EARLY LIFE HISTORY DYNAMICS OF A STOCKED STRIPED BASS (*MORONE SAXATILIS*) POPULATION AND ASSESSMENT OF STRATEGIES FOR IMPROVING STOCKING SUCCESS IN SMITH MOUNTAIN LAKE, VIRGINIA

by
Trent M. Sutton

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APPROVED:

John J. Ney, Chair

Alan G. Heath
Brian R. Murphy

Donald J. Orth
Eric P. Smith

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(ABSTRACT)

The early life history dynamics of stocked, fingerling striped bass (*Morone saxatilis*) were evaluated in Smith Mountain Lake, Virginia, from 1994-96 and incorporated into an individual-based model to assess various stocking strategies in terms of their largest percent increases in first-year growth, overwinter survival, and recruitment to age 1. Age-0 striped bass exhibited dissimilar patterns of dispersion and size-dependent spatial distribution as a result of differences in habitat availability between stocking sites and water temperature preferences. Although size increased over the growing season, a bimodal length distribution developed by fall during both 1994 and 1995; this distribution consisted of large-mode juveniles (>180 mm TL) that weighed several times more than small-mode fish (<140 mm TL). Differential growth was attributed primarily to size-dependent differences in food habits and diet quality: small-mode striped bass maintained a mixed, low quality diet of invertebrates and small, age-0 cyprinids, while large-mode juveniles consumed only larger, energetically more profitable age-0 alewives. This disparity in food habits, largely due to the inability of small-mode striped bass to consume distributionally- and morphologically-invulnerable age-0 alewives, resulted in size-dependent differences in physiological well-being as large-mode juveniles

had amassed greater absolute energy stores than small-mode fish by the end of the growing season. Spring sampling revealed that the bimodal length distribution had become unimodal and was comprised almost entirely of large-mode juveniles. Because the few surviving small-mode striped bass collected during spring were extremely emaciated, it appears that this size group exhausted their energy stores and, consequently, starved over the winter.

Individual-based model simulation results indicated that stocking juvenile striped bass at a median total length of 52 mm on 08 June, while maintaining the current stocking density at 300,000 fingerlings, would result in the largest percent increases in first-year growth, survival, and number of age-1 recruits. This strategy was also less sensitive to perturbations in alewife population parameters and water temperature regime, and was more robust to these variations than the existing stocking scheme (300,000 fingerling striped bass with a median total length = 42 mm introduced on 15 June).

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INTRODUCTION

The discovery in the mid-1950s that the striped bass (*Morone saxatilis*) could successfully complete its life cycle in freshwater (Scruggs 1957) resulted in the development of a nationally-recognized sport fishery in Santee-Cooper Reservoir, South Carolina (Stevens 1958). The popularity of this fishery led other state fisheries management agencies to examine the possible utility of this anadromous sportfish for stocking in the large multipurpose impoundments that had been created throughout the southern United States. Because most of these systems contained resident populations of gizzard shad (*Dorosoma cepedianum*) and threadfin shad (*D. petense*), ostensibly underutilized by indigenous shore-oriented predator species such as largemouth bass (*Micropterus salmoides*), fisheries managers were hopeful that striped bass would not only control overabundant populations of these forage fishes, but also fill the vacant ecological niche (i.e. the pelagic zone) created during the formation of these impoundments (Radonski and Martin 1986).

Although introductions of newly-hatched striped bass fry were initiated by a number of state agencies throughout the South, several years of evaluation demonstrated that stocking this life stage was almost completely ineffective. As a result, more efficient artificial propagation and rearing techniques were developed in the 1960s that permitted rearing of fry to fingerling size prior to stocking (Stevens 1967a; Bailey 1975). The dramatic increase over the past several decades in the number of striped bass sport fisheries created in freshwater impoundments throughout the southern United States can be viewed as a testament to this change in stocking strategy (Axon and Whitehurst 1985). However, because striped bass require long stretches of free-flowing river for successful reproduction (Scott and Crossman 1973; Crance 1984), a characteristic lacking from most inland impoundments, self-maintaining populations have rarely been established. Consequently, most landlocked striped bass fisheries have been maintained strictly on a put-grow-take basis through annual stockings of fingerlings. These stockings have been largely a trial-and-error process with regards to stocking densities and the size and time at stocking; large numbers of small (<50 mm total length) fingerlings are stocked during summer months to offset the low (<20%) survival rates often observed for this species (Bailey 1975). Although striped bass fisheries have been established successfully in many of these systems, a paucity of information exists on the mechanisms influencing recruitment of stocked juveniles to the adult population. More knowledge concerning the early life history dynamics of striped bass stocked into freshwater impoundments should not only make stocking efforts more efficient, but management of this species less uncertain.

Smith Mountain Lake, an 8,343-ha hydroelectric impoundment in southcentral Virginia, is in many respects typical of other freshwater systems in which striped bass populations have been supported on a put-grow-take basis. Since 1964, the stocking of striped bass (between 180,000 and 800,000 fingerlings annually) has led to the development and maintenance of a successful sport fishery. Initial stockings of striped bass throughout the 1970s established an exceptional trophy fishery, with growth and harvest rates among the highest reported for freshwater systems throughout the United States (Hart 1978). Despite the success of this fishery, fingerling stocking density and survival to age 1 varied inversely from 1973-83 (Figure I.1; Moore 1988). Based on marginal yield analysis, it was determined that an annual

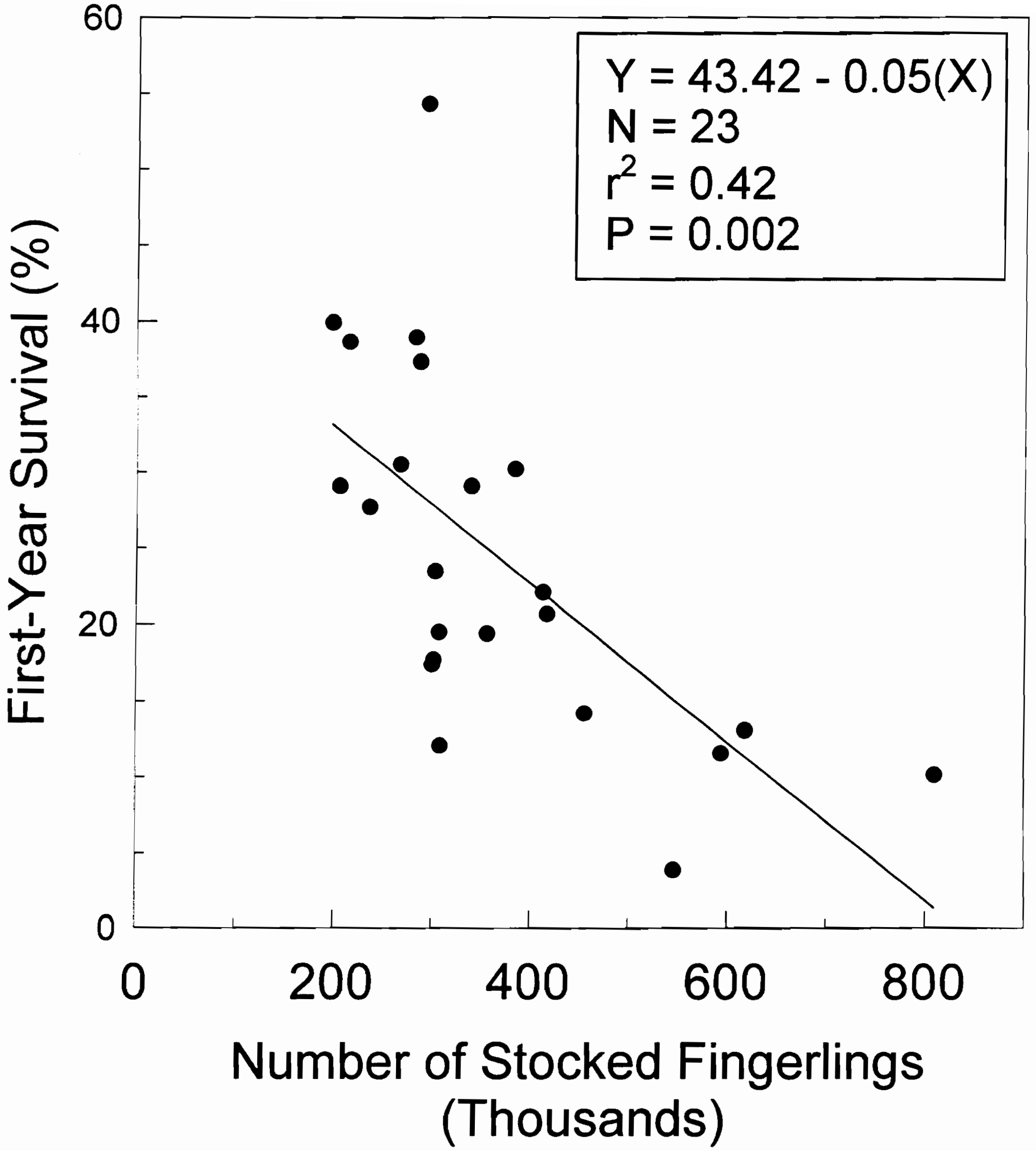


Figure I.1. First-year survival versus fingerling stocking density for striped bass in Smith Mountain Lake, 1973-96.

stocking density between 250,000 and 300,000 fingerlings would optimize the number of year-class recruits in this system (Figure I.2; Moore et al. 1991). In response, the number of striped bass stocked annually in Smith Mountain Lake by the Virginia Department of Game and Inland Fisheries (VDGIF) has fluctuated between 200,000 and 400,000 fingerlings since 1984. However, the inverse pattern continues to the present; first-year survival estimates have ranged from 12% to 40% at these stocking densities (Table I.1).

Despite a significant decline in harvest rates for striped bass in Smith Mountain Lake since the late 1970s (LaRoche 1981), growth rates for adults continue to remain above the national average (Duval 1996). It is thus quite possible that this system can support more harvestable fish than are now produced under the current stocking regime. However, production of more adult fish can only occur if the recruitment bottleneck observed at higher stocking densities for juvenile striped bass is identified and overcome.

