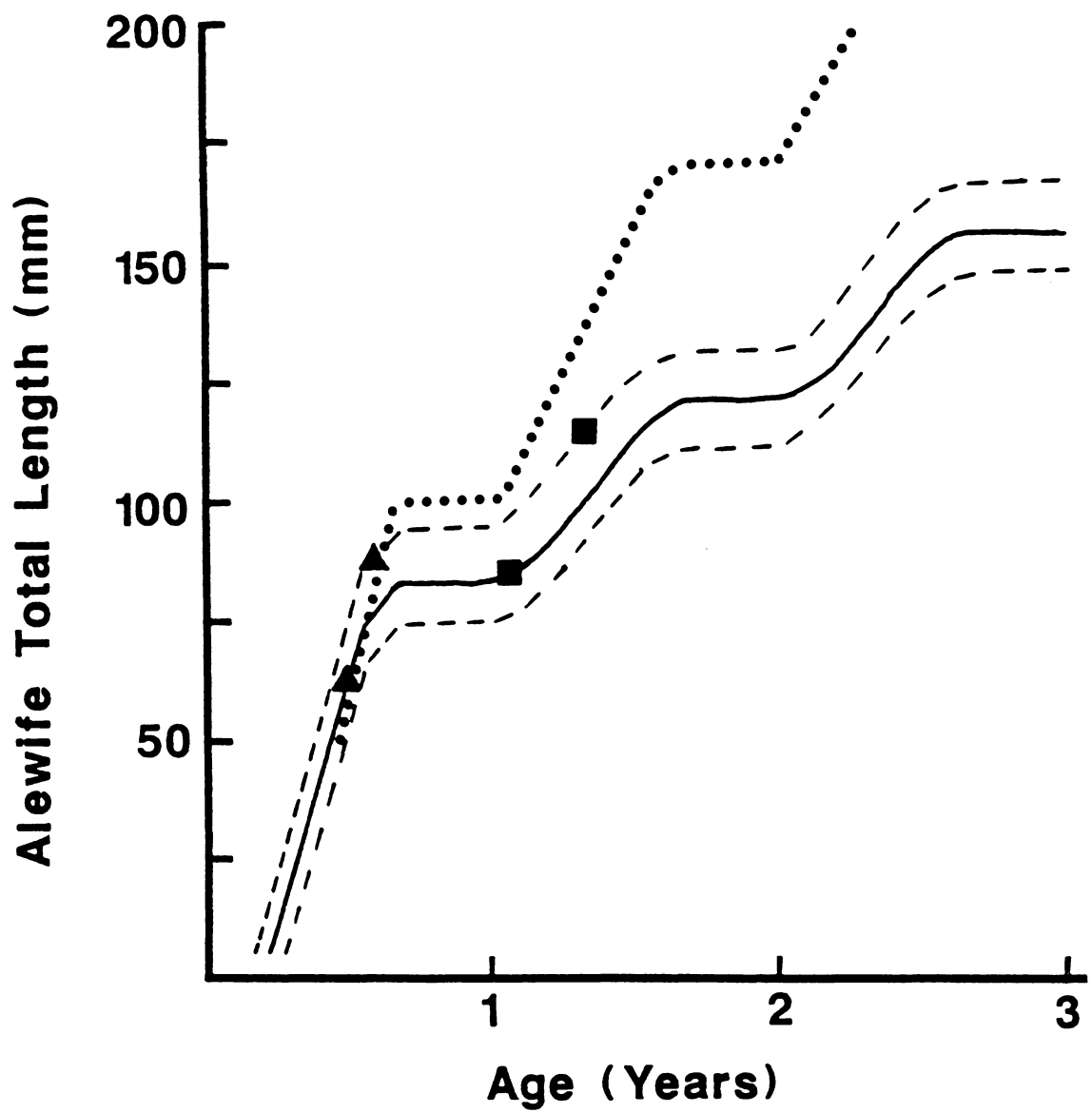
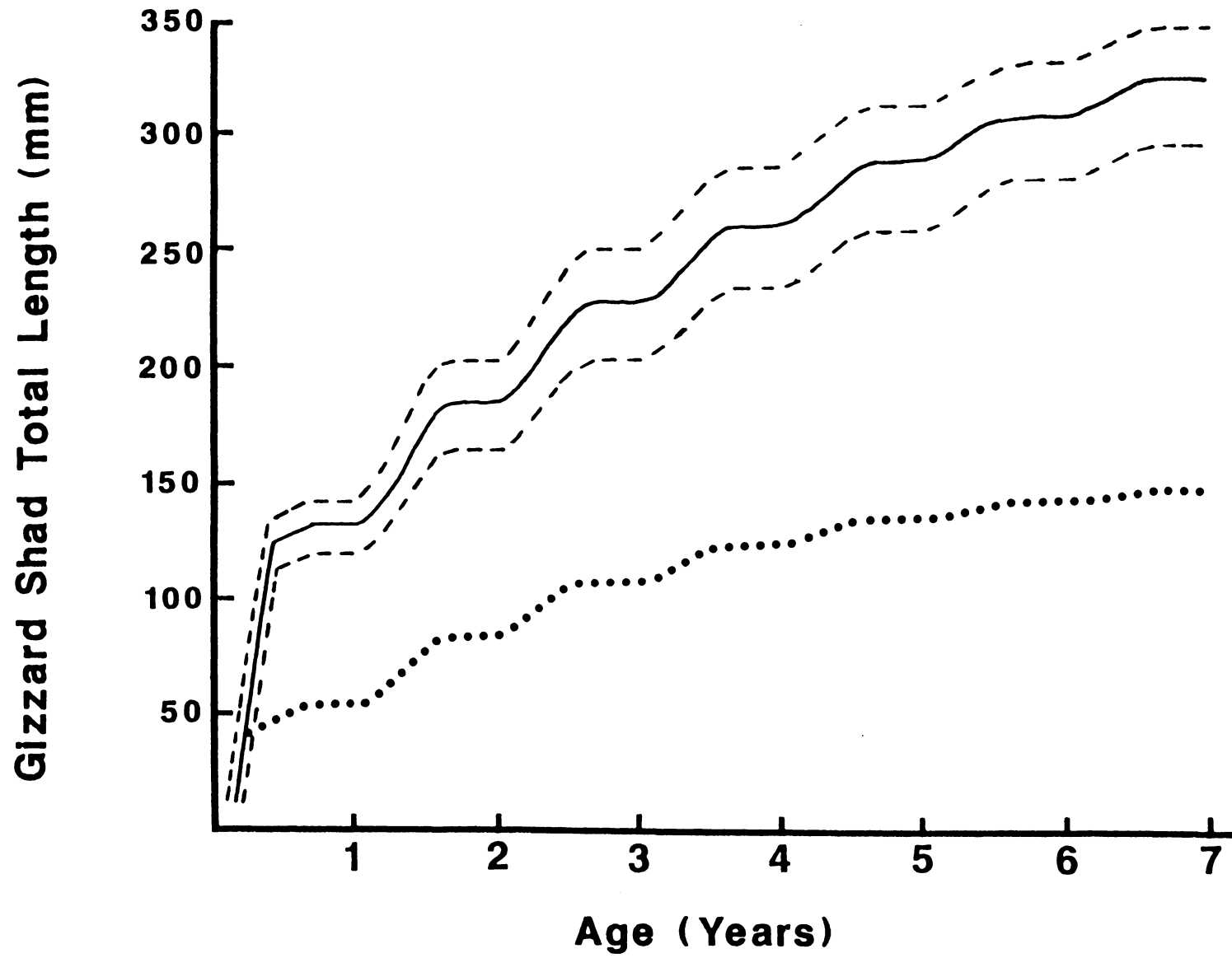


Figure 20. Growth of gizzard shad (median total length = solid line with semi-quartile range represented by dashed lines) versus the maximum total lengths of gizzard shad ingestible by same-age walleye (median total length = dotted line) in Smith Mountain Lake, Virginia. Same-age gizzard shad remain morphologically invulnerable to even the largest walleye (75th percentile).

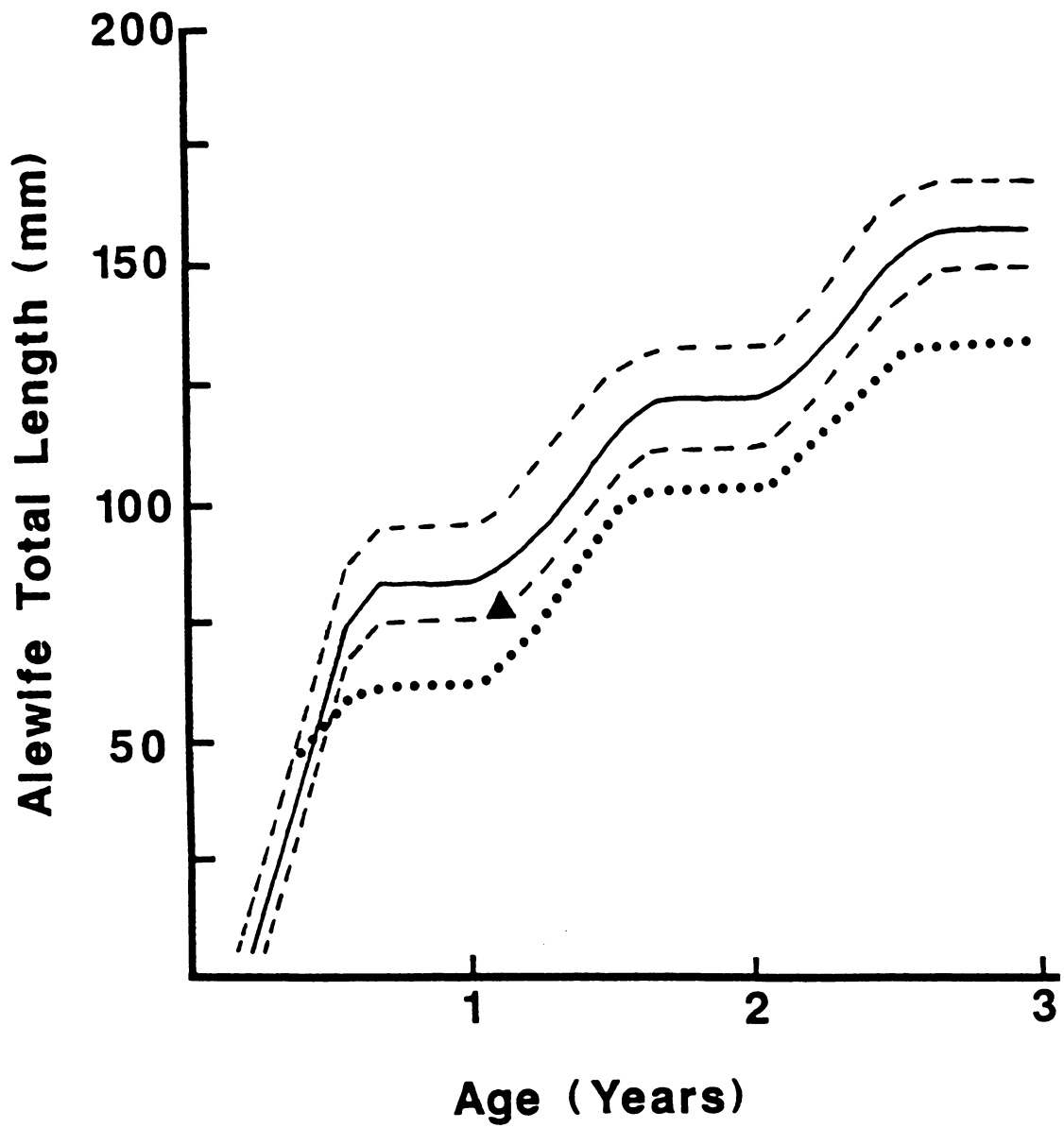


walleye ages 3-6. Gizzard shad are morphologically vulnerable for the first one to one and one half years of their life, then outgrow the ingestibility limits of even the oldest and largest walleye.

All walleye can consume some alewives of the same cohort at age-0. However, unlike striped bass, walleye cannot fully utilize same-age alewives throughout the alewife lifespan. Alewives, like gizzard shad, become and remain morphologically invulnerable to all walleye of the same age by the end of the first growing season (Fig. 21). The larger walleye, however, can resume feeding on the smaller alewives by mid May of their second year, but never again can consume average or larger size alewives of the same year class (Fig. 21).

Older walleye cohorts are more able to capitalize on an alewife cohort throughout its life. Walleye one year older (25th percentile) than an alewife cohort can consume the smaller alewives until September of the walleye's fourth year of life. These smaller $n + 1$ walleye can also consume 75th percentile and median-length alewives until April and November of their third year of life, respectively. Median-length walleye one year older than an alewife cohort have the smaller alewives available to them for the life of the alewives (3 years). Also morphologically available to them are the 75th percentile and median-length alewives until April and October of the walleye's fourth year of life, respectively. Larger walleye, one year older than an alewife cohort, can feed on that cohort throughout its three-year lifespan. The alewife cohort is also morphologically available to all walleye ages 2-6 through its lifespan with a single exception: smaller walleye, two years older than alewives, can only consume the larger alewives until mid July of their fifth year. At the time these walleye can no longer ingest the larger alewives, only about one year remains in the alewives' lifespan. In summary, the differ-

Figure 21. Growth of alewife (median total length = solid line with semi-quartile range represented by dashed lines) versus the maximum total lengths of alewife ingestible by same-age walleye (median total length = dotted line) in Smith Mountain Lake, Virginia. Triangle indicates point in time where 75th percentile-length walleye catch up to smaller alewives. Median and 25th percentile-length walleye never catch up to same-age alewives.

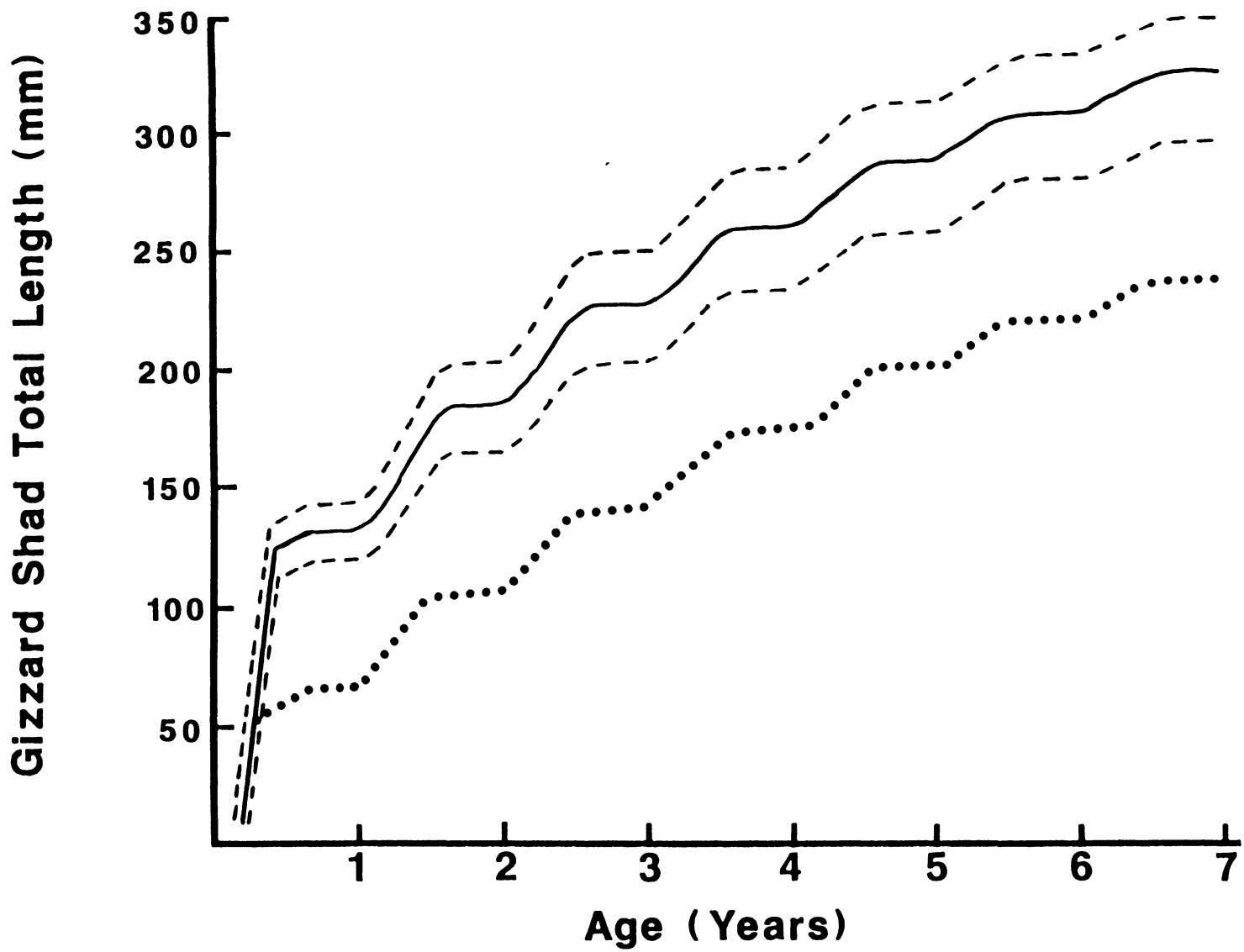


ence in morphological availability of gizzard shad versus alewife renders the walleye heavily dependent on alewife over most of the lifespan, but deficiency in even ingestible alewife can occur for age-1 walleye in spring.

Largemouth bass: Largemouth bass, like striped bass and walleye, can consume some gizzard shad of the same cohort at age-0, but gizzard shad soon outgrow them. Median, 25th, and 75th percentile length-groups of largemouth bass never catch up to gizzard shad once they initially lose them during that first year (Fig. 22). The situation does not improve much for largemouth bass one year older ($n+1$) than a gizzard shad cohort (n). These largemouth bass are never again able to resume predation after the gizzard shad cohort initially outgrows them near the end of its first growing season. Largemouth bass ($n+2$) in the 25th percentile length-group can consume the smaller gizzard shad until mid September of the largemouth bass' fourth year of life, but large and median-length gizzard shad are never available to them. Median-length largemouth bass ($n+2$) have the smaller gizzard shad available to them until June of their fifth year of life. They also can consume median-length gizzard shad until mid August of the largemouth bass' fourth year of life, but are unable to take advantage of larger gizzard shad. Largemouth bass (75th percentile), two years older than a cohort of gizzard shad, can eat gizzard shad in the 25th percentile-length group until mid November of the largemouth bass' sixth year of life. Largemouth bass $n+2$ (75th percentile), however, are outgrown by the large and average-size gizzard shad by July and October, respectively, in the largemouth bass' fourth year of life.

When largemouth bass are three years older than a cohort of gizzard shad, all gizzard shad are morphologically vulnerable to them for at least one year and as much as three

Figure 22. Growth of gizzard shad (median total length = solid line with semi-quartile range represented by dashed lines) versus the maximum total lengths of gizzard shad ingestible by same-age largemouth bass (median total length = dotted line) in Smith Mountain Lake, Virginia. Same-age gizzard shad remain morphologically invulnerable to even the largest bass (75th percentile).



years of the gizzard shad's life. At ages 4-6, largemouth bass are virtually no longer restricted to the size of gizzard shad they can ingest. The time they have to utilize that gizzard shad cohort, however, is limited by the time remaining in their own lifespan (e.g., a largemouth bass cohort four years older than a cohort of gizzard shad may only be able to utilize that gizzard shad cohort for two years because few largemouth bass in Smith Mountain Lake live beyond six years).

Largemouth bass are able to catch up to alewives of the same cohort and do so early in life (Fig. 23). Largemouth bass (75th percentile) of the same cohort as alewives can feed on them (25th, median, 75th length-groups) as soon as they become piscivorous until the alewife cohort is extinguished at age 3. Median-length largemouth bass can feed on the smaller alewives as soon as they become piscivorous and catch up to median and 75th percentile-length alewives by early May and mid August, respectively, during their second year of life (Fig. 23). Largemouth bass in the 25th percentile length-group catch up to the smaller alewives in mid July of the largemouth bass' second year of life and to median-length alewives in June of the largemouth bass' third year; however, the 75th percentile length-group of alewives always remain too large for them to eat (Fig. 23). Like striped bass, largemouth bass one year older ($n + 1$) than a cohort of alewives (n) can feed on that alewife cohort throughout that alewives' three-year lifespan.

Patterns of Cohort Production

Forage fish: Cohort production for both alewives and gizzard shad peaks in the first year of life and drops sharply thereafter (Fig. 24). Gizzard shad, despite the fact that their lifespan is four years longer than that of alewives, achieve 96 percent of their life-

Figure 23. Growth of alewife (median total length = solid line with semi-quartile range represented by dashed lines) versus the maximum total lengths of alewife ingestible by same-age largemouth bass (median total length = dotted line) in Smith Mountain Lake, Virginia. Squares and triangles indicate points in time where 25th and 75th percentile-length largemouth bass catch up to same-age alewives, respectively.

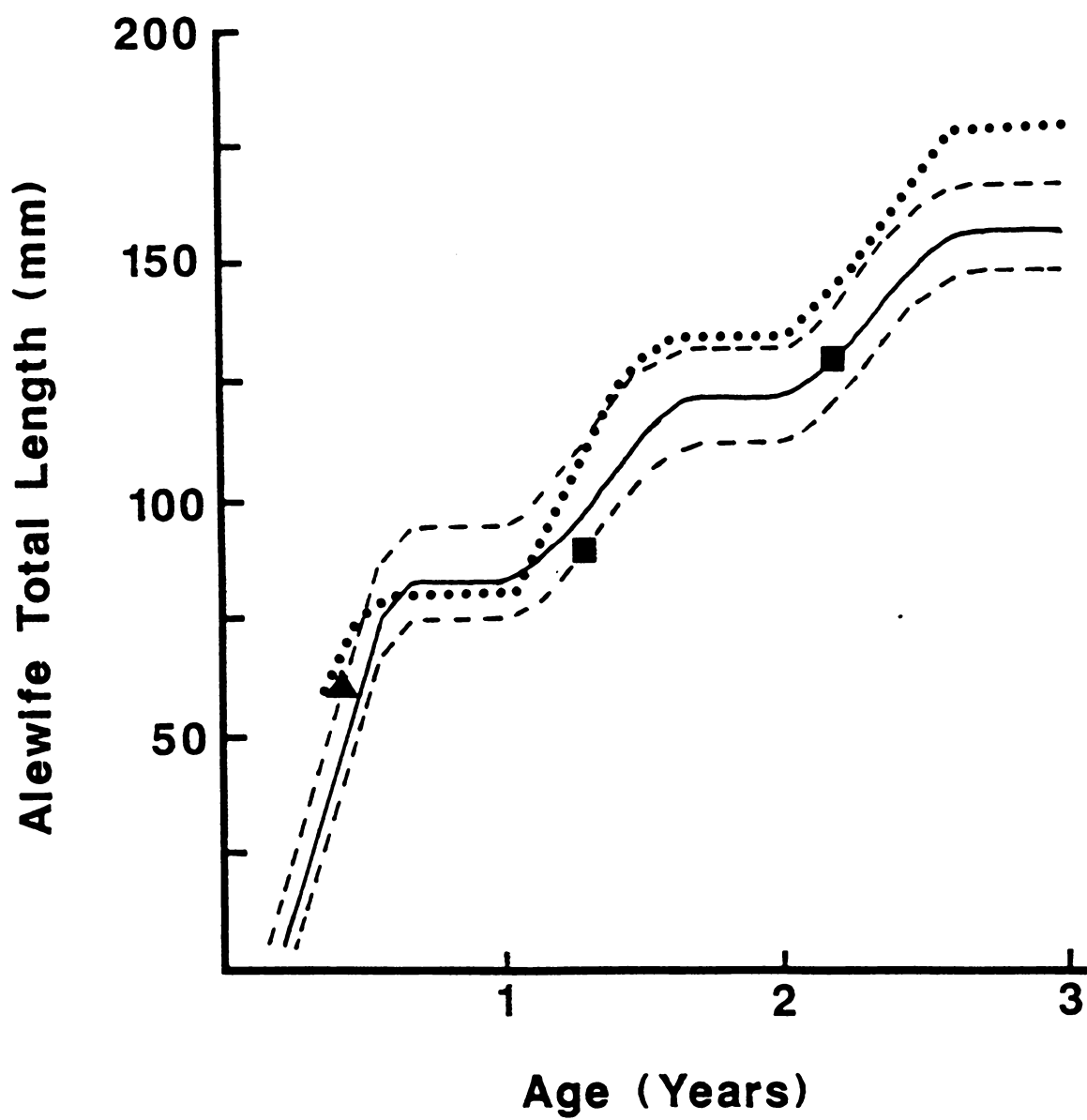
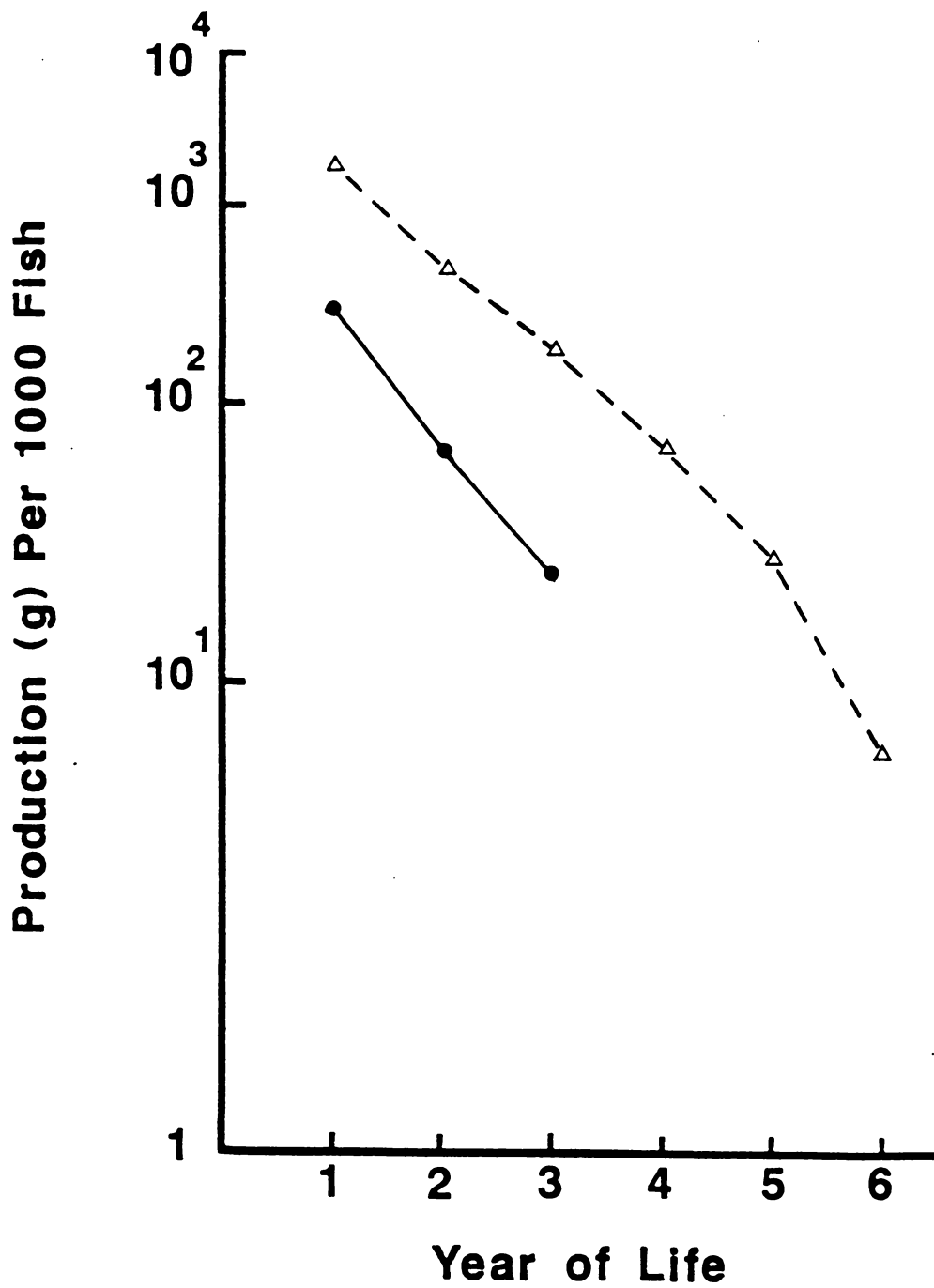


Figure 24. Lifespan production for initial 1000-fish cohorts of gizzard shad (dashed line/triangles) and alewife (solid line/dots) in Smith Mountain Lake.



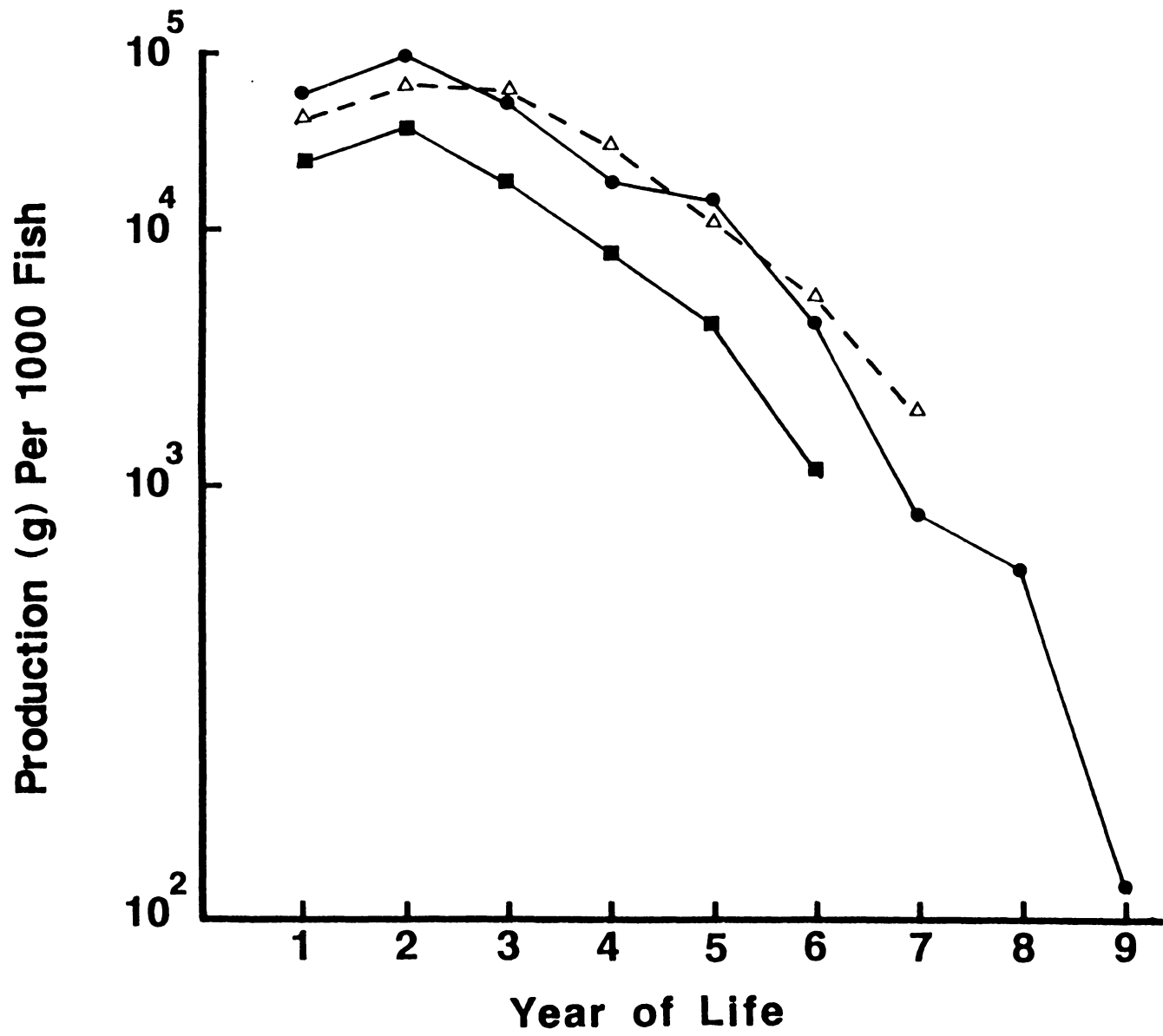
time production within the first three years. The absolute difference in cohort production, however, is seven times greater per 1000 gizzard shad compared to 1000 alewives over the course of their lifetime. The degree of difference in total production between these two species in Smith Mountain Lake is not known, largely because alewife abundance cannot be accurately determined with available technology.