Van Den Avyle and Higginbotham (1979) reported a similar inverse relationship between density of stocked fingerling striped bass and first-year survival in Watts Bar Reservoir, Tennessee. Although the authors could not determine the cause(s) of this empiric relationship, they believed that size at stocking, rather than density-dependent mechanisms, was primarily responsible for the observed relationship. White (1989) reported that natural recruitment of juvenile striped bass in the Santee-Cooper system had declined substantially since 1980. Bulak et al. (1997) demonstrated that spring flow rates from upstream dams in this system played a significant role in influencing recruitment variability. By managing water releases relative to the timing of striped bass spawning events, these authors believe that increased recruitment could be achieved through optimizing temperature and flow regimes so that striped bass

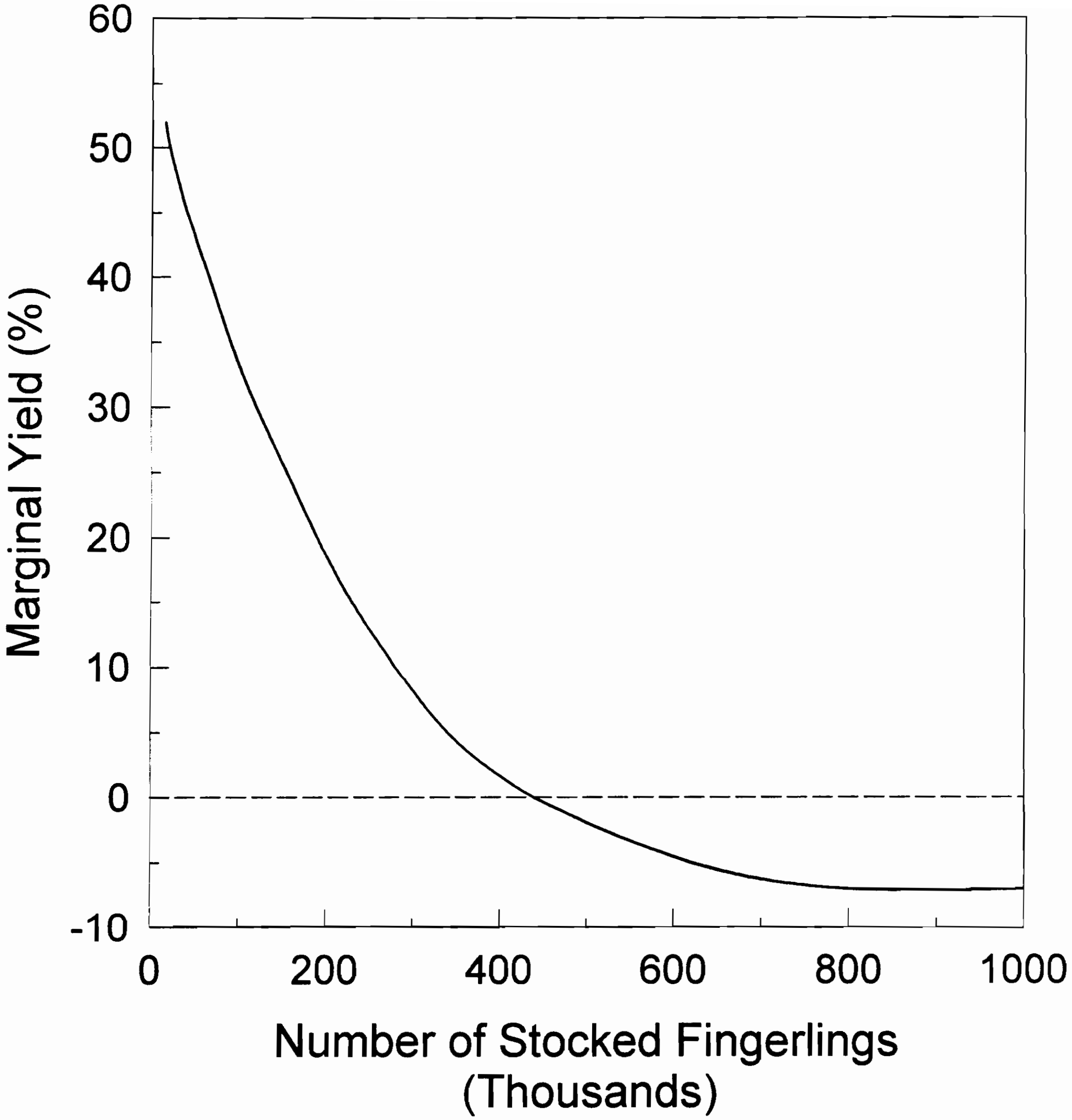


Figure I.2. Relationship between the number of stocked, fingerling striped bass and their marginal yield. Marginal yield is the number of age-1 recruits produced per additional stocking of fingerling striped bass (from Moore et al. 1991).

Table I.1. Numbers of juvenile striped bass stocked, actual and corrected catch-per-unit-effort (CPUE) for fish the following year, estimated first-year survival, and estimated number of age-1 striped bass in Smith Mountain Lake, 1973-1996. For methodology used to calculate estimates, see Moore et al. 1991.

Year Interval	Number Stocked	Actual CPUE	Corrected CPUE	First-Year Survival (%)	Number Age-1 Recruits
1973-74	293,925	0.296	0.296	54.3	159,601
1974-75	306,884	0.111	0.309	19.5	59,850
1975-76	455,241	0.120	0.458	14.2	64,703
1976-77	618,020	0.150	0.622	13.1	80,879
1977-78	416,732	0.160	0.420	20.7	86,271
1978-79	546,354	0.040	0.550	3.9	21,568
1979-80	809,246	0.153	0.815	10.2	82,497
1980-81	593,978	0.128	0.598	11.6	69,017
1981-82	412,790	0.169	0.416	22.1	91,124
1982-83	267,153	0.151	0.269	30.5	81,418
1983-84	205,654	0.111	0.207	29.1	59,850
1984-85	214,860	0.154	0.216	38.6	83,036
1985-86	308,501	0.069	0.311	12.1	37,204
1986-87	384,047	0.215	0.387	30.2	115,927
1987-88	355,936	0.128	0.358	19.4	69,017
1988-89	302,992	0.132	0.305	23.5	71,174
1989-90	197,534	0.146	0.199	39.9	78,722
1990-91	300,131	0.097	0.302	17.4	52,302
1991-92	301,346	0.099	0.303	17.7	53,380
1992-93	282,281	0.184	0.271	38.9	108,736
1993-94	287,054	0.174	0.253	37.3	93,820
1994-95	339,337	0.162	0.303	29.1	87,349
1995-96	236,100	0.118	0.231	27.7	63,625

eggs hatch in more suitable regions of the impoundment. Although density-independent processes, strongly influenced by the environment, have been shown to regulate recruitment of larval striped bass in both freshwater (Bulak et al. 1997) and tidal ecosystems (Ulanowicz and Polgar 1980; Uphoff 1989; Rutherford and Houde 1995), these mechanisms most likely have little influence on recruitment of striped bass in Smith Mountain Lake because: (1) no natural reproduction occurs; (2) fish are stocked as larger, less vulnerable juveniles; and (3) reservoir hydrology and water quality are relatively stable (Ney et al. 1988, 1990). Consequently, the cause(s) of this compensatory phenomenon appear to be trophic in nature.

Identifying the mechanisms resulting in the recruitment bottleneck of age-0 striped bass in Smith Mountain Lake is further constrained because fish are not monitored until fifteen months post-stocking when the VDGIF conducts its annual fall gillnet survey; it is during this time that the bottleneck manifests itself. To determine the cause(s) of the inverse pattern between stocking density and first-year survival, it is necessary to increase the understanding of the ecology and life history dynamics of striped bass during the first year of life so that scientifically sound stocking and management strategies can be identified and applied in Smith Mountain Lake.

Variability in recruitment has been identified as a central problem in fisheries research (Sissenwine et al. 1988). Although it has long been understood that year-class strength of most fish populations is set early in life, knowledge of the mechanisms affecting recruitment of age-0 fishes is generally poor. Whereas fish recruitment can be affected by many different biotic and abiotic factors, size-dependent mechanisms such as growth, cannibalism, predation, and starvation-induced overwinter mortality have been hypothesized to explain survival and recruitment variability of age-0 fish populations (Sissenwine 1984; Gutreuter and Anderson 1985; Miller et al. 1988; Cushing 1995). Because recruitment is affected by such a large suite of factors, their impacts may vary on a system-by-system, as well as temporal basis, for many species.

For juvenile piscivores in lakes and reservoirs, the principal factor limiting growth is the availability of forage-fish prey throughout the first year of life (Jenkins 1979; Noble 1981). The problem of forage-fish availability is immediate and acute for fingerlings that become piscivorous at or soon after stocking but are limited in their consumption to very small forage fish, usually of the same year class (Ney and Orth 1986). For these fingerlings, a lack of small, ingestible fish prey, resulting in poor or negligible growth, can have a tremendous impact on the size distribution of juveniles by the end of their first growing season (Shelton et al. 1979; Timmons et al. 1980; Keast and Eadie 1985) because many of them are relegated to feeding on prey types, such as invertebrates, that have a lower caloric content per unit body mass than fish prey (Cummins and Wuycheck 1971; Prus 1975; Penczak et al. 1984; Moore 1988). Aggus and Elliott (1975) reported that in Bulls Shoal Lake, Missouri-Arkansas, age-0 largemouth bass were able to grow twice as large in length by the end of the first growing season by feeding on gizzard shad, threadfin shad, and brook silversides (*Labidesthes sicculus*) than did their cohorts which consumed predominantly invertebrates. Forney (1976) reported that in Oneida Lake, New York, when age-0 yellow perch (*Perca flavescens*) were too large to be preyed upon by juvenile walleyes (*Stizostedion vitreum*), first-year growth was relatively slow because walleyes could consume only invertebrates. Conversely, when yellow perch were small enough to be vulnerable to walleye predation, age-0 walleye growth was rapid.

For piscivorous fishes in temperate climates, rapid growth during the first months of life is particularly critical for survival. Age-0 fishes that grow at less than the maximal rate are vulnerable to predation for longer periods of time and, as a result, subsequent recruitment is typically poorer than that exhibited by populations of faster-growing individuals (Ricker and Foerster 1948). This premise has been observed for walleyes in both Oneida Lake, New York, and Lake Mendota, Wisconsin, in which cannibalism by older fish on slow-growing juveniles was one of the most important factors governing recruitment (Chevalier 1973; Forney 1976, 1980; Madenjian et al. 1991). Additionally, size-dependent predation has been shown to have a significant influence on recruitment variability in populations of largemouth bass (Minton and McLean 1982) and yellow perch (Nielsen 1980; Craig 1982; Post and Prankevicius 1987).

Size-dependent predation may be particularly acute in systems that rely on stocked fingerlings, not only because these fish may be "naive", lacking the necessary predator avoidance behaviors that wild fish exhibit (Stein et al. 1981; Santucci and Wahl 1993), but because they may remain concentrated at high densities in nearshore regions, further exacerbating the problem by attracting predators. Carline et al. (1986) found that 168-184 mm total length (TL) tiger muskellunge (*Esox lucius x E. masquinongy*) stocked in sixteen small ponds and impoundments in Ohio suffered losses as high as 100% within 50 days post-stocking from predation by largemouth bass. The authors hypothesized that these mortality events were largely a result of two factors: (1) tiger muskellunge <250 mm TL were within the ingestibility limits of most adult largemouth bass; and (2) thermal stratification in these systems, coupled with an anoxic hypolimnion, forced largemouth bass and tiger muskellunge to concentrate in nearshore areas. Comparable results on post-stocking predation by nearshore piscivores (primarily largemouth bass) have also been reported for other stocked juvenile esocids (Stein et al. 1981; Wahl and Stein 1989; Szendrey and Wahl 1996), percids (Johnson et al. 1988), ictalurids (Krummrich and Heidinger 1973), and salmonids (Keith and Barkley 1971) in similar systems. However, in sharp contrast, Michaelson (1996) demonstrated through both field-collected data and bioenergetics modeling that predation on juvenile striped bass by largemouth bass in Smith Mountain Lake immediately post-stocking until dispersal from nearshore regions by the end of the first summer of life was negligible (0.1% in 1994 and 1.2% in 1995). Although size-dependent predation on juvenile fishes, particularly smaller, slower-growing individuals, may be a significant factor regulating first-year recruitment in some freshwater systems, this mechanism does not appear to contribute to the recruitment bottleneck for fingerling striped bass stocked in Smith Mountain Lake.

Alternatively, size-dependent survival may be a result of differential starvation. Body size of age-0 fishes at the end of the first growing season has been identified as a critical factor in influencing overwinter survival (Forney 1976; Oliver et al. 1979; Shuter et al. 1980; Toneys and Coble 1980; Adams et al. 1982; Carline et al. 1986; Adams and DeAngelis 1987; Henderson et al. 1988; Post and Evans 1989; Post and Shuter 1990; Thompson et al. 1991; Miranda and Hubbard 1994; Johnson and Evans 1996). Smaller individuals within a cohort have higher maintenance requirements per unit body mass than larger ones (Paloheimo and Dickie 1966). During winter at temperate latitudes when activity is slowed by cold temperatures and food density is low (Keast 1968), smaller individuals have been shown to exhaust stored energy earlier to meet basal metabolic requirements (Shuter et al. 1980; Henderson et al. 1988; Post and Evans 1989). As a consequence, smaller individuals are more vulnerable to overwinter mortality due to starvation than larger fish of the same cohort. These results have been demonstrated in a number of studies on juvenile fishes. Larger age-0 black basses (*Micropterus* spp.) tend to accumulate more stored lipid reserves (Adams et al. 1982) and utilize these energy stores at a slower rate (Oliver et al. 1979; Shuter et al. 1980; Miranda and Hubbard 1994) than smaller fish of the same cohort. Larger bass also are more likely to encounter ingestible-sized prey in early spring (Adams et al. 1982; Adams and DeAngelis 1987), a critical period for young piscivores because appropriate-sized prey and energy reserves are often limiting (Adams and DeAngelis 1987; Tisa 1988). Adams et al. (1982) reported disproportionately greater overwinter survival for age-0 largemouth bass that were >160-mm TL at the end of the growing season than bass smaller than this size. A similar result was also reported for walleyes >175 mm TL (Forney 1976) and tiger muskellunge >200-mm TL (Carline et al. 1986). Because size-dependent, overwinter survival has not been examined for populations of juvenile striped bass, it may be possible that this mechanism is the primary factor driving the recruitment bottleneck for this stocked piscivore in Smith Mountain Lake.

One approach to aid the analysis of first-year recruitment variability of piscivorous fishes is the use of an individual-based model (IBM; Huston et al. 1988). An IBM provides the framework to realistically conceptualize a complex system by synthesizing empirical data in order to simulate biotic and abiotic mechanisms. By incorporating dynamic processes such as feeding success, bioenergetic constraints on growth and consumption, and size-dependent mortality, this approach tracks the growth and survival of individual fish through an iterative, time-step basis and aggregates them to provide an opportunity to test hypotheses, examine the consequences of and generate insights into population-level variation in life-history strategies, and evaluate existing data. Through the process of parameter alteration, IBMs are able to identify essential mechanisms that drive biotic ecosystems (Van Winkle et al. 1993). The expectation is that these more realistic, detailed models will improve the identification of factors ultimately responsible for population variability. Individual-based models have been shown to accurately simulate growth of age-0 largemouth bass in a Tennessee reservoir (Adams and DeAngelis 1987), growth and recruitment of age-0 walleye in the Great Lakes drainage basin (Madenjian 1991; Madenjian and Carpenter 1991; Madenjian et al. 1996), size-dependent predation on age-0 smallmouth bass in boreal North American lakes (DeAngelis et al. 1991, 1993), predator-prey interactions between alewife (*Alosa pseudoharengus*) and larval/juvenile bloater (*Coregonus hoyi*) in Lake Michigan (Rice et al. 1993), and competitive interactions between rainbow trout (*Oncorhynchus mykiss*) and brook trout (*Salvelinus fontinalis*) in southern Appalachian streams (Clark and Rose 1997a, 1997b, 1997c).

An IBM has also been developed for striped bass in the Potomac River, Maryland (Rose and Cowan 1993). In its present state, the IBM is highly precise for both the egg and larval stages but is considerably more speculative regarding dynamics of the juvenile life stage. Simulations using the model, in combination with site-specific data, can help to identify those factors having the most influence on growth, survival, and recruitment when they operate. Cowan et al. (1993) used the above-mentioned IBM to determine which factors had the greatest impact on recruitment of age-0 striped bass. Analysis and predictive assessment of the factors affecting striped bass recruitment also will provide an opportunity to simulate the consequences of changes in size distribution, day of introduction, and density at stocking, both singly and in combination. Madenjian et al. (1991) used an IBM to simulate and assess various stocking strategies for fingerling walleyes in Lake Mendota, Wisconsin. The IBM approach thus provides a framework within which to conceptualize life-history dynamics, combine empirical studies and modeling in a synergistic fashion, and provide quantitative justification for making scientifically sound management decisions.

Quantitative assessments are generally lacking regarding the biotic mechanisms influencing recruitment variability of age-0 fishes in freshwater systems, in particular stocked juvenile piscivores in reservoirs. The goal of this study was to quantitatively assess the relationship between recruitment to age 1 and first-year growth and survival of stocked juvenile striped bass in Smith Mountain Lake, Virginia. Additionally, an individual-based model was utilized to assess various stocking strategies in terms of their utility for maximizing first-year growth, survival, and recruitment to age 1. Ancillary information required for this individual-based model includes spatial dispersion from stocking sites, growth patterns, overwinter survival, food habits, and predator-prey size relationships. This dissertation incorporates these data in two chapters.

Chapter I details the early life history dynamics of juvenile striped bass stocked into Smith Mountain Lake, Virginia, during 1994-95 and 1995-96. Specifically I evaluated, through an extensive field-collected data set, the following: (1) temporal patterns of spatial dispersion and distribution of striped bass juveniles from the time of stocking through the first overwintering period; (2) temporal patterns and trends in size distribution and growth of juvenile striped bass during the first year of life; (3) food habits of age-0 striped bass and black basses by size class and season (to assess competitive interactions); (4) size relationships between juvenile striped bass and consumed fish prey; and (5) a suite of physiological indices of health (relative condition, liver-somatic index, lipid index, and stomach-fullness index) to assess both temporal and size-dependent trends in feeding success and energetic well-being

Chapter II utilizes an individual-based model, that was tailored using the above field-collected data, to assess various scenarios for stocking juvenile striped bass in Smith Mountain Lake. Specifically, I examined the influence of size distribution at stocking, day of stocking, and stocking density to determine which scenario(s) maximized first-year growth, overwinter survival, and, consequently, the number of age-1 recruits. I then examined the effects of IBM perturbations in age-0 alewife cohort density, timing of adult alewife spawning, and age-0 alewife growth and mortality rates, as well as Smith Mountain Lake water temperature, singly and in combination, to determine the sensitivity and robustness of the proposed, "new" versus the existing, "old" stocking strategy.

CHAPTER I

EARLY LIFE HISTORY DYNAMICS OF STOCKED, FINGERLING STRIPED BASS IN SMITH MOUNTAIN LAKE, VIRGINIA

INTRODUCTION

Management of inland fish populations can be improved by gaining knowledge of the factors controlling growth, survival, and recruitment of early life stages (Hayes et al. 1993). Identification of the mechanisms affecting early growth and survival of fishes should not only allow the successful prediction of future recruitment, but it may also permit fisheries managers to take appropriate remedial actions that will increase recruitment to the adult population, thereby dampening population fluctuations or reversing long-term population declines. For fisheries biologists managing populations of stocked piscivores, this is particularly true because a considerable degree of control potentially exists in managing these fish populations through the regulation of size, time, and/or density at stocking (Stein et al. 1981; Carline et al. 1986; Hume and Parkinson 1987; Madenjian et al. 1991; Fielder 1992a, 1992b; Santucci and Wahl 1993; Stahl and Stein 1994; Szendrey and Wahl 1996). Therefore, an increased understanding of the specific mechanisms regulating the early life history dynamics of stocked piscivores should not only allow stocking efforts to become more efficient, but management of these fish populations less uncertain.

The literature is replete with studies examining the early life-history dynamics of striped bass (*Morone saxatilis*) in marine environments and associated tributaries (Merriman 1941; Rathjen and Miller 1957; Mansueti

1961; Trent 1962; Heubach et al. 1963; Chadwick 1966; Markle and Grant 1970; Schaefer 1970; Bason 1971; Turner and Chadwick 1972; Koo and Ritchie 1973; Manooch 1973; Wigfall and Barkuloo 1975; Ulanowicz and Polgar 1980; Boynton et al. 1981; Dey 1981; Kernehan et al. 1981; Setzler-Hamilton et al. 1981; Polgar 1982; Martin et al. 1985; Setzler-Hamilton et al. 1987; Boreman and Klauda 1988; McGovern and Olney 1988; Uphoff 1989; Rulifson and Manooch 1990; Dorazio et al. 1991; Wells et al. 1991; Chesney 1993; Pace et al. 1993; Wallin et al. 1993; Rutherford and Houde 1995; Secor and Houde 1995). Additionally, hatchery studies have been conducted to identify factors influencing growth and survival of age-0 striped bass in freshwater culture environments (Sandoz and Johnston 1965; Logan 1967; Harper et al. 1968; Harper and Jarman 1971; Humphries and Cumming 1971, 1973). However, little comparative data exist on the early life history dynamics of striped bass post-stocking in freshwater impoundments. Although numerous investigators have conducted research on stocked juvenile striped bass, these studies have focused primarily on first-year growth and/or food habits (Stevens 1967b; Gomez 1970; Mensinger 1970; Ware 1970; Erickson et al. 1970; Weaver 1975; Axon 1979; Van Den Avyle and Higginbotham 1979; Saul 1981; Saul and Wilson 1981; Nifong 1982; Richardson 1982; Humphreys 1983; Van Den Avyle et al. 1983; Matthews et al. 1992), with little attempt to link these dynamics to the recruitment process. As a result, information is lacking on the specific interactions regulating recruitment to the adult population for this species in freshwater impoundments.

The purpose of this investigation was to assess the factors influencing first-year growth, overwinter survival, and recruitment to age 1 for stocked juvenile striped bass in Smith Mountain Lake, Virginia. Specific objectives were to: (1) describe the temporal patterns of dispersion and spatial distribution of juvenile striped bass post-stocking during their first year of life; (2) characterize temporal changes in growth patterns and size distribution of juvenile striped bass through the critical overwintering period; (3) determine the relationship among juvenile striped bass size and food habits, feeding success, physiological indices of health, and overwinter survival during the first year of life; and (4) assess the constraints on feeding success of juvenile striped bass in terms of availability of forage-fish prey and the diets of other juvenile predators (black basses).

STUDY AREA

Smith Mountain Lake is an 8,343-ha (20,600-acre) impoundment in south-central Virginia. The lake 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 10.5 km above the dam (Figure 1.1). This deep storage reservoir (3.2-yr retention time) was created in 1965 and is operated by American Electric Power (formerly Appalachian Power Company) as a run-of-the-river and pump-storage hydroelectric facility in concert with downstream Leesville Reservoir. Smith Mountain Lake has a maximum pool elevation of 242.4 m, a maximum depth of 63.7 m, a mean depth of 16.8 m, and an 805-km (500-mi) shoreline that is highly dendritic (Simmons and Neff 1969; Duval 1996). The average annual vertical water fluctuation due to hydroelectric operation is 0.56 m (LaRoche 1981; Duval 1996).