Piscivores: Striped bass, walleye, and largemouth bass cohort production peak in the second year of life, one year out-of-phase with both forage species (Fig. 25). Their peaks are also much lower as a percentage of lifetime production ($\approx 40\%$) than either gizzard shad (69%) or alewife (76%) and decline more gradually over their remaining lifespans. The later peak in production for each of the predators, together with their longer lifespans, assure that alewife and gizzard shad of the same cohort will not be present in sufficient abundance to fulfill the lifespan demands of these predators. Like the forage species, the absolute difference in cohort production for a given initial cohort number (e.g. 1000 fish) varies among the three predator species with highest annual production estimates for striped bass, followed by walleye and then largemouth bass. Absolute production of walleye and striped bass will vary each year based on the numbers stocked. Largemouth bass will vary each year with spawning and recruitment success.

Available Forage Supply versus Predator Demand

This analysis relies on the previously derived cohort production data to estimate age and cohort-specific forage supply and predator demand as percentages of lifespan values. It does not address supply and demand in terms of absolute values, but rather analyzes

Figure 25. Lifespan production for initial 1000-fish cohorts of striped bass (solid line/dots), walleye (dashed line/triangles) and largemouth bass (solid line/squares) in Smith Mountain Lake.



when and where prey deficiencies might occur. Supply is further constrained by ingestibility limits.

The underlying assumptions are that: 1) cohort production patterns simulate prey supply and predator demand over the lifespans; and 2) for each prey-predator combination, total supply (100% of lifespan prey production) would exactly balance predator demand (100% of predator lifespan production) in the absence of ingestibility limitations. In actuality, production only approximates (percentage-wise) the lifespan patterns of supply and predator demand. However, biomass is also inadequate in itself to portray lifespan supply or demand; production offers a more reasonable depiction (see Discussion). Of course, absolute prey and predator production will never perfectly balance but rather will be in a constant state of flux, depending on population dynamics. In the regrettable but unavoidable absence of accurate estimates of absolute abundance for every species, I assumed that supply and demand production were in balance to develop a lifespan assessment of the comparative importance of alewife and gizzard shad to the three major predators as impacted by morphological limitations. Consequently, statements regarding the adequacy of prey cohorts to meet predator demand should be understood to apply only in the context of equal prey supply and predator demand.

The supply-demand relationship is first examined from the perspective of the vulnerability of a forage cohort to coexistent predator cohorts over its lifespan. Then the perspective is shifted to the predator to address the question of which prey cohorts are available to it to meet its age-specific trophic demands. The analysis, assuming constant recruitment, mortality and growth rates for successive prey cohorts, is performed separately for gizzard shad and then alewife and finally for the combination of the two species.

Striped Bass

Gizzard shad supply: A gizzard shad cohort is almost completely invulnerable to the same-age cohort of striped bass. Although 69% of gizzard shad cohort production is achieved in its first year, only 0.14% (0.10% of total lifetime production) is available to age-0 striped bass because of rapid growth of gizzard shad. Striped bass catch up to the gizzard shad cohort when both are age 5, but supply and demand production are both very low in the two years when gizzard shad remain in the system (Table 8). A gizzard shad cohort (age-0) should face the most intense predation from one-year old striped bass. Although age-0 gizzard shad are not completely vulnerable to age-1 striped bass, the available supply (in terms of percent of lifespan production) is adequate to meet the heavy demand on it (Table 8). For the remainder of their mutual lifespans, the n gizzard shad cohort and the $n + 1$ striped bass cohort are virtually equivalent in terms of production in available supply and concurrent demand as measured by production. A gizzard shad cohort is completely vulnerable to striped bass cohorts two or more years older than itself for as long as they remain in the system. Despite this, the production demand of these older striped bass cohorts is much less than the production supply of the gizzard shad cohort; vulnerability is mitigated by low demand (Table 8).

From the striped bass perspective, only age-0 striped bass experience a deficiency in available gizzard shad supply (Table 9). Age-1 striped bass are also restricted to age-0 gizzard shad, but the fraction of gizzard shad cohort production available to them is theoretically adequate to meet their demand (Table 9). Striped bass $\geq$ age 2 can feed

Table 8. Available supply of a gizzard shad cohort age n versus demand by coexistent striped bass cohorts. Age-specific available supply of gizzard shad and demand by striped bass are estimated in terms of percent of lifetime cohort production.

<u>Striped Bass Cohort: n</u>										
Striped Bass Age	0	1	2	3	4	5	6	7	8	Total
Supply/Demand	0.10/23.9	0.00/39.0	0.00/21.2	0.00/7.7	0.00/6.0	0.02/1.6	0.03/0.3	-	-	0.15/99.7
<u>Striped Bass Cohort: n+1</u>										
Striped Bass Age	0	1	2	3	4	5	6	7	8	Total
Supply/Demand	-	45.7/39.0	19.5/21.2	7.2/7.7	2.7/6.0	1.0/1.6	0.27/0.3	0.03/0.2	-	76.40/76.0
<u>Striped Bass Cohort: n+2</u>										
Striped Bass Age	0	1	2	3	4	5	6	7	8	Total
Supply/Demand	-	-	69.3/21.2	19.5/7.7	7.2/6.0	2.7/1.6	1.0/0.3	0.27/0.2	0.03/0.1	100/37.1
<u>Striped Bass Cohort: n+3</u>										
Striped Bass Age	0	1	2	3	4	5	6	7	8	Total
Supply/Demand	-	-	-	69.3/7.7	19.5/6.0	7.2/1.6	2.7/0.3	1.0/0.2	0.27/0.1	99.97/15.9
<u>Striped Bass Cohort: n+4</u>										
Striped Bass Age	0	1	2	3	4	5	6	7	8	Total
Supply/Demand	-	-	-	-	69.3/6.0	19.5/1.6	7.2/0.3	2.7/0.2	1.0/0.1	99.70/8.2
<u>Striped Bass Cohort: n+5</u>										
Striped Bass Age	0	1	2	3	4	5	6	7	8	Total
Supply/Demand	-	-	-	-	-	69.3/1.6	19.5/0.3	7.2/0.2	2.7/0.1	98.70/2.2
<u>Striped Bass Cohort: n+6</u>										
Striped Bass Age	0	1	2	3	4	5	6	7	8	Total
Supply/Demand	-	-	-	-	-	-	69.3/0.3	19.5/0.2	7.2/0.1	96.00/0.6
<u>Striped Bass Cohort: n+7</u>										
Striped Bass Age	0	1	2	3	4	5	6	7	8	Total
Supply/Demand	-	-	-	-	-	-	-	69.3/0.2	19.5/0.1	88.80/0.3
<u>Striped Bass Cohort: n+8</u>										
Striped Bass Age	0	1	2	3	4	5	6	7	8	Total
Supply/Demand	-	-	-	-	-	-	-	-	69.3/0.1	69.30/0.1

Table 9. Percentage of lifespan production (supply) of alewife (A) and gizzard shad (G) morphologically vulnerable to meet age-specific demand (% of lifespan production) of striped bass.

Age of Prey	Age of Striped Bass																	
	0		1		2		3		4		5		6		7		8	
	A	G	A	G	A	G	A	G	A	G	A	G	A	G	A	G	A	G
0	43.7	0.10	75.6	45.7	75.6	69.3	75.6	69.3	75.6	69.3	75.6	69.3	75.6	69.3	75.6	69.3	75.6	69.3
1	-	-	17.8	-	17.8	19.5	17.8	19.5	17.8	19.5	17.8	19.5	17.8	19.5	17.8	19.5	17.8	19.5
2	-	-	0.8	-	6.6	-	6.6	7.2	6.6	7.2	6.6	7.2	6.6	7.2	6.6	7.2	6.6	7.2
3	-	-	-	-	-	-	-	-	-	2.7	-	2.7	-	2.7	-	2.7	-	2.7
4	-	-	-	-	-	-	-	-	-	-	-	1.0	-	1.0	-	1.0	-	1.0
5	-	-	-	-	-	-	-	-	-	-	-	-	-	0.3	-	0.3	-	0.3
6	-	-	-	-	-	-	-	-	-	-	-	-	-	0.03	-	0.03	-	0.03
Total Supply	43.7	0.10	94.2	45.7	100.0	88.8	100.0	96.0	100.0	98.7	100.9	99.7	100.0	100.0	100.0	100.0	100.0	100.0
Age-Specific Demand	23.9		39.0		21.2		7.7		6.0		1.6		0.3		0.2		0.1	

on successively more age groups of gizzard shad, and the supply is much more than adequate if each group is considered alone (Table 9). However, the cumulative demand of multiple striped bass cohorts on particular age groups of gizzard shad could exceed the available supply. To investigate this possibility, I compared the available supply of the oldest age groups of gizzard shad to the oldest cohorts of striped bass that could consume them, assuming that striped bass would eat the largest gizzard shad that they could ingest before turning to smaller gizzard shad. My analysis indicated that production demand does not exceed available production supply for any age group of gizzard shad (Table 10). This results because older striped bass are not morphologically constrained from consuming older gizzard shad. The supply deficiency experienced by age-0 striped bass is completely a function of ingestibility limits and is not exacerbated by competing demands on age-0 gizzard shad.

Alewife supply: In contrast to gizzard shad, an alewife cohort is vulnerable to all cohorts of striped bass. Both same-age and one-year older striped bass cohorts will potentially have the strongest impacts on an alewife cohort (Table 11). The impacts of these cohorts are virtually equivalent but for opposite reasons. Same-age striped bass can consume only 68% of the lifespan production of the alewife cohort; they do not feed on age-0 alewives until they turn piscivorous in August. The available alewife supply pattern is thus not adequate to meet the simultaneous production demand of the same-age striped bass cohort (84% of lifespan) over the alewife's three-year life (Table 11). In contrast, the $n+1$ striped bass cohort has 100 percent of the alewife cohort lifespan production available to it, but only 68% of its lifespan production occurs during the three years that the alewife cohort is extant (Table 11). Although the alewife cohort is

Table 10. Multiple cohort demand by striped bass for gizzard shad cohorts in Smith Mountain Lake, Virginia. All values in percent of lifespan production.

Striped Bass Age	Demand	Percent of Demand Met by Gizzard Shad of Age:						
		6	5	4	3	2	1	0
8	0.1	0.03	0.07	-	-	-	-	-
7	0.2	-	0.20	-	-	-	-	-
6	0.3	-	-	0.30	-	-	-	-
5	1.6	-	-	0.70	0.90	-	-	-
4	6.0	-	-	-	1.80	4.20	-	-
3	7.7	-	-	-	-	3.00	4.70	-
2	21.2	-	-	-	-	-	14.80	6.40
1	39.0	-	-	-	-	-	-	39.00
0	23.9	-	-	-	-	-	-	*23.90
Age-Specific Supply		0.03	0.27	1.00	2.70	7.20	19.50	69.30

*Not Completely Ingestible by Age-0 Striped Bass.

Table 11. Available supply of an alewife cohort age n versus demand by coexistent striped bass cohorts. Age-specific available supply of alewives and demand by striped bass are estimated in terms of percent of lifetime cohort production.

Striped Bass Age Supply/Demand	<u>Striped Bass Cohort: n</u>									Total
	0	1	2	3	4	5	6	7	8	
Striped Bass Age Supply/Demand	43.7/23.9	17.8/39.0	6.6/21.2	-	-	-	-	-	-	68.1/84.1
Striped Bass Age Supply/Demand	<u>Striped Bass Cohort: $n+1$</u>									Total
	0	1	2	3	4	5	6	7	8	
Striped Bass Age Supply/Demand	-	75.6/39.0	17.8/21.2	6.6/7.7	-	-	-	-	-	100/67.9
Striped Bass Age Supply/Demand	<u>Striped Bass Cohort: $n+2$</u>									Total
	0	1	2	3	4	5	6	7	8	
Striped Bass Age Supply/Demand	-	-	75.6/21.2	17.8/7.7	6.6/6.0	-	-	-	-	100/34.9
Striped Bass Age Supply/Demand	<u>Striped Bass Cohort: $n+3$</u>									Total
	0	1	2	3	4	5	6	7	8	
Striped Bass Age Supply/Demand	-	-	-	75.6/7.7	17.8/6.0	6.6/1.6	-	-	-	100/15.3
Striped Bass Age Supply/Demand	<u>Striped Bass Cohort: $n+4$</u>									Total
	0	1	2	3	4	5	6	7	8	
Striped Bass Age Supply/Demand	-	-	-	-	75.6/6.0	17.8/1.6	6.6/0.3	-	-	100/7.9
Striped Bass Age Supply/Demand	<u>Striped Bass Cohort: $n+5$</u>									Total
	0	1	2	3	4	5	6	7	8	
Striped Bass Age Supply/Demand	-	-	-	-	-	75.6/1.6	17.8/0.3	6.6/0.2	-	100/2.1
Striped Bass Age Supply/Demand	<u>Striped Bass Cohort: $n+6$</u>									Total
	0	1	2	3	4	5	6	7	8	
Striped Bass Age Supply/Demand	-	-	-	-	-	-	75.6/0.3	17.8/0.2	6.6/0.1	100/0.6
Striped Bass Age Supply/Demand	<u>Striped Bass Cohort: $n+7$</u>									Total
	0	1	2	3	4	5	6	7	8	
Striped Bass Age Supply/Demand	-	-	-	-	-	-	-	75.6/0.2	17.8/0.1	93.4/0.3
Striped Bass Age Supply/Demand	<u>Striped Bass Cohort: $n+8$</u>									Total
	0	1	2	3	4	5	6	7	8	
Striped Bass Age Supply/Demand	-	-	-	-	-	-	-	-	75.6/0.1	75.6/0.1

completely vulnerable to older striped bass cohorts, their progressive decline in production demand limits their predation impacts (Table 11).

From the striped bass perspective, age-0 striped bass are constrained to feeding on age-0 alewife, and striped bass $\geq$ age 1 can eat all three age groups of alewives in Smith Mountain Lake (Table 9). The simultaneous demand of nine striped bass cohorts on only three alewife cohorts could create supply deficiencies. However, if as assumed for gizzard shad, the oldest striped bass first consume the oldest and largest alewife, production supply balances production demand at all ages, principally, because older striped bass are not limited in their consumption (Table 12).

Combined clupeid supply:

The only age-specific prey deficiency for striped bass occurs at age-0, when only 0.10% of gizzard shad lifespan production (supply) is available for 23.9% of striped bass lifespan production demand. Based on cohort production estimates, a gizzard shad cohort is one year out-of-phase with a same-age striped bass cohort; striped bass stocked in any year are dependent on production of the following gizzard shad cohort. However, when ingestibility limits (availability patterns) are factored into the analysis, striped bass are two years out-of-phase with same-age shad cohorts (i.e. striped bass have to be $n + 2$ to fully utilize a shad cohort, Table 8). Alewives in Smith Mountain Lake, however, remedy this deficiency; 43.7 percent of alewife lifespan production is available to age-0 striped bass. An alewife cohort is of principal benefit to both the same-age and one-year older striped bass cohorts. Alewives provide a continuous supply of forage to age-0 striped bass from the time they become piscivorous through the end of the growing season and into the following spring. In the absence of alewives, age-1 striped bass may

Table 12. Multiple cohort demand by striped bass for alewife cohorts in Smith Mountain Lake, Virginia. All values in percent of lifespan production.

<u>Striped Bass</u>		<u>Percent of Demand Met by Alewife of Age:</u>		
<u>Age</u>	<u>Demand</u>	<u>2</u>	<u>1</u>	<u>0</u>
8	0.1	0.1	-	-
7	0.2	0.2	-	-
6	0.3	0.3	-	-
5	1.6	1.6	-	-
4	6.0	4.4	1.6	-
3	7.7	-	7.7	-
2	21.2	-	8.5	12.7
1	39.0	-	-	39.0
0	23.9	-	-	23.9
Age-Specific Supply		6.6	17.8	75.6

face spring prey deficiencies until a new cohort of young-of-the-year gizzard shad becomes available in the summer.

Walleye

Gizzard shad supply: A gizzard shad cohort is virtually invulnerable to the same cohort of walleye. Gizzard shad have only 0.047% of their first-year production (0.03% of lifetime shad cohort production) vulnerable to predation by age-0 walleye because of their rapid growth and remain invulnerable for the rest of the shad lifespan (Table 13). Gizzard shad are partially vulnerable in their first year of life to walleye one, two, and three years older than themselves and face the most intensive potential predation from two-year old walleye (Table 13). Age-0 gizzard shad are fully vulnerable to walleye four to six years older than themselves. One year old gizzard shad ($n+1$) are also partially vulnerable to walleye four and five years older than themselves (Table 13).

From the walleye perspective, age-0 and age-1 walleye experience a deficiency in available gizzard shad supply, being able to consume only a few age-0 gizzard shad (Table 14). Walleye ages 2-4 are also restricted to age-0 gizzard shad, but the fraction of gizzard shad cohort production available to them is more than adequate to meet their demand (Table 14). Walleye ages 5 and 6 can feed on some age-1 as well as age-0 gizzard shad. Production supply for these five and six-year old walleye exceeds their demands by 30 and 94 times, respectively.

Table 13. Available supply of a gizzard shad cohort age n versus demand by coexistent walleye cohorts. Age-specific supply of gizzard shad and demand by walleye are estimated in terms of percent of lifetime cohort production.

Walleye Age	<u>Walleye Cohort: n</u>							Total
Supply/Demand	0	1	2	3	4	5	6	
	0.03/21.2	0.00/31.5	0.00/26.1	0.00/12.9	0.00/5.1	0.00/2.4	0.00/0.8	0.03/100
Walleye Age	<u>Walleye Cohort: $n+1$</u>							Total
Supply/Demand	0	1	2	3	4	5	6	
	-	14.7/31.5	0.00/26.1	0.00/12.9	0.00/5.1	0.00/2.4	0.00/0.8	14.7/78.8
Walleye Age	<u>Walleye Cohort: $n+2$</u>							Total
Supply/Demand	0	1	2	3	4	5	6	
	-	-	34.0/26.1	0.00/12.9	0.00/5.1	0.00/2.4	0.00/0.8	34.0/47.3
Walleye Age	<u>Walleye Cohort: $n+3$</u>							Total
Supply/Demand	0	1	2	3	4	5	6	
	-	-	-	57.8/12.9	0.00/5.1	0.00/2.4	0.00/0.8	57.8/21.2
Walleye Age	<u>Walleye Cohort: $n+4$</u>							Total
Supply/Demand	0	1	2	3	4	5	6	
	-	-	-	-	69.3/5.1	2.4/2.4	0.00/0.8	71.7/8.3
Walleye Age	<u>Walleye Cohort: $n+5$</u>							Total
Supply/Demand	0	1	2	3	4	5	6	
	-	-	-	-	-	69.3/2.4	6.1/0.8	75.4/3.2
Walleye Age	<u>Walleye Cohort: $n+6$</u>							Total
Supply/Demand	0	1	2	3	4	5	6	
	-	-	-	-	-	-	69.3/0.8	69.3/0.8

Table 14. Percentage of lifespan production (supply) of alewife (A) and gizzard shad (G) morphologically vulnerable to meet age-specific demand (% of lifespan production) of walleye.

Age of Prey	Age of Walleye													
	0		1		2		3		4		5		6	
	A	G	A	G	A	G	A	G	A	G	A	G	A	G
0	26.9	0.03	71.7	14.7	75.6	34.0	75.6	51.8	75.6	69.3	75.6	69.3	75.6	69.3
1	-	-	-	-	17.8	-	17.8	-	17.8	-	17.8	2.4	17.8	6.1
2	-	-	-	-	-	-	5.0	-	6.6	-	6.6	-	6.6	-
3	-	-	-	-	-	-	-	-	-	-	-	-	-	-
4	-	-	-	-	-	-	-	-	-	-	-	-	-	-
5	-	-	-	-	-	-	-	-	-	-	-	-	-	-
6	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Total Supply	26.9	0.03	71.7	14.7	93.4	34.0	98.4	51.8	100.0	69.3	100.0	71.7	100.0	75.4
Age-Specific Demand	21.2		31.5		26.1		12.9		5.1		2.4		0.8	

The cumulative demand of multiple walleye cohorts on younger age groups of gizzard shad, however, could result in intensive competition because even the oldest and largest walleye are morphologically restricted to gizzard shad less than two years old. As with striped bass, I compared the available supply (percent of lifespan cohort production) of successive age groups of gizzard shad to the demand (same parameter) of the various cohorts of walleye). I assumed that predators would consume the largest gizzard shad morphologically vulnerable to them first, and so the analysis proceeds from the oldest to youngest age groups. This analysis indicates that walleye $\leq$ age 4 are all limited to feeding on age-0 gizzard shad. If it is also assumed that older walleye will be more successful in fulfilling their trophic needs (i.e. first in line), a gizzard shad prey deficiency occurs for walleye ages 0 and 1 (Table 15). For age-0 walleye, the deficiency is irrelevant because few age-0 gizzard shad are small enough for them to eat. The deficiency is also mitigated for age-1 walleye for the same reason: supply remaining after older walleye cohorts have been satiated is sufficient to meet 80% of age-1 walleye demand, but ingestibility limits reduce the morphologically available age-0 gizzard shad supply to 47% of the demand.

Alewife supply: In contrast to gizzard shad, an alewife cohort is vulnerable to some degree to all cohorts of walleye. An alewife cohort is least vulnerable to walleye of the same cohort and faces the greatest pressure based on prey availability and production patterns from walleye one year older than themselves. The available alewife supply is more than adequate to meet the total lifetime production demand by $n + 1$ walleye that occurs during the three years the alewife cohort is extant (Table 16). Although the alewife cohort is completely vulnerable to older walleye cohorts, their progressive decline in trophic demand limits their predation impacts (Table 16).

Table 15. Multiple cohort demand by walleye for gizzard shad cohorts in Smith Mountain Lake, Virginia. All values in percent of lifespan production.

Age	Walleye Demand	Percent of Demand Met by Gizzard Shad of Age:						
		6	5	4	3	2	1	0
6	0.8	-	-	-	-	-	0.8	-
5	2.4	-	-	-	-	-	2.4	-
4	5.1	-	-	-	-	-	-	5.1
3	12.9	-	-	-	-	-	-	12.9
2	26.1	-	-	-	-	-	-	26.1
1	31.5	-	-	-	-	-	-	*25.2
0	21.2	-	-	-	-	-	-	0
Age-Specific Supply		0.0	0.0	0.0	0.0	0.0	3.2	69.3

*Not Completely Ingestible by Age-1 Walleye.

Table 16. Available supply of an alewife cohort age n versus demand by coexistent walleye cohorts. Age-specific available supply of alewives and demand by walleye are estimated in terms of percent of lifetime cohort production.

Walleye Age Supply/Demand	<u>Walleye Cohort: n</u>							Total
	0	1	2	3	4	5	6	
Walleye Age Supply/Demand	26.9/21.2	0.00/31.5	0.00/26.1	-	-	-	-	26.9/78.8
Walleye Age Supply/Demand	<u>Walleye Cohort: $n+1$</u>							Total
	0	1	2	3	4	5	6	
Walleye Age Supply/Demand	-	74.7/31.5	17.8/26.1	5.0/12.9	-	-	-	97.5/70.5
Walleye Age Supply/Demand	<u>Walleye Cohort: $n+2$</u>							Total
	0	1	2	3	4	5	6	
Walleye Age Supply/Demand	-	-	75.6/26.1	17.8/12.9	6.6/5.1	-	-	100/44.1
Walleye Age Supply/Demand	<u>Walleye Cohort: $n+3$</u>							Total
	0	1	2	3	4	5	6	
Walleye Age Supply/Demand	-	-	-	75.6/12.9	17.8/5.1	6.6/2.4	-	100/20.4
Walleye Age Supply/Demand	<u>Walleye Cohort: $n+4$</u>							Total
	0	1	2	3	4	5	6	
Walleye Age Supply/Demand	-	-	-	-	75.6/5.1	17.8/2.4	6.6/0.8	100/8.3
Walleye Age Supply/Demand	<u>Walleye Cohort: $n+5$</u>							Total
	0	1	2	3	4	5	6	
Walleye Age Supply/Demand	-	-	-	-	-	75.6/2.4	17.8/0.8	93.4/3.2
Walleye Age Supply/Demand	<u>Walleye Cohort: $n+6$</u>							Total
	0	1	2	3	4	5	6	
Walleye Age Supply/Demand	-	-	-	-	-	-	75.6/0.8	75.6/0.8

From the walleye perspective, walleye $\leq$ age 1 walleye are constrained to feeding on age-0 alewife. However, the fraction of the production supply available is 1.3 and 2.4 times as great as their age-specific demand, respectively (Table 14). Age-2 walleye have age-0 and 1 alewives morphologically vulnerable to them in excess of demand, while the remaining year classes can eat all three age groups of alewives in the system (Table 14). The simultaneous demand of seven walleye cohorts on only three alewife cohorts could also create supply deficiencies. However, like striped bass, if the oldest walleye first consume the oldest and largest alewife, age-specific demand balances with cohort supply (Table 17).

Combined clupeid supply: Age-specific prey deficiencies for walleye are most likely to occur at ages 0 and 1 when only 0.03% and 14.7% of gizzard shad lifespan production, respectively, is morphologically available for 21.1% and 31.5% of walleye lifetime production demand. Gizzard shad cohorts are one year out-of-phase with same-age walleye cohorts based on their respective age-specific production estimates (peak prey supply versus maximum piscivore demand). Ingestibility patterns, however, indicate that walleye (all ages) are never able to fully utilize the entire lifetime production potential of a given cohort of shad (Table 13). In fact, walleye must be at least four-years older than a cohort of shad before they are able to take full advantage of all age-0 shad production. Alewives, however, can remedy this deficit because 26.9% of alewife lifetime production is morphologically available to age-0 walleye (versus 0.03% for shad) and virtually all first-year alewife production (representing 75.6% of total alewife production) is ingestible to walleye $\geq$ age 1 (Table 16). In the absence of alewife, walleye would be apt to confront severe food shortages for the entire growing season. Even with alewives, age-1 walleye probably experience prey deficiencies during the early spring

Table 17. Multiple cohort demand by walleye for alewife cohorts in Smith Mountain Lake, Virginia. All values in percent of lifespan production.

Age	Walleye Demand	Percent of Demand Met by Alewife of Age:		
		2	1	0
6	0.8	0.8	-	-
5	2.4	2.4	-	-
4	5.1	3.4	1.7	-
3	12.9	-	12.9	-
2	26.1	-	3.2	22.9
1	31.5	-	-	31.5
0	21.2	-	-	21.2
Age-Specific Supply		6.6	17.8	75.6

months, because unlike striped bass, age-1 walleye cannot eat age-1 alewives. Therefore, alewives in providing a summer/fall food resource are probably crucial to the over-winter/spring survival of age-0 walleye. If reproductive failure of gizzard shad occurred in any year, alewives of all age groups would also become vitally important to other age groups of walleye because they are all restricted to feeding on primarily age-0 shad. Alewives are also critical to walleye ages 2-4 which must otherwise depend on age-0 gizzard shad that are not present for the first three months of the growing season. Unlike age-1 walleye, older walleye cohorts are able to consume age-1 alewife in the spring, thereby filling what would potentially be a prey deficient period (Table 14).

Largemouth Bass

Gizzard shad supply: A gizzard shad cohort is almost completely invulnerable to the same cohort of largemouth bass. Gizzard shad are vulnerable only part of their first year and then remain invulnerable to largemouth bass the remainder of their lifespan (Table 18). They are also invulnerable to largemouth bass one year older than themselves, except during their first year. Most of the gizzard shad cohort is available to largemouth bass cohorts two or more years older than themselves for as long as the largemouth bass remain in the system (in Smith Mountain lake largemouth bass live more than 6 years). Despite this, the percentage of lifespan production (demand) remaining for these older largemouth bass cohorts is much less than the concurrent percentage of lifespan production (supply) of the gizzard shad cohort (Table 18); vulnerability should be mitigated by low demand as was the case with striped bass and walleye. Most gizzard shad eaten will be consumed as young-of-the-year by largemouth bass ages 1 and 2.

Table 18. Available supply of a gizzard shad cohort age n versus demand by coexistent largemouth bass cohorts. Age-specific available supply of gizzard shad and demand by largemouth bass are estimated in terms of percent of lifetime cohort production.

Largemouth Bass Age Supply/Demand	<u>Largemouth Bass Cohort: n</u>						Total
	0	1	2	3	4	5	
	0.13/26.1	0.00/40.4	0.00/19.3	0.00/8.7	0.00/4.2	0.00/1.3	0.13/100
Largemouth Bass Age Supply/Demand	<u>Largemouth Bass Cohort: $n+1$</u>						Total
	0	1	2	3	4	5	
	-	32.5/40.4	0.00/19.3	0.00/8.7	0.00/4.2	0.00/1.3	32.5/73.9
Largemouth Bass Age Supply/Demand	<u>Largemouth Bass Cohort: $n+2$</u>						Total
	0	1	2	3	4	5	
	-	-	69.3/19.3	11.0/8.7	0.00/4.2	0.00/1.3	80.3/33.5
Largemouth Bass Age Supply/Demand	<u>Largemouth Bass Cohort: $n+3$</u>						Total
	0	1	2	3	4	5	
	-	-	-	69.3/8.7	19.5/4.2	4.5/1.3	93.3/14.2
Largemouth Bass Age Supply/Demand	<u>Largemouth Bass Cohort: $n+4$</u>						Total
	0	1	2	3	4	5	
	-	-	-	-	69.3/4.2	19.5/1.3	88.8/5.5
Largemouth Bass Age Supply/Demand	<u>Largemouth Bass Cohort: $n+5$</u>						Total
	0	1	2	3	4	5	
	-	-	-	-	-	69.3/1.3	69.3/1.3

Largemouth bass $\leq$ age 1, like walleye, also experience a deficiency in available gizzard shad supply, being able only to consume some age-0 gizzard shad. The deficiency is not nearly as severe for age-1 largemouth bass as it is for age-0 largemouth bass (Table 19). Age-2 largemouth bass are also morphologically constrained to feeding on age-0 gizzard shad, but their available supply is 3.6 times as great as their age-specific demand on the basis of percentage of lifespan production (Table 19). Largemouth bass ages 3 and 4 can both feed on gizzard shad $\leq$ age 1, while five year old largemouth bass can feed on gizzard shad ages 0-2.