Smith Mountain Lake is oligotrophic at its lower end, mesotrophic at the confluence of its tributary arms, and eutrophic further upstream (Benfield and Hendricks 1975; Obenshain and McLeod 1981). Littoral areas (<5 m in depth) in the lower lake section contain only sparse fish cover and grade sharply into the profundal zone. Oxygen concentrations in the cool hypolimnetic waters of this region of the lake are reduced to approximately 2-4 $mg \cdot L^{-1}$ during the summer months (Ney et al. 1988). In contrast, the lake is riverine in the upper tributary arms with expansive and vegetated littoral areas that slope more gradually into the main channel. During summer months, these upper reservoir waters may be devoid of oxygen 5 m below the surface (Ney et al. 1988). Because of these habitat differences, Smith Mountain Lake is divided into two distinct regions with arbitrary boundaries: (1) the upper reservoir, which

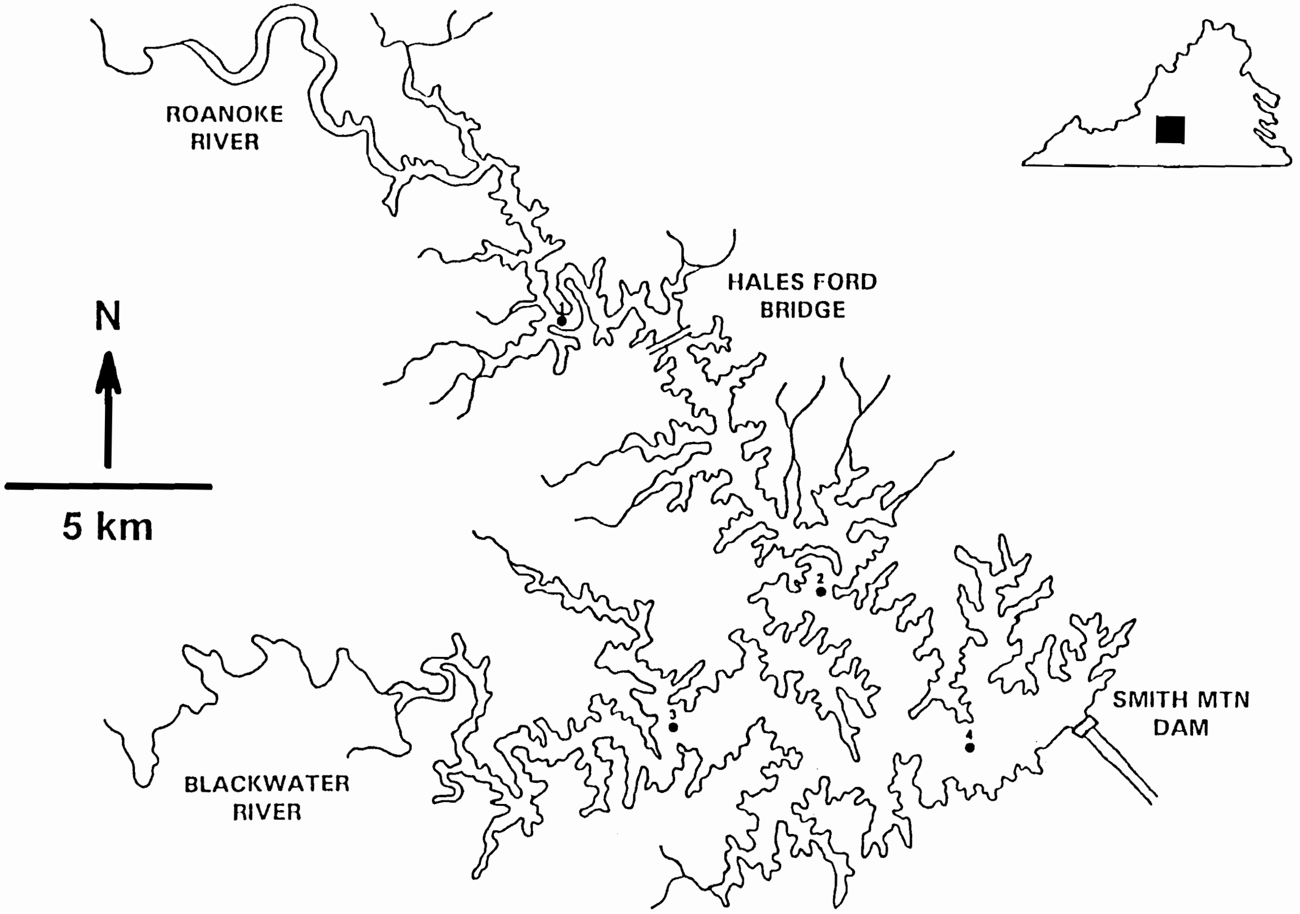


Figure 1.1. Map of Smith Mountain Lake, Virginia, with locations of striped bass sampling ranges: (1) upper s-curve (USC) of the Roanoke River; (2) lower s-curve (LSC) of the Roanoke River; (3) Gills Creek confluence (GCC) of the Blackwater River; and (4) upper lower lake (ULL) region.

consists of the Roanoke River above the upper s-curve area (USC) and the Blackwater River above the Gills Creek confluence (GCC); and (2) the lower reservoir, which consists of the Roanoke River below the upper s-curve area, the Blackwater River below the confluence of Gills Creek, and the lower lake region (Figure 1.1). For the purposes of this study, sampling was confined primarily to the lower reservoir because few juvenile striped bass were collected from regions above the stocking sites of both river arms.

The lake's fish assemblage is diverse, consisting of 45 species of indigenous and introduced fishes (Hart 1978). Largemouth bass (*Micropterus salmoides*) and smallmouth bass (*M. dolomieu*) were the primary game species after the initial formation of the reservoir and continue to provide an important sport fishery. Native centrarchids (*Lepomis* and *Pomoxis* spp.) and ictalurids (*Ictalurus* and *Ameiurus* spp.), and the introduced flathead catfish (*Pylodictus olivaris*), white bass (*Morone chrysops*), and white perch (*M. americana*), also contribute to the sportfishery in Smith Mountain Lake. The forage complex consists of age-0 sportfish as well as various cyprinids (*Cyprinella*, *Pimephales*, *Notemigonus*, and *Notropis* spp.), percids (*Etheostoma* spp.), and crayfish (*Orconectes* spp.), but it is dominated by the native gizzard shad (*Dorosoma cepedianum*) and the introduced alewife (*Alosa pseudoharengus*; Tisa 1988). Threadfin shad (*D. petense*), sometimes numerically abundant in Smith Mountain Lake, were first detected in 1993 and probably made their way into the lake as an angler introduction in 1991 or 1992 (M.C. Duval, VDGIF, personal communication). Stocking of piscivorous pelagic sport species on a put-grow-take basis, such as striped bass, walleye (*Stizostedion vitreum*), muskellunge (*Esox masquinongy*), and tiger muskellunge (*E. lucius x E. masquinongy*), began in 1965 to utilize the open-water habitat and to both diversify and augment the sportfish harvest. Although the Virginia Department of Game and Inland Fisheries (VDGIF) still stocks fingerling muskellunge and tiger muskellunge at low densities, walleye are no longer stocked due to poor angling success for this species (LaRoche 1981). However, striped bass, the primary pelagic sport fish sought in this system, are stocked annually at high densities in two locations: the Penhook state boat ramp (PSB) on the Blackwater River arm and Hales Ford state boat ramp (HFSB) on the Roanoke River arm (Figure 1.1).

STRIPED BASS STOCKINGS, 1994 & 1995

1994. - Running-ripe striped bass from Kerr Reservoir (approximately 100-km downriver from Smith Mountain Lake) were collected from the Roanoke River by VDGIF personnel from Brookneal Hatchery (Brookneal, Virginia) in early May and used as broodstock for striped bass stocking in Smith Mountain Lake. After hatching, 5-6 day old fry were transported to rearing ponds at the hatchery and allowed to grow to stocking size (30-50 mm TL). After grow-out (approximately 42 d), these Phase I fingerlings were seined from the rearing ponds, loaded into an aerated 2500-L tank, and transported (approximately a 2-h trip) to Smith Mountain Lake. Upon arrival, fish were tempered gradually using lake water over a 45-60 min period within the transport tank and stocked in the early afternoon.

A total of 300,447 Phase I striped bass fingerlings were stocked at the Penhook (Blackwater River arm; 140,342) and Hales Ford (Roanoke River arm; 160,105) state boat ramps in mid- to late June (Table 1.1). Additionally, accelerated-growth Phase II fingerling striped bass (38,890 total), reared at the Virginia Tech Aquaculture Facility (Blacksburg, Virginia), were stocked at the Hales Ford state boat ramp in two equal groups one week apart in early to mid-July (Table 1.1). These fish were obtained from the Brookneal Hatchery as 35-day-old fry on 27 May and reared indoors on an artificial diet in circular, 2,200-gallon recirculating aquaculture chambers. In addition, to differentiate between Phase I and Phase II juveniles, Phase II fish were batch marked as 4-day-old fry in a solution of oxytetracycline hydrochloride (OTC) by VDGIF hatchery personnel at the Brookneal Hatchery according to the procedure of Secor et al. (1991b).

Table 1.1. Summary of juvenile striped bass stockings during 1994 and 1995 at Smith Mountain Lake, Virginia. Total lengths and wet weights are medians; values in parentheses are the minimum and maximum total lengths and wet weights. PBR = Penhook Boat Ramp (Blackwater River); HFBR = Hales Ford Boat Ramp (Roanoke River).

Year	Phase Type	Date Stocked	Number Stocked	Stocking Site	Rearing Site	Total Length (mm)	Wet Weight (g)
1994	I	15 June	140,342	PBR	Brookneal Fish Hatchery - VDGIF (Brookneal, VA)	42 (30-54)	0.65 (0.22-1.53)
	I	22 June	160,105	HFBR	Brookneal Fish Hatchery - VDGIF (Brookneal, VA)	32 (24-41)	0.30 (0.10-0.67)
	II	06 July	19,469	HFBR	Virginia Tech Aquaculture Facility (Blacksburg, VA)	70 (53-86)	3.70 (1.55-6.78)
	II	13 July	19,421	HFBR	Virginia Tech Aquaculture Facility (Blacksburg, VA)	76 (55-97)	5.00 (1.93-13.31)
1995	II	10 July	7,300	HFBR	Virginia Tech Aquaculture Facility (Blacksburg, VA)	66 (45-97)	3.06 (0.98-11.09)
	I	12 July	66,000	HFBR	McKinney Fish Hatchery - NCWRC (Rockingham, NC)	47 (31-64)	0.99 (0.24-2.97)
	I	14 July	37,000	HFBR	Watha Fish Hatchery - USFWS (Cape Fear, NC)	47 (41-70)	1.05 (0.74-3.64)
	I	14 July	110,000	PBR	Watha Fish Hatchery - USFWS (Cape Fear, NC)	48 (38-74)	1.02 (0.51-3.87)
	I	20 July	15,800	PBR	Watha Fish Hatchery - USFWS (Cape Fear, NC)	57 (40-81)	1.96 (0.69-6.07)

1995. - Phase I fingerling striped bass from the Brookneal Hatchery were not stocked in Smith Mountain Lake in 1995 because heavy rainfall and severe flooding at the hatchery in mid-June washed all fish from rearing ponds into the Roanoke River. Instead, Phase I fingerlings for stocking were obtained from both the McKinney (Rockingham, North Carolina) and Watha (Cape Fear, North Carolina) Hatcheries. Although these fish were brought from North Carolina, they were of the same brood-stock origin (Roanoke River strain) and were reared in a similar fashion as Phase I striped bass in Virginia (S. Arthur, VDGIF Brookneal Hatchery, personal communication).

A total of 228,800 Phase I fingerling striped bass were stocked at the Penhook (125,800) and Hales Ford (103,000) state boat ramps during mid-July (Table 1.1). An additional 7,300 accelerated-growth Phase II fingerling striped bass from the Virginia Tech Aquaculture Center were stocked at the Hales Ford state boat ramp in early July (Table 1.1). These fish, reared as in 1994, were obtained from the Brookneal Hatchery as 30-day-old fry on 25 May. However, accelerated-growth Phase II striped bass were not batch-marked with OTC in 1995. Instead, Phase I fish that were washed out of the Brookneal Hatchery rearing ponds had been OTC marked. Therefore, collected Phase I and Phase II juvenile striped bass could not be differentiated during this sampling year.

METHODS

This study involved two years (1994-95 and 1995-96) of field collection and laboratory analysis. Most of the effort during the first year of sampling consisted of logistical arrangements, learning general patterns of fish distributions within Smith Mountain Lake, and developing analytical laboratory procedures. Through an intensive sampling effort, I was able to gain a very good understanding of the dynamics of stocked juvenile striped bass in this system so that the remaining year could be devoted strictly to research collections and finishing laboratory analyses.