The shad supply is more than adequate, except for bass ages 0 and 1, if each age group is considered alone (Table 19). The cumulative demand of multiple largemouth bass cohorts on particular age groups of gizzard shad could, however, exceed the available supply. Multiple cohort demand by largemouth bass is intense on gizzard shad ages 0 and 1 because of ingestibility constraints; age-5 largemouth bass are limited to gizzard shad two years old and younger. When age-specific demand is compared to age-specific supply (in terms of percent of lifetime cohort production), it is apparent that age-0 largemouth bass could experience a deficiency with gizzard shad as prey if the demand of older largemouth bass is first satiated (Table 20). However, as with walleye, age-0 largemouth bass cannot consume age-0 gizzard shad to any degree because of ingestibility limits. The large size of age-0 gizzard shad overrides the competitive effects of multiple cohort demand in creating the gizzard shad prey deficiency for age-0 largemouth bass.

Alewife supply: In contrast to gizzard shad, an alewife cohort is vulnerable to all cohorts of largemouth bass. Both same-age and one-year older largemouth bass cohorts

Table 19. Percentage of lifespan production (supply) of alewife (A) and gizzard shad (G) morphologically vulnerable to meet age-specific demand (% of lifespan production) of largemouth bass.

Age of Prey	Age of Largemouth Bass											
	0		1		2		3		4		5	
	A	G	A	G	A	G	A	G	A	G	A	G
0	41.8	0.13	75.6	32.5	75.6	69.3	75.6	69.3	75.6	69.3	75.6	69.3
1	-	-	15.6	-	17.8	-	17.8	11.0	17.8	19.5	17.8	19.5
2	-	-	-	-	6.6	-	6.6	-	6.6	-	6.6	4.5
3	-	-	-	-	-	-	-	-	-	-	-	-
4	-	-	-	-	-	-	-	-	-	-	-	-
5	-	-	-	-	-	-	-	-	-	-	-	-
6	-	-	-	-	-	-	-	-	-	-	-	-
Total Supply	41.8	0.13	91.2	32.5	100.0	69.3	100.0	80.3	100.0	88.8	100.0	93.3
Age-Specific Demand	26.1		40.4		19.3		8.7		4.2		1.3	

Table 20. Multiple cohort demand by largemouth bass for gizzard shad cohorts in Smith Mountain Lake, Virginia. All values in percent of lifespan production.

<u>Largemouth Bass</u>		<u>Percent of Demand Met by Gizzard Shad of Age:</u>							
Age	Demand	6	5	4	3	2	1	0	
5	1.3	-	-	-	-	1.3	-	-	
4	4.2	-	-	-	-	-	4.2	-	
3	8.7	-	-	-	-	-	8.7	-	
2	19.3	-	-	-	-	-	-	19.3	
1	40.4	-	-	-	-	-	-	*40.4	
0	26.1	-	-	-	-	-	-	*9.6	
Age-Specific Supply		0.0	0.0	0.0	0.0	1.3	12.9	69.3	

*Not Completely Ingestible by Largemouth Bass Ages 0 and 1.

should have the strongest impacts on an alewife cohort (Table 21). Like striped bass, the impacts of these cohorts are virtually equivalent but for opposite reasons. Same-age largemouth bass can consume only 64% of the lifetime production of the alewife cohort; they do not begin feeding on age-0 alewives until they turn piscivorous in August. The available alewife supply is not adequate to meet the simultaneous production demand of the same-age largemouth bass cohort (86%) over the alewife's three-year lifespan. Largemouth bass one-year older than an alewife cohort have 100% of the alewife lifespan production available to them; but only 68% of their (age-1 bass) lifespan production occurs during the three years that the alewife cohort is extant. Although the alewife cohort is completely vulnerable to older largemouth bass cohorts, their (bass) progressive decline in production demand limits their predation impacts (Table 21).

From the largemouth bass perspective, age-0 largemouth bass are morphologically constrained to age-0 alewife while age-1 largemouth bass can consume age-0 and most of age-1 alewife production (Table 19). Older bass have all age groups of alewives available to them. I also evaluated the simultaneous demand of all largemouth bass cohorts on the three alewife cohorts. If the oldest largemouth bass first consume the oldest and largest alewife, multiple cohort demand of the bass does not of itself cause alewife supply deficiencies for juvenile largemouth bass (Table 22).

Combined clupeid supply:

Age-specific prey deficiencies for largemouth bass are most probable at ages 0 and 1 when only 0.13% and 32.5% of gizzard shad lifespan production, respectively, are available for 26.1% (age-0) and 40.4% (age 1) of the largemouth bass production demand. Based strictly on production patterns, largemouth bass are one year out-of-phase

Table 21. Available supply of an alewife cohort age n versus demand by coexistent largemouth bass cohorts. Age-specific available supply of alewives and demand by largemouth bass are estimated in terms of percent of lifetime cohort production.

Largemouth Bass Age Supply/Demand	<u>Largemouth Bass Cohort: n</u>						Total
	0	1	2	3	4	5	
	41.8/26.1	15.6/40.4	6.6/19.3	-	-	-	64.0/85.8
Largemouth Bass Age Supply/Demand	<u>Largemouth Bass Cohort: $n+1$</u>						Total
	0	1	2	3	4	5	
	-	75.6/40.4	17.8/19.3	6.6/8.7	-	-	100/68.4
Largemouth Bass Age Supply/Demand	<u>Largemouth Bass Cohort: $n+2$</u>						Total
	0	1	2	3	4	5	
	-	-	75.6/19.3	17.8/8.7	6.6/4.2	-	100/32.2
Largemouth Bass Age Supply/Demand	<u>Largemouth Bass Cohort: $n+3$</u>						Total
	0	1	2	3	4	5	
	-	-	-	75.6/8.7	17.8/4.2	6.6/1.3	100/14.2
Largemouth Bass Age Supply/Demand	<u>Largemouth Bass Cohort: $n+4$</u>						Total
	0	1	2	3	4	5	
	-	-	-	-	75.6/4.2	17.8/1.3	93.4/5.5
Largemouth Bass Age Supply/Demand	<u>Largemouth Bass Cohort: $n+5$</u>						Total
	0	1	2	3	4	5	
	-	-	-	-	-	75.6/1.3	75.6/1.3

Table 22. Multiple cohort demand by largemouth bass for alewife cohorts in Smith Mountain Lake, Virginia. All values in percent of lifespan production.

<u>Largemouth Bass</u>		<u>Percent of Demand Met by Alewife of Age:</u>		
<u>Age</u>	<u>Demand</u>	<u>2</u>	<u>1</u>	<u>0</u>
5	1.3	1.3	-	-
4	4.2	4.2	-	-
3	8.7	1.1	7.6	-
2	19.3	-	10.2	9.1
1	40.4	-	-	40.4
0	26.1	-	-	26.1
Age-Specific Supply		6.6	17.8	75.6

with gizzard shad cohorts. When ingestibility patterns are also considered, largemouth bass are two years out-of-phase with shad; two-year old largemouth bass have all age-0 shad production (which represents 69% of shad total lifetime production) available to them. In theory, alewives can remediate this deficiency for age-0 and 1 largemouth bass in Smith Mountain Lake; 41.8% and 91.2% of alewife total lifetime production is available to these two age groups of bass, respectively.

An alewife cohort is of principal potential benefit to largemouth bass cohorts of the same-age and one year older. In the absence of alewives, age-0 largemouth bass are without a principal source of clupeid forage once shad rapidly outgrow largemouth bass ingestibility limits in late August. At this time, age-0 largemouth bass would have to switch to other food sources (e.g minnows, crayfish, sunfish, etc.) until the following summer when a new cohort of shad becomes available. Alewives also provide an available forage to age-1 largemouth bass during the spring; a period when same-age gizzard shad are not morphologically available to them.

Distributional Availability

The seasonal distribution (uplake/downlake, littoral/pelagic) of alewife and gizzard shad relative to their predators determines the probability of feeding encounters. Information on prey and predator distributions is not comprehensive because it was largely obtained as a by-product of efforts to capture clupeids and piscivores to determine life history parameters utilized elsewhere in this study. Nevertheless, my data are sufficiently detailed to provide a general description of the seasonal aspects of prey and predator

distributions and to develop an overview of the complementarity of gizzard shad and alewife in providing potential feeding encounters for predators in Smith Mountain Lake.

Forage-Fish Distributions

Trawling was the only method that proved successful in the capture of juvenile alewives, and it was performed primarily to describe first-year growth of clupeids. Seven midwater trawl sampling trips were conducted between late June and early September, 1984 in main channel locations of the lower lake, mid lake (Hales Ford Bridge area) and upper lake. Initially (first 5 sampling trips), only the largest juvenile alewives and gizzard shad were removed from the catch and measured for total length; remaining clupeids were not enumerated and were discarded. On the final two sampling trips (8/20/84 and 9/10/84), bioacoustical transects were conducted concurrently with midwater trawl collections. All trawl-caught clupeids were enumerated on those two dates to estimate relative abundance and to determine if bioacoustical data reflected trawl catches.

Only alewives were captured in the mid and lower-lake regions of Smith Mountain Lake (based on all midwater trawl collections conducted). On the August (8/20) sampling trip, average CPUE (CPUE defined as a 15 minute haul at 2m/s; depth 2 m) for juvenile alewives in the lower lake (69.5; $N = 2$) was similar to the upper lake catch (58.0; $N = 1$). However, the average catch of adult alewives in the lower lake was twice as high as the upper lake on that same date (Table 23). September (9/10) catches of alewives in the lower lake, both juvenile and adults, were substantially less than the August numbers from the same location (Table 23). Relative abundances of juvenile and adult alewives were also higher in the upper lake compared to the lower lake at the time

Table 23. Catch-per-unit-effort, based on mid-water trawl collections (15 minute haul at 2 m/s), for juvenile and adult clupeids in Smith Mountain Lake, Virginia 1984.

Location	Sampling Date	Juvenile		Adult	
		Alewives	Gizzard shad	Alewives	Gizzard shad
Lower lake	August 28	58	0	27	0
Lower lake	August 28	81	0	13	0
Lower lake	September 10	0	0	0	0
Lower lake	September 10	7	0	2	0
Mid lake	September 10	56	0	43	0
Mid lake	September 10	15	0	51	0
Upper lake	August 28	58	7	9	0
Upper lake	September 10	22	2	7	0

of the September collection (Table 23). Juvenile alewives, however, were found in the highest numbers during the September sampling date in the immediate vicinity of the Hales Ford Bridge (mid lake region). Adult alewives were also captured in the highest densities around the Hales Ford Bridge area in September (Table 23). No adult gizzard shad were taken by midwater trawling at any time. In all 1984 trawl samples, only nine juvenile gizzard shad were captured, all from the upper-main channel site (Table 23).

Daytime bioacoustic transects revealed scattered and clumped distributions of small fish suspended between 8 and 12 m depth in the upper and mid-lake regions (e.g. Fig. 26). In contrast to mid and upper-lake areas, no fish at all were recorded during daytime transects in the lower lake (Fig. 27). Bioacoustics readings taken at night revealed greater densities of fish in both the upper and mid-lake sites compared to the densities observed in those same areas during the daytime (e.g. Fig. 26). Concurrent trawl samples captured only alewives in the mid-lake area and primarily alewives and a few gizzard shad in the upper-lake site. In contrast to the scattered and clumped distribution patterns observed during the daytime, distribution during the night appeared more homogeneous, with fish concentrated in the top 5 m of the water column (Fig. 26). In the lower lake, night bioacoustic transects revealed some fish in the upper 5 m of the water column, but their density appeared to be significantly less than at mid and upper-lake sites (Fig. 27); concurrent trawl samples in the lower lake contained only juvenile and adult alewives.

Shoreline electrofishing during the spring and summer did not result in the capture of any juvenile alewives at any location. CPUE data were not collected on forage fish while electrofishing. Adult alewives were captured at lower-lake and mid-lake locations until the end of June. Juvenile gizzard shad were collected along the shoreline only in

Figure 26. Graph recordings from bioacoustical transects conducted during the day and night in the mid-lake area of Smith Mountain Lake, Virginia, on August 28, 1984. A = probable forage fish; B = probable predators.

Mid Lake
day
night

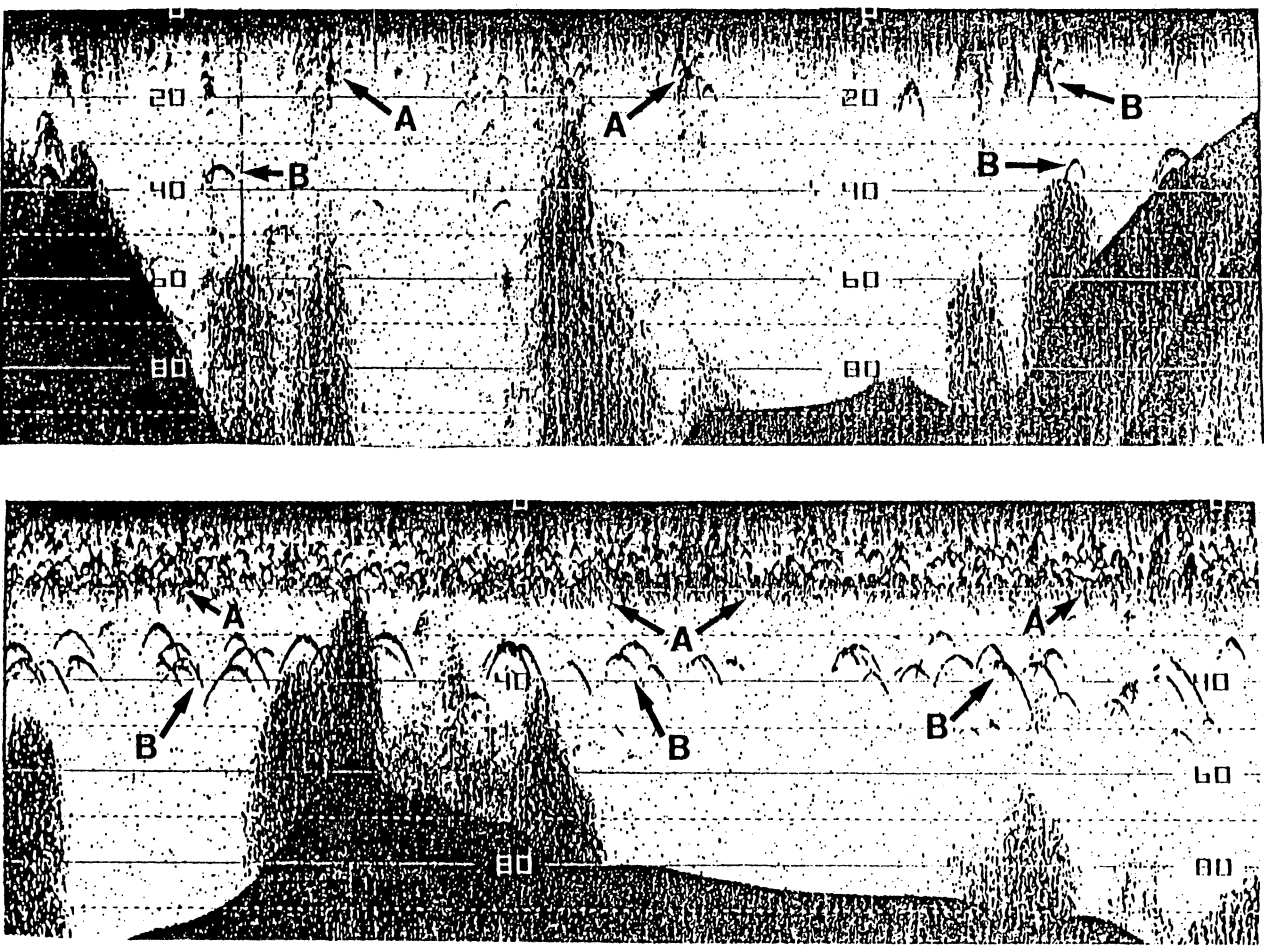
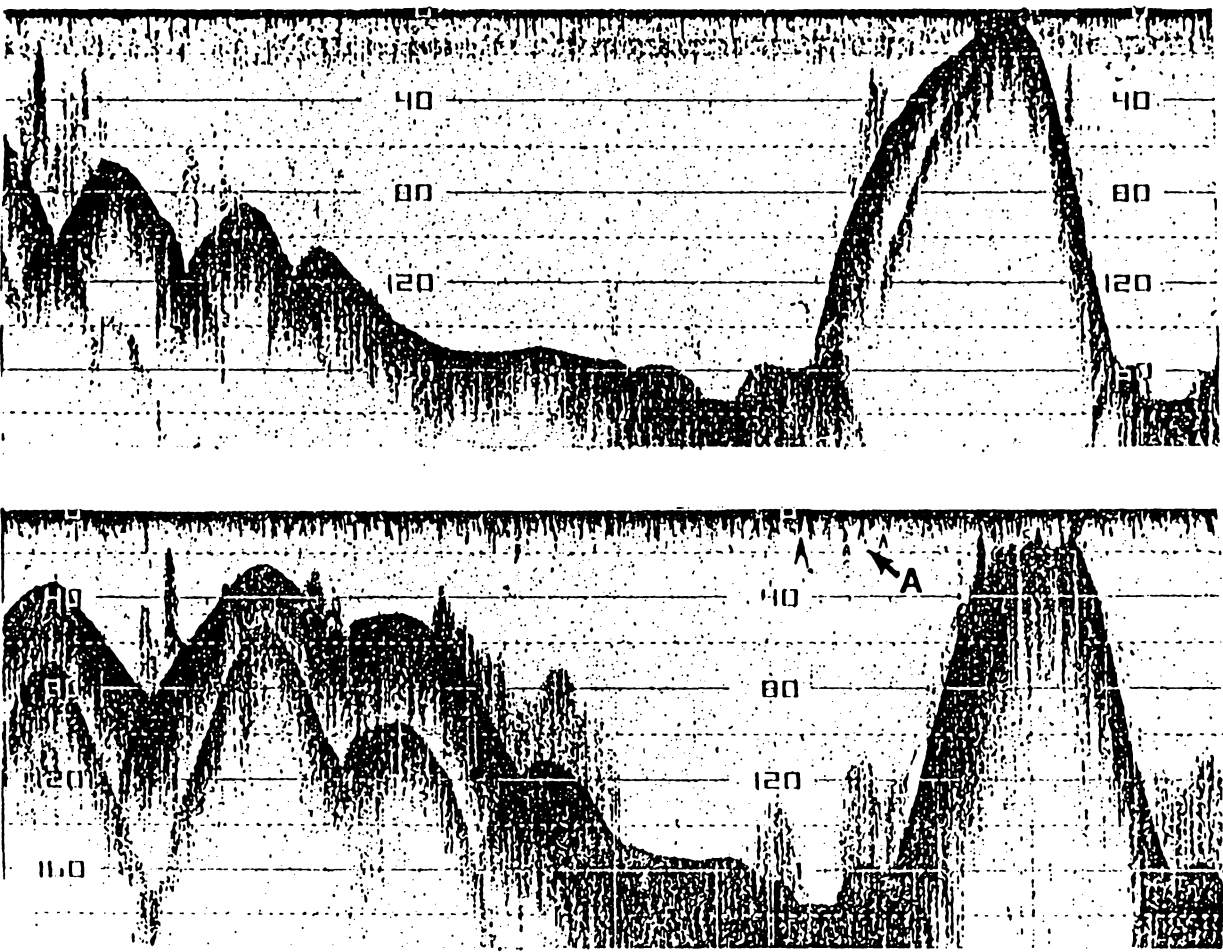


Figure 27. Graph recordings from bioacoustical transects conducted during the day and night in the lower lake of Smith Mountain Lake, Virginia, on September 10, 1984. A = probable forage fish.

Lower Lake
day night



the upper lake, with numbers increasing upstream; they were extremely abundant from Beaverdam Creek to the Hardy Bridge (Fig. 1). Adult gizzard shad were electroshocked in all three shoreline areas, but were most abundant in the upper lake.

Gill nets were set weekly from April to September to capture both predators and prey. However, nets were not routinely set in the upper lake, but rather at Hale's Ford Bridge in the mid-lake area because preliminary surveys indicated that striped bass and walleye were largely absent from the upper lake from May through October. Gillnet placement was intended to sample pelagic areas, with sets running off points into deep water, and littoral areas, with sets perpendicular to the shoreline in shallow water. However, almost all fish caught in sets off points were in the 30 m of net nearest shore. As a result, all collections were used to describe relative abundance (CPUE) of prey and predators in the littoral habitat of the mid-lake and lower-lake regions by season (spring - April, May, June; summer - July, August, September). Catch-per-unit-effort (CPUE) was defined as the total number of each species captured in all four nets fished overnight. I could not use vertical gill nets to sample pelagic habitat because they would have posed a safety hazard to boaters.

Seasonally, gillnet catches of alewives were significantly higher by number in the spring compared to the summer in both the lower and mid-lake regions (Table 24). Summer catches of alewives in both areas of the lake amounted to only 5% of the springtime catch. In contrast to alewives, gizzard shad were significantly more abundant inshore during the summer compared to the spring in the lower lake, with twice the number of shad being captured during the summer (Table 24). The mid-lake region, however, did not differ significantly in catches of gizzard shad between the spring and summer seasons (Table 24). Between species, alewives were significantly more abundant

Table 24. Comparison of catch-per-unit-effort (median CPUE with semi-quartile range in parentheses) in gillnet sets between seasons for forage and predator species in Smith Mountain Lake. CPUE is catch per 243.2 m of net fished overnight (12 hours). Statistical comparisons were made using the Wilcoxon Rank Sum test. N = sample sizes for spring/summer (1983/84 data combined).

Species	N	Location	Spring	Summer	P-value
Alewife	14/13	Lower Lake	166.00(88.75-239.50)	8.00(0.50-68.00)	0.002
Alewife	10/06	Mid Lake	123.50(97.75-285.50)	6.00(0.00-44.75)	0.013
Gizzard Shad	14/13	Lower Lake	23.50(10.00-46.00)	53.00(38.00-79.00)	0.016
Gizzard Shad	10/06	Mid Lake	64.00(32.00-94.50)	72.00(22.75-102.25)	0.828
Striped Bass	14/13	Lower Lake	10.50(6.25-11.00)	5.00(3.00-7.50)	0.007
Striped Bass	10/06	Mid Lake	9.50(7.25-12.00)	5.00(0.75-8.75)	0.037
Walleye	14/13	Lower Lake	15.50(8.75-23.25)	2.00(1.00-7.00)	0.002
Walleye	10/06	Mid Lake	4.50(2.50-9.25)	1.00(0.00-3.25)	0.049

than gizzard shad in both the lower and mid-lake areas in the spring (Table 25). During the summer months, relative abundance reversed. Gizzard shad were significantly more abundant in the littoral regions of the lake during the summer months compared to alewives. In the lower and mid-lake regions, gizzard shad outnumbered alewives 8:1 and 12:1, respectively (Table 25). Examination of mid-lake versus lower-lake distribution of alewives during the spring and summer revealed no significant difference in abundance between the two areas in either season (Table 26). In contrast to alewives, gizzard shad were more abundant in the mid-lake area compared to the lower lake in the spring; however, during the summer months, there was no significant difference in abundance (Table 26).

To summarize, alewives were found in lower, mid and upper-lake areas but only in pelagic habitat except during the spring when they move inshore to spawn. No juvenile gizzard shad were collected at anytime in the lower or mid-lake areas, but I was able to collect them in increasing numbers in an upstream direction from the mouth of Beaverdam Creek to the Hardy Bridge. Adult gizzard shad were collected in all three littoral regions of the lake, but were most abundant in the upper lake.

Piscivore Distributions

Striped bass were significantly more abundant in gillnet catches during the spring compared to the summer in both mid-lake and lower-lake regions (Table 24). Striped bass collected in littoral areas during the spring were twice as numerous as those collected in the littoral areas during the summer months in both parts of the lake. Walleye,

Table 25. Comparison of catch-per-unit-effort by species (median CPUE with semi-quartile range in parentheses) in gillnet sets and for black basses by electrofishing in Smith Mountain Lake. Gillnet CPUE is catch per 243.2 m of net fished overnight (12 hours) and electrofishing CPUE is catch per hour. Statistical comparisons were made using the Wilcoxon Rank Sum test. N = sample size (1983/84 data combined).

Location	Season	N	Species CPUE		P-Value
			<u>Alewife</u>	<u>Gizzard shad</u>	
Mid Lake	Spring	10	123.50(97.75-285.50)	64.00(32.00-94.50)	0.023
Mid Lake	Summer	6	6.00(0.00-44.75)	72.00(22.75-102.25)	0.037
Lower Lake	Spring	14	166.00(88.75-239.50)	23.50(10.00-46.00)	0.002
Lower Lake	Summer	13	8.00(0.50-68.00)	53.00(38.00-79.00)	0.038
			<u>Striped bass</u>	<u>Walleye</u>	
Mid Lake	Spring	10	9.50(7.25-12.00)	4.50(2.50-9.25)	0.030
Mid Lake	Summer	6	5.00(0.75-8.75)	1.00(0.00-3.25)	0.167
Lower Lake	Spring	14	10.50(6.25-11.00)	15.50(8.75-23.25)	0.018
Lower Lake	Summer	13	5.00(3.00-7.50)	2.00(1.00-7.00)	0.180
			<u>Largemouth bass</u>	<u>Smallmouth bass</u>	
Upper Lake	§	11	11.30(8.70-14.00)	0.00(0.00-0.67)	0.001
Lower Lake	§	7	5.00(4.00-6.00)	2.00(1.67-4.00)	0.034

§All samples combined.

Table 26. Comparison of catch-per-unit-effort of clupeid and sportfish species by location (median CPUE with semi-quartile range in parentheses) in overnight gillnet sets and for black basses by electrofishing in Smith Mountain Lake. Gillnet CPUE is catch per 243.2 m of net fished overnight (12 hours) and electrofishing CPUE is catch per hour. Statistical comparisons were made using the Wilcoxon Rank Sum test. N = sample sizes for mid/lower lake (1983/84 data combined).

Species	N	Season	CPUE		P-value
			Mid Lake	Lower Lake	
Alewife	10/14	Spring	123.50(97.75-285.50)	166.00(88.75-239.50)	0.619
Alewife	6/13	Summer	6.00(0.00-44.75)	8.00(0.50-68.00)	0.658
Gizzard Shad	10/14	Spring	64.00(32.00-94.50)	23.50(10.00-46.00)	0.035
Gizzard Shad	6/13	Summer	72.00(22.75-102.25)	53.00(38.00-79.00)	0.660
Striped Bass	10/14	Spring	9.50(7.25-12.00)	10.50(6.25-11.00)	0.494
Striped Bass	6/13	Summer	5.00(0.75-8.75)	5.00(3.00-7.50)	0.859
Walleye	10/14	Spring	4.50(2.50-9.25)	15.50(8.75-23.25)	0.003
Walleye	6/13	Summer	1.00(0.00-3.25)	2.00(1.00-7.00)	0.212
Largemouth Bass	11/07	-A	11.30(8.70-14.00)B	5.00(4.00-6.00)	0.001
Smallmouth Bass	11/07	-A	0.00(0.00-0.67)B	2.00(1.67-4.00)	0.001

A: All samples combined.

B: Collected in upper lake.

like striped bass, were also significantly more abundant in littoral areas during the spring compared to the summer at both mid-lake and lower-lake areas (Table 24). Striped bass exhibited no significant difference in relative abundance between mid-lake and lower-lake regions in either season (Table 26).

Median CPUE for walleye, however, was approximately three times higher in the lower lake compared to the mid-lake region during the spring and summer. Walleye were about 1.5 times more abundant than striped bass in the gill nets during the spring in the lower lake (Table 25). In contrast, CPUE for striped bass during the spring in the mid-lake area was twice as high as CPUE for walleye (Table 25). During the summer months, CPUE was not significantly different for striped bass and walleye in the mid-lake or lower-lake areas (Table 25).

Bioacoustic transects done in September showed fish of relatively large size in 12 to 15 m of water both during the day and night around the mid-lake area (Fig. 26). In the lower lake, however, I was unable to locate any fish the size of adult predators using bioacoustic equipment during the day or night (Fig. 27). Personal communications with fishermen regarding fishing spots during the spring and summer months substantiate the bioacoustics' data. During the spring, anglers fished for striped bass and walleye in littoral areas. In summer months, most striped bass fishing is done at night or early morning by locating fish in pelagic habitat using depth recorders, and vertically fishing for them with live bait or tackle. Fishermen have reported finding striped bass as deep as 21 m during the summer months. Most striped bass fishermen I spoke with fished the lower lake during the spring months and shifted to the mid-lake region during the summer. Catch rates in the lower lake during the summer months for striped bass appeared

to decline dramatically but increased in the mid-lake region. Several fishermen told me they fished where they were able to locate schools of forage fish with their depth finders.

Largemouth and smallmouth bass are primarily littoral species (Scott and Crossman 1973) and are known to avoid gill nets (Bennett 1970); analysis of their distributions focused on up-lake versus down-lake differences as indicated by electrofishing data (catch-per-hour of electrofishing). Distribution was not analyzed by season for the black basses. Only 1 and 3 electrofishing trips were conducted in the lower and upper lake, respectively, during the summer months (1983 and 1984 electrofishing data combined). Therefore, all electrofishing samples were pooled (seasons and years) by lake region (i.e. upper vs. lower lake) for intra-region (e.g., CPUE of largemouth bass vs. smallmouth bass in the upper lake) and inter-region (e.g., CPUE of smallmouth bass in the lower lake vs. upper lake) comparisons. Largemouth bass were significantly more abundant in the upper lake than in the lower lake, with the reverse true for smallmouth bass. Although smallmouth bass were more abundant in the lower lake than in the upper lake, CPUE for largemouth bass was still significantly greater than for smallmouth bass in the lower lake (Table 25). Largemouth bass in the upper lake completely dominated the catch with virtually no smallmouth bass collected there (Table 25).

In summary, striped bass were twice as abundant in nearshore areas during the spring compared to the summer. Catch-per-unit-effort was equivalent in each season for striped bass in both the mid and lower-lake regions. In contrast, walleyes were 2-3 times more abundant in the lower-lake gillnet catches. Walleye CPUE dropped several fold from spring to summer in both locations. Largemouth bass were significantly more abundant in the upper lake than in the lower lake. The reverse was true for smallmouth

bass, but largemouth bass were still captured in greater frequencies than smallmouth bass in the lower lake.

DISCUSSION

Alewife and gizzard shad life history patterns, population dynamics, and distributions in Smith Mountain Lake differ in numerous respects. These are considered in the context of relative availability of the two clupeids to piscivores to evaluate the compatibility and complementarity of these forage fishes in enhancing feeding opportunities for game fishes.

Clupeid Early Life History

Reproduction

Alewife and gizzard shad larvae exhibited strong spatial segregation in Smith Mountain Lake. Gizzard shad larvae were primarily uplake and littoral while alewife larvae were mainly downlake and pelagic. My sampling design was not sufficiently extensive to determine the degree to which overlap might have occurred. I suspect, however, it would be greatest in the mid-lake region (where the habitat characteristics are intermediate between those of the lower and upper lake) and vary annually. For example, low densities of larval alewives were collected in the upper main channel in 1984, but were absent in 1983. Significantly, no alewife larvae were taken in the upper lake cove, where

gizzard shad were the most abundant in both years. Therefore, it appears that even when these two species overlap in general lake regions, partial segregation may still be achieved via differences in their horizontal distributions (i.e., gizzard shad onshore and alewife offshore).

The larval distributions of these species is consistent with reports from other, morphometrically similar reservoirs where each occurs alone. Densities of larval shad are commonly higher in upper tributary arms of reservoirs than in broader and deeper downstream areas (Eley et al. 1967; Taber 1969; Storck et al. 1978; Krause and Van Den Avyle 1979; Shelton et al. 1982; Storck et al. 1982), perhaps due to the differential availability of suitable spawning areas (Downey and Toetz 1983). Gizzard shad spawn principally in low gradient tributaries, where large spawning aggregations move upstream as far as water depth will allow (Shelton 1972; Pierce 1977; Trautman 1981; Becker 1983). In Smith Mountain Lake, Virginia, gizzard shad apparently spawn in the upper arm of the Roanoke River, the principal tributary of the reservoir. In lakes, May (1968) found that shad preferred cover such as brush and aquatic vegetation for spawning and avoided steep banks which provided little shallow water and cover. The littoral zone in the upper region of Smith Mountain Lake contains more cover and slopes much more gradually toward the main channel than it does in the lower lake. In contrast, alewives spawn less discriminately over sand and gravel substrata (Rothschild 1966; Norden 1967b). In Claytor Lake, Virginia, the major spawning site of alewives is also adjacent to deep water near the dam (Nigro and Ney 1982).