Field Collections

Age-0 striped bass and black basses (largemouth and smallmouth bass) were collected from the Hales Ford and Penhook cove stocking sites of Smith Mountain Lake using a suite of gear types. Shoreline seining (six to ten hauls per night using a 10-m long and 1-m deep beach seine with a 3.18-mm bar mesh bag and wings) was conducted at least two nights each week from mid-June through August 1994 and mid-July through August 1995 because some juvenile striped bass and black basses <50 mm TL inhabited shallow (<1 m), littoral areas of the stocking coves and, as a result, were inaccessible to electrofishing. Additionally, the entire shoreline of both stocking coves was electrofished at least two nights each week during this time period to collect juveniles in deeper, littoral areas (1-2 m) using a 4.3-m aluminum-hulled boat with a boom-type Smith-Root Model 3.5 Gas-Powered Pulsator, AC-DC electrofishing unit (3-6 A pulsed DC at a frequency of 60 pulses per second) powered by a 200-W generator. For the remainder of each sampling year (at least one night each week from August through mid-December 1994 and August through November 1995; at least two nights each week during March 1995 and March through mid-April 1996), boat electrofishing was the primary gear type used to collect juvenile striped bass and black basses in nearshore areas of the stocking coves.

Horizontal gillnets were used at least one night each week from August through mid-December 1994 and August through November 1995, and at least four nights each week during March 1995 and March through mid-April 1996 to collect larger age-0 striped bass (≥90 mm TL) that had dispersed from the stocking coves to deeper, more pelagic areas of the main channels in Smith Mountain Lake. Because juvenile striped bass rarely frequented the upper reservoir following dispersion from the stocking areas, collections using gillnets were conducted from the Roanoke River arm below Hales Ford Bridge (HFB) and the Blackwater River arm below the Gills Creek confluence (GCC) to the upper lower lake (ULL) region (Figure 1.1). Fifteen bi-panel monofilament gillnets (50-m long and 2-m deep consisting of two 25-m long panels with bar mesh sizes of 12.7 mm and 19.05 mm, 12.7 mm and 25.4 mm, or 19.05 mm and 25.4 mm; five nets of each mesh size combination) were set perpendicularly from the shore along the lake bottom and anchored using one 4.5-kg weight on the offshore end. Suspension of the gillnet float line underwater was maintained using three one-gallon plastic floats spaced equidistantly along the length of each net from the top of float line. Additionally, juvenile striped bass collected by the VDGIF as part of their annual fall gillnet survey (two nights per month in October, November, and December 1994 and 1995) were used to supplement field collections. All gillnets were set in late afternoon, and captured striped bass were removed the following dawn.

I sought to collect at least 60 juvenile striped bass and 30 black basses (both largemouth and smallmouth bass in combination) in total using all gear types employed during each weekly sampling period. All striped bass and black basses collected were immediately sacrificed with an overdose of MS-222 (tricaine methanesulfonate) and preserved on ice. Upon returning from sampling, all fish were measured for total length to the nearest 1 mm, weighed to the nearest 0.01 g (fresh wet weight), and frozen pending further laboratory analysis.

Contribution of Phase II Fingerlings

Because of equipment and time constraints, a random sample (N = 100) of all age-0 striped bass collected from the Roanoke River arm of Smith Mountain Lake during the 1994-95 sampling year was examined for OTC marks. Juvenile striped bass captured from the Blackwater River arm during 1994-95 were not examined for marks because Phase II fish were only stocked in the Roanoke River arm. Removal and preparation of the saggital otoliths from these fish was conducted according to Secor et al. (1991a). Otoliths were examined whole and in cross-section using an epifluorescence microscope at 10x magnification under phase-contrast conditions. Presence of an OTC mark was noted as a gold-yellow ring near the center of the otolith. Because no striped bass stocked in Smith Mountain Lake during 1995 were marked with OTC, otolith removal and analysis was not conducted for juveniles collected during this sampling year.

Dispersal and Spatial Distribution

Dispersal and spatial distribution of juvenile striped bass within and out of the Hales Ford (Roanoke River) and Penhook (Blackwater River) stocking coves during both the 1994 and 1995 growing seasons were examined by comparing temporal trends in catch-per-unit-effort (CPUE) from shoreline electrofishing and gillnetting data. Data were evaluated by standardizing CPUE by gear type as follows: number of fish collected per minute of electrofishing and number of fish collected per gillnet night. Beach seine data were not used to evaluate dispersal and spatial distribution of juveniles because suitable locations in which to conduct seine hauls were limited. As a result, few juvenile striped bass were captured using this gear type.

Transects within each stocking cove were classified as inner (INN), intermediate (INT), and outer (OUT) regions according to the shoreline distance from the stocking site (0 to 100 m, 100 to 400 m, and >400 m, respectively), and right (R) or left (L) of the stocking site (Figures 1.2 and 1.3). Spatial distribution of juvenile striped bass throughout main channel areas was described by examining temporal trends only in gillnetting CPUE data because no fish were collected using electrofishing equipment in these regions of the lake. Because the primary purpose of this study was to collect juvenile striped bass and not to characterize all regions of Smith Mountain Lake in which fish did/did not occur, these data serves only as a relative description of temporal trends in dispersion and spatial distribution within this system.

First-Year Striped Bass Growth

The median length and weight of juvenile striped bass collected from the Roanoke and Blackwater River arms were calculated at bi-weekly intervals and plotted over the growing season (mid-June through mid-December 1994; mid-July through November 1995) to describe temporal patterns in growth.

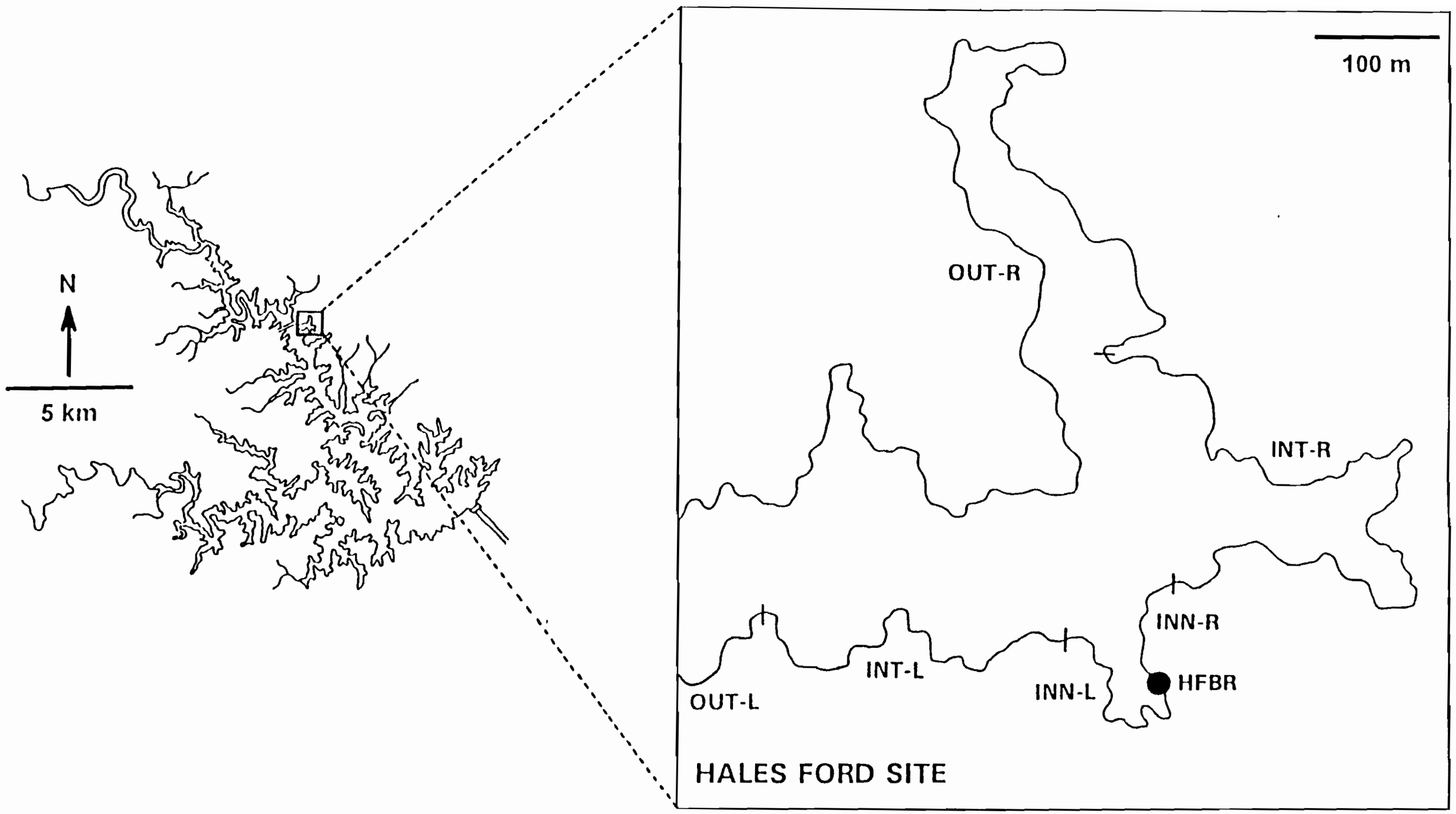


Figure 1.2. Close-up of the Hales Ford site on the Roanoke River arm of Smith Mountain Lake, Virginia, showing locations of sampling transects used to estimate dispersion patterns of age-0 striped bass from the Hales Ford Boat Ramp (HFBR) stocking site; L and R indicate left and right of stocking site, respectively, and INN, INT, and OUT indicate inner, intermediate, and outer sampling transects, respectively.