Spatial segregation of alewife and gizzard shad larvae effectively minimizes the potential for direct (interference) trophic competition which could impact the production of either species. However, the possibility of exploitative competition still exists. If

alewives in the lower lake rely on downstream drift of zooplankton from the tributary arms of the reservoir, they could experience shortages when gizzard shad produce a strong year-class. Larval gizzard shad can decimate zooplankton populations to the apparent detriment of other larval fishes (R.A. Stein, Ohio State University, personal communication). However, gizzard shad larvae in Smith Mountain Lake are more abundant in coves than in the main channel, where zooplankton would be transported. In addition, adult alewives are piscivorous (Kohler and Ney 1980) and could consume larval gizzard shad, because adult alewives do show some overlap with larval gizzard shad in the upper lake. Assessment of exploitative competition and predation between gizzard shad and alewife larvae would require a focused investigation which does not appear warranted at this time because overlaps are not severe.

Spatial segregation should also increase feeding opportunities for juvenile piscivores throughout systems that contain both forage species versus systems that have only one. However, it is not yet possible to generalize the occurrence and degree of spatial segregation between larval alewives and gizzard shad in lentic waters. In particular, systems that differ from the shallow upstream and deep downstream configuration may also experience different distributions of these larval clupeids. Where alewife and gizzard shad larvae do share a horizontal distribution, they are also likely to occur at the same depths. In Smith Mountain Lake, both species were nocturnally present in greatest abundance in the upper 3 m of the water column. Similar vertical distributions for larval gizzard shad, from both day and night samples, have been reported in Melvern Reservoir, Kansas (Willis 1987), Center Hill Reservoir, Tennessee (Van Den Avyle and Fox 1980), Barkley Reservoir, Kentucky (Graser 1979), Lake Norman, North Carolina (Edwards et al. 1977) and Beaver Reservoir, Arkansas (Netsch et al 1971). Larval alewives were

also most abundant near the surface in Claytor Lake, Virginia (Nigro 1980), Lake Huron (O'Gorman 1983) and Lake Ontario (Graham 1956).

The higher densities of larval gizzard shad recorded at the cove site versus the main channel location in both 1983 and 1984 in Smith Mountain Lake do not reflect a general distributional pattern for the species in other systems. Mayhew (1974) also found that larval gizzard shad (in Lake Rathbun, Iowa) were more numerous in embayments and shallow water habitat along the shoreline. In contrast, Edwards et al. (1977) and Shelton (1972) observed that some shad spawning activity occurred in open water, and Storck et al. (1982) reported that larval gizzard shad were more abundant in mainlake areas than in embayments in Lake Shelbyville, Illinois. Larval gizzard shad in Melvern Reservoir, Kansas, were more abundant in open water compared to nearshore habitat (Willis 1987). Netsch et al. (1971), however, found shad to be equally abundant at nearshore and offshore sites in Beaver Reservoir, Arkansas.

Abundance of larval alewives in Lake Michigan (Wagner (1972), Lake Huron (O'Gorman 1983) and Claytor Lake, Virginia (Nigro 1980) was closely related to shoreline topography, with greatest densities occurring in littoral areas, coves and embayments. In Smith Mountain Lake, greater larval alewife densities occurred near shore in 1983. In 1984, larvae were equally abundant at cove and main channel sites. Alewife larvae will usually remain on the spawning grounds until the late larval stage (19 mm TL) and then move offshore to deeper water (Wagner 1972; Scott and Crossman 1973; O'Gorman 1983). Higher densities recorded offshore in 1984 may be the result of an earlier offshore movement of larvae. Although larval gizzard shad densities were usually higher than alewife densities in Smith Mountain Lake samples, their separate

spatial distributions make it impossible to extrapolate the relative abundance of one to the other without much more extensive sampling.

Clupeid populations are characterized by large fluctuations in year-class strength, attributable to a variety of causes (Lasker 1985). In Smith Mountain Lake, relative abundance of larval alewives did not vary significantly between the two years, but densities of larval gizzard shad varied more than five-fold. Bross (1967) reported that the relative abundance of young-of-the-year gizzard shad can vary forty-fold over consecutive years in Canton Reservoir, Oklahoma, and observed that low abundance was associated with low water levels and temperatures during the spring. Dewey and Moen (1982) reported that interannual densities of larval gizzard shad varied two-fold in DeGray Lake, Arkansas and suggested that this might be partially due to competition for food resources with threadfin shad and young sunfishes. Aggus and Lewis (1978) found that high spring water levels and/or nutrient inflows were correlated with strong year classes of both prey and predators in some southeastern reservoirs. In Smith Mountain Lake, the higher densities of larval gizzard shad observed in 1983 compared to 1984 were also associated with greater water levels/inflows. Water temperatures were similar in 1983 and 1984 (Figs. 4 and 5), but total rainfall for the months of April, May and June was higher in 1983 (13.5 inches) compared to 1984 (10.7 inches) (National Oceanic and Atmospheric Administration, Climatological Data, Virginia, Vols. 93 and 94). In 1983, the lake reached its maximum level in April (795.7 feet) compared to 1984 when elevation peaked in February (795.1 feet). There are many causes other than water levels or inflows which could alone or in combination affect larval clupeid abundance (e.g. competition for food and reproductive habitat, predation, disease, abundance and condition of spawning stock, temperature, wind, etc.). Investigation of the role of all these variables was not warranted on the basis of only two years' data. Information in

the literature pertaining to interannual variations in abundance of larval alewives is lacking. Independent of whatever caused the fluctuations in the relative abundance of larval gizzard shad in Smith Mountain Lake, it is evident that gizzard shad and alewife did not respond in synchrony to the same variable(s).

Relative abundance of larval gizzard shad (5-30 mm TL) appears to provide a useful index of late summer abundance of age-0 shad in Smith Mountain Lake. Gizzard shad were 5.3 times more abundant in larval fish tows (based on median densities) in 1983 compared to 1984. This difference in relative abundance was also later reflected in August VDGIF cove rotenone samples (Whitehurst 1984, 1985); age-0 shad in 1983 outnumbered the 1984 cohort 5.8 to 1. Houser and Netsch (1971) also found that the relative abundance of larval shad provided a reasonable index of year-class strength. Crecco et al. (1983) suggested, based on survivorship curves, that year-class strength of American shad is established prior to the juvenile stage and that relative abundance of juvenile shad provides a useful index for detecting strong and weak year classes. Whether relative abundance of larval shad can be used as a reliable predictor (index) of age-0 shad abundance in Smith Mountain Lake will need to be further determined by correlating larval shad densities and later age-0 shad abundance over several years. The use of larval indices to assess year-class strength of alewives could not be evaluated because alewives are not collected in cove rotenone surveys in proportion to their abundance.

Water temperature has often been cited as an important factor in regulating gonadal maturation and initiating spawning activity in fish (LeCren 1951; Nikolsky 1963; Mathur and Ramsey 1974; Muth and Tarter 1975). Alewife spawning begins at approximately the same water temperature (18°C) in Smith Mountain Lake as in other lacustrine sys-

tems. Gross (1959) observed that in Lake Hopatcong, New Jersey, alewives first appeared inshore (< 5 m) in late April at water temperatures of 10 to 13°C. Spawning subsequently began in late May at water temperatures of 17 to 18°C. Norden (1967b) reported that alewives moved inshore in Milwaukee Harbor, Lake Michigan, toward the end of April and first part of May and began spawning in late June at 17.5°C. Edsall (1970) noted that alewives in the Kalamazoo River, Michigan entered shallow areas as water temperatures approached 10°C, but did not spawn until late May or early June when water temperatures reached 16°C. Rothschild (1966) observed that alewives first entered littoral areas of Cayuga Lake, New York, in late May as water temperatures approached 12°C. The onset of courtship and spawning, however, did not occur until mid-June when water temperatures reached approximately 17°C. In Claytor Lake, Virginia, alewives began spawning when water temperatures reached 16°C in early May (Nigro 1980).

Although alewives in Smith Mountain Lake initiate spawning at the same approximate water temperature as alewives in other systems, temporal differences are evident. Alewives in Smith Mountain Lake begin spawning approximately one month later than those in Claytor Lake, Virginia (Nigro 1980) and one month earlier than alewives in Milwaukee Harbor, Lake Michigan (Norden 1967a) or Cayuga Lake, New York (Rothschild 1966).

Gizzard shad spawning also begins at approximately the same water temperature in Smith Mountain Lake (17°C) as in other impoundments. In Center Hill Reservoir, Tennessee (Krause and Van Den Avyle 1979) and Lake Rathbun, Iowa (Mayhew 1974) gizzard shad began spawning when water temperatures reached 17°C in early May. Shelton et al. (1982) reported that gizzard shad in Lake Texoma, Oklahoma- Texas,

began spawning in March when water temperatures reached 18°C. Gizzard shad in Lake Norman, North Carolina (Edwards et al. 1977) and Beaver Reservoir, Arkansas (Netsch et al. 1971) initiated spawning activities in April also at water temperatures of 18°C. Downey and Toetz (1983) also observed that gizzard shad in an Oklahoma reservoir began spawning in April, but not until water temperatures were 21°C.

Temporal differences in the onset of spawning were also evident for gizzard shad, like alewives, among different systems. Gizzard shad in Smith Mountain Lake began spawning approximately 4 to 6 weeks later than those in Lake Carl Blackwell, Oklahoma (Downey and Toetz 1983), DeGray Lake, Arkansas (Dewey and Moen 1982), Lake Norman, North Carolina (Edwards et al. 1977) and Beaver Reservoir, Arkansas (Netsch et al. 1971) and 8 to 10 weeks later than observed in Lake Texoma, Oklahoma-Texas (Shelton et al. 1982). Increases in water temperature vary between systems primarily due to differences in latitudinal, climatological, and limnological characteristics. Consequently, water temperatures reach levels necessary to elicit physiological and behavioral responses associated with spawning at different times in the season and ultimately may cause variation in onset of spawning.

Alewife and gizzard shad in Smith Mountain Lake appear to possess very similar temperature preferenda (18-29°C and 17-29°C, respectively) for spawning; however, alewives begin spawning later than gizzard shad. The differences in the timing of spawning observed in Smith Mountain Lake may be partially explained by the thermal regime: the upper lake warmed more rapidly than did the lower lake. Shelton et al. (1982) noted that initiation of spawning by most temperate fishes is closely correlated with water temperature, and initial spawning is usually observed in the suitable habitat that warms earliest. Shelton et al. (1982) and Netsch et al. (1971) reported that gizzard

shad in the upper end of reservoirs (tributary arms) spawned several weeks earlier than gizzard shad further downstream.

Nigro (1980) noted that peak spawning for alewives in Claytor Lake occurred during the third week of May at water temperatures of 21 to 24°C. Spawning, however, continued well into the summer and ended during the first week of August at water temperatures of 24 to 27°C. Alewives in Milwaukee Harbor, Lake Michigan, also spawned until early August, but peak spawning occurred in July (Norden 1967b). In Smith Mountain Lake, peak spawning for alewives occurred close to July 1 in 1983 and mid July in 1984 at water temperatures of 28 and 26°C, respectively. Spawning was completed by the first or second week of August at surface water temperatures of 27-28°C. Only Edsall (1970) discussed possible upper temperature limits for alewife spawning. He found that in Kalamazoo River, Lake Michigan, alewife spawning was interrupted when the water temperature rose above 28°C. Although an upper temperature limit for successful alewife spawning exists, that temperature is rarely reached in northern lakes where alewives occur and thus may not be a primary determinant of spawning period in those systems. However, in southern reservoirs where water temperatures may exceed the upper temperature limit, alewife spawning may be interrupted and spawning period significantly curtailed. In Smith Mountain Lake in 1984, lower-lake water temperatures rose to 29°C during the second week of June and may have interrupted alewife spawning. Densities of larval alewives decreased by 55% that week compared to the previous week. The following week, however, lower lake temperatures dropped back to 26°C, and larval alewife densities rose by 200%.

Peak spawning of gizzard shad occurred at approximately the same time in Smith Mountain Lake as in other lakes and reservoirs. Edwards et al. (1977) reported that

peak spawning for gizzard shad in Lake Norman, North Carolina, occurred in mid-June at water temperatures 24 to 28°C. In Center Hill Reservoir, Tennessee, peak spawning for gizzard shad occurred when water temperatures reached 24°C in early June (Krause and Van Den Avyle 1979). Downey and Toetz (1983) noted that peak spawning for gizzard shad in Lake Carl Blackwell, Oklahoma, occurred during the third week of May at a water temperature of 22°C. In Lake Rathbun, Iowa, (Mayhew 1974) and Lake Texoma, Oklahoma-Texas, (Shelton et al. 1982) peak spawning for gizzard shad also occurred at a temperature of 22°C. In both years at Smith Mountain Lake, peak spawning for gizzard shad occurred in mid June at water temperatures of 28°C. In 1983, spawning was completed by the last week of June at surface water temperatures of 29°C with temperatures climbing to 30°C by the following week. In 1984, however, gizzard shad were spawning until late July at water temperatures of 27°C. At no time in 1984 did water temperatures exceed 28°C. To my knowledge, no studies have been conducted to determine the upper temperature limits for gizzard shad spawning. However, in 1983, water temperatures in the upper lake may have exceeded some upper limit for gizzard shad spawning which may be near 29°C. Gizzard shad in Lake Norman, North Carolina, were observed spawning until early September at water temperatures to 29°C (Edwards et al. 1977). Spawning ceased after the first week of July when water temperatures the previous week reached 29°C in Lake Carl Blackwell, Oklahoma (Downey and Toetz 1983). Mayhew (1974) also noted that gizzard shad spawning ended in Lake Rathbun, Iowa, when water temperatures reached 29°C in mid-August; while Krause and Van Den Avyle (1979) reported that gizzard shad continued to spawn in Center Hill Reservoir, Tennessee, until water temperatures reached 28°C in early August.

Variation in the duration of spawning period in Smith Mountain Lake and elsewhere appears to be a function of the thermal regime. In 1984, gizzard shad in Smith Moun-

tain Lake spawned over a period nearly twice as long as in 1983, 11 versus 6 weeks, respectively. Spawning periods in other systems were reported to last approximately 4 weeks in western Lake Erie (Bodala 1966); 6 weeks in Melvern Reservoir, Kansas (Willis 1987); 7 to 9 weeks in Lake Texoma, Oklahoma-Texas (Shelton et al. 1982) and Lake Carl Blackwell, Oklahoma (Downey and Toetz 1983); 11 to 13 weeks in Beaver Reservoir, Arkansas (Netsch et al. 1971), Lake Rathbun, Iowa (Mayhew 1974), Center Hill Reservoir, Tennessee (Krause and Van Den Avyle 1979) and DeGray Lake, Arkansas (Dewey and Moen 1982); 15 weeks in Lake Norman, North Carolina (Edwards et al. 1977) and 17 to 18 weeks in Barkley Reservoir, Kentucky (Graser 1979).

Stock (1971) found that spawning periods were brief in ponds where the condition of gizzard shad was poor. Willis (1987) reported that larger gizzard shad (270-299 mm; $\geq$ age 5) appeared at spawning areas early in the season and completed most spawning within 2-3 weeks compared to smaller gizzard shad (170-219 mm; $\leq$ age 4) which spawned for 6 weeks. After 3 to 4 years of age, gizzard shad fecundity begins to decrease; for example, a two year-old female may produce over 300,000 eggs while a four year-old female may only produce 70,000 eggs (Miller 1960; Kilambi and Baglin 1969). Gizzard shad populations dominated by younger individuals ($\leq$ age 4) may therefore, have longer spawning seasons compared to populations dominated by older individuals (Willis 1987). Age-5 and older gizzard shad composed 19%, by numbers, of all gizzard shad $\geq$ age 1 in 1983 cove rotenone samples from Smith Mountain Lake; gizzard shad spawning lasted 6 weeks that year. In 1984, gizzard shad $\geq$ age 5 composed only 2% of the cove rotenone sample; spawning that year lasted 11 weeks.

Spawning period of alewives in Smith Mountain Lake was approximately 13 weeks, compared to 13 weeks in Claytor Lake (Nigro 1980), nine weeks in Cayuga Lake

(Rothschild 1966) and Lake Michigan (Norden 1967a) and four weeks in Lake Hopatcong (Gross 1959). Time and place of spawning are adaptations which assure optimum conditions for growth and survival of young (Nikolsky 1963). As latitude decreases, conditions favorable for spawning may occur earlier and persist longer if the upper temperature limit is not reached, thus allowing for more individual variation in timing of spawning. A general review of extant early life history information on both species indicates that alewives will probably spawn longer and later than gizzard shad if thermal limits are not exceeded. Prolonged spawning of alewife in Smith Mountain Lake may be due in part both to longitudinal temperature gradient in the reservoir and the fact that adult alewives can locate in cooler, oxygenated water in the lower reservoir all spring and summer and are not closely attuned to surface temperatures to induce spawning. Alewives might also be fractional, repeat spawners, which would contribute to an extended reproductive period (Nigro and Ney 1982). Observations on spawning behavior of several species of fish (Fabricus and Gustafson 1954; Jones and Ball 1954) indicate that repeated spawning acts, with the extrusion of small numbers of eggs each time together with wide distribution of eggs and a protracted spawning period, increases the likelihood that some eggs will survive unfavorable periods during development. Spawning periods of alewife and gizzard shad will likely overlap in other systems as they do in Smith Mountain Lake. The potential for trophic competition among the larvae may be high unless, as in Smith Mountain Lake, they are spatially segregated.

In summary, alewife and gizzard shad larvae exhibited strong spatial segregation in Smith Mountain Lake. Gizzard shad larvae were primarily uplake and littoral while alewife larvae were mainly downlake and pelagic. Spatial segregation should increase feeding opportunities for piscivores and minimize the potential for direct (interference) trophic competition, especially during the larval stages when it would be the most in-

tense and could impact the production of either. Alewives spawned later and over a longer period of time (≈ 13 weeks) than gizzard shad (≈ 6 weeks) in Smith Mountain Lake. Peak spawning for gizzard shad occurred in June while alewives peaked in July. Differences in the timing and duration of these clupeid spawning periods are complementary in providing temporal feeding opportunities for Smith Mountain Lake piscivores.

First-Year Growth

The pattern of a linear increase in total length, from first capture through August, observed for age-0 alewives in Smith Mountain Lake is consistent with growth patterns observed in other waters. Nigro and Ney (1982) found that first-year growth in length of alewives in Claytor Lake, Virginia, proceeds at a linear daily rate from first capture through September. Estimated daily growth increments were 0.84 mm/day in 1978 and 0.68 mm/day in 1979 (Nigro and Ney 1982), versus a similar rate of 0.84 mm/day in Smith Mountain Lake in 1984. Temporal patterns of first-year growth of landlocked alewives have not been described explicitly for other waters. Total lengths of age-0 alewives captured on successive dates, however, have been reported from Lake Hopatcong, New Jersey (Gross 1959), Cayuga Lake, New York (Rothschild 1966) and Lake Michigan (Norden 1967b). These data indicate that growth in length also proceeds at a linear daily rate through the summer period. Daily growth increments derived from these data were very similar to the growth rate of alewives in Smith Mountain Lake: 0.77 mm/day (Lake Hopatcong), 0.82 mm/day (Cayuga Lake), and 0.86 mm/day (Lake Michigan). Although growth rates of alewives among these systems were similar, the maximum size attained at the end of their first year of life varied considerably (Table 27).

Table 27. Total length (mm) at age of landlocked alewife from various locations in the United States.

Water and Source	Age				
	I	II	III	IV	V
Cayuga Lake, NY (Rothschild 1965)	102	121	130	138	144
Claytor Lake, VA (Kohler 1980)	160	182	200	208	-
Lake Michigan (Norden 1967b)	94	140	159	173	-
Lake Hopatcong, NJ (Gross 1959)	76	108	150	-	-
Seneca Lake, NY (Odell 1934)	68	144	151	168	172
Wautauga Reservoir, TN (Daniel 1984)	70	103	-	-	-
Smith Mountain Lake, VA (This study)	84	120	157	-	-

Nigro (1980) suggested that alewives in Claytor Lake have greater first-year growth compared to alewives in northern systems due to a longer growing season rather than any variation in physiology or genetics. The growing season in Smith Mountain Lake should be approximately the same length as the growing season in Claytor Lake because of their close geographic proximity. Alewives in Claytor Lake, however, achieve a greater total length at the end of their first year of growth compared to alewives in Smith Mountain Lake (Table 27). Smith Mountain Lake contains 5.6 times the volume of water as Claytor Lake and has 30 times the retention rate; it probably takes considerably longer than Claytor Lake to warm during the spring. Alewives in Smith Mountain Lake begin spawning about a month later than alewives in Claytor Lake, resulting in a shorter growing season.

The trophic state of Smith Mountain Lake may be of more importance than length of growing season (i.e. water temperature) as a factor affecting first-year growth of alewives. Hayward and Margraf (1987) suggested that growth rates of yellow perch (Perca flavescens) varied between the central and western basins of Lake Erie because of differences in the trophic states of the two basins rather than temperature. Reservoirs characteristically experience species shifts and declines in standing stock, harvest, and growth rates as initial fertility declines (Kohler et al. 1986). Claytor Lake, Virginia, differs from this pattern in that fertility has increased sharply in the last decade (Kohler et al. 1986), while nutrient concentrations in Smith Mountain Lake have declined significantly since the installation of an advanced waste-water treatment plant on the Roanoke River in 1975 (Whitehurst 1984). The mesotrophic conditions in the lower lake of Smith Mountain Lake (Benfield and Hendricks 1975), versus the eutrophic conditions in Claytor Lake (Kohler 1980), may explain the differences in first-year growth of alewives between these two systems. In addition, possible competition for food re-

sources may also be an important factor affecting first-year growth of alewives in Smith Mountain Lake. A massive alewife die-off in Claytor Lake, Virginia, during the exceptionally cold winter of 1977-78 and the resultant effect of the die-off on prey abundance and intensity of competition may have caused the disparity in the total first-year alewife growth between 1978 (148 mm TL) and 1979 (160 mm TL) (Nigro and Ney 1982). Brown (1972) speculated that reduction in population density of alewives in Lake Michigan following a massive die-off in 1967 was most likely responsible for the corresponding increase in growth rate. Other investigators (Brooks 1968; Wells 1970) have described a direct relation between changes in growth of alewives and their selective depletion of larger zooplankton species.

Gizzard shad, like alewives, also exhibited a linear increase in total length from first capture through the end of August in Smith Mountain Lake; gizzard shad growth also appeared to decelerate by early September. Temporal patterns of first-year growth of gizzard shad have not been described explicitly for other waters. Total lengths of age-0 gizzard shad captured on successive dates, however, have been reported for Lake Erie (Bodala 1966), Beaver and Bull Shoals Reservoirs, Arkansas (Kersh 1970) and the Wisconsin River (Becker 1983). These data indicate that growth also proceeds at a linear rate, but unlike shad growth in Smith Mountain Lake, does not decelerate until late September or October. Daily growth rates of young-of-the-year gizzard shad in Smith Mountain Lake (1.33 mm/day) were higher than those estimated for the other systems: Lake Erie and the Wisconsin River (1.16 mm/day), Beaver Reservoir (0.83 mm/day) and Bull Shoals Reservoir (0.77 mm/day). However, total length attained by gizzard shad in Smith Mountain Lake at the end of their first season of growth was in the range of lengths reported for gizzard shad from other waters around the country (Table 28). Why shad in Smith Mountain Lake should grow faster but decelerate earlier than in other

Table 28. Total length (mm) at age of gizzard shad from various locations in the United States

Water and Source	Age										
	I	II	III	IV	V	VI	VII	VIII	IX	X	XI
Elephant Butte Lake, NM (Jester and Jensen 1972)	95	151	183	219	254	273	391	324	-	-	-
Conchas Lake, NM (Jester 1962)	76	154	225	284	320	343	360	371	379	387	412
Ft. Gibson Reservoir, OK (Jenkins 1953)	143	258	325	-	-	-	-	-	-	-	-
Lake Erie (Boloda 1966)	259	366	403	429	467	428	-	-	-	-	-
Beaver Dam Lake, IL (Lager and Van Meter 1951)	240	278	330	375	-	-	-	-	-	-	-
Lake Wappapello, MO (Patriarche 1953)	103	170	208	230	245	258	273	293	300	293	-
Herrington Lake, KY (Turner 1953)	110	196	259	311	334	-	-	-	-	-	-
Lake Newnan, FL (Berry 1958)	254	317	338	-	-	-	-	-	-	-	-
Smith Mountain Lake, VA (This Study)	134	186	224	257	290	314	320	-	-	-	-

systems is not readily explicable. First-year growth of fish is determined by the integration of climatological and biological conditions that may influence food availability, competition for food and space, and predation (Ney and Smith 1975). The high first-year growth rate of gizzard shad in Smith Mountain Lake may be linked to predation by sportfish on young-of-the-year shad which can rapidly reduce intraspecific competition. In 1973-75, when gizzard shad were much more abundant, first-year growth averaged about 10% less than in the period 1979-84 (age and growth data from Hart 1978; La Roche 1981; Whitehurst 1984, 1985), providing support for the hypothesis of density-dependent control of growth. Eutrophic conditions in the upper lake, where young-of-the-year gizzard shad were most abundant, may also be a major factor contributing to the high growth rates.

Growth rates of clupeids are extremely plastic and can be expected to vary annually in Smith Mountain Lake. Both the absolute abundance of zooplankton (for alewives) and periphyton/phytoplankton (for post-larval shad) and the density of competitors will cause growth rates to vary between years to some degree. My analyses are necessarily based on the assumption that first-year growth rates and patterns observed in 1983-84 are typical for Smith Mountain Lake.

In summary, total lengths of gizzard shad and alewife young-of-the-year increased at a linear rate through August, but shad daily growth was about 40% greater than alewife. This, coupled with earlier spawning by shad means they were approximately 50% greater in total length at age-1 than alewives. Later spawning and slower first-year growth of alewives should assure a better degree of morphological availability throughout the growing season to piscivores that share a similar spatial distribution.

Mortality Rates

Larval clupeids: Mortality estimates which I derived from growth rate and length-frequency data will be unbiased estimates only if 1) larvae were consistently sampled in proportion to their abundance, and 2) growth rates were constant over the range of lengths being considered (Ricker 1975; Mansfield and Jude 1986). Sampling gear, towing speed and water clarity can all affect vulnerability of fish larvae to capture (Thayer et al. 1983; Snyder 1983). Collection gear and towing speed used in this study were selected based on previous larval fish studies which successfully captured larval shad and alewives up to 25-30 mm TL. I also sampled at night to minimize net avoidance (Silliman 1943; Bridges 1956; Ehrlich 1975) along with thoroughly cleaning the net after each haul to minimize back-flushing resulting from a plankton-clogged net (Snyder 1983). The effect of back-wash (from the engine's prop) on the capture of larval fish was reduced by towing from the side of the boat rather than directly behind the engine (Snyder 1983). In addition, prolarvae (< 5 mm TL) and larvae (> 30 mm TL) which were not fully vulnerable to the sampling gear based on catch data, were excluded from analyses. Prolarvae were less abundant than 5-10 mm larvae in standardized hauls while larvae > 30 mm TL were virtually absent from the catch. The assumption of constant growth over the range of lengths (5-30 mm TL) being considered is reasonable: growth rates appeared to be strongly linear in the range used to derive mortality estimates for both gizzard shad ($R^2 = 0.96$) and alewife ($R^2 = 0.97$) larvae in Smith Mountain Lake (see Fig. 6).

My mortality estimates are also consistent with those reported in the literature, although estimates of daily mortality rates specifically derived for larval gizzard shad and

alewife are limited. Mayhew (1976) estimated daily mortality rates for larval gizzard shad (5-16 mm TL) in Lake Rathbun, Iowa, using the catch curve method. Mortality rates with 95% confidence intervals ranged from 6.1%/day $\pm$ 2.6% to 13.0%/day $\pm$ 1.1% over a three-year period (Mayhew 1976) and compared favorably to my estimates for gizzard shad 5-17 mm (12.7%/day, semi-quartile range 7.8% to 14.0%).

Daily larval mortality rates have been derived for two alewife populations. Essig and Cole (1986) estimated daily mortality rates for larval alewives from a small Massachusetts coastal pond using three methods, two based on otoliths and one using catch curves. Mortality rates ($\pm$ 95% confidence limits) for 6-14 mm alewives using the two otolith methods (otolith increment-frequency and the otolith converted length-frequency) were 13.6%/day $\pm$ 10% and 8.8%/day $\pm$ 8.0%, respectively. Based on the catch curve method, daily mortality rates were 8.8%/day $\pm$ 5.0%. Essig and Cole (1986) concluded, however, that significant differences were not generally found among mortality rates derived by these three methods. Larval alewife (5.5-25.0 mm TL) mortality rates derived from length-frequency data, averaged 6.4%/day $\pm$ 6.3 SD in Lake Michigan (Mansfield and Jude 1986). Daily mortality estimates for alewives in Smith Mountain Lake were similar (7.1%/day, semi-quartile range 4.8% to 9.8%) to those derived in both of these studies.

Larval mortality rates of gizzard shad and alewife in Smith Mountain Lake are also consistent with the reported values for another closely related species. Crecco et al. (1983) estimated mortality rates for American shad (*Alosa sapidissima*) in the Connecticut River. The natural logarithm of abundance at each 1 mm length group was linearly regressed against its corresponding age determined from otoliths. Highest larval mortality rates (19.8 to 25.6%/day) were with first-feeding larvae (10-13 mm) and lowest

rates (4.3 to 8.7%/day) among larvae approaching metamorphosis (14-25 mm). In Smith Mountain Lake, smaller larval gizzard shad (5-17 mm TL) also had a higher estimated daily mortality rate than larger larvae (18-30 mm TL); 12.7%/day and 8.3%/day, respectively. Improved survival with size may, in part, be related to the development of fins which would facilitate feeding and predator avoidance (May 1974; Dahlberg 1979; Blaxter and Hunter 1982; Mansfield and Jude 1986). Alewife mortality (7.1%/day), however, did not vary over this same length range, indicating that size (length) may not be as critical a factor in early survival of alewives as compared to gizzard shad.

The mortality rate of fishes during the larval stage is generally considered an important factor in the determination of year-class strength (Crecco et al. 1983; Alderdice and Houston 1985; Smith 1985; Essig and Cole 1986). It is generally thought that disease, parasitism and inimical environmental conditions of temperature, salinity or oxygen are usually of minor importance in mortality and that the main causes are starvation and predation in the early prerecruit stages (Blaxter and Hunter 1982). Higher mortality rates of younger larval gizzard shad compared to alewives in Smith Mountain Lake might be attributable to more intense trophic interactions and resultant starvation. Densities of larval gizzard shad in the upper lake were usually higher than densities of alewives in the lower lake. Zooplankton production may be insufficient to support the observed densities of larval gizzard shad and other littoral planktivores which are abundant uplake. Gizzard shad, which begin as zooplanktivores and gradually become phytoplanktivores at approximately 35 mm TL (Cramer and Marzolf 1970), also may not be as efficient zooplanktivores as alewives which are zooplanktivorous their entire life (Odell 1934). Larval gizzard shad could also suffer a higher incidence of predation because of their nearshore distribution and the higher densities of largemouth bass and other littoral predators in the upper lake compared to the lower lake. Precise definition

of causes of larval mortality, however, was beyond the scope of this study. Based on the review of the literature, my estimates on the daily mortality rates of larval gizzard shad and alewives in Smith Mountain Lake seem very reasonable. As with growth, it must be assumed that my estimates represent typical mortality rates for larval gizzard shad and alewives for Smith Mountain Lake.