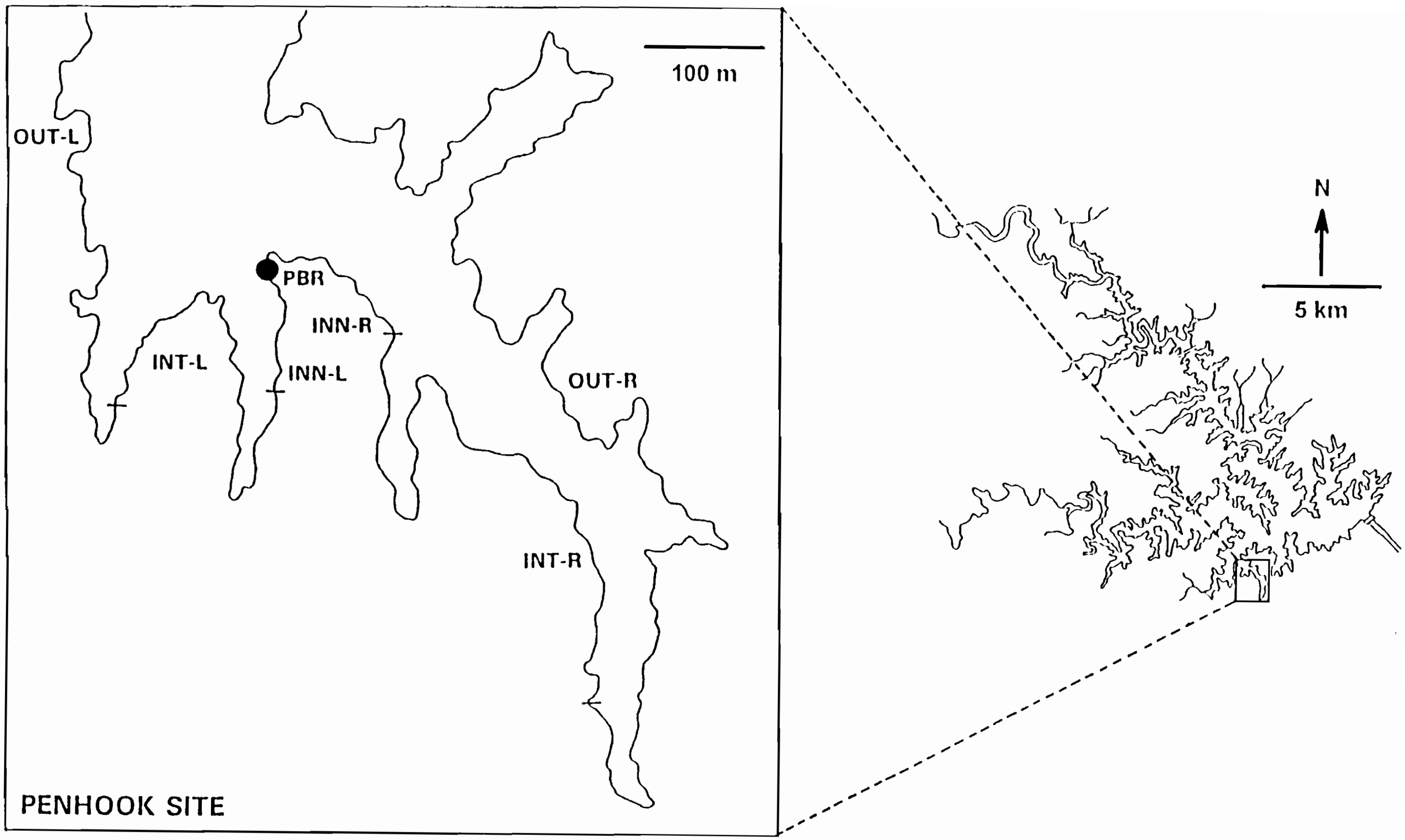


Figure 1.3. Close-up of the Penhook site on the Blackwater River arm of Smith Mountain Lake, Virginia, showing locations of sampling transects used to estimate dispersion patterns of age-0 striped bass from the Penhook Boat Ramp (PBR) stocking site; L and R indicate left and right of stocking site, respectively, and INN, INT, and OUT indicate inner, intermediate, and outer sampling transects, respectively.

Additionally, monthly length-frequency histograms for 1994-95 and 1995-96 (Roanoke and Blackwater River arm data pooled for each sampling year) were developed to further describe patterns in juvenile striped bass growth and size distribution.

Overwinter Survival

Length-frequency histograms of juvenile striped bass before and after winter were compared (November-December 1994 versus March 1995; November 1995 versus March-April 1996; Roanoke and Blackwater River arm data pooled for each sampling year) to evaluate whether divergences in length distribution through summer and fall resulted in differential size-dependent overwinter mortality in Smith Mountain Lake. Because length-frequency distributions were not significantly different between November and December 1994 ($\chi^2=3.16$, df=15, $P=0.68$) or March and April 1996 ($\chi^2=3.15$, df=8, $P=0.99$), these months were pooled to increase sample sizes in order to facilitate comparisons between fall and spring samples.

Determination of size-dependent overwinter mortality was based on the assumption that if the median length of fish increased over the winter while the variability in length decreased, the decrease in variability should be due to an upward shift in the minimum but not the maximum length (i.e. small fish were lost from the population). It was also assumed that smaller striped bass were not growing at a faster rate over the winter than their larger conspecifics and, as a result, catching up in length. This assumption is reasonable because several studies have documented that age-0 striped bass discontinue feeding after water temperatures have declined below 10°C (Scofield 1931; Vladykov and Wallace 1952; Koo and Ritchie 1973). Because water temperatures in

Smith Mountain Lake were below 10°C from the end of November through mid-March during both sampling years, it is unlikely that juvenile striped bass, regardless of size, were growing during winter months. Additionally, if fish were growing over this period and there was no or little length-based overwinter mortality, both the median and variance in size would be expected to increase.

Food Habits

In the laboratory, fish were thawed and stomachs (from the base of the esophagus to anterior portion of the intestine) were removed from both striped bass and black basses, and preserved in 10% buffered formalin for subsequent analysis. Stomach contents were examined under magnification using a dissecting microscope, identified to the lowest practical taxa, and each prey item was blotted to remove excess fluid before being weighed to the nearest 0.01 g. Diet composition for striped bass and black basses was expressed as the average percent contribution of each prey type consumed to the total food weight during each month of the growing season and 10-mm size class interval for each river arm using the following equation:

$$\%WTP_i = (\Sigma WTP_i/\Sigma WT_i)/N,$$

where $\%WTP_i$ is the average percent contribution by weight for prey type i, ΣWTP_i is the summed weight of prey i consumed by each predator, ΣWT_i is the summed weight of prey type i consumed by each predator, and N is the total number of predators sampled, including those with empty stomachs (Hyslop 1980). This approach was chosen because it allows food types to be quantified in directly comparable mass units so that the relative importance of these diet items can be estimated in terms of approximate nutrition gained by the predator (Bowen 1996).

Diet Overlap

Diet overlap, as an index of potential interspecific trophic competition, was calculated between juvenile striped bass and black basses by month and 10-mm size class interval separately for both the Roanoke and Blackwater River arms during the 1994 and 1995 growing season using diet composition weight percentages and Schoener's overlap index (1970), which is defined as:

$$C_{xy} = 1.0 - 0.5 \sum_{i=1}^{n} |p_{xi} - p_{yi}|,$$

where C_{xy} is the overlap index, p_{xi} is the proportion of food type i used by species x (striped bass), p_{yi} is the proportion of food type i used by species y (black basses), and n is the total number of food categories. Wallace (1981) determined that this symmetrical index, used with weight percentages, was the most appropriate method for calculating overlap when accurate data on prey abundance were unavailable. The index ranges from 0 (no overlap) to 1 (complete overlap). Values greater than 0.6 are considered indicative of substantial overlap and potential resource competition (Zaret and Rand 1971).

Only samples which adequately described the diet of striped bass and black basses, as determined by cumulative prey species curves (Brodeur and Pearcy 1984), were used in diet comparisons because small sample sizes often lead to spurious results (Smith 1985). Cumulative prey species curves for both striped bass and black basses (by month and 10-mm size class interval for the Roanoke and Blackwater River arms separately during both 1994 and 1995) were obtained by plotting the cumulative number of prey taxa found in a progressively larger number of randomly-ordered stomachs. The asymptote of the curve corresponded to the minimum number of stomachs needed to adequately describe the diet. If an asymptote was not reached, the sample was considered inadequate for subsequent comparisons.

Predator-Prey Size Relationships

To quantify size relationships between age-0 striped bass and forage-fish prey, total, standard, and backbone lengths of identifiable fish in the stomachs of juvenile striped bass were measured to the nearest 1 mm. Standard lengths (SL) and backbone lengths (BL.) of consumed age-0 alewives and spottail shiners (*Notropis hudsonius*; hereafter termed cyprinids), the two primary forage fish species consumed by juvenile striped bass, were converted to total lengths (TL) using linear regression equations developed from specimens collected in Smith Mountain Lake. Additionally, linear regression equations were developed to back-calculate maximum body depth (BD, measured as the linear distance from the anterior origin of the dorsal fin to the ventral surface) from total length (TL) estimates for these two forage-fish prey at the time of consumption. The regression equations for alewife were:

$$TL = -1.99 + 1.26(SL),\ N=400,\ r^2=0.99$$

$$TL = -2.99 + 1.62(BL.),\ N=400,\ r^2=0.98$$

$$BD = -0.72 + 0.22(TL),\ N=400,\ r^2=0.97.$$

Similar equations for cyprinids were:

$$TL = 1.90 + 1.16(SL),\ N=450,\ r^2=0.98$$

$$TL = 8.85 + 1.15(BL.),\ N=450,\ r^2=0.97$$

$$BD = -0.95 + 0.16(TL),\ N=450,\ r^2=0.97.$$

Morphological constraints on forage-fish prey utilization were evaluated to determine whether the maximum size of cyprinids and alewives consumed were consistent with juvenile striped bass ingestibility limitations. Because the nutritional value of a prey item is directly proportional to its mass (Bowen 1996), the relationship between the weight of consumed cyprinid and alewife prey relative to striped bass weight was also evaluated to estimate differences in energetic gains from these two forage fishes. Linear regression equations were developed to compare: (1) TL of cyprinids and alewives consumed versus striped bass TL; (2) the ratio of consumed fish prey TL to striped bass TL versus striped bass TL; (3) body weight of cyprinids and alewives consumed versus striped bass body weight; and (4) the ratio of consumed fish prey body weight to striped bass body weight versus striped bass TL. In other studies examining the size relationship between consumed forage-fish prey and juvenile piscivores, fish prey body depth relative to predator gape width has been shown to be a factor limiting ingestibility (Lawrence 1958; Kerby 1979; Dennerline 1990; Hambright 1991). To further assess ingestibility limitations, the estimated maximum total lengths of cyprinids and alewives that could be consumed by a given size striped bass were predicted based on linear regression relationships between predator gape width (measured as the horizontal distance between the maxillary bones) and fish prey body depth. These relationships were compared to measured total lengths of cyprinids and alewives actually consumed to determine whether fish prey were consumed at or near the maximum ingestibility limits of juvenile striped bass. Ingestibility limits were applied to growth data for both predators and fish prey to identify periods over the growing season when cyprinids and alewives could/could not be consumed by different sizes of juvenile striped bass.

To estimate growth rates and size distributions of age-0 cyprinids, fish were collected monthly from June through November 1995 by shoreline seine hauls in nearshore areas of both stocking coves. During each month of sampling, three seine hauls were conducted using a 10-m long and 1-m deep seine with a 3.18-mm bar mesh bag and wings. At least 200 age-0 cyprinids were collected during each monthly sampling period. These fish were measured for TL to the nearest 1 mm, weighed to the nearest 0.01 g, and temporal trends in size distribution were described. Although size distributions over the growing season were not determined in 1994, 1995 data were used for both years because age-0 cyprinid size distributions from cove rotenone sampling in August of both 1994 and 1995 were not significantly different ($\chi^2 = 5.45$, df = 7, $P = 0.68$).

Because monthly growth and size distribution data for age-0 alewives in Smith Mountain Lake already exist (Tisa 1988), this species was only collected during the annual VDGIF cove rotenone survey in August 1994 and 1995 to ensure that growth dynamics had not changed significantly since the study was conducted from 1982-1984. Because age-0 alewife length-frequency distributions from cove rotenone surveys did not differ significantly between these two studies ($\chi^2 = 10.51$, df = 10, $P = 0.35$), it was assumed that alewife growth rates had not changed appreciably over the past twelve years in Smith

Mountain Lake. As a result, age-0 alewife growth and size distribution data from Tisa (1988) was compared to juvenile striped bass ingestibility limits to identify periods during the growing season when this forage-fish prey species could be consumed by different size modes of striped bass. These periods were then transformed to determine the percentage of the age-0 alewife cohort biomass ingestible by both small- and large-mode juvenile striped bass (estimated as the 25th and 75th percentiles, respectively, from first-year growth data).

Physiological Indices of Health

The performance and physiological health of juvenile striped bass from stocking to age 1 were monitored using a suite of physiological measures indicative of relative well-being. Because these parameters do not directly measure a change in size (i.e. growth), they can only be used as a surrogate for the rate of growth or performance of individual fish. The value of these parameters is in their ability to describe changes in growth rate over short periods of time, particularly growth in response to changing environmental conditions or food type and supply (Busacker et al. 1990).

Relative Condition. - Body condition of each juvenile striped bass was calculated using the relative condition factor (K_n), which is defined as:

$$K_n = W/W' \times 100,$$

where W is the measured wet weight (nearest 0.01 g) and W' is the length-specific expected wet weight (nearest 0.01 g) for fish in the population as predicted by the weight-length regression equation for that population (LeCren

1951). Weight-length equations used to determine K_n for juvenile striped bass were calculated from fish collected in this study using the following linear regression equations:

1994-95 LogWT = $-5.12 + 3.06(\text{LogTL})$, $N=1628$, $r^2=0.99$, $P<0.0001$
1995-96 LogWT = $-5.08 + 3.04(\text{LogTL})$, $N=1272$, $r^2=0.99$, $P<0.0001$,

where LogWT is the base ten logarithm of the wet weight and LogTL is the base ten logarithm of the total length. Juvenile striped bass from both the Roanoke and Blackwater River arms were pooled for each sampling year to develop each weight-length regression equation.

Although the traditional approach to the assessment of condition involves the use of the Fulton factor (K; Fulton 1904), this index is length-dependent, thereby preventing comparisons of individuals of the same species with disparate lengths (Bagenal and Tesch 1978). The relative weight index (W_r) represents a refinement of K_n (Wege and Anderson 1978; Murphy et al. 1991) and allows assessment of how energy is allocated across length classes within a species (Brown and Murphy 1991b). However, this index does not work for striped bass <150 mm TL due to high variability in the length at which the growth form changes for this species (Brown and Murphy 1991a).

Because relative condition is only affected by changes in weight, a K_n value equal to 100 reflects the expected, "average" condition for a fish at a given length (i.e. has attained 100% of its expected weight for its particular length). Juvenile striped bass with K_n values greater than or equal to 100 indicate better than expected physiological condition (i.e. "good plumpness") within the population. Conversely, K_n values less than 100 indicate that physiological condition within the population is "poor" (i.e. weight is less than expected for a particular length).

Liver-Somatic Index. - Because fish accumulate energy in the form of glycogen in their liver (Hinton et al. 1972) during periods of high energy intake and utilize this energy when not feeding, the relative size of the liver should be positively correlated with nutritional state of a fish (Anderson and Gutreuter 1983). Thus, a high liver weight relative to body weight should correspond to profitable forage and growth conditions and a low liver weight relative to body weight should indicate the converse. This indirect measure of condition is referred to as the liver-somatic index (LSI; Anderson and Neumann 1996).

In the laboratory, striped bass were thawed, and livers were removed by dissection (minus the gall bladder) before weighing to the nearest 0.01 g. LSI was calculated for each fish as:

$$LSI = (LVW/WT) \times 100,$$

where LVW is the wet weight of the liver minus the gall bladder and WT is the measured liver-free wet body weight (nearest 0.01 g) of the fish. By subtracting liver weight from body weight, liver weight is removed from the denominator, thereby eliminating bias from the estimator. Since LSI is a more sensitive indicator of recent energy dynamics than condition factor (Heidinger and Crawford 1977; Adams and McLean 1985), this parameter was used as a measure of short-term food consumption and metabolic energy demand.

Lipid Index. - Although lipids may be transient body materials, they are a very important source of potential chemical energy during periods of low food availability or environmental stress. As a consequence, their presence reflects the physiological capacity of the fish. The capacity to store energy and rate of usage of these energy reserves often vary with body size; large fish typically have accumulated more lipid reserves, on a per unit mass basis, and utilize this energy source at a slower rate than smaller fish (Oliver et al. 1979; Miranda and Hubbard 1994). This suggests that overwinter survival, a period when fish feed very little, could be a problem for juvenile fishes that do not attain some minimum size (and consequently adequate lipid reserves) prior to their first overwintering period.

All juvenile striped bass were frozen, freeze-dried to a constant weight (4-7 d) at -60°C, reweighed (to the nearest 0.01 g dry weight), and ground with a commercial Waring blender. Weight loss (due to the freeze-drying process) provided an estimate of body water content, which was used to develop a linear regression relationship between percent water and lipid content because these physiological measures are inversely related (Love 1970; Niimi 1972; Toneys and Coble 1980; Cunjak and Power 1986). A random sample (N = 250) of all freeze-dried striped bass was chosen for the lipid extraction procedure. Samples (dried homogenate) were oven dried at 105°C for 24 h to reach a constant weight and cooled in a desiccation chamber at 0% humidity for 24 h, reweighed to the nearest 0.01 g, and stored in the chamber pending lipid extraction. Filter paper was oven dried at 105°C to a constant weight (24 h), cooled in a desiccation chamber at 0% humidity for 24 h, and weighed to the nearest 0.01 g. Dry homogenate (1-2 g from each individual striped bass) was then packaged in filter paper and reweighed to the nearest 0.01 g. The filter paper packages plus contents were placed in a Soxhlet lipid extraction apparatus, and lipid was extracted from the packages over a 24-h period using anhydrous (ethyl) ether as the solvent. Extraction was conducted with anhydrous ether because this solvent removes nonpolar, storage lipids (i.e. usable energy stores) with little removal of polar, structural lipids (i.e. unusable energy stores; Dobush et al. 1985; Reznick and Braun 1987). There is some indication that petroleum ether may be a more appropriate solvent for quantifying storage lipids because anhydrous ether may remove small quantities of structural lipids. However, Dobush et al. (1985) found that anhydrous ether removed, on average, only 3.3% more material than did petroleum ether and this difference was not found to be significant.

Following extraction, sample packages were oven dried for 24 h to constant weight, cooled in a desiccation chamber, and reweighed to the nearest 0.01 g. Lipid index (LI) was calculated as:

$$LI = (LPW/LFDW) \times 100,$$

where LPW is the weight of extracted lipid and LFDW is the lipid-free dry body weight. This index scales the lipid content by a measure of structural size (Owen and Cook 1977) in recognition that 1 g of lipid has different meaning to a fish of 5 g dry weight than to one of 50 g dry weight. This scaling is particularly important for life stages, such as juveniles, that vary considerably in size (Johnson and Stewart 1973; Johnson et al. 1985). Schmidt-Nielsen (1979) illustrated how a ratio such as lipid index is preferable for portraying the importance of a body constituent. Likewise, Morton et al. (1990) demonstrated that changes in lipid index are proportional to incremental changes in lipid weight for a given lipid-free dry weight, while percent lipid changes at a decreasing rate as lipid weight increases incrementally for a given lipid-free dry weight.

Linear regression was used to express the relationship between lipid index and percent body water (Figure 1.4). This equation was used to estimate the lipid index for the remainder of the juvenile striped bass samples based on their percent body water content as determined from the freeze-drying process.

Stomach-Fullness Index. - As an index of feeding intensity, stomach-fullness index (SFI) was calculated for each striped bass as the ratio of the blotted wet weight of food contents to the wet body weight minus the stomach contents x 100 (Bowen 1996). By subtracting stomach content weight from body weight, food content weight is removed from the denominator, thereby eliminating bias from the estimator. This permits more reasonable comparisons between age-0 striped bass with varying degrees of stomach fullness.

Statistical Analyses

Statistical procedures used to analyze data sets in this dissertation are listed in Table 1.2. Although no formal statistical tests were performed on spatial distribution (except for comparisons of length-frequency distributions), those data were examined and compared among sampling periods in order to describe temporal trends in dispersion within and out of each stocking cove site. Differences in median size and size range at the time of stocking were compared among sites, and between Phase I and Phase II striped bass. Size distributions of juvenile striped bass were compared sequentially month versus month to describe differences in growth, and between fall and spring to evaluate size-based overwinter mortality. For growth and overwinter mortality analyses, size distribution data from both river arms were pooled to more meaningfully describe these trends in juvenile striped bass growth. Additionally, tests for skewness (symmetry of observed data about the median, where values >0

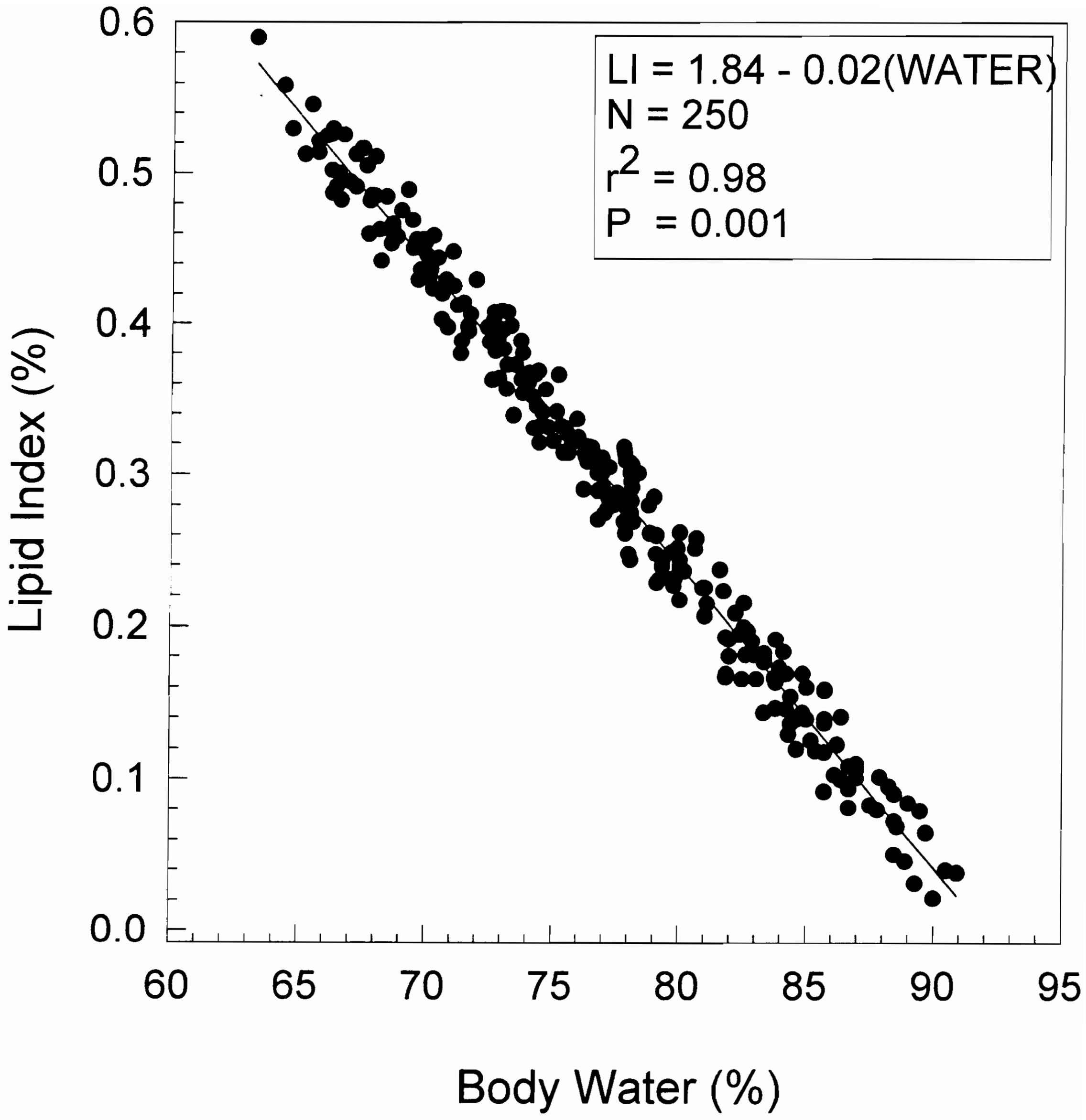


Figure 1.4. Regression relationship between lipid index (LI) and percent body water (WATER) for juvenile striped bass collected from Smith Mountain Lake.