Juvenile clupeids:

By necessity, mortality rates for juvenile clupeids in Smith Mountain Lake were extracted from the literature. Mortality estimates for juvenile clupeids and other juvenile species appear to average approximately 2%/day in the early juvenile stages (30-60 mm TL) and 1%/day for fish 61 to 80 mm TL (Table 5). Declining mortality rates with increasing size probably reflects an increasing ability of larvae and juveniles to feed and avoid predators (May 1974; Dahlberg 1979; Blaxter and Hunter 1982; Mansfield and Jude 1986). I felt it was reasonable to assume those same mortality rates for juvenile clupeids in Smith Mountain Lake for the following reasons: 1) the published estimates of juvenile mortality for clupeid and other prey fishes showed good agreement and; 2) the larval mortality estimates derived in my study compared well to those reported for the species for which juvenile mortality estimates were also derived.

Clupeid Availability to Age-0 and -1 Piscivores

Production analyses for all species assumed that the initial size of each cohort was 1000 individuals. I used this approach because it permitted me to compare cohort sup-

ply and demand patterns in the absence of absolute abundance estimates. The technology to make accurate absolute abundance estimates is not yet developed for the forage species, and abundance of piscivores varies with annual stocking. When actual numbers become available, information generated from this analysis can be used to derive actual supply and demand estimates. Since actual numbers are not known, this analysis assumes the same total production for each clupeid. The emphasis in this study is on the generalized comparative patterns of availability of these two clupeids to young piscivores. Supply and demand relationships, therefore, are based on percentage of first-year or lifespan production rather than actual production.

The differing life history characteristics of piscivores and forage fish species indicate that stocked sport fish may encounter food deficiencies in many instances, most critically early in life (Ney and Orth 1986). Analyses of ingestibility limits and cohort production patterns demonstrate that alewives play a crucial role in Smith Mountain Lake in providing potential prey for juvenile piscivores. Age-0 gizzard shad are largely invulnerable to first-year striped bass, walleye, and largemouth bass in Smith Mountain Lake, but many age-0 alewives are small enough to be eaten by these newly stocked sport fish. Later spawning and slower first-year growth rate both contribute to enhancing the morphological availability of alewife to juvenile piscivores. Whether alewives do indeed remedy the prey deficiency caused by the rapid growth of gizzard shad depends on the co-occurrence of both predators and prey and their interactive behavior. Information on the food habits of juvenile piscivores in Smith Mountain Lake provides supporting evidence for this thesis. Ricci and Ney (1978) examined the stomachs of 87 age-0 striped bass (58-134 mm) captured in August 1977 rotenone collections from Smith Mountain Lake and found that they consumed significant numbers of alewives but contained no identifiable gizzard shad. In one cove sampled, they found that alewives occurred in

75% of the striped bass stomachs. Fingerling striped bass ate large quantities of benthic invertebrates, but this component of the diet was replaced by fish (including alewives, *Lepomis* spp. and golden shiners, *Notemigonus crysoleucas*) in larger striped bass (≥ 100 mm TL).

Striped bass appear to depend on an abundant supply of young clupeids to achieve good growth and survival during the first year of life. Young-of-the-year striped bass in Cherokee (Saul 1981; Humphreys 1983) and Norris (Richardson 1982) reservoirs, Tennessee, which contain both gizzard shad and threadfin shad, appeared starved and in extremely poor condition in years when the threadfin shad populations were low. Humphreys (1983) also reported that in these years, age-0 striped bass stocked in July attained an average total length of only 94 mm by December and that 96% of their diet was composed of invertebrates. In other years when age-0 striped bass exhibited good growth (318 mm TL at the end of their first growing season), fish, mostly threadfin shad, composed 67% of their diet. Van Den Avyle and Higginbotham (1979) reported a strong correlation between size and date of stocking of striped bass in Watts Bar Reservoir, Tennessee, and growth and cohort survival, presumably due to greater early food availability for larger fingerlings. Axon (1979) reported that first-year growth and survival of one of five year classes of striped bass in Herrington Lake, Kentucky, were poor due to low standing stock of threadfin shad and forage-size gizzard shad that year. In Smith Mountain Lake, first-year survival of striped bass is inversely proportional to stocking density (Ney et al. 1988), indicating that food availability is a likely limiting factor.

The presence of alewives in Smith Mountain Lake should also significantly enhance feeding opportunities for age-1 striped bass by extending morphological availability

through time. Analysis of prey availability patterns indicates that age-0 shad begin to exceed the ingestibility limits of age-1 striped bass by early September, with more than one-third of the growing season still remaining. Striped bass can, however, continue to feed on age-0 alewives for the remainder of the growing season and thereby avoid a potential autumn prey deficiency. Prey availability patterns also indicate that age-1 striped bass can consume same-age alewives during the spring, a period when no gizzard shad are morphologically vulnerable to them and neither clupeid species has produced a new cohort. As summer approaches, age-1 striped bass have both newly spawned cohorts of gizzard shad and alewife morphologically available to them as well as age-1 alewives. Consequently, striped bass should have more to eat in Smith Mountain Lake, and in-season patterns of growth should begin earlier and extend later than in reservoirs that contain only gizzard shad.

Unfortunately, I was not able to acquire any data on either in-season growth (length-at-capture data throughout the growing season) or total annual growth increments for juvenile striped bass in reservoir/lakes which only contain gizzard shad. In attempting to locate these data, I contacted the fish and wildlife agencies in all states in the climatic region and also discussed my data needs with many state biologists in person. In addition, I also contacted fisheries faculty at universities throughout the region. The basic problem that I encountered was that reservoirs and lakes with striped bass also contained both species of shad and in some cases, alewives (e.g., Cherokee Reservoir, Tennessee). Even in waters which contain both gizzard shad and threadfin shad, available age and growth data on striped bass were usually derived by back-calculation from older fish.

Walleye undergo a similar early prey availability experience pattern as do striped bass in Smith Mountain Lake, and it is probable that alewife are available to remedy the deficiency in gizzard shad. I have no data, however, on the food habits of juvenile walleye because there were few age-0 and age-1 walleye in Smith Mountain Lake during the 1982-84 period when Moore (1988) conducted his concurrent study on the food habits of these piscivores. Walleye, like striped bass, are likely to co-occur with alewives in Smith Mountain Lake because they are primarily pelagic and inhabit the mid to down-lake regions. In the absence of alewives, age-0 walleye in Smith Mountain Lake would probably encounter severe prey deficiencies from mid August until late spring to early summer when, as age-1 piscivores, the next cohort of gizzard shad emerge. Even then, most of the gizzard shad cohort will be lost to age-1 walleye by late July, but almost all age-0 alewives remain available to them. Mitzner and McWilliams (1986) found that juvenile walleye in Lake Rathbun, Iowa, often faced near starvation by mid summer when gizzard shad outgrew the size they could feed upon. In addition, they found that young walleye lacked sufficient quantities of food until the following summer. As indicated by this analysis, age-0 walleye can consume young-of-the-year alewives through most of the fall in Smith Mountain Lake, enabling them to build and store energy necessary to survive the winter and spring. Age-1 walleye, unlike same-age striped bass, must rely principally on energy reserves accumulated during the previous fall because gizzard shad and alewives are not morphologically vulnerable to them during the spring. Age-0 alewives outgrow the ingestibility limits of same-age walleye at just about the end of their first growing season (late November). Minton et al. (1981) stated that sauger (Stizostedion canadense) in Tennessee cope with large seasonal variations in threadfin shad availability by increasing their consumption of vulnerable cold-stressed shad in early winter and storing this excess energy in large fat deposits which are metabolized in the spring and early summer when shad are scarce. The fact that stocked walleye do

survive to maturity in Smith Mountain Lake indicates that juveniles are either finding alternative food during the spring period of clupeid deficiency or that winter and spring metabolic demands are not sufficiently stressful to cause large scale starvation. Predatory species are somewhat resistant to food shortages, a characteristic developed through evolution, and may survive starvation for longer times than prey and resume growth when food is again available (Ivlev 1961).

Analysis of prey availability patterns indicate that age-0 largemouth bass in Smith Mountain Lake, like age-0 striped bass and walleye, are only able to feed upon young-of-the-year gizzard shad for a few weeks after they become piscivorous in August. Storck (1986) reported that only the largest age-0 largemouth bass in Lake Shelbyville, Illinois were able to consume age-0 gizzard shad. Intermediate-sized young-of-the-year bass consumed sunfish, miscellaneous fish and invertebrates, while the smallest bass ate invertebrates only. The period in early development during which age-0 largemouth bass switch from macroinvertebrates to fish has been well documented as a period of stress (Aggus and Elliot 1975; Shelton et al 1979; Timmons et al. 1980, 1981; Adams and DeAngelis 1987; Wicker and Johnson 1987). In those studies, a shortage of morphologically vulnerable prey resulted in differential growth which in turn increased vulnerability of smaller largemouth bass to predation and to overwinter starvation. Patterns of availability also indicate that age-0 shad begin to rapidly outgrow the ingestibility limits of even age-1 largemouth bass by mid August in Smith Mountain Lake. Alewives have the potential to fill trophic voids for both age 0 and 1 largemouth bass. Age-0 largemouth bass have same-age alewives morphologically available to them from the time they become piscivorous in August through their first season of growth. Prey availability patterns reveal that age-1 largemouth bass have all first-year alewife production available to them as well as some age-1 alewives during the spring where

distributions overlap. However, Ricci and Ney (1978) found that unlike striped bass, age-0 largemouth bass (80 mm-114 mm TL) did not consume alewives and that they primarily ate larval sunfish (Lepomis spp.) and catfish (Ictalurus spp.) in Smith Mountain Lake after becoming piscivorous. The latter finding could be anticipated because largemouth bass are primarily littoral and uplake and consequently spatially isolated from alewives (pelagic and downlake) but in proximity to both sunfish and catfish.

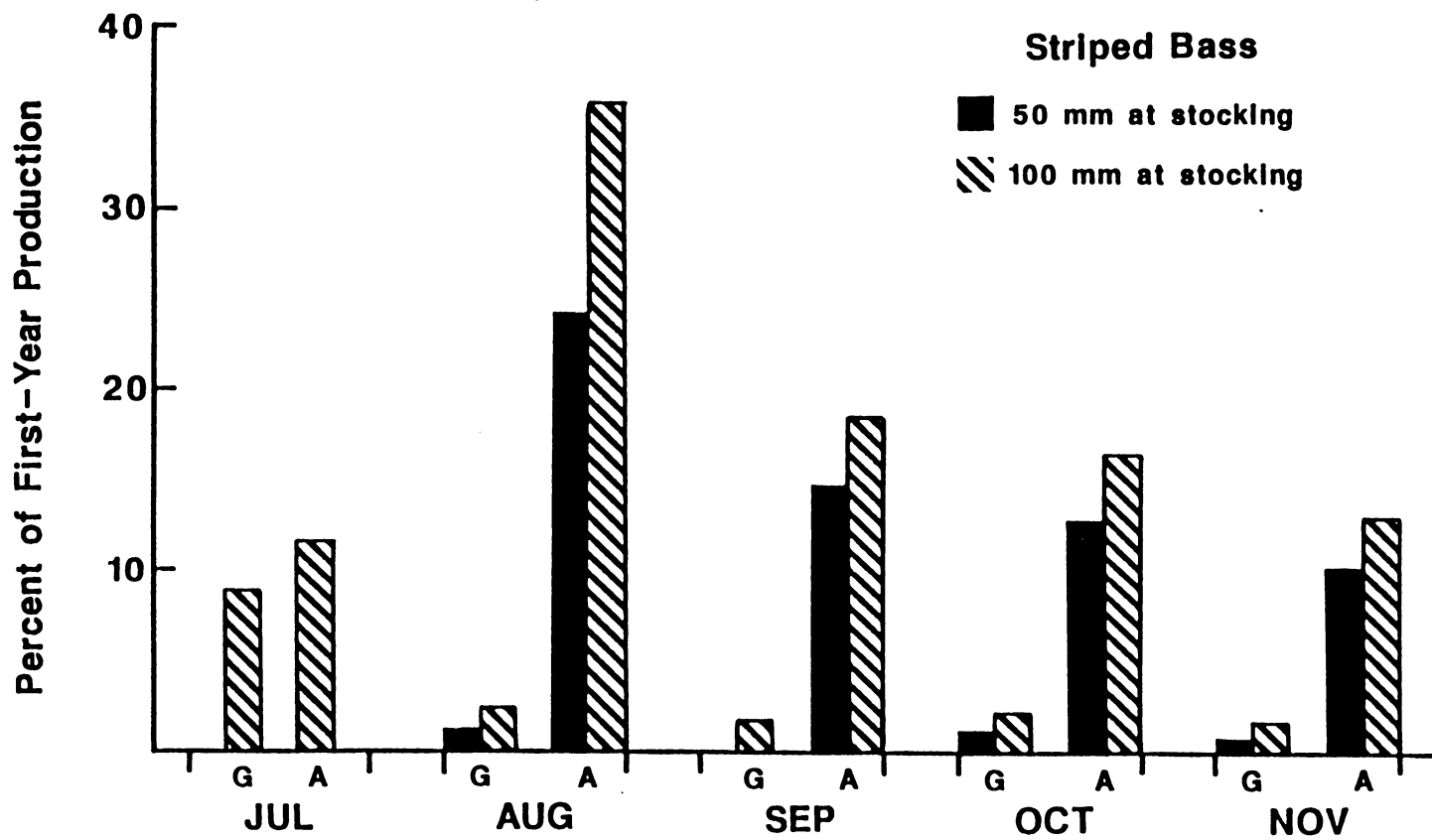
In the virtual absence of morphologically vulnerable age-0 gizzard shad and the spatial segregation of alewives and largemouth bass, the availability of the other prey species is probably paramount to the overwinter/spring survival of age-0 largemouth bass in Smith Mountain Lake. Aggus and Elliott (1975) reported that largemouth bass that could not shift to a fish diet may have suffered nearly total mortality during the winter in Bull Shoals Lake, Arkansas. Adams et al. (1982a) found that, for largemouth bass to maintain condition in a system where their prey undergoes large fluctuations in seasonal abundance, they must maximize caloric growth in the fall, store visceral fat, minimize standard and active metabolic demands, and undertake some winter feeding. Depending on the severity of the winter, largemouth bass that do not attain 250 mm $\pm$ 50 mm by the end of their first growing season in Watts Bar Reservoir, Tennessee, do not survive to annulus I formation because of the unavailability of appropriate-size prey in the spring and the inability of small bass to store sufficient energy reserves (Adams et al. 1982b). In Smith Mountain Lake, the median length at age 1 for largemouth bass was 144 mm TL (semi-quartile range 109 mm to 197 mm). Although the alewife could compensate for the deficiency of forage-sized gizzard shad available to juvenile largemouth bass, the distributions of alewife and largemouth bass overlap poorly. Therefore, alewives are probably not important to the success of largemouth bass in Smith Mountain Lake. Storck (1986) reported that when gizzard shad were

morphologically unavailable to largemouth bass in Lake Shelbyville, Illinois, crayfish and sunfish (*Lepomis* spp.) contributed most to their diet. He also noted that yearling bass would also consume large numbers of young-of-the-year bass in the spring, a period when no shad were small enough to be eaten. Juvenile largemouth bass probably survive by eating other prey items (e.g., sunfish, minnows, crayfish, etc.) to sustain themselves during the winter and spring months in Smith Mountain Lake.

Initial morphological availability of young-of-the-year gizzard shad and alewife to age-0 piscivores may be enhanced by stocking striped bass and walleye fingerlings earlier and/or at larger sizes (Van Den Avyle and Higginbotham 1979). I analyzed morphological availability of both gizzard shad and alewife to age-0 walleye and striped bass, assuming that these piscivores were stocked at 100 mm TL on July 1 instead of 50 mm TL on that same date as was the practice during my study. I used a conservative approach and applied the growth rates calculated in this study for piscivores stocked at 50 mm TL to piscivores stocked at 100 mm TL to project their size over the growing season. Lengths were then used to estimate maximum-size prey that could be ingested based on Jenkins and Morais' (1978) equations as outlined in the Methods section. The approach is conservative because in all probability, growth rates of age-0 striped bass and walleye would accelerate if they could feed on an abundant forage-fish supply from date of stocking; actual availability of gizzard shad and alewife would probably increase over the conservative estimates I have projected in the following scenario.

My analysis indicates that the percent of total first-year alewife production available on a monthly basis throughout the growing season is substantially higher for striped bass stocked at 100 mm TL versus 50 mm TL (Fig. 28). Larger striped bass (stocked at 100 mm) could utilize 94% of total first-year alewife production compared to only

Figure 28. Percent of total first-year production of gizzard shad (G) and alewife (A) morphologically available, by month, to striped bass stocked at 50 mm and 100 mm TL on July 1.

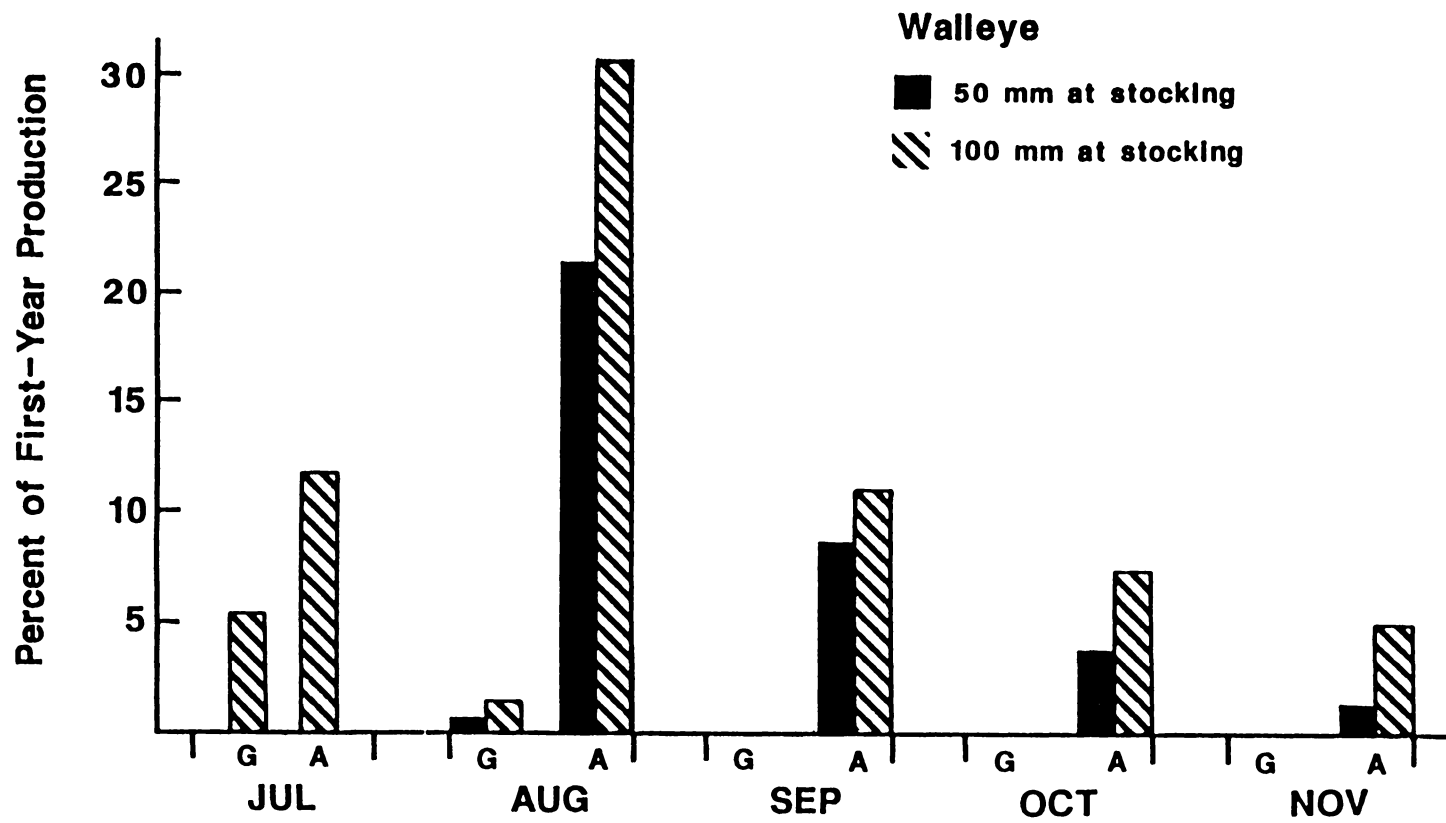


58% for smaller stocked fish. Striped bass would also have more gizzard shad production available to them. Available first-year gizzard shad production would increase from less than 1% to over 6% for larger striped bass, with the bulk of the increase in available supply coming in July (Fig. 28). The larger striped bass could capitalize on early spawned cohorts of both gizzard shad and alewife in July compared to smaller stocked predators which are still morphologically and behaviorally restricted to a non-piscine diet during that month.

Walleye stocked at larger sizes may also experience an increase in available first-year clupeid production. Based on monthly production estimates over the growing season, available first-year alewife production could increase from 36% for smaller walleye (50 mm TL), to over 65% for larger stocked fish (100 mm TL; Fig. 29). Available gizzard shad production would also increase from less than 1% to over 5%, with most of the increase in July, when walleye stocked at 50 mm TL in July are unable to take advantage of young-of-the-year clupeids (Fig. 29). Perhaps more importantly, walleye stocked at this larger size are able to gain a size advantage by the end of their first season of growth which allows them, like striped bass, to utilize alewives the following spring when they might normally experience prey deficiencies when stocked at the smaller size.

In summary, age-0 gizzard shad become too large for age-0 striped bass, walleye and largemouth bass to consume shortly after they become piscivorous and even begin to outgrow the ingestibility limits of older (age 1) piscivores by mid to late summer. However, later spawning and slower growth of the alewife assures its morphological availability to these predators for the remainder of the growing season. The alewife appears to be compatible with gizzard shad, and the species are complementary in providing spatial and temporal feeding opportunities for juvenile piscivores in Smith Mountain

Figure 29. Percent of total first-year production of gizzard shad (G) and alewife (A) morphologically available, by month, to walleye stocked at 50 mm and 100 mm TL on July 1.



Lake. In particular, because alewives are pelagic and primarily mid/down-lake, they should be critical to the early growth and survival of stocked coolwater piscivores in Smith Mountain Lake. Initial morphological availability of both gizzard shad and alewife may also be enhanced by stocking striped bass and walleye earlier and/or at larger sizes. Age-1 striped bass can also consume same-age alewives during the spring, a period when no gizzard shad are morphologically available to them. Unlike striped bass, age-1 walleye probably encounter spring prey deficiencies because they cannot eat age-1 alewives or gizzard shad. The spring deficiency in clupeid prey may not be critical for walleye if this is not a period of high food demand. Alewives are unlikely to have any significant impact on the success of largemouth bass recruitment in Smith Mountain Lake because of the differences in their spatial distributions.

Clupeid Availability to Older Piscivores

This analysis provides a clearer understanding of the trophic relationships in Smith Mountain Lake but is not without its limitations. Actual abundance estimates of prey and predators were not used in the analysis because a method has not yet been perfected to estimate accurately alewife standing stock in any waterbody, including the Great Lakes (Stewart et al. 1981). Bioacoustic procedures, perhaps in conjunction with open-water trawling, appear to have the most promise for quantifying abundance of small, pelagic schooling fishes such as alewife, but interpretation of sonar recordings has not been perfected. My analysis assumes that the overall abundance of both clupeids is adequate to meet demand, and that ingestible prey will be consumed upon encounter (i.e., are behaviorally available) by piscivores. In reality, of course, supply and demand de-

depends on how many clupeids and predators are present at any one time in the system and their production rate. In addition, this analysis also assumes that predators eat the largest prey that they can ingest before turning to smaller prey. Some piscivorous fish usually prefer the largest prey they can swallow (Ivlev 1961). Studies of striped bass (Stevens 1958; Humphreys 1983), walleye (Wagner 1972; Daniel 1984), and largemouth bass (Timmons and Pawaputanon 1980) indicate that these species will feed on successively larger clupeid prey as they grow, if that prey is available. If not, however, the cumulative demand of multiple predator cohorts on particular age groups of gizzard shad and alewife could exceed the available supply.

Morphological availability of prey to predators of particular lengths was determined from the Jenkins and Morais (1978) ingestibility equation. This equation was developed for largemouth bass versus gizzard shad; other predators were converted to largemouth bass length equivalents on the basis of their relative throat diameter. Moore (1988) found that some striped bass less than 300 mm TL ate gizzard shad larger than predicted by the Jenkins and Morais equation. Walleye also consumed some shad larger than projected, but maximum prey size agreed well with empirical observations for largemouth bass. Maximum available prey estimates for smaller piscivores derived from this predictive equation could be somewhat conservative. The throat diameter ratios between largemouth bass and both striped bass and walleye should probably be revised based on direct comparison of these species.

Population Dynamics of Prey and Predators

Growth and longevity of alewife and gizzard shad in Smith Mountain Lake are intermediate in the range to what has been reported elsewhere (Tables 27 and 28). Both species show great variation in growth rates across their geographic distributions which probably reflect both food availability and length of growing season. In Virginia, growth rates for alewives in Smith Mountain Lake are greater than those obtained by alewives in Flannagan Reservoir, an oligotrophic system, but less than those achieved by alewives in eutrophic waters of Claytor Lake (Ney et al. 1982).

Length variation at first annulus among clupeids was less than the observed variation among age-1 sport fish in Smith Mountain Lake (Tables 1 and 2). Lack of size variation among these clupeids in comparison to piscivores at age 1 is surprising, given the protracted spawning seasons of both gizzard shad and alewives. It may be due to the fact that most spawning of gizzard shad ($> 70\%$) and alewife ($> 50\%$) occurs within a much shorter period of time, two and three weeks, respectively. Alternately, it may reflect differential overwinter mortality of smaller age-0 clupeids (Adams et al. 1982; White et al. 1986) and/or size-selective predation (Bagenal and Tesch 1978). Greater variation in first-year growth of sport fishes may be caused by differential availability of food resources and/or physiological-genetic differences. Timmons et al. (1980) found a clear bimodal length-frequency distribution for age-0 largemouth bass by the end of their first season of growth and concluded it was the result of an inadequate prey supply for later spawned (smaller-sized) bass. In Smith Mountain Lake, largemouth bass had the greatest degree of variation in length during their first season of growth; the semi-

quartile range was 65% of age-1 total length, followed by walleye (39%) and then striped bass (34%).

Growth rates for adult clupeids ($\geq$ age 1), like juveniles, will vary to some degree between years based on available food supply, densities of competitors and predators as well as environmental conditions. By comparison to gizzard shad and alewives in other waters (Tables 27 and 28), growth and longevity of Smith Mountain Lake clupeids are about average and appear reasonable. My analyses are therefore necessarily based on the assumption that adult clupeid growth rates and patterns observed in 1983-84 are typical for Smith Mountain Lake.

The annual mortality rates I calculated for gizzard shad (70%) and alewife (80%) in Smith Mountain Lake are reasonable and consistent with reported estimates for other systems. Mayhew (1976) estimated annual mortality of gizzard shad in Lake Rathbun, Iowa using the catch curve method; over a four year period, annual mortality ranged from 57% to 84% with a mean of 69%. Derived from age composition data presented by Bodola (1966), annual mortality of gizzard shad (ages II-VI) was 86% in Lake Erie where winter die-offs are common. Annual mortality of alewives in Lake Ontario after their fourth growing season averaged 75% based on age composition (O'Gorman and Schneider 1986), while Brown (1972) reported 79% annual mortality for Lake Michigan alewives after their fifth year of life, which he calculated from fall mean-age frequencies. In Long Pond, Maine, total annual mortality rates for anadromous alewives based on age composition were 79% between ages 5 and 6 and 74% between ages 6 and 7 (Havey 1961). Havey (1973) also reported that adult alewife mortality in Love Lake, Maine, averaged 91% and ranged from 66% to 100% over an 11-year study period. As with

clupeid growth, it must be assumed that my estimates represent typical mortality rates for Smith Mountain Lake.

Piscivore growth curves were derived from observed data and realistically reflect (based on observed vs. predicted values) 25th, median and 75th percentile growth of individuals in each cohort. Mortality estimates derived for Smith Mountain Lake predators (Moore 1988) were consistent with those reported in the literature for exploited populations.

Cohort Supply and Demand Relationships

Lifespan cohort production patterns of both prey and predators were used to estimate the percent of prey production morphologically available to meet cohort and age-specific predator demand. Production is a maximum estimate of prey supply inasmuch as some fish must die from causes other than predation. Predator production is not itself equivalent to predator demand for food in that several times as much prey must be consumed to produce a given biomass of predator. If that ratio is constant over the predator lifespan (e.g. 5 g of prey to produce 1 g of predator; Brett and Groves 1979), then the pattern of production over the lifespan is identical to the pattern of consumption. In reality, fish require an increasing ratio of prey to growth as they age (e.g. Eck and Wells 1983; Moore 1988), but the fraction of total predator biomass represented by older fish ($\geq$ age 3) is small, and resulting errors should not greatly affect a production-based analysis of prey supply and predator demand.

In Smith Mountain Lake, lifespan cohort production patterns indicate that prey supply peaks one year earlier than does predator demand for same-aged fish. Piscivores and prey typically exhibit different life history characteristics; forage fish grow more rapidly toward their maximum size and also experience higher mortalities and significantly shorter lifespans than do their predators. Differences in growth and mortality rates between piscivores and forage species assure that piscivore cohorts will lag one year behind forage cohorts in achieving peak production in Smith Mountain Lake. In a management context, this discrepancy means that stocking densities of piscivores cannot be adjusted to the abundance of new clupeid cohorts because the prey demand of the piscivores will peak when the supply of same-age prey is declining (Stewart et al. 1981; Ney and Orth 1986). Therefore, abundance of forage fish at the time of their stocking is not particularly relevant to the piscivores in Smith Mountain Lake with the exception that the abundance of age-0 alewives can soon be consumed to newly stocked piscivores. Even if piscivores can immediately profit from an available forage supply (such as the age-0 piscivores), the differential in lifespans between predators and prey causes them to ultimately depend on the abundance of forage cohorts spawned in the next and succeeding years (Ney and Orth 1986). For example, an individual cohort of alewives will be in Smith Mountain Lake only three years. For striped bass which live nine years, at least two more strong year classes of alewives will be required at three-year intervals to assure an abundant lifelong food supply. Striped bass out-live gizzard shad by two or more years in Smith Mountain Lake and again this would necessitate the utilization of succeeding prey cohorts. Largemouth bass and walleye have shorter lifespans (6 and 7 years, respectively) than striped bass, but both would still rely heavily on future cohorts of clupeids.

Stewart et al. (1981) used the term "predation inertia" to describe the time from predator stocking until the majority of predation impact has occurred. Predation inertia is two years for striped bass, walleye and largemouth bass in Smith Mountain Lake. Although all three piscivores have similar predatory inertia, their total predation impacts on the forage supply differ. Lifespan cohort production patterns indicate that striped bass will have greatest demand (per 1000 individuals) for forage resources. At peak demand, the potential predatory impacts by striped bass may be 44% and 157% greater than those of walleye and largemouth bass, respectively. Over their lifespans, striped bass demand (per 1000 fish) exceeds those of walleye by 17% and largemouth bass by 166%. In a management context, piscivore species with high predatory impacts could be used to curtail clupeid population increases or reduce high standing stocks of forage fish. However, in the event of low or widely fluctuating prey standing stocks, piscivore species with less of an impact should be stocked in place of high-impact species. Another alternative to stocking different predator species would be to relax harvest regulations and encourage the rapid exploitation of predator species and/or reduce size limits.

When growth rates of forage species are compared to ingestibility limits of piscivores in Smith Mountain Lake, it is evident that there is considerable delay in the utilization of these prey once alewife and especially gizzard shad initially outgrow the ingestibility limits of juvenile piscivores in their first year of life. On an equivalent size basis, largemouth bass can ingest the largest prey items based on mouth sizes, followed by striped bass and then walleye. Striped bass, however, grow faster than largemouth bass and walleye in Smith Mountain Lake and are able to utilize gizzard shad and alewife earlier in life compared to the other two piscivores. Because alewives do not grow as fast or as large as gizzard shad, piscivores are able to take advantage of alewives earlier in

life compared to gizzard shad. In fact, striped bass have most of the production of a same-age cohort of alewives available to them. Largemouth bass are intermediate between striped bass and walleye in terms of when they are able to utilize alewives on a sustained basis. Older cohorts of piscivores will naturally be able to commence feeding on clupeid cohorts on a sustained basis sooner in life than same-age piscivores. The pattern, however, is similar to the same-age predators with striped bass being the first to “intercept” the forage species, followed second by largemouth bass, then walleye.

Cohort production patterns and ingestibility limitations on prey assure that most predation pressure in Smith Mountain Lake will come from piscivores ages 0-2 and be morphologically constrained to alewives ages 0 and 1 and young-of-the-year gizzard shad. Alewives should experience the most intense levels of predation from striped bass, walleye and largemouth bass ages 0-2, while gizzard shad should encounter the greatest predation pressure from striped bass and largemouth bass ages 1 and 2. In Smith Mountain Lake, alewives appear to have potential to prevent clupeid prey deficiencies which might occur if gizzard shad was the only abundant forage species in the system. Cohort production patterns, coupled with prey availability analyses, clearly indicate that walleye are particularly dependent on alewives because almost all age groups of walleye are morphologically constrained to feeding on age-0 shad only. Striped bass ($\leq$ age 1) and largemouth bass ($\leq$ age 2) also have only age-0 gizzard shad morphologically available to them without alewives. Therefore, poor recruitment or year-class failure of shad in the absence of alewives could significantly impact growth and survival of these predators.

In summary, the great majority of predator demand ($\approx 75\%$) is contained in the first three age groups of striped bass, walleye and largemouth bass in Smith Mountain Lake,

and this is size-limited primarily to age-0 gizzard shad and alewives ages 0-2. Cohorts of alewife and gizzard shad should encounter the most intensive predation from piscivores one and two years older than themselves. Analysis of lifespan cohort production patterns in Smith Mountain Lake indicate that prey supply and predator demand are one year out-of-phase. When ingestibility limits are factored into this analysis, piscivores may be as much as two years out of synchrony with gizzard shad cohorts. In Smith Mountain Lake, alewives appear to have potential to prevent clupeid prey deficiencies which might occur, especially for piscivores ages 0 and 1, if gizzard shad were the only abundant forage species in the system.

Distributional Limits on Availability

Data from the various techniques of fish survey as well as from angler interviews provide a general description of the seasonal distributions of predators and prey in Smith Mountain Lake. Alewives are primarily residents of the lower and mid-lake region in the pelagic zone, but move nearshore in spring and summer to spawn. Landlocked alewives in other systems have also been reported to inhabit deep, pelagic waters during most of the year and move into shallow water to spawn during the spring and summer (Odell 1934; Gross 1951; Rothschild 1966; Wells 1968; Wagner 1972; Scott and Crossman 1973; Kohler 1980; Becker 1983; O'Gorman and Schneider 1986). Preferred temperature for adult alewives has been estimated at 16-21°C (Coutant 1977; Stewart and Binkowski 1986). Water of this temperature and with sufficient dissolved oxygen (≥ 4 mg/l) occurs primarily in the lower lake during summer. In the summer of 1982 and 1983, these conditions were also observed in the mid-lake area (Hales Ford bridge vicinity). Surprising, these conditions were not observed in the mid-lake area during the summer of

1984, but forage fish abundance, as revealed by bioacoustics, was much higher offshore there than in the lower lake, and trawling indicated that these fish were predominately alewives. It appears likely that most of these were juvenile alewives which have a preferred temperature of 25°C (Stewart and Binkowski 1986) and a critical thermal maximum of 33°C (Otto et al. 1976). Alternately, alewives might be found in mid-lake and uplake regions near thermal refugia (e.g. cool springs or tributaries). In general, it appears that alewives move uplake in the summer as far as the temperature and dissolved oxygen regime will permit. Their migration is likely a response to trophic conditions; fertility and presumably zooplankton abundance increase in an upstream gradient. If Smith Mountain Lake continues to decrease in fertility in response to the reduced phosphorus load (Ney et al. 1988), then acceptable summer habitat for alewives might be progressively increased upstream; the alewives can be expected to respond.

In contrast to alewives, gizzard shad are primarily found uplake and in the littoral regions of Smith Mountain Lake. Abundance of adult gizzard shad in the lower and mid-lake regions appeared to be somewhat evenly distributed along the shoreline in the spring and summer, but I only found juvenile (age-0) gizzard shad in the upper reaches of the Roanoke River arm, where they were very abundant. Gizzard shad have been widely reported to prefer upper tributary arms and coves in reservoirs (Bodola 1966; Eley et al. 1967; Houser and Bryant 1967; Mayhew 1974; Rainwater and Houser 1982; Willis 1987). The nearshore and uplake distributions of gizzard shad complements that of alewife very well and assures that clupeid prey are distributed throughout most of Smith Mountain Lake during the growing season. The reduced fertility of Smith Mountain Lake is most strongly evident in the lower-lake region. Gizzard shad densities in the lower lake may have responded with a shift to the upper lake which is richer in periphyton and algae. Alewives also move uplake in the summer as far as temperature

and dissolved oxygen conditions permit. As bioacoustics transects indicated, the deep, pelagic waters of the lower lake have a low abundance of these clupeids in the summer which is reflected in the distribution of their predators as well.

Striped bass and walleye in Smith Mountain Lake were more abundant in littoral areas during the spring than summer in both lower and mid-lake areas. Change in distribution of these two predators from nearshore during the spring to offshore in the summer may be in response to thermal conditions and/or offshore movements of prey (alewives) after spawning activities are terminated. Coutant and Carroll (1980) reported that ultrasonic-tagged striped bass in two rock quarry lakes in Oak Ridge, Tennessee moved into deeper, cooler waters during the summer months and occupied a temperature band of about 22-23°C. Combs and Peltz (1982) found that striped bass concentrated in the lower, deep regions of Keystone Reservoir, Oklahoma during the summer. Walleye have a thermal preferendum of approximately 21 to 23°C (Coutant 1977), indicating habitat requirements similar to striped bass during the summer months. Fitz and Holbrook (1978) reported that during the summer months, walleye in Norris Reservoir, Tennessee occupied the thermocline and avoided temperatures above 24°C, even to the point of entering relatively deoxygenated waters below the thermocline if necessary. Striped bass, walleye, and alewives are therefore likely to co-occur in the same habitat during the summer months because of similar thermal preferences. This pattern was evident in Smith Mountain Lake. During the summer, striped bass and to a lesser degree, walleye, concentrated in the mid-lake region of Smith Mountain Lake. This concentration appears to be a response to the location of greatest abundance of forage fish within the temperature and dissolved oxygen habitat available to these coolwater piscivores. Walleye, and especially striped bass, move far upstream in the fall when the thermal barrier dissipates as stratification breaks down, probably to take advantage of

the abundant young-of-the-year gizzard shad concentrated in the upper reaches of the Roanoke River (Hardy Bridge vicinity, Fig 1). The seasonal cycle in distribution of both striped bass and walleye (Spring: downlake; Summer/Fall: mid-lake; Winter: uplake) undoubtedly is only a general pattern with numerous exceptions. However, it is a strong pattern explicable by the distribution of prey and the trophic gradient of Smith Mountain Lake and should continue to recur annually unless either of these factors changes.

The distribution of black basses in Smith Mountain Lake is primarily a function of habitat. Largemouth bass are oriented to shoreline habitat which is relatively shallow and contains cover (Heidinger 1975), while smallmouth bass prefer rocky substrata at or near greater depths (Scott and Crossman 1973); these are the prevailing characteristics in the upper and lower regions of Smith Mountain Lake, respectively. There is also more suitable largemouth bass habitat in the lower reservoir than smallmouth bass habitat in the upper part of the system. The habitats of smallmouth and largemouth bass seldom overlap extensively when the two species occur in the same systems (Scott and Crossman 1973). In Smith Mountain Lake, largemouth bass, like gizzard shad, were more abundant in the upper lake compared to smallmouth bass and alewives, which were more numerous in the lower lake. Therefore, alewives are probably not important to the success of largemouth bass in Smith Mountain Lake.

Availability Versus Diet

Morphological and spatial availability of prey does not alone assure utilization by predators. Availability also includes a behavioral component; i.e., the predator must recognize the clupeid as prey and successfully pursue it. Moore (1988) performed a

concurrent study (1982-84) of the seasonal diets of Smith Mountain lake piscivores. I compared his findings to my analysis of availability of gizzard shad and alewife to assess how well availability analysis can predict consumption patterns.

My analysis of production and distributional patterns indicate that alewives should be the principal food item in the diet of striped bass, particularly for young-of-the-year and age-1 striped bass. For age-0 striped bass, my analysis predicts that they will have alewives available to them from the time they become piscivorous (early August) through the end of their first season of growth. Gizzard shad should only be vulnerable to them for a few weeks in early August and again in the late fall. My analysis also predicts that during the spring, these same striped bass (now age 1), have age-1 alewives but not gizzard shad available to them. In addition, age-1 striped bass also have all age-0 alewife production available to them as well as age-1 alewives throughout their entire second season of growth.

Diet data (Moore, unpublished data) for striped bass in Smith Mountain Lake substantiate my findings based on analysis of availability patterns. As predicted, stomach analysis revealed that age-0 striped bass did eat alewives (62%, by number) throughout the late summer and fall in Smith Mountain Lake. Gizzard shad were only found in the stomachs of age-0 striped bass (9%, by number) in late fall (October/November) as projected by my analysis (see Fig. 10). Age-1 striped bass did consume more alewives (65%, by number, during the spring) than any other age group of striped bass which also corresponded perfectly with my availability predictions. My analysis of lifespan cohort production patterns and ingestibility limitations indicate that age-2 striped bass should have the strongest impact on a shad cohort. More gizzard shad were consumed by age-2 striped bass than any other striped bass cohort (Moore, unpublished data).

Alewives should be the most important food items for walleye in Smith Mountain Lake based on the following: 1) both species are pelagic and co-occur in the same areas of the lake; and 2) alewives remain morphologically vulnerable to walleye longer than do gizzard shad. My analysis of prey availability and lifespan supply/demand relationships predicts that walleye will eat predominately alewives, except perhaps in the late fall when thermal barriers to the upper lake break down and some gizzard shad may be consumed. Actual walleye diets ($\geq$ age 4; very few younger walleye were collected because they were last stocked in 1979) consisted primarily of alewives ($\approx 85\%$, by weight) during the spring and summer (Ney et al. 1988). During late fall, walleye fed almost exclusively on young-of-the-year gizzard shad (91% , by weight); however, walleye were only collected in the upper lake at this time of year where age-0 shad are most abundant. Although diet analysis did show that walleye in Smith Mountain Lake consumed alewives during the spring, approximately 90% of the stomachs examined at that time of year were empty and may reflect a seasonal feeding pattern. My analysis of availability patterns indicates that walleye ($>$ age 1) should have adult alewives morphologically available to them during the spring/early summer in Smith Mountain Lake. Perhaps the spring may be a period of innately low feeding activity as a means of coping with food shortages for this predator (Ivlev 1961). Knight et al. (1984) also found that walleye did little feeding during the spring/early summer in Lake Erie where both gizzard shad and alewife are present. In other studies, Daniel (1984) reported that walleye consumed alewives throughout the year in greater percentages than gizzard shad except during the fall when both species were consumed in equal abundance in Watauga Reservoir, Tennessee. In Claytor Lake, Virginia, alewives were the principal items in the diet of walleye during all seasons (Ney et al. 1982) and in Lake Michigan, alewives were heavily utilized by walleye during the spring (Wagner 1972).

My analysis of prey availability and lifespan supply/demand relationships for largemouth bass is also consistent with and supported by the diet data (Moore, unpublished data). Prey and predator distributional patterns in Smith Mountain Lake indicate that largemouth bass, being primarily uplake and littoral, should eat more gizzard shad than alewives. Largemouth bass consumed 8.6 times as much gizzard shad (by weight) as alewives and 3 times as much shad as striped bass and walleye combined in Smith Mountain Lake (Moore, unpublished data). Young-of-the-year gizzard shad were found in the stomachs of some age-0 largemouth bass (21%, by number), but only in the August samples. This is consistent with my projections on availability which indicated that age-0 largemouth bass could eat some young-of-the-year shad until mid August, after which time, shad are too large to be eaten for the balance of the growing season (see Fig. 11). Prey availability patterns indicate that young-of-the-year alewives could fill this trophic void for young largemouth bass, however, morphological availability appears to be negated by spatial segregation; no alewives were found in the stomachs of age-0 largemouth bass (Moore, unpublished data). My analysis of prey availability patterns indicates that gizzard shad should not be morphologically vulnerable to age-1 largemouth bass during the spring and is again supported by the diet data. Gizzard shad represented only 2% (by number) of the food items consumed by age-1 largemouth bass during the spring; crayfish and minnows composed approximately 18% and 23% (by number), respectively, of their spring diet. Largemouth bass (all age groups) ate some alewives (3% by number), many of which were consumed during the spring. This is not surprising because some spatial overlap probably occurs between these two species during the spring, especially in the mid-lake region.

In contrast to largemouth bass, smallmouth bass were more abundant in downlake areas and are less littoral; therefore, they should consume more alewives than gizzard

shad in Smith Mountain Lake. Again, the diet data supports my prediction. Smallmouth bass ate more alewives during each season than gizzard shad; 37% more alewives (by weight) than gizzard shad were consumed over the entire year (Moore, unpublished data). Alewives were an especially important component of their diet during the spring and summer months. This is consistent with my projections which indicate that alewives, during their spawning season (late spring/early summer), should be spatially available to smallmouth bass in Smith Mountain Lake. Alewives were consumed in greater amounts than gizzard shad during each season; however, crayfish were the dominant prey item in the stomachs of smallmouth bass during the fall (Moore, unpublished data). Again, given that smallmouth bass are primarily down-lake and "semi-pelagic", my projections indicated greater utilization of alewives than gizzard shad by this piscivore.

In summary, the use of prey availability and production patterns as a predictor of piscivore diets worked well in Smith Mountain Lake. My predictions agreed closely with actual diets for the various predator-prey location, season and age combinations.

SUMMARY

This study resulted in a number of findings concerning the population dynamics of alewives and gizzard shad and their relationships with piscivores in Smith Mountain Lake.

1. Alewife and gizzard shad exhibit strong reproductive segregation in Smith Mountain Lake. Alewives spawn primarily in the lower lake and over a longer period of time (≈ 13 weeks) than gizzard shad (≈ 6 weeks) which spawn primarily in the upper tributary arms. Peak spawning occurs earlier for gizzard shad (mid June) than alewife (early or mid July), but the water temperatures at which peak spawning occurs are similar (26-28°C).
2. No larval gizzard shad were taken in the lower lake and a few alewife larvae were found in the upper lake, but only in 1984. Larval gizzard shad were consistently more abundant in nearshore versus offshore areas, while alewife larvae appear equally abundant in cove and main channel locations.
3. First-year growth of both gizzard shad and alewife appears to proceed in two linear phases: 1) hatch through August, and 2) September through the end of the growing season. Gizzard shad grew faster than alewives during the first linear period, 1.33 mm/day versus 0.84 mm/day, respectively. Growth decelerated in the September through November period, but still approximated a linear pattern. Over these months, shad increased at 0.20 mm/day while alewife gained 0.30 mm/day. Median

total first-year growth of gizzard shad and alewife was 134 mm TL and 84 mm TL, respectively.

4. Estimated mortality rates for larval gizzard shad (5-17 mm TL) decreased from 12.7%/day to 8.3%/day for larger shad (18-30 mm TL). The estimated daily mortality rate of alewives (7.1%/day) remained constant over this same size range (5-30 mm TL). Mortality rates for juvenile clupeids were, by necessity, extracted from the literature and assumed for both species to average 2%/day in the early juvenile stages (30-60 mm TL) and 1%/day for fish (61-80 mm TL). Annual mortality estimates for adult gizzard shad and alewife were derived from cove rotenone and gillnet data from Smith Mountain Lake and averaged 70% and 80%, respectively.
5. First-year production patterns for gizzard shad and alewife are similar in that they both peak in August, but differ in that nearly 50% of the alewife production occurs in the latter portion of the growing season (September-November) compared to only 25% for gizzard shad.
6. Analyses of ingestibility limits and cohort production patterns indicate that age-0 gizzard shad are largely invulnerable to first-year striped bass, walleye and largemouth bass in Smith Mountain Lake, but many age-0 alewives (36-58% of the first-year production) are small enough to be eaten by these newly stocked or hatched piscivores. Later spawning and slower first-year growth rates both contribute to enhancing the morphological availability of alewife to juvenile piscivores.
7. Prey availability patterns indicate that age-0 shad begin to outgrow the ingestibility limits of age-1 piscivores as early as July for age-1 walleye. Age-0 gizzard shad begin to exceed the morphological ingestibility limits of age-1 largemouth bass and striped

bass by August and September, respectively. In Smith Mountain Lake, alewives can mitigate declining availability of gizzard shad; almost all age-0 alewife production is available to age-1 piscivores.

8. Age-1 striped bass and, to a lesser degree, largemouth bass can eat age-1 alewives during the spring in Smith Mountain Lake and thereby remediate a potential spring forage deficiency. Age-1 walleye, however, cannot consume same-age alewives during the spring period when no gizzard shad are morphologically available to age-1 piscivores. The spring deficiency in clupeid prey may not be critical for age-1 walleye if this is not a period of high food demand.
9. Whether alewives remedy trophic voids created by the rapid growth of gizzard shad depends on the co-occurrence of both predators and prey and their interactive behavior. Distributional patterns indicate that gizzard shad are well segregated from alewives most of the year in Smith Mountain Lake. Spatial segregation of clupeid species should increase feeding opportunities for piscivores where they co-occur. Gizzard shad are primarily uplake and littoral in distribution, while alewives are downlake and pelagic. Alewives co-occur with striped bass and walleye during the growing season and therefore should be more important to their success than gizzard shad. Largemouth bass share a more common distribution pattern with gizzard shad and should be more dependent on them as a source of clupeid forage.
10. Cohort production patterns, coupled with prey availability analyses, indicate that alewives play a crucial role in providing prey for walleye and striped bass in Smith Mountain Lake. Walleye are particularly dependent on alewives because almost all age groups of walleye are morphologically constrained to feeding on only age-0 shad. In the absence of alewives, poor recruitment or year-class failure of shad

could significantly impact growth and survival of several age-groups of walleye. Striped bass are less vulnerable to this situation because older striped bass (age ≥ 2) have more than one age group of shad vulnerable to them. Striped bass $\leq$ age 1, however, could still be impacted because like walleye, they too would have only age-0 shad morphologically available to them if alewives were not present in the reservoir.

11. Analysis of lifespan cohort production patterns in Smith Mountain Lake reveals that alewife and gizzard shad production peak in the first year of life while their predators' cohort production peaks in the second year. Consequently, prey supply and predator demand are one year out of phase. When ingestibility patterns are also factored into the analysis, piscivores may be as much as two years out of synchrony with shad cohorts. Differential lifespans between predators and prey will also cause predators to ultimately depend on the abundance of future forage cohorts.
12. Although cohort production patterns for striped bass, walleye and largemouth bass in Smith Mountain Lake are similar, impacts on the forage supply differ among the species. Cohort production estimates indicate that over their lifespan, striped bass demand (per 1000 fish) exceeds those of walleye and largemouth bass by 17% and 166%, respectively. At peak demand, the predatory impacts by striped bass may be 44% and 157% greater than those of walleye and largemouth bass, respectively.
13. Cohort production patterns and ingestibility limitations on prey assure most predation pressure in Smith Mountain Lake will come from piscivores ages 0-2 and be size-limited to alewives ages 0 and 1 and young-of-the-year gizzard shad.

14. Prediction of comparative piscivore consumption patterns of alewife and gizzard shad was derived from analysis of relative morphological and distributional availability and cohort lifespan production patterns. Predictions agreed closely with actual diets for most predator-prey location, season and age combinations.

CONCLUSIONS AND MANAGEMENT IMPLICATIONS

The alewife was introduced into Smith Mountain Lake to augment native gizzard shad as the forage base. As with any planned introduction, it was assumed that the net impact on the fishery would be positive. My objectives for this study focused on the assessment of alewife and gizzard shad as complementary forage species in enhancing forage-fish availability for native and stocked piscivores. This assessment of alewife and gizzard shad as coexistent forage species for piscivores resulted in several conclusions relevant to the management of reservoir fisheries in general as well as for Smith Mountain Lake.

Alewife and gizzard shad appear compatible with one another in a reservoir of morphometric configuration and trophic conditions (containing both broad, deep, mesotrophic and narrow, shallow, eutrophic regions) of Smith Mountain Lake. Total forage-fish production will be strongly influenced by the degree to which these two clupeid species compete. Spatial segregation minimizes the potential for direct trophic competition between alewife and gizzard shad and increases feeding opportunities for piscivores in Smith Mountain Lake. Later spawning and slower growth enhances temporal and morphological availability of alewives to piscivores and reduces the potential for exploitative competition between the clupeids. The presence of alewives is of particular benefit to stocked walleye and striped bass which would likely experience

both seasonal and early life prey deficiencies without them. Alewives co-occur with striped bass and walleye throughout the growing season. Largemouth bass share a common distribution with gizzard shad and are more trophically dependent than other piscivores on them.

Although alewives are both complementary to and compatible with gizzard shad in Smith Mountain Lake, its introduction into other waters should be made with caution. The alewife will be of little value as a forage species for littoral predators because their distributions will overlap poorly most of the year. Littoral predators, such as the black basses, may be able to utilize some alewives during the spring when alewives move in-shore to spawn. However, any value they may provide in terms of a seasonal forage is probably offset by their potential negative attributes. In particular, alewives have been shown to compete with and/or consume juvenile sport fishes (Kohler and Ney 1980; Ney et al. 1982). Self-sustaining walleye populations have also been adversely impacted after alewives were introduced (Daniel 1984; Kohler et al. 1986). Consequently, I strongly recommend that alewives be introduced only in systems managed primarily for pelagic predators which are stocked as fingerlings (50-100 mm TL) to minimize time of trophic overlap with, and predation by, alewives. In addition, it is critical that alewives not be introduced into waters where they could emigrate and potentially impact other waters by their unintended introduction.

Morphological invulnerability of gizzard shad to striped bass and walleye in Smith Mountain Lake can be partially remedied by stocking these piscivores earlier and at larger sizes. My analysis indicates that striped bass and walleye stocked at approximately 100 mm TL by July can immediately begin to take advantage of age-0 gizzard shad as well as alewives spawned over the previous month. The ability to consume

piscine prey earlier in life should accelerate predator growth rates and extend morphological availability of clupeids later into the growing season for juvenile piscivores. In the case of walleye, this added size advantage gained by stocking earlier and at larger sizes should extend morphological availability of same-age alewives into the next growing season and increase initial availability of gizzard shad. Acceleration of striped bass growth rates due to earlier initial clupeid utilization (July vs. August) should permit them to continue feeding on same-age shad as well as alewives into their second season of growth, and perhaps for the duration of their concurrent lifespans.

Stocking piscivores earlier and larger, however, will have the same effect as increasing stocking densities of smaller fish. Stocking larger fingerlings at the same densities as smaller piscivores will increase mortality on the prey base because of higher predator survival rates. In some instances, this may be counterproductive if prey abundance is not adequate to support the increase in predator numbers. Therefore, larger fingerlings should be stocked at lower densities to compensate for their higher survival rates as compared to smaller stocked piscivores. Appropriate stocking densities for larger-sized fingerlings can be estimated by comparing first-year survival rates between smaller and larger stocked fingerlings. As a hypothetical example, stocking records indicate that when 300,000 striped bass fingerlings are stocked at an initial size of 50 mm TL, 20% survive to age 1. When the same number of larger fingerlings (100 mm TL) are stocked and 40% survived to age 1, then only 150,000 fingerlings (50% reduction) need to be stocked the following year to achieve the same end point as stocking 300,000 of the smaller-size fingerlings. There is little doubt that estimating appropriate stocking densities for larger fingerlings will initially be by trial and error; however, the estimate should always be slanted toward the conservative end of the scale.

From a practical and economic perspective, consideration must also be given to the hatcheries' capabilities to grow and hold larger fish and the associated cost/benefits. It may be more cost effective to put out more smaller fish (which is often the case) than fewer larger ones. The cost effectiveness of raising fewer but larger striped bass and/or walleye fingerlings will vary with the differential in first-year mortality rates and hatchery production capabilities; it can only be determined on a case-by-case basis.

Location of stocking sites, as well as the size and date at which piscivores are stocked, can also be used to maximize clupeid availability to young piscivores. Densities of gizzard shad were greatest in the upper tributary arms of Smith Mountain Lake, while alewives were most numerous in the mid and lower lake regions. By stocking fingerling striped bass and walleye (100 mm TL) in both these areas, good growth and survival should be assured for at least some portion of the cohort even in the event one clupeid species should suffer reproductive failure or produce a weak year-class. Juvenile striped bass and walleye can tolerate warmer temperatures than the adults (Wrenn and Forsythe 1978; Coutant 1985); therefore, the thermal regime of the upper lake should not pose any significant problems in terms of their survival. Predation by littoral piscivores (e.g., largemouth bass) in the upper lake could adversely impact juvenile sportfish survival. However, the ability of larger stocked fingerlings to consume piscine prey earlier in life should accelerate their growth rates and thereby minimize predation mortality.

The asynchrony of predator demand and prey supply in Smith Mountain Lake and other systems (Stewart et al. 1981) negates the possibility of matching the number of predators stocked each year to the abundance of age-0 clupeids. In Smith Mountain Lake, predator and prey cohorts are one year out of phase with each other based on my analysis of lifespan cohort production patterns. In particular, gizzard shad of the

same age as stocked striped bass and walleye are virtually irrelevant to them over their mutual lifespans.

Stocked piscivores will have the greatest predatory impact on gizzard shad and alewives one to two years younger than themselves. Most predation pressure by Smith Mountain Lake piscivores is focused on only three age groups of clupeids, age-0 shad and alewives ages 0 and 1. This creates an unstable balance between predator and prey species, especially with the high degree of interannual variability associated with the reproductive success of clupeid populations. Therefore, stocking densities of pelagic predators should not exceed moderate levels which have produced desirable growth and survival rates in the past. Increased stockings above moderate levels to capitalize on an apparently strong year class of prey would not be successful because of the inherent asynchrony between predator demand and prey supply and the characteristic variability of the latter. In the event of low clupeid standing stocks, piscivore stocking should be reduced and/or harvest regulations relaxed (both size and bag limits) to encourage the rapid exploitation of predator species to reduce overall predation pressure. Harvest of young sportfish (ages 0-2) should be particularly encouraged because they consume the most clupeid prey in Smith Mountain Lake. Reductions in size limits would be necessary to achieve this management objective because two-year old striped bass (406 mm TL) and largemouth bass (263 mm TL) in Smith Mountain Lake are considered sub-legal fish under current regulations (minimum size lengths are 508 mm TL and 356 mm TL, respectively).

The use of prey availability and production patterns as a predictor of piscivore diets and supply/demand relationships worked well in Smith Mountain Lake. Availability analysis, however, is not without limitations. Other species of recreational value that

also consume clupeid prey such as muskellunge (Esox masquinongy), crappie (Pomoxis nigromaculatus), catfish (Ictalurus spp.) and white bass (Morone chrysops) were not included in my analysis because of their low relative abundance and the study's time and manpower constraints. The development of prey availability and production patterns hinges on estimates of growth and survival for both predators and prey which are sometimes not easily or accurately obtained (e.g., determination of age and growth of fishes in less temperate regions of the country). The use of median or average growth rates with some incorporated measure of variance (such as the semi-quartile range) to define morphological availability can be an intractable task if all possible combinations are considered. Reliance on only average or median growth rates will be erroneous in proportion to their variance about the "average" growth estimate. Morphological availability is itself only a one-dimensional analysis of availability, as distributional (temporal and spatial) and behavioral factors also influence available forage supply. In addition, production is only an indicator of supply and demand relationships, especially for older piscivore and forage cohorts because biomass may still be high, but actual production is low. My approach does not require estimation of actual abundance of either predator or prey species, but the realism of this analysis would be greatly improved if these data could be incorporated. However, methods of estimating actual abundance such as bioacoustics and/or trawling are often time consuming, labor intensive and costly, which puts such methods beyond the reach of many state fisheries agencies. Within these limitations, prey availability analysis provides a reasonable and useful approach that can be applied by most fisheries managers, without actual abundance estimates or use of complex bioenergetic models, to gain an initial understanding of the potential utilization of forage fish species by various piscivores.

LITERATURE CITED

- 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 W.C. Kerfoot and A. Sih, editors. Predation: Direct and indirect impacts on aquatic communities. University Press of New England, London.
- Adams, S.M., R.B. McLean and J.A. Parrotta. 1982a. Energy 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.
- Ager, L.M. 1978. Evaluation of predator fish introduction in Lake Sinclair. Georgia Department of Natural Resources, Game and Fish Division, Atlanta, Georgia.
- Aggus, L.R. and G.V. Elliott. 1975. Effects of cover and food on year-class strength of largemouth bass. Pages 317-322 in R.H. Stroud and H. Clepper, editors. Black bass biology and management. Sport Fishing Institute, Washington, District of Columbia.
- Aggus, L.R. and S.A. Lewis. 1978. Environmental conditions and standing crops of fishes in the predator stocking evaluation reservoirs. Proceedings of the Annual Conference Southeastern Association of Fish and Wildlife Agencies 30:131-140.
- Alderdice, D.F. and A.S. Houston. 1985. Factors influencing development and survival of Pacific herring (*Clupea harengus pallasii*) eggs and larvae to beginning of exogenous feeding. Canadian Journal of Fisheries and Aquatic Sciences 42 (Supplement 1):56-68.
- Axon, J.R. 1979. An evaluation of striped bass introductions in Herrington Lake. Kentucky Department of Fish and Wildlife Resources, Fisheries Bulletin 63.
- Bagenal, T.B. and F.W. Tesch. 1978. Age and growth. Pages 101-136 in T. Bagenal, editor. Methods for assessment of fish production in fresh waters. Blackwell Scientific Publications, Oxford, England.
- Baker, C.D. and E.H. Schmitz. 1971. Food habits of adult gizzard and threadfin shad in two Ozark reservoirs. Pages 3-11 in G.E. Hall, editor. Reservoir fisheries and limnology. American Fisheries Society Special Publication Number 8.

- Barger, L.E. and R.V. Kilambi. 1980. Feeding ecology of larval shad, Dorosoma, in Beaver Reservoir, Arkansas. Pages 136-145 in Lee A. Fuiman, editor. Proceedings of the Fourth Annual Larval Fish Conference. U.S. Fish and Wildlife Service FWS/OBS-80/43.
- Becker, G.C. 1983. Fishes of Wisconsin. University of Wisconsin Press, Madison.
- Benfield, E.F. and A.C. Hendricks. 1975. Eutrophic gradient in Smith Mountain Lake, Virginia. Virginia Journal of Science 26(1):20-26.
- Bennett, G.W. 1970. Management of lakes and ponds. Van Nostrand Reinhold Company, New York.
- Berry, F.H. 1958. Age and growth of the gizzard shad (Dorosoma lacepedi) (LeSueur) in Lake Newman, Florida. Proceedings of the Conference Southeastern Association of Game and Fish Commissioners 11:318-331.
- Billy, A.J. 1982. The effects of formalin and isopropyl alcohol on length and weight measurements of Sarotherodon mossambicus Trewavas. Journal of Fish Biology 21:107-112.
- Blaxter, J.H.S. and J.R. Hunter. 1982. The biology of the clupeoid fishes. Pages 3-194 in J.H.S. Blaxter, Sir F.S. Russel, and Sir M. Yonge, editors. Advances in marine biology (Volume 20). Academic Press, New York.
- Bodola, A. 1966. Life history of the gizzard shad, Dorosoma cepedianum (LeSueur), in western Lake Erie. U.S. Fish and Wildlife Service Fishery Bulletin 65:391-425.
- Braum, E. 1978. Part II. The eggs and larval phase. Pages 178-201 in T. Bagenal, editor. Methods for assessment of fish production in fresh waters. Blackwell Scientific Publications, Oxford, England.
- Brett, J.R. and T.S. Groves. 1979. Physiological energetics. Pages 279-352 in W.S. Hoar, D.J. Randall, and J.R. Brett, editors. Fish physiology, Volume VIII: Bioenergetics and growth. Academic Press, New York.
- Bridges, J.P. 1956. On day and night variation in catches of fish larvae. Journal du Conseil, Conseil International pour l'Exploration de la Mer 22:42-57.
- Brooks, J.L. 1968. The effects of prey size selection by lake planktivores. Systemic Zoology 17:272-291.
- Bross, M.C. 1967. Fish samples and year-class strength (1965-1967) from Canton Reservoir, Oklahoma. Proceedings of the Oklahoma Academy of Science 48:194-199.
- Brown, E.H., Jr. 1972. Population biology of alewives, Alosa pseudoharengus, in Lake Michigan, 1949-70. Journal of the Fisheries Research Board of Canada 29:447-500.

- Bryant, H.E. and A. Houser. 1969. Growth of threadfin shad in Bull Shoals Reservoir. *Proceedings of the Annual Conference Southeastern Association of Game and Fish Commissioners* 22:275-283.
- Colby, P.J. 1973. Response of the alewives to environmental change. Pages 163-198 *in* W. Chavin, editor. *Responses of fish to environmental changes*. Thomas, Springfield, Illinois.
- Combs, D.L. and L.R. Peltz. 1982. Seasonal distribution of striped bass in Keystone Reservoir. *North American Journal of Fisheries Management* 2:66-73.
- Coutant, C.C. 1977. Compilation of temperature preference data. *Journal of the Fisheries Research Board of Canada* 34:739-745.
- 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. and D.S. Carroll. 1980. Temperatures occupied by ten ultrasonic-tagged striped bass in freshwater lakes. *Transactions of the American Fisheries Society* 109:195-202.
- Cramer, J.D. and G.R. Marzolf. 1970. Selective predation on zooplankton by gizzard shad. *Transactions of the American Fisheries Society* 99:320-332.
- Crecco, V., T. Savoy, and L. Gunn. 1983. Daily mortality rates of larval and juvenile American shad (*Alosa sapidissima*) 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. 1986. Ecological and morphological shifts in Lake Michigan fishes: Glimpses of the ghost of competition past. *Environmental Biology of Fishes* 16:147-157.
- 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 Research Center, Bulletin* 23.
- Dahlberg, M.D. 1979. A review of survival rates of fish eggs and larvae in relation to impact assessments. *Marine Fisheries Review*, U.S. Department of Commerce, March 1979:1-12.
- Daniel, K.L. 1984. Food habits, age and growth, and forage value of the alewife in Watauga Reservoir, Tennessee. Master's thesis. University of Tennessee, Knoxville.
- Davies, W.D., B.W. Smith, and W.L. Shelton. 1979. Predator-prey relationships in management of small impoundments. Pages 449-458 *in* R.H. Stroud and H.

- Clepper, editors. Predator-prey systems in fisheries management. Sport Fishing Institute, Washington, District of Columbia.
- Dewey, M.R. and T.E. Moen. 1982. The temporal and spatial distribution of some young-of-the-year fishes in DeGray Lake, Arkansas, 1975-1978. Pages 37-41 in D.F. Bryan, J.V. Conner, and F.M. Truesdale, editors. Proceedings of the fifth annual larval fish conference. Louisiana Cooperative Fishery Research Unit, Louisiana State University, Baton Rouge.
- Dey, W.P. 1981. Mortality and growth of young-of-the-year striped bass in the Hudson River Estuary. Transactions of the American Fisheries Society 110:151-157.
- Downey, P. and D. Toetz. 1983. Distribution of larval gizzard shad (Dorosoma cepedianum) in Lake Carl Blackwell, Oklahoma. American Midland Naturalist 109:23-33.
- Eaton, S.W. and L.P. Kardos. 1972. The fishes of Canadaiqua Lake, 1971. Science Studies St. Bonaventure University 28:23-44.
- Eck, G.W. and E.H. Brown, Jr. 1985. Lake Michigan's capacity to support lake trout (Salvelinus namaycush) and other salmonines: An estimate based on the status of prey populations in the 1970's. Canadian Journal of Fisheries and Aquatic Sciences 42:449-454.
- Eck, G.W. and L. Wells. 1983. Biology, population structure, and estimated forage requirements of lake trout in Lake Michigan. U.S. Fish and Wildlife Service Technical Paper III.
- Edsall, T.A. 1970. The effect of temperature on the rate of development and survival of alewife eggs and larvae. Transactions of the American Fisheries Society 99:376-380.
- Edwards, T., W. Hunt, and L. Olmsted. 1977. Density and distribution of larval shad (Dorosoma spp.) in Lake Norman, North Carolina, entrainment at McGuire nuclear station. Pages 143-158 in L.L. Olmsted, editor. Proceedings of the first symposium on freshwater larval fish. Charlotte, North Carolina.
- Ehrlich, K.F. 1975. A preliminary study of the chemical composition of sea-caught larval herring and plaice. Comparative Biochemistry and Physiology 51B:25-28.
- Eley, R.L., N.E. Carter, and T.C. Dorris. 1967. Physiochemical limnology and related fish distribution of Keystone Reservoir. Pages 333-357 in Reservoir fishery resources symposium. Southern Division, American Fisheries Society, Bethesda, Maryland.
- Essig, R.J. and C.F. Cole. 1986. Methods of estimating larval fish mortality from daily increments in otoliths. Transactions of the American Fisheries Society 115:34- 40.
- Fabricus, E. and K.J. Gustafson. 1954. Further aquarium observations on the spawning behavior of the char Salvelinus alpinus. Laboratory Report of the Institute of Freshwater Research Drottingholm 35:58-104.

- Farris, D.A. 1960. The effect of three different types of growth curves on estimates of larval fish survival. *Journal du Conseil, Conseil International pour l'Exploration de la Mer* 42:116-124.
- Fitz, R.B. 1968. Fish habitat and population changes resulting from impoundment of Clinch River by Melton Hill Dam. *Journal of the Tennessee Academy of Science* 43:7-15.
- Fitz, R.B. and J.A. Holbrook II. 1978. Sauger and walleye in Norris Reservoir, Tennessee. Pages 82-88 in R.L. Kendall, editor. *Selected coolwater fishes of North America*. American Fisheries Society Special Publication Number 11.
- Gaschutz, G, D. Pauley and N. David. 1980. A versatile BASIC program for fitting weight and seasonally oscillating length growth data. *International Council for the Exploration of the Sea*. CM/1980/D:6 Statistics Committee.
- Graham, J.J. 1956. Observations on the alewife, *Pomolobus pseudoharengus* (Wilson), in fresh water. *University of Toronto Studies Biological Series Publication* 62, Publication of the Ontario Fisheries Research Laboratory, 74, Toronto.
- Graser, L.F. 1979. Spatio-temporal distribution of clupeid larvae in Barkley Reservoir. Pages 120-138 in R. Hoyt, editor. *Proceedings of the third symposium on larval fish*. Western Kentucky University, Bowling Green.
- Gomez, R. 1970. Food habits of young-of-the-year striped bass *Morone saxatilis* (Walbaum), in Canton Reservoir. *Proceedings of the Oklahoma Academy of Science* 50:57-83.
- Gross, R. 1951. Some observations on the landlocked alewife, *Pomolobus pseudoharengus* (Wilson) in New Jersey. *New Jersey Fisheries Survey Report* No. 2.
- Gross, R. 1959. A study of the landlocked alewife, *Alosa pseudoharengus*, Wilson, in some New Jersey lakes with special reference to Lake Hopatcong. Master's thesis. Rutgers University, New Jersey.
- Hart, L.G. 1978. Smith Mountain Lake Research Study. Virginia Commission of Game and Inland Fisheries, Dingell-Johnson Project F-30-R, Project Completion Report.
- Havey, K.A. 1961. Restoration of anadromous alewives at Long Pond, Maine. *Transactions of the American Fisheries Society* 90:281-286.
- Havey, K.A. 1973. Production of juvenile alewives at Love Lake, Washington County, Maine. *Transactions of the American Fisheries Society* 102:434-437.
- Hayward, R.S. and F.J. Margraf. 1987. Eutrophication effects on prey size and food available to yellow perch in Lake Erie. *Transactions of the American Fisheries Society* 116:210-223.

- Heidinger, R.C. 1975. Life history and biology of the largemouth bass. Pages 11-20 in R.H. Stroud and H. Clepper, editors. Black bass biology and management. Sport Fishing Institute, Washington, District of Columbia.
- Hollander, M. and D.A. Wolfe. 1973. Nonparametric statistical methods. Wiley and Sons, New York.
- Houser, A. and H.E. Bryant. 1967. Sampling reservoir fish populations using midwater trawls. Pages 391-404 in Reservoir fishery resources symposium. Southern Division, American Fisheries Society, Bethesda, Maryland.
- Houser, A. and N.F. Netsch. 1971. Estimates of young-of-the-year shad population in Beaver Reservoir. Pages 359-370 in G.E. Hall, editor. Reservoir fisheries and limnology. American Fisheries Society Special Publication Number 8.
- Humphreys, M. 1983. Effects of forage variations on young-of-the-year striped bass and other young predators in Cherokee Reservoir, Tennessee. Master's thesis. University of Tennessee, Knoxville.
- Hutchinson, B.P. 1971. The effect of fish predation on the zooplankton of ten Adirondack lakes, with particular reference to the alewife, Alosa pseudoharengus. Transactions of the American Fisheries Society 100:325- 335.
- Ivlev, V.S. 1961. Experimental ecology of the feeding of fishes. (Translated from Russian by D. Scott). Yale University Press, New Haven, Connecticut.
- Jearld, A. Jr. 1983. Age determination. Pages 301-324 in L.A. Nielsen and D.L. Johnson, editors. Fisheries techniques. American Fisheries Society, Bethesda, Maryland.
- Jenkins, R.M. 1953. A pre-impoundment survey of Fort Gibson Reservoir, Oklahoma (summer 1952). Oklahoma Fisheries Research Laboratory Report No. 29.
- Jenkins, R.M. 1967. The influence of some environmental factors on standing crop and harvest of fishes in U.S. reservoirs. Pages 298-321 in Reservoir fishery resource symposium. Southern Division, American Fisheries Society, Bethesda, Maryland.
- Jenkins, R.M. 1979. Predator-prey relations in reservoirs. Pages 123-134 in R.H. Stroud and H. Clepper, editors. Predator-prey systems in fisheries management. Sport Fishing Institute, Washington, District of Columbia.
- Jenkins, R.M. and D.J. Morais. 1978. Prey-predator relations in the predator-stocking-evaluation reservoir. Proceedings of the Annual Conference Southeastern Association of Fish and Wildlife Agencies 30:141-157.
- Jester, D.B. 1962. Fisheries study of Conchas Lake. New Mexico Department of Game and Fish, Federal Aid Project F-22, R-3, Work Plan 2, Job B-1 (3), Job Completion Report.

- Jester, D.B. and B.L. Jensen. 1972. Life history and ecology of the gizzard shad, Dorosoma cepedianum (LeSueur) with reference to Elephant Butte Lake. New Mexico State University Agricultural Experiment Station Research Report 218.
- Jones, J.W. and J.N. Ball. 1954. The spawning behavior of brown trout and salmon. Behavior 2:103-114.
- Kersh, G.B., Jr. 1970. Growth and distribution of larval and early juvenile gizzard shad and threadfin shad in Beaver and Bull Shoals Reservoirs. Master's thesis. University of Arkansas, Fayetteville.
- Kilambi, R.V. and R.E. Baglin. 1969. Fecundity of the gizzard shad, Dorosoma cepedianum (LeSueur) in Beaver and Bull Shoals Reservoirs. American Midland Naturalist 82:444-449.
- Kilch, B.L. 1976. Horizontal distribution and relative abundance of larval fishes in Center Hill Reservoir, Tennessee. Master's thesis. Tennessee Technological University, Cookeville.
- Kimsey, J.B. 1957. Fisheries problems in impounded waters of California and the lower Colorado River. Transactions of the American Fisheries Society 87:319- 332.
- Kirchis, F.W. and J.G. Stanley. 1981. Theory and practice of forage-fish management in New England. Transactions of the American Fisheries Society 110:729-737.
- Knight, R.L., F.J. Margraf and R.F. Carline. 1984. Piscivory by walleyes and yellow perch in western Lake Erie. Transactions of the American Fisheries Society 113:677-693.
- Kohler, C.C. 1980. Trophic ecology of an introduced, landlocked alewife (Alosa pseudoharengus) population and assessment of alewife impact on resident sportfish and crustacean zooplankton communities in Claytor Lake, Virginia. Doctoral dissertation. Virginia Polytechnic Institute and State University, Blacksburg.
- Kohler, C.C. and J.J. Ney. 1980. Piscivory in a land- locked alewife (Alosa pseudoharengus) 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 Southeastern Association of Fish and Wildlife Agencies 34:272-286.
- Kohler, C.C., J.J. Ney, and W.E. Kelso. 1986. Filling the void: Development 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.
- Krause, R.A. and M.J. Van Den Avyle. 1979. Temporal and spatial variations in abundance and species composition of larval fishes in Center Hill Reservoir,

- Tennessee. Pages 167-184 in R. Hoyt, editor. Proceedings of the third symposium on larval fish. Western Kentucky University, Bowling Green.
- Kutkuhn, J.H. 1957. Utilization of plankton by juvenile gizzard shad in a shallow prairie lake. Transactions of the American Fisheries Society 87:80-103.
- Lackey, R.T. 1968. Seasonal abundance and availability of forage fish and their utilization by land-locked Atlantic salmon and brook trout in Echo Lake, Mount Desert Island, Maine. Master's thesis. University of Maine, Orono.
- Lagler, K.F. and H. Van Meter. 1951. Abundance and growth of gizzard shad, Dorosoma cepedianum (LeSueur), in a small Illinois lake. Journal of Wildlife Management 15:357-360.
- LaRoche, A.L., III. 1981. Region II reservoir investigations, Smith Mountain Lake. Virginia Commission of Game and Inland Fisheries, Dingell-Johnson Project F-39.
- Lasker, R. 1985. What limits clupeoid production? Canadian Journal of Fisheries and Aquatic Sciences 42(Supplement 1):31-38.
- LeCren, E.D. 1951. The length-weight relationship and seasonal cycle in gonad weight and condition in the perch (Perca fluviatilis). Journal of the Animal Ecology 20:201-219.
- Leslie, J.K. and J.E. Moore. 1986. Changes in lengths of fixed and preserved young freshwater fish. Canadian Journal of Fisheries and Aquatic Sciences 43:1079-1081.
- Lippson, A.J. and R.L. Moran. 1974. Manual for identification of early developmental stages of fishes of the Potomac River estuary. Power Plant Siting Program, Maryland Department of Natural Resources.
- Lockwood, S.J. 1973. Weight and length changes of O-group plaice (Pleuronectes platessa L.) after preservation in 4% neutral formalin. Journal du Conseil, Conseil International pour l'Exploration de la Mer 35:100-101.
- Lockwood, S.J. 1981. Density dependent mortality in O- group plaice, Pleuronectes platessa, populations. Journal du Conseil, Conseil International pour l'Exploration de la Mer 39:148-153.
- Mansfield, P.J. and D.J. Jude. 1986. Alewife (Alosa pseudoharengus) survival during the first growth season in southeastern Lake Michigan. Canadian Journal of Fisheries and Aquatic Sciences 43:1318-1326.
- Marquess, K., G. Pardue, R. Neves, L. Fortunato, and A. Tipton. 1982. Computer program for the computation of age and growth statistics of fish populations, (IBM 370, Fortran IV, Level G1). Management Publication Number 1, Department of Fisheries and Wildlife Services, Virginia Polytechnic Institute and State University, Blacksburg.

- Mathur, D. and J.S. Ramsey. 1974. Reproductive biology of the rough shiner, Notropis baileyi, in Halawokee Creek, Alabama. Transactions of the American Fisheries Society 103:88-93.
- May, B. 1968. Biology of the threadfin shad. Final report, North Carolina Wildlife Resources Commission, Division of Inland Fisheries, Job X-B, Project F-16-R.
- May, R.C. 1974. Larval mortality in marine fishes and the critical period concept. Pages 3-19 in J.H.S. Blaxter, editor. The early life history of fish. Springer-Verlag, Heidelberg.
- Mayhew, J. 1974. Abundance, distribution, mortality and production of 0-age fish (0-Age Fish Production at Lake Rathbun). Iowa Conservation Commission, Federal Aid Project F-88-R-1.
- Mayhew, J. 1976. Abundance, distribution, mortality and production of 0-age fish (0-Age Fish Production at Lake Rathbun). Iowa Conservation Commission, Federal Aid Project F-88-R-3.
- Miller, R.R. 1960. Systematics and biology of the gizzard shad, Dorosoma cepedianum (LeSueur), and related fishes. U.S. Fish and Wildlife Service Fishery Bulletin 60(173).
- Miller, R.V. 1967. Food of the threadfin shad, Dorosoma petenense, in Lake Chicot, Arkansas. Transactions of the American Fisheries Society 96:243-246.
- Minton, J.W., R.B. McLean, and P.T. Singley. 1981. Bioenergetics of sauger in Watts Bar Reservoir. Oak Ridge National Laboratory, ORNL/TM-7630, Oak Ridge, Tennessee.
- Mitzner, L. and D. McWilliams. 1986. Walleye research on large lakes. Iowa Conservationist 45(11):21-23.
- Momot, W.T., J. Erickson and F. Stevenson. 1977. Maintenance of a walleye, Stizostedion vitreum vitreum, fishery in a eutrophic reservoir. Journal of the Fisheries Research Board of Canada 34:1725-1733.
- 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.
- Moreau, J. 1987. Mathematical and biological expression of growth in fishes: recent trends and further developments. Pages 81-114 in R.C. Summerfelt and G.E. Hall, editors. Age and growth of fish. Iowa State University Press, Ames.
- Morsell, J.W. and C.R. Norden. 1968. Food habits of the alewife, Alosa pseudoharengus (Wilson), in Lake Michigan. Proceedings Conference of Great Lakes Research 11:96-102.

- Muth, S.E. and D.C. Tarter. 1975. Reproductive biology of the trout perch, Percopsis omiscomaycus (Walbaum), in Beech Fork of Twelve-Pole Creek, Wayne County, West Virginia. *American Midland Naturalist* 93:434-439.
- Netsch, N.F., G.M. Kersh, Jr., A. Houser, and R.V. Kilambi. 1971. Distribution of young gizzard shad and threadfin shad in Beaver Reservoir. Pages 95-105 in G.E. Hall, editor. *Reservoir fisheries and limnology*. American Fisheries Society Special Publication Number 8.
- Ney, J.J. 1978. A synoptic review of yellow perch and walleye biology. Pages 1-12 in R.L. Kendall, editor. *Selected coolwater fishes of North America*. American Fisheries Society Special Publication Number 11.
- Ney, J.J. 1981. Evolution of forage-fish management in lakes and reservoirs. *Transactions of the American Society* 110:725-728.
- Ney, J.J. 1989. Trophic economics in fisheries: assessment of demand/supply relationships between predators and prey. *Reviews in Aquatic Science* 1:(In press).
- Ney, J.J., C.C. Kohler, and A.A. Nigro. 1982. Landlocked alewife in Claytor lake, Virginia: Evaluation as a forage species for inland waters. Management Publication Number 4, Department of Fisheries and Wildlife Sciences, Virginia Polytechnic Institute and State University, Blacksburg.
- 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 Services, Virginia Polytechnic Institute 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. and L.L. Smith, Jr. 1975. First-year growth of the yellow perch, Perca flavescens, in the Red Lakes, Minnesota. *Transactions of the American Fisheries Society* 104:718-725.
- Nigro, A.A. 1980. Reproduction and early life history of a landlocked population of alewife (Alosa pseudoharengus) in Claytor Lake, Virginia. Master's thesis. Virginia Polytechnic Institute and State University, Blacksburg.
- Nigro, A.A. and J.J. Ney. 1982. Reproduction and early-life accommodations of landlocked alewives to a southern range extension. *Transactions of the American Fisheries Society* 111:559-569.
- Nikolsky, G.V. 1963. *The ecology of fishes*. Academic Press, New York.
- Noble, R.L. 1981. Management of forage fishes in impoundments of the southern United States. *Transactions of the American Fisheries Society* 110:738- 750.

- Norden, C.R. 1967a. Development and identification of the larval alewife, in *Alosa pseudoharengus* (Wilson), in Lake Michigan. Proceedings Conference on Great Lakes Research 10:70-78.
- Norden, C.R. 1967b. Age, growth, and fecundity of the alewife, *Alosa pseudoharengus* (Wilson), in Lake Michigan. Transaction of the American Fisheries Society 96:387-393.
- Odell, T.T. 1934. The life history and ecological relationships of the alewife, (*Pomolobus pseudoharengus* Wilson) in Seneca Lake, New York. Transactions of the American Fisheries Society 64:118-126.
- O'Gorman, R. 1983. Distribution and abundance of larval fish in the nearshore waters of western Lake Huron. Journal of the Great Lakes Research 9:14-22.
- O'Gorman, R. and C.P. Schneider. 1986. Dynamics of alewives in Lake Ontario following a mass mortality. Transactions of the American Fisheries Society 115:1-14.
- Otto, R.G., M.A. Kitchel, and J. O'Hara Rice. 1976. Lethal and preferred temperatures of the alewife (*Alosa pseudoharengus*) in Lake Michigan. Transactions of the American Fisheries Society 105:96-106.
- Parker, R.R. 1963. Effects of formalin on length and weight of fishes. Journal of the Fisheries Research Board of Canada 20:1441-1455.
- Patriarche, M.H. 1953. The fishery in Lake Wappapello, a flood-control reservoir on the St. Francis River, Missouri. Transactions of the American Fisheries Society 82(1952):242-254.
- Pierce, R.J. 1977. Life history and ecological energetics of the gizzard shad (*Dorosoma cepedianum*) in Acton Lake, Ohio. Doctoral dissertation. Miami University, Oxford, Ohio.
- Pirie, W.R. and W.A. Hubert. 1977. Assumptions in statistical analysis. Transactions of the American Fisheries Society 106:646-648.
- 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.
- Rhodes, R.J. 1971. The food habits of the alewife in Indiana waters of Lake Michigan in 1970. Master's thesis. Ball State University, Muncie, Indiana.
- Ricci, E. and J.J. Ney. 1978. Food habits of young-of-the- year largemouth bass and striped bass in Smith Mountain Lake, Virginia. Independent study report. Virginia Polytechnic Institute and State University, Blacksburg.
- Richardson, J.M. 1982. Food habits and growth of young-of- the-year striped bass in Norris Reservoir, Tennessee. Master's thesis. University of Tennessee, Knoxville.

- Ricker, W.E. 1946. Production and utilization of fish populations. *Ecological Monographs* 16:373-391.
- Ricker, W.E. 1975. Computation and interpretation of biological statistics of fish populations. *Fisheries Research Board of Canada Bulletin* 191.
- Riggs, C.D. and G.A. Moore. 1957. The occurrence of *Signalosa petenensis* in Lake Texoma. *Proceedings of the Oklahoma Academy of Science* 37:64-67.
- Rothschild, B.J. 1965. Aspects of the population dynamics of the alewife, *Alosa pseudoharengus* (Wilson), in Cayuga Lake, New York. *American Midland Naturalist* 74:479-496.
- Rothschild, B.J. 1966. Observations on the alewife (*Alosa pseudoharengus*) in Cayuga Lake. *New York Fish and Game Journal* 13:188-195.
- Saul, B.M. 1981. Food habits and growth of young-of-the-year striped bass in Cherokee Reservoir, Tennessee. Master's thesis. University of Tennessee, Knoxville.
- Scott, W.B. and E.J. Crossman. 1973. Freshwater fishes of Canada. *Fisheries Research Board of Canada Bulletin* 184.
- Shelton, W.L. 1972. Comparative reproductive biology of the gizzard shad, *Dorosoma cepedianum* (LeSueur), and the threadfin shad, *D. petenense* (Gunther), in Lake Texoma, Oklahoma. Doctoral dissertation. University of Oklahoma, Norman.
- Shelton, W.L., W.D. Davis, 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* 108:1142-1149.
- Shelton, W.L., C.D. Riggs, and L.G. Hill. 1982. Comparative reproductive biology of threadfin and gizzard shad in Lake Texoma, Oklahoma-Texas. Pages 47-51 in C.F. Bryan, J.V. Conner, and F.M. Truesdale, editors. *Proceedings of the fifth annual larval fish conference*. Louisiana State University, Baton Rouge.
- Shields, J.T. 1957. Fish management problems of large impoundments of the Missouri River. *Transactions of the American Fisheries Society* 87:356-362.
- Silliman, R.P. 1943. Thermal and diurnal changes in the vertical distribution of eggs and larvae of the pilchard (*Sardinops caerulea*). *Journal of the Marine Research* 5:118-129.
- 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.
- Smith, P.E. 1985. Year-class strength and survival of 0-group clupeoids. *Canadian Journal of Fisheries and Aquatic Sciences* 42(Supplement 1):69-82.

- Smith, S.H. 1968. Species succession and fishery exploitation in the Great Lakes. *Journal of the Fisheries Research Board of Canada* 25:667-693.
- Smith, S.H. 1970. Species interactions of the alewife in the Great Lakes. *Transactions of the American Fisheries Society* 99:754-765.
- Snyder, D.E. 1983. Fish eggs and larvae. Pages 165-197 in L.A. Nielsen and D.L. Johnson, editors. *Fisheries techniques*. American Fisheries Society, Bethesda, Maryland.
- Stein, R.A. 1979. Behavioral response of prey to fish predators. Pages 343-353 in R.H. Stroud and H. Clepper, editors. *Predator-prey systems in fisheries management*. Sport Fishing Institute, Washington, D.C.
- 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 Commissioners* 11:253-264.
- Stewart, D.J. and F.P. Binkowski. 1986. Dynamics of consumption and food conversion by Lake Michigan alewives: An energetics-modeling synthesis. *Transactions of the American Fisheries Society* 115:643- 661.
- 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.
- Stock, J.N. 1971. A study of some effects of population density on gizzard shad and bluegill growth and recruitment in ponds. Master's thesis. University of Missouri, Columbia.
- 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.
- Storck, T.W., W. Dimond, and S. Miller. 1982. Determination of factors affecting the survival of larval fish and an evaluation of their utilization as food by predators. Illinois Natural History Survey, Federal Aid in Fish Restoration Project F-31-R, Final Report. Submitted to the Illinois Department of Conservation, Springfield.
- Storck, T.W., D.W. Dufford, and K.T. Clement. 1978. The distribution of limnetic fish larvae in a flood control reservoir in central Illinois. *Transactions of the American Fisheries Society* 107:419-424.
- Strawn, K. 1965. Resistance of threadfin shad to low temperatures. *Proceedings of the Annual Conference Southeastern Association of Game and Fish Commissioners* 17:290-293.
- Taber, C.A. 1969. The distribution and identification of larval fishes in the Buncombe Creek arm of Lake Texoma with observations on spawning habits and relative abundance. Doctoral dissertation. University of Oklahoma, Norman.

- Thayer, G.W., D.R. Colby, M.A. Kjelson, and M.P. Weinstein. 1983. Estimates of larval-fish abundance: Diurnal variation and influences of sampling gear and towing speed. *Transactions of the American Fisheries Society* 112:272-279.
- Timmons, T.J. and O. Pawaputanon. 1980. Relative size relationships in prey selection by largemouth bass in West Point Lake, Alabama-Georgia. *Proceedings of the Annual Conference Southeastern Fish and Wildlife Agencies* 34:248-252.
- 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.
- Timmons, T.J., W.L. Shelton, and W.D. Davies. 1981. Early growth and mortality of largemouth bass in West Point Reservoir, Alabama-Georgia. *Transactions of the American Fisheries Society* 110:489-491.
- Tin, H.T. 1982. Clupeidae. Pages 64-73 in N.A. Auer, editor. Identification of larval fishes of the Great Lakes Basin with emphasis on the Lake Michigan drainage. Great Lakes Fishery Commission Special Publication 82-3, Ann Arbor.
- Tranter, D.J. and P.E. Smith. 1968. Filtration performance. Pages 27-55 in D.J. Tranter and J.H. Fraser, editors. Zooplankton sampling. United Nations Educational, Scientific, and Cultural Organization, Monographs on Oceanographic Methodology 2, Paris, France.
- Trautman, M.B. 1981. The fishes of Ohio. Ohio State University Press, Columbus.
- Turner, W.R. 1953. The age and growth of the gizzard shad *Dorosoma cepedianum* (LeSueur) in Herrington Lake, Kentucky, Kentucky Department of Fish and Wildlife Resources, Fisheries Bulletin 13.
- Van Den Avyle, M.J. and D.D. Fox. 1980. Diel, vertical, and horizontal variations in abundance of larval Dorosoma spp. in Center Hill Reservoir, Tennessee. Pages 116-122 in L.A. Fuiman, editor. Proceedings of the fourth annual larval fish conference. University of Mississippi, Oxford.
- Van Den Avyle, M.J. and B.J. Higginbotham. 1979. 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.
- Wagner, W.C. 1972. Utilization of alewives by inshore piscivorous fishes in Lake Michigan. *Transactions of the American Fisheries Society* 101:55-63.
- Warner, E.N. 1940. Studies on the embryology and early life history of the gizzard shad Dorosoma cepedianum LeSueur. Doctoral dissertation. Ohio State University, Columbus.
- Wells, L. 1968. Seasonal depth distribution of fish in southeastern Lake Michigan. U.S. Fish and Wildlife Service Fishery Bulletin 67.

- Wells, L. 1970. Effects of alewife predation on zooplankton populations in Lake Michigan. *Limnology and Oceanography* 15:556-565.
- Wells, L. 1980. Food in alewives, yellow perch, spottail shiners, trout-perch, and slimy and fourhorn sculpins in southeastern Lake Michigan. U.S. Fish and Wildlife Service, Technical Paper 98.
- White, A.M., N.A. Aldridge, F.D. Moore, and D.M. Loucks. 1986. The effects of natural winter stresses on the mortality of the eastern gizzard shad in Lake Erie. Report to the Cleveland Electric Illuminating Company/Ohio Edison, Akron, Ohio.
- Whitehurst, D.K. 1984. Smith Mountain Lake, Annual Report, 1 April 1983 - 31 March 1984. Virginia Commission of Game and Inland Fisheries.
- Whitehurst, D.K. 1985. Smith Mountain Lake, Annual Report, 1 April 1984 - 31 March 1985. Virginia Commission of Game and Inland Fisheries.
- Wicker, A.M. and W.E. Johnson. 1987. Relationship among fat content, condition factor, and first-year survival of Florida largemouth bass. *Transactions of the American Fisheries Society* 116:254-271.
- Willis, D.W. 1987. Reproduction and recruitment of gizzard shad in Kansas Reservoirs. *North American Journal of Fisheries Management* 7:71-80.
- Wrenn, W.B. and T.D. Forsythe. 1978. Effects of temperature on production and yield of juvenile walleyes in experimental ecosystems. Pages 66-73 in R.L. Kendall, editor. *Selected coolwater fishes of North America*. American Fisheries Society Special Publication Number 11.

APPENDIX TABLES

Table 1. Weight-length relationships for gizzard shad and alewife in Smith Mountain Lake. N = sample size.

Species	Size Class (mm)	N	Weight-Length Equation	R ²
Gizzard shad	4-20	170	$\ln W = -15.59 + 3.98 * \ln L$	.98
Gizzard shad	21-50	209	$\ln W = -14.95 + 3.90 * \ln L$	.99
Gizzard shad	51-389	874	$\ln W = -11.67 + 3.01 * \ln L$	.99
Alewife	5-20	160	$\ln W = -15.48 + 3.91 * \ln L$	.99
Alewife	21-32	101	$\ln W = -17.40 + 4.64 * \ln L$	.95
Alewife	33-178	684	$\ln W = -11.35 + 1.91 * \ln L$	.99

Table 2. Linear regression equations for back calculation of length-at-age of prey and predators in Smith Mountain Lake, Virginia. L = length of fish when annulus was formed and S = radius of annulus (in millimeters). N = sample size.

Species	Year	Equation	N	R ²
Gizzard shad	1983	$L = 43.36 + 1.01 (S)$	72	0.94
Gizzard shad	1984	$L = 34.70 + 1.06 (S)$	86	0.96
Alewife	1984	$L = 28.11 + 0.89 (S)$	97	0.91
Striped bass	1983	$L = 51.44 + 2.86 (S)$	225	0.95
Striped bass	1984	$L = 47.58 + 2.87 (S)$	365	0.98
Walleye	1983	$L = 80.45 + 3.05 (S)$	142	0.69
Walleye	1984	$L = 79.59 + 2.99 (S)$	243	0.65
Largemouth bass	1983	$L = 38.06 + 1.26 (S)$	146	0.94
Largemouth bass	1984	$L = 41.70 + 1.22 (S)$	234	0.95

Table 3. First-year production (in grams) of the 1984 gizzard shad cohort, by week, assuming 1000 individuals hatched.

Percent of Annual Spawn	2	9	2	0	26	50	1	0	1	0	1	Cohort Production By Interval
Interval	5/14	5/21	5/31	6/4	6/11	6/19	6/26	7/2	7/9	7/16	7/25	
5/21	0.173	.	.	.	.	.	.	.	.	.	.	0.173
5/31	1.045	2.784	.	.	.	.	.	.	.	.	.	3.829
6/04	0.590	1.443	0.064	.	.	.	.	.	.	.	.	2.097
6/11	1.631	4.260	0.478	0.690	.	.	.	.	.	.	.	7.059
6/19	1.626	0.066	0.910	2.933	2.991	.	.	.	.	.	.	17.326
6/26	2.052	5.919	1.397	4.085	8.718	4.312	.	.	.	.	.	26.403
7/02	2.108	7.810	1.168	5.675	10.566	12.732	0.065	.	.	.	.	40.124
7/09	2.902	10.870	1.786	5.487	21.200	21.748	0.205	.	.	.	.	64.278
7/16	3.300	13.058	2.230	7.950	17.833	37.827	0.435	.	0.095	.	.	82.808
7/25	5.113	20.240	3.568	12.914	34.382	47.801	1.088	.	0.429	.	.	125.535
8/01	4.520	17.925	3.361	12.239	33.675	51.285	0.658	.	0.546	.	0.088	124.297
8/08	4.986	20.341	3.886	14.508	39.778	61.802	1.026	.	0.933	.	0.309	147.569
8/15	5.361	22.439	4.320	15.933	47.152	75.583	1.236	.	0.654	.	0.474	173.152
8/22	5.904	24.122	4.824	18.080	51.783	87.563	1.512	.	1.057	.	0.815	195.660
8/29	6.077	26.567	5.245	19.946	58.762	100.021	1.751	.	1.295	.	0.686	220.350
9/05	2.379	10.846	2.232	8.230	22.555	42.824	0.755	.	0.547	.	0.331	90.699
9/12	0.999	3.999	0.735	2.704	9.983	15.612	0.254	.	0.201	.	0.121	34.608
9/19	0.957	3.837	0.708	2.606	9.644	15.136	0.247	.	0.197	.	0.118	33.450
9/26	0.916	3.680	0.681	2.510	9.313	14.667	0.241	.	0.193	.	0.112	32.313
10/03	0.877	3.529	0.655	2.416	6.742	14.205	0.234	.	0.190	.	0.112	28.960
10/10	0.840	3.383	0.629	2.326	6.505	13.752	0.228	.	0.186	.	0.112	27.961
10/17	0.803	3.243	0.605	2.238	6.274	13.307	0.221	.	0.182	.	0.095	26.960
10/24	0.769	3.107	0.581	2.153	6.049	12.870	0.214	.	0.178	.	0.095	26.016
10/31	0.735	2.976	0.558	2.070	5.830	12.442	0.208	.	0.174	.	0.094	25.087
11/07	0.703	2.850	0.537	1.990	5.617	12.022	0.201	.	0.170	.	0.093	24.183
11/14	0.672	2.729	0.514	1.912	5.409	11.613	0.196	.	0.166	.	0.092	23.303
11/21	0.642	2.612	0.493	1.837	5.207	11.212	0.189	.	0.129	.	0.091	22.412
11/28	0.409	2.500	0.473	1.764	5.012	8.115	0.183	.	0.126	.	0.090	18.672
11/30	0.199	0.810	0.154	0.573	1.629	2.643	0.045	.	0.031	.	0.030	6.114
Total Annual Production = 1651.486												

Table 4. First-year production (in grams) of the 1984 alewife cohort, by week, assuming 1000 individuals hatched.

Percent of Annual Spawn	1	8	4	8	12	7	4	24	10	5	16	1	Cohort Production By Interval
Interval	5/31	6/5	6/12	6/21	6/26	7/2	7/9	7/16	7/25	7/30	8/6	8/13	
6/05	0.022	.	.	.	.	.	.	.	.	.	.	.	0.022
6/12	0.063	0.305	.	.	.	.	.	.	.	.	.	.	0.360
6/21	0.220	1.167	0.243	.	.	.	.	.	.	.	.	.	1.630
6/26	0.161	1.015	0.211	0.170	.	.	.	.	.	.	.	.	1.557
7/02	0.230	1.502	0.630	0.396	0.340	.	.	.	.	.	.	.	3.106
7/09	0.232	1.997	0.900	1.184	0.797	0.267	.	.	.	.	.	.	5.377
7/16	0.261	1.096	0.999	0.834	2.102	0.498	0.174	.	.	.	.	.	6.764
7/25	0.301	2.915	1.266	2.607	3.056	1.756	0.503	1.447	.	.	.	.	14.091
7/30	0.229	1.760	0.802	1.350	2.041	1.241	0.507	1.266	0.212	.	.	.	9.400
8/06	0.341	2.554	1.213	2.096	2.044	1.734	0.963	4.460	0.620	0.190	.	.	17.017
8/13	0.302	2.764	1.277	2.350	3.277	1.729	0.991	5.777	1.614	0.356	0.600	.	21.133
8/20	0.403	3.096	1.302	2.518	3.630	1.977	0.908	6.007	2.120	0.931	1.137	0.030	24.235
8/27	0.450	3.374	1.540	2.727	3.031	2.117	1.130	5.928	2.619	1.203	4.340	0.072	29.347
9/03	0.343	2.640	1.206	2.153	2.952	1.608	0.840	4.563	1.632	0.905	2.400	0.119	21.369
9/10	0.166	1.211	0.590	1.090	1.432	0.756	0.399	2.149	0.016	0.372	1.111	0.050	10.150
9/17	0.166	1.214	0.603	1.108	1.464	0.763	0.307	2.113	0.766	0.350	0.956	0.041	10.702
9/24	0.166	1.215	0.607	0.999	1.493	0.704	0.374	2.067	0.765	0.340	0.690	0.032	9.532
10/01	0.165	1.214	0.534	1.011	1.518	0.722	0.336	1.845	0.705	0.319	0.672	0.028	9.069
10/08	0.141	1.212	0.535	1.021	1.369	0.730	0.343	1.700	0.642	0.319	0.646	0.024	8.778
10/15	0.141	1.208	0.537	1.031	1.307	0.753	0.318	1.572	0.633	0.297	0.616	0.021	8.514
10/22	0.141	1.031	0.537	0.907	1.401	0.600	0.326	1.559	0.567	0.271	0.570	0.021	8.019
10/29	0.130	1.022	0.534	0.909	1.410	0.607	0.331	1.594	0.549	0.264	0.573	0.010	8.029
11/05	0.136	1.013	0.531	0.910	1.240	0.693	0.336	1.471	0.530	0.235	0.526	0.016	7.637
11/12	0.134	1.005	0.453	0.909	1.244	0.699	0.303	1.504	0.469	0.220	0.479	0.015	7.442
11/19	0.133	0.993	0.449	0.900	1.246	0.703	0.306	1.534	0.472	0.221	0.469	0.014	7.440
11/26	0.131	0.981	0.446	0.905	1.246	0.610	0.310	1.560	0.405	0.196	0.419	0.013	7.310
11/30	0.065	0.406	0.221	0.515	0.711	0.354	0.156	0.077	0.247	0.117	0.224	0.007	3.980
Total Annual Production = 262.91													

Table 5. Maximum-size prey ingestible by age-0 striped bass from August through November (end of the growing season) and available first-year gizzard shad and alewife biomass (per 1000-fish cohort).

Date	Age-0 striped bass total length (mm)	Maximum total length (mm) of ingestible prey		First-year biomass available (g)		Percent of first-year biomass available	
		Shad	Alewife	Shad	Alewife	Shad	Alewife
8/8	101	45	52	0.228	23.521	0.01	8.94
8/15	111	47	54	0.568	33.386	0.03	12.69
8/22	122	49	57	1.224	36.673	0.07	13.94
8/29	132	51	59	0	35.122	0	13.35
9/5	141	53	62	0	40.641	0	15.45
9/12	151	55	64	0	39.996	0	15.21
9/19	161	58	67	0	40.237	0	15.30
9/26	171	60	70	0	39.999	0	15.21
10/3	181	62	72	0	56.772	0	21.59
10/10	190	65	76	0	56.744	0	21.58
10/17	199	67	83	1.581	69.697	0.10	26.50
10/24	207	69	86	1.569	70.047	0.10	26.63
10/31	215	71	88	1.556	70.368	0.09	26.76
11/7	222	73	90	1.556	70.718	0.09	26.88
11/14	228	75	93	1.524	70.996	0.09	26.99
11/21	234	76	95	1.506	71.351	0.09	27.13
11/28	239	78	97	1.486	71.599	0.09	27.22
11/30	241	78	98	1.480	71.731	0.09	27.27

Table 6. Maximum-size prey ingestible by age-1 striped bass from May through November (the end of the growing season) and available first-year gizzard shad and alewife biomass (per 1000-fish cohort).

Date	Age-1 striped bass total length (mm)	Maximum total length (mm) of ingestible prey		First-year biomass available (g)		Percent of first-year biomass available	
		Shad	Alewife	Shad	Alewife	Shad	Alewife
5/21	245	80	100	0.146	0.000	0.01	0.00
5/31	248	80	100	1.856	0.005	0.11	0.01
6/4	249	81	101	3.276	0.600	0.20	0.02
6/11	252	82	102	8.399	0.306	0.51	0.12
6/19	256	83	104	20.435	1.295	1.24	0.49
6/26	261	84	105	37.449	2.234	2.27	0.85
7/2	266	86	107	66.489	4.040	4.02	1.54
7/9	271	87	109	114.927	7.560	6.97	2.87
7/16	277	89	112	167.231	12.418	10.12	4.72
7/25	285	92	115	200.479	21.239	12.14	8.11
8/1	290	94	117	280.625	27.267	16.99	10.37
8/8	299	96	119	364.692	37.967	22.08	14.44
8/15	306	99	122	411.078	50.864	24.88	19.34
8/22	314	101	126	410.191	66.513	24.81	25.29
8/29	322	104	129	408.561	84.377	24.73	32.08
9/5	329	106	132	396.217	95.442	23.98	36.29
9/12	337	109	135	393.941	95.529	23.83	36.32
9/19	344	112	138	384.093	96.384	23.25	36.65
9/26	352	114	142	372.216	96.643	22.53	36.75
10/3	359	117	145	360.527	96.798	21.82	36.81
10/10	366	120	149	349.038	96.854	21.13	36.83
10/17	373	122	152	337.756	96.993	20.45	36.88
10/24	379	124	155	326.688	97.137	19.78	36.93
10/31	385	127	157	315.843	97.217	19.12	36.96
11/7	390	129	160	305.225	97.352	18.48	37.02
11/14	395	130	162	294.837	97.385	17.84	37.03
11/21	399	132	165	284.684	97.465	17.23	37.05
11/28	403	134	167	274.769	97.408	16.63	37.04
11/30	406	134	168	271.980	97.356	16.46	37.02

Table 7. Maximum-size prey ingestible by age-0 walleye from August through November (the end of the growing season) and available first-year gizzard shad and alewife biomass (per 1000-fish cohort).

Date	Age-0 walleye total length (mm)	Maximum total length (mm) of ingestible prey		First-year biomass available (g)		Percent of first-year biomass available	
		Shad	Alewife	Shad	Alewife	Shad	Alewife
8/8	102	40	47	0.228	23.522	0.01	8.94
8/15	111	41	49	0.568	25.952	0.03	9.87
8/22	120	43	50	0	24.928	0	9.48
8/29	128	44	51	0	28.108	0	10.69
9/5	134	45	53	0	29.374	0	11.17
9/12	141	46	54	0	28.898	0	10.99
9/19	147	47	55	0	29.037	0	11.04
9/26	153	48	56	0	28.727	0	10.92
10/3	158	49	57	0	28.285	0	10.75
10/10	163	49	58	0	27.758	0	10.55
10/17	166	50	59	0	11.807	0	4.49
10/24	170	50	59	0	11.551	0	4.39
10/31	172	51	61	0	11.238	0	4.27
11/7	174	51	61	0	10.967	0	4.17
11/14	176	51	61	0	10.747	0	4.09
11/21	177	52	61	0	5.941	0	2.26
11/28	178	52	61	0	5.800	0	2.20
11/30	178	52	61	0	3.796	0	1.44

Table 8. Maximum-size prey ingestible by age-1 walleye from May through November (end of the growing season) and available first-year gizzard shad and alewife biomass (per 1000-fish cohort).

Date	Age-1 walleye total length (mm)	Maximum total length (mm) of ingestible prey		First-year biomass available (g)		Percent of first-year biomass available	
		Shad	Alewife	Shad	Alewife	Shad	Alewife
5/21	215	58	69	0.146	0.000	0.01	0.00
5/31	222	60	70	1.856	0.005	0.11	0.01
6/4	227	60	71	3.276	0.600	0.20	0.02
6/11	233	62	73	8.399	0.306	0.51	0.12
6/19	241	63	75	20.435	1.295	1.24	0.49
6/26	247	64	76	32.293	2.234	1.95	0.85
7/2	253	66	82	59.599	4.040	3.61	1.54
7/9	260	67	84	74.691	7.560	4.52	2.87
7/16	266	68	85	119.701	12.418	7.25	4.72
7/25	274	70	87	161.505	21.239	9.78	8.11
8/1	279	71	88	131.470	27.267	7.96	10.37
8/8	286	72	90	4.279	37.967	0.26	14.44
8/15	291	73	91	2.448	50.864	0.15	19.34
8/22	297	75	93	3.938	66.513	0.24	25.29
8/29	302	76	94	5.456	84.377	0.33	32.08
9/5	306	76	95	1.791	95.442	0.10	36.29
9/12	311	77	96	1.672	95.529	0.10	36.32
9/19	314	78	98	1.605	96.384	0.10	36.65
9/26	318	79	99	1.603	96.643	0.10	37.75
10/3	321	80	99	1.598	96.798	0.10	36.81
10/10	324	80	100	1.591	96.854	0.10	36.83
10/17	326	81	101	1.581	96.993	0.10	36.88
10/24	328	81	101	1.569	97.137	0.09	36.93
10/31	330	82	102	1.556	94.938	0.09	36.10
11/7	331	82	102	1.541	95.100	0.09	36.16
11/14	332	82	102	1.524	95.161	0.09	36.18
11/21	333	82	102	1.506	78.812	0.09	29.97
11/28	334	83	103	1.486	78.992	0.09	30.03
11/30	334	83	103	1.480	79.082	0.09	30.10

Table 9. Maximum-size prey ingestible by age-0 largemouth bass from August through November (the end of the growing season) and available first-year gizzard shad and alewife biomass (per 1000-fish cohort).

Date	Age-0 largemouth bass total length (mm)	Maximum total length (mm) of ingestible prey		First-year biomass available (g)		Percent of first-year biomass available	
		Shad	Alewife	Shad	Alewife	Shad	Alewife
8/8	92	48	56	1.701	27.437	0.10	10.43
8/15	98	50	59	0.568	33.385	0.03	12.69
8/22	104	52	61	1.224	45.485	0.07	17.29
8/29	109	53	63	0	48.928	0	18.60
9/5	114	54	64	0	56.362	0	21.43
9/12	118	56	66	0	39.996	0	15.21
9/19	122	57	67	0	40.237	0	15.30
9/26	126	58	69	0	39.999	0	15.21
10/3	129	59	70	0	39.771	0	15.12
10/10	132	60	71	0	39.512	0	15.02
10/17	134	61	72	0	39.302	0	14.94
10/24	137	62	73	0	30.942	0	11.77
10/31	139	62	73	0	31.084	0	11.82
11/7	141	63	74	0	31.261	0	11.89
11/14	142	63	74	0	31.442	0	11.96
11/21	143	64	75	0	27.919	0	10.62
11/28	144	64	75	0	28.170	0	10.71
11/30	144	64	75	0	28.338	0	10.77

Table 10. Maximum-size prey ingestible by age-1 largemouth bass from May through November (the end of the growing season) and available first-year gizzard shad and alewife biomass (per 1000-fish cohort).

Date	Age-1 largemouth bass total length (mm)	Maximum total length (mm) of ingestible prey		First-year biomass available (g)		Percent of first-year biomass available	
		Shad	Alewife	Shad	Alewife	Shad	Alewife
5/21	170	73	91	0.146	0.000	0.01	0.00
5/31	176	75	94	1.856	0.005	0.11	0.01
6/4	179	76	95	3.276	0.060	0.20	0.02
6/11	184	78	98	8.399	0.306	0.51	0.12
6/19	189	80	100	20.435	1.295	1.24	0.49
6/26	194	82	102	37.449	2.234	2.27	0.85
7/2	198	83	104	66.489	4.040	4.02	1.54
7/9	204	85	107	114.927	7.560	6.97	2.87
7/16	208	87	109	167.230	12.418	10.12	4.72
7/25	214	90	112	200.479	21.329	12.14	8.11
8/1	218	91	114	280.624	27.267	16.99	10.37
8/8	223	93	116	313.856	37.967	19.00	14.44
8/15	227	95	118	411.078	50.864	24.88	19.34
8/22	231	97	120	316.196	66.513	19.14	25.29
8/29	235	98	122	11.605	84.377	0.70	32.08
9/5	238	100	124	12.277	95.442	0.74	36.29
9/12	241	101	126	11.917	95.529	0.72	36.32
9/19	244	102	127	11.607	96.384	0.70	36.65
9/26	247	103	129	11.361	96.643	0.69	36.75
10/3	249	104	130	11.112	96.798	0.67	36.81
10/10	251	105	131	10.861	96.854	0.66	36.83
10/17	252	106	132	10.608	96.993	0.64	36.88
10/24	254	107	134	10.353	97.137	0.63	36.93
10/31	255	107	134	4.990	97.217	0.30	36.96
11/7	256	107	134	4.894	97.352	0.30	37.02
11/14	256	107	134	4.795	97.385	0.29	37.03
11/21	256	107	134	4.695	97.465	0.28	37.05
11/28	256	107	134	4.593	97.408	0.28	37.04
11/30	256	107	134	4.564	97.356	0.28	37.02

Table 11. Maximum-size prey ingestible by age-0 striped bass over the growing season and available first-year gizzard shad and alewife production (per 1000-fish cohort).

Date	Age-0 striped bass total length (mm)	Maximum total length (mm) of ingestible prey		First-year production available (g/wk)		Percent of first-year production available	
		Shad	Alewife	Shad	Alewife	Shad	Alewife
8/8	101	45	52	0.309	12.909	0.019	4.910
8/15	111	47	54	0.474	16.710	0.029	6.356
8/22	122	49	57	0.815	16.836	0.049	6.404
8/29	132	51	59	0	17.417	0	6.625
9/5	141	53	62	0	12.067	0	4.590
9/12	151	55	64	0	5.653	0	2.150
9/19	161	58	67	0	5.384	0	2.048
9/26	171	60	70	0	5.052	0	1.922
10/3	181	62	72	0	6.1452	0	2.337
10/10	190	65	76	0	5.869	0	2.232
10/17	199	67	83	0.095	8.514	0.006	3.238
10/24	207	69	86	0.095	6.310	0.006	2.400
10/31	215	71	88	0.094	6.335	0.006	2.410
11/7	222	73	90	0.093	5.957	0.006	2.266
11/14	228	75	93	0.092	5.850	0.005	2.224
11/21	234	76	95	0.091	5.873	0.005	2.233
11/28	239	78	97	0.090	5.752	0.005	2.188
11/30	241	78	98	0.030	3.208	0.002	1.220

Table 12. Maximum-size prey ingestible by age-1 striped bass over the growing season and available first-year gizzard shad and alewife production (per 1000-fish cohort).

Date	Age-1 striped bass total length (mm)	Maximum total length (mm) of ingestible prey		First-year production available (g/wk)		Percent of first-year production available	
		Shad	Alewife	Shad	Alewife	Shad	Alewife
5/21	245	80	100	0.173	0	0.010	0
5/31	248	80	100	3.829	0	0.232	0
6/4	249	81	101	2.097	0.022	0.127	0.008
6/11	252	82	102	7.059	0.368	0.427	0.140
6/19	256	83	104	17.326	1.630	1.049	0.620
6/26	261	84	105	26.483	1.557	1.604	0.592
7/2	266	86	107	40.124	3.186	2.430	1.212
7/9	271	87	109	64.278	5.377	3.892	2.045
7/16	277	89	112	79.428	6.764	4.809	2.573
7/25	285	92	115	100.182	14.891	6.066	5.664
8/1	290	94	117	101.852	9.408	6.167	3.578
8/8	299	96	119	118.356	17.017	7.167	6.472
8/15	306	99	122	125.099	21.133	7.575	8.038
8/22	314	101	126	90.947	24.235	5.507	9.218
8/29	322	104	129	103.753	29.347	6.282	11.162
9/5	329	106	132	44.457	21.369	2.692	8.128
9/12	337	109	135	16.188	10.150	0.980	3.860
9/19	344	112	138	15.698	10.702	0.951	4.071
9/26	352	114	142	15.213	9.532	0.921	3.626
10/3	359	117	145	14.741	9.069	0.893	3.449
10/10	366	120	149	14.278	8.778	0.865	3.339
10/17	373	122	152	13.805	8.514	0.836	3.238
10/24	379	124	155	13.357	8.019	0.809	3.050
10/31	385	127	157	12.918	8.029	0.782	3.054
11/7	390	129	160	12.486	7.637	0.756	2.905
11/14	395	130	162	12.067	7.442	0.730	2.831
11/21	399	132	165	11.621	7.448	0.704	2.833
11/28	403	134	167	8.514	7.310	0.516	2.780
11/30	406	134	168	2.749	3.980	0.166	1.514

Table 13. Maximum-size prey ingestible by age-0 walleye over the growing season and available first-year gizzard shad and alewife production (per 1000-fish cohort).

Date	Age-0 walleye total length (mm)	Maximum total length (mm) of ingestible prey		First-year production available (g/wk)		Percent of first-year production available	
		Shad	Alewife	Shad	Alewife	Shad	Alewife
8/8	102	40	47	0.309	12.909	0.019	4.910
8/15	111	41	49	0.474	14.352	0.029	5.459
8/22	120	43	50	0	13.198	0	5.020
8/29	128	44	51	0	15.300	0	5.819
9/5	134	45	53	0	9.619	0	3.659
9/12	141	46	54	0	4.498	0	1.711
9/19	147	47	55	0	4.234	0	1.610
9/26	153	48	56	0	3.894	0	1.481
10/3	158	49	58	0	3.569	0	1.357
10/10	163	49	58	0	3.419	0	1.300
10/17	166	50	59	0	1.567	0	0.596
10/24	170	50	59	0	1.437	0	0.547
10/31	172	51	60	0	1.404	0	0.534
11/7	174	51	61	0	1.307	0	0.497
11/14	176	51	61	0	1.191	0	0.453
11/21	177	52	61	0	0.704	0	0.268
11/28	178	52	61	0	0.628	0	0.239
11/30	178	52	61	0	0.231	0	0.088

Table 14. Maximum-size prey ingestible by age-1 walleye over the growing season and available first-year gizzard shad and alewife production (per 1000-fish cohort).

Date	Age-1 walleye total length (mm)	Maximum total length (mm) of ingestible prey		First-year production available (g/wk)		Percent of first-year production available	
		Shad	Alewife	Shad	Alewife	Shad	Alewife
5/21	215	58	69	0.173	0	0.010	0
5/31	222	60	70	3.829	0	0.232	0
6/4	227	60	71	2.097	0.022	0.127	0.008
6/11	233	62	73	7.059	0.368	0.427	0.140
6/19	241	63	75	17.326	1.630	1.049	0.620
6/26	247	64	76	24.431	1.557	1.479	0.592
7/2	253	66	82	38.016	3.186	2.302	1.212
7/9	260	67	84	48.720	5.377	2.950	2.045
7/16	266	68	85	64.140	6.764	3.884	2.573
7/25	274	70	87	83.700	14.891	5.068	5.664
8/1	279	71	88	52.577	9.408	3.184	3.578
8/8	286	72	90	2.268	17.017	0.137	6.472
8/15	291	73	91	1.128	21.133	0.068	8.038
8/22	297	75	93	1.872	24.235	0.113	9.218
8/29	302	76	94	1.981	29.347	0.120	11.162
9/5	306	76	95	0.331	21.369	0.020	8.128
9/12	311	77	96	0.121	10.150	0.007	3.860
9/19	314	78	98	0.118	10.702	0.007	4.071
9/26	318	79	99	0.112	9.532	0.007	3.626
10/3	321	80	99	0.112	9.069	0.007	3.449
10/10	324	80	100	0.112	8.778	0.007	3.339
10/17	326	81	101	0.095	8.514	0.006	3.238
10/24	328	81	101	0.095	8.019	0.006	3.050
10/31	330	82	102	0.094	7.891	0.006	3.002
11/7	331	82	102	0.093	7.501	0.006	2.853
11/14	332	82	102	0.092	7.308	0.006	2.780
11/21	333	82	102	0.091	6.322	0.006	2.405
11/28	334	83	103	0.090	6.198	0.005	2.357
11/30	334	83	103	0.030	3.492	0.002	1.304

Table 15. Maximum-size prey ingestible by age-0 largemouth bass over the growing season and available first-year gizzard shad and alewife production (per 1000-fish cohort).

Date	Age-0 largemouth bass total length (mm)	Maximum total length (mm) of ingestible prey		First-year production available (g/wk)		Percent of first-year production available	
		Shad	Alewife	Shad	Alewife	Shad	Alewife
8/8	92	48	56	1.242	14.122	0.075	5.371
8/15	98	50	59	0.474	16.710	0.029	6.356
8/22	104	52	61	0.815	19.354	0.049	7.361
8/29	109	53	63	0	21.248	0	8.082
9/5	114	54	64	0	15.019	0	5.713
9/12	118	56	66	0	5.653	0	2.150
9/19	122	57	67	0	6.147	0	2.338
9/26	126	58	69	0	5.052	0	1.922
10/3	129	59	70	0	4.627	0	1.760
10/10	132	60	71	0	5.500	0	1.712
10/17	134	61	72	0	4.210	0	1.601
10/24	137	62	73	0	3.322	0	1.264
10/31	139	62	73	0	3.329	0	1.266
11/7	141	63	74	0	3.114	0	1.184
11/14	142	63	74	0	2.998	0	1.140
11/21	143	64	75	0	2.710	0	1.030
11/28	144	64	75	0	2.673	0	1.017
11/30	144	64	75	0	1.472	0	0.560

Table 16. Maximum-size prey ingestible by age-1 largemouth bass over the growing season and available first-year gizzard shad and alewife production (per 1000-fish cohort).

Date	Age-1 largemouth bass total length (mm)	Maximum total length (mm) of ingestible prey		First-year production available (g/wk)		Percent of first-year production available	
		Shad	Alewife	Shad	Alewife	Shad	Alewife
5/21	170	73	91	0.173	0	0.010	0
5/31	176	75	94	3.829	0	0.232	0
6/4	179	76	95	2.097	0.022	0.127	0.008
6/11	184	78	98	7.059	0.368	0.427	0.140
6/19	184	80	100	17.326	1.630	1.049	0.620
6/26	194	82	102	26.483	1.557	1.604	0.592
7/2	198	83	104	40.124	3.186	2.430	1.212
7/9	204	85	107	64.278	5.377	3.892	2.045
7/16	208	87	109	79.428	6.764	4.809	2.573
7/25	214	90	112	100.182	14.891	6.066	5.664
8/1	218	91	114	101.852	9.408	6.168	3.578
8/8	223	93	116	103.848	17.017	6.288	6.472
8/15	227	95	118	125.099	21.133	7.575	8.038
8/22	231	97	120	90.947	24.235	5.507	9.218
8/29	235	98	122	3.732	29.347	0.226	11.162
9/5	238	100	124	1.633	21.369	0.099	8.128
9/12	241	101	126	0.576	10.150	0.035	3.860
9/19	244	102	127	0.562	10.702	0.034	4.071
9/26	247	103	129	0.546	9.532	0.033	3.626
10/3	249	104	130	0.536	9.069	0.033	3.449
10/10	251	105	131	0.526	8.778	0.032	3.339
10/17	252	106	132	0.498	8.514	0.030	3.238
10/24	254	107	134	0.487	8.019	0.029	3.050
10/31	255	107	134	0.268	8.029	0.016	3.054
11/7	256	107	134	0.263	7.637	0.016	2.905
11/14	256	107	134	0.258	7.442	0.016	2.831
11/21	256	107	134	0.220	7.448	0.013	2.833
11/28	256	107	134	0.216	7.310	0.013	2.780
11/30	256	107	134	0.061	3.980	0.004	1.514

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