Table 1.2. Statistical procedures used to analyze Smith Mountain Lake data sets, 1994-96.

Data Set	Statistical Procedure
Contribution of Phase II striped bass to the age-0 population	Chi-square test for association
Length-frequency distributions within the stocking cove versus outside the stocking cove at the end of the growing season (both Roanoke and Blackwater sites pooled for 1994 and 1995)	Chi-square test for association
Length-frequency distributions of juvenile striped bass at time of stocking - Hales Ford site versus Penhook site for 1994 and 1995.	Chi-square test for association
Sequential month versus month (i.e. Jun versus Jul; Jul versus Aug) comparison of juvenile striped bass length-frequency distributions over the growing season (both Roanoke and Blackwater River sites pooled for 1994 and 1995).	Chi-square test for association
Symmetry of juvenile striped bass length-frequency distributions (both Roanoke and Blackwater River sites pooled for 1994-95 and 1995-96).	Skewness of distribution
Juvenile striped bass length-frequency distributions versus normal distribution (both Roanoke and Blackwater River sites pooled for 1994-95 and 1995-96).	Kurtosis of distribution
Length-frequency distributions of juvenile striped bass - fall 1994 versus spring 1995 and fall 1995 versus spring 1996 (both Roanoke and Blackwater River sites pooled).	Chi-square test for association
Variance of length-frequency distribution of juvenile striped bass - fall 1994 versus spring 1995 and fall 1995 versus spring 1996 (both Roanoke and Blackwater River sites pooled).	Variance ratio test (F-test)
Fish prey (cyprinid and alewife) body meristic relationships (TL vs. SL, TL vs. BL, BD vs. TL).	Linear regression analysis
Consumed fish prey (cyprinid and alewife) size versus juvenile striped bass size (fish prey TL versus striped bass TL; fish prey TL/striped bass TL versus striped bass TL; fish prey WT versus striped bass WT; fish prey WT/striped bass WT versus striped bass TL; both Roanoke and Blackwater River sites pooled for 1994-1996).	Linear regression analysis

Table 1.2 continued. Statistical procedures used to analyze Smith Mountain Lake data sets, 1994-96.

Data Set	Statistical Procedure
TL of cyprinids consumed versus TL of alewives consumed and WT of cyprinids consumed versus WT of alewives consumed for the above regression relationships (both Roanoke and Blackwater River sites pooled for 1994-96).	t-test for regression coefficients
Distribution of physiological indices of well-being (K_n, LSI, LI, SFI) by month and 10-mm size class interval versus normal distribution.	Kolmogorov-Smirnov goodness of fit test for normality
Juvenile striped bass wet body weight (Log WT) versus total body length (Log TL; Roanoke River site, Blackwater River site, and both sites combined for 1994-95 and 1995-96).	Linear regression analysis
Juvenile striped bass lipid index versus percent body water.	Linear regression analysis
Juvenile striped bass physiological indices of well-being (K_n, LSI, LI, SFI) versus month (both Roanoke and Blackwater River sites for 1994-95 and 1995-96).	Kruskal-Wallis (analysis of variance by ranks) and Dunn's multiple comparisons test
Juvenile striped bass physiological indices of well-being (K_n, LSI, LI, SFI) versus juvenile striped bass 10-mm size class interval (both Roanoke and Blackwater River sites for 1994-95 and 1995-96).	Kruskal-Wallis (analysis of variance by ranks) and Dunn's multiple comparisons test
Juvenile striped bass physiological indices of well-being (K_n, LSI, LI, SFI) - fall small-mode fish versus fall large-mode fish and spring small-mode fish versus spring large-mode fish (both Roanoke and Blackwater sites pooled for 1994-95 and 1995-96).	Mann-Whitney rank sum test
Juvenile striped bass physiological indices of well-being (K_n, LSI, LI, SFI) - small-mode fish (fall 1994 versus spring 1995; fall 1995 versus spring 1996) and large-mode fish (fall 1994 versus spring 1995; fall 1995 versus spring 1996).	Mann-Whitney rank sum test

indicate a positively skewed distribution and values <0 indicate a negatively skewed distribution; Zar 1984) and kurtosis (shape of observed data about the median, where positive kurtosis indicates a unimodal distribution and negative kurtosis indicates a bimodal distribution; Sokal and Rohlf 1981) were conducted to further aid interpretation of age-0 striped bass length-frequency distributions.

Diet composition data were tabulated by location (Roanoke and Blackwater River arms), month of the growing season (mid-June through mid-December 1994 and mid-July through November 1995), and 10-mm size class intervals to evaluate differences in food habits and feeding success. Relationships using linear regression analysis between consumed forage-fish prey and juvenile striped bass size were pooled for both the 1994-95 and 1995-96 sampling seasons to increase sample sizes to facilitate comparisons among the two forage fish prey types. All the above statistical analyses (size distribution and diet composition data) were performed as in Zar (1984).

Preliminary tests (Kolmogorov-Smirnov) revealed that physiological measures of health data were not normally distributed ($D=0.31$, $P<0.0001$). Because parametric statistical analyses can lead to misinterpretation of results when assumptions of normality and homoscedasticity are not met (Pirie and Hubert 1977), nonparametric statistical procedures (Gibbons 1985) were used to analyze these data sets. Data were grouped by location (Roanoke or Blackwater River arm), month, and 10-mm size class interval to facilitate comparisons of changes in well-being. Additionally, comparisons between fall and spring were made for relative condition, liver-somatic index, and lipid index by 10-mm size class intervals to detect differences in physiological health over winter. Statistical analyses, both parametric and nonparametric, were considered significant at $P<0.05$ for Type I error.

RESULTS

Temporal patterns of juvenile striped bass dispersion within and out of the stocking coves were described to assess size-dependent differences in spatial distribution. Additionally, growth of juvenile striped bass was evaluated to assess temporal patterns in size distributions over the growing season and after the overwintering period. Finally, trends in food habits, diet overlap with black basses, forage-fish prey-predator ingestibility relationships, and physiological indices of health were examined for juvenile striped bass to aid analysis of growth and size distribution patterns, size-dependent overwinter mortality, and recruitment to age 1.

Field Collections

A total of 3,649 age-0 piscivores (N=2,299 for striped bass; N=1,350 for black basses) were collected from Smith Mountain Lake during the 1994-95 and 1995-96 sampling seasons (Table 1.3). Juvenile striped bass, the target species for this study, were most commonly collected in nearshore areas of the stocking coves during the summer months before they dispersed to more pelagic regions of the main channels of Smith Mountain Lake. Following dispersion from the stocking coves, the range of striped bass distribution extended primarily from the upper s-curve of the Roanoke River arm and the Gills Creek Confluence of the Blackwater River arm to the upper lower lake region (for a more thorough description, see Dispersal and Spatial Distribution). In contrast, age-0 black basses (about 95% largemouth bass) occupied nearshore regions throughout Smith Mountain Lake, typically areas containing underwater timber and/or aquatic vegetation.

Table 1.3. Total number of juvenile predators collected by sampling season, sampling period, and location from Smith Mountain Lake.

		Striped Bass			Black Bass		
Sampling Season	Sampling Period	Roanoke River	Blackwater River	Total	Roanoke River	Blackwater River	Total
1994-95	16-30 Jun	52	58	110	41	64	105
	01-15 Jul	137	80	217	24	30	54
	16-31 Jul	111	63	174	75	59	134
	01-15 Aug	93	86	179	38	56	94
	16-31 Aug	71	55	126	46	31	77
	01-15 Sep	48	32	80	36	33	69
	16-30 Sep	37	21	58	32	39	71
	01-15 Oct	66	25	91	14	10	24
	16-31 Oct	34	15	49	28	17	45
	01-15 Nov	53	16	69	6	8	14
	16-30 Nov	28	6	34	4	8	12
	01-15 Dec	7	5	12	2	0	2
	15-31 Mar	125	113	128	0	0	0
	Total	862	575	1327	346	355	701
1995-96	16-31 Jul	64	64	128	110	63	173
	01-15 Aug	74	92	166	80	51	131
	16-31 Aug	35	66	101	65	60	125
	01-15 Sep	17	66	83	42	41	83
	16-30 Sep	42	78	120	27	47	74
	01-15 Oct	26	53	79	10	26	36
	16-31 Oct	29	57	86	7	5	12
	01-15 Nov	22	52	74	4	6	10
	16-30 Nov	22	38	60	1	4	5
	15-31 Mar	8	6	14	0	0	0
	01-15 Apr	26	35	61	0	0	0
	Total	365	607	972	346	303	649

Although more juvenile striped bass were collected during 1994-95 than 1995-96 (1,327 versus 972; Table 1.3), the numbers of age-0 black basses collected during each sampling year were approximately equal (701 during 1994-95 and 649 during 1995-96; Table 1.3). Additionally, despite similar sampling effort in both river arms, greater numbers of juvenile striped bass were captured from the Roanoke River arm during the 1994-95 sampling season (862 versus 575 in the Blackwater River arm), whereas more were collected from the Blackwater River arm during the 1995-96 sampling season (607 versus 365 for the Roanoke River arm). In contrast, approximately equal numbers of black basses were collected from both the Roanoke and Blackwater River arms during each sampling season (346 versus 355, respectively, in 1994-95; 346 versus 303, respectively, in 1995-96).

Contribution of Phase II Fingerlings

Only two of the 100 otoliths examined to estimate the contribution of Phase II fish to the total number of age-0 striped bass in the Roanoke River arm during 1994-95 exhibited a discernable fluorescent mark when examined using epifluorescence microscopy. Chi-square analysis revealed that these results were significantly different than expected ($\chi^2 = 13.36$, df = 1, $P < 0.0001$). Had the contribution of Phase II striped bass been proportional to the total number of fish stocked, twenty juveniles would have been expected to display the fluorescent mark. Interestingly, by factoring in the high initial stocking mortality observed for Phase II striped bass during 1994 (99.5% and 51.0% for those stocked on 06 and 13 July, respectively; Michaelson 1996), only six of the 100 otoliths would have been expected to contain a fluorescent mark. Although this adjusted estimate is still greater than the observed percentage (six versus two), these proportions were not significantly different ($\chi^2 = 1.92$, df = 1, P = 0.13). However, the apparently poor contribution of Phase II fingerlings to the striped bass population during 1994-95 should be interpreted with caution because: (1) the small number of otoliths examined may not be representative of the entire sample collected; (2) Phase I striped bass, because of their affinity for nearshore areas and greater susceptibility of capture, may have been collected at a greater frequency than their occurrence in the age-0 striped bass population; and (3) the inability to distinguish OTC marks from background fluorescence may have resulted in misidentified Phase II fish.

Dispersal and Spatial Distribution

Dispersion patterns for age-0 striped bass stocked from the Hales Ford state boat ramp, as characterized by catch-per-unit-effort (CPUE) data, were nearly identical in 1994 and 1995. During both years, CPUE was highest within 100 m of the stocking site (INN-L and INN-R) during the first week post-stocking before slowly declining over the remainder of the growing season as juveniles dispersed throughout the stocking cove (electrofishing only; Figures 1.5 and 1.6). Although striped bass were collected within the cove for the duration of the growing season, the outermost sampling regions (OUT-L and OUT-R; both electrofishing and gillnetting; Figures 1.5 and 1.6) yielded the highest CPUE during fall sampling, particularly shallow, structureless zones containing a mixture of sand and gravel that graded gradually to deep water. Because fish were rarely collected from intermediate (INT-L and INT-R) or innermost (INN-L and INN-R) regions of the cove after early fall (both electrofishing and gillnetting; Figures 1.5 and 1.6), it would appear that juvenile striped bass had dispersed to areas containing the most suitable habitat (for a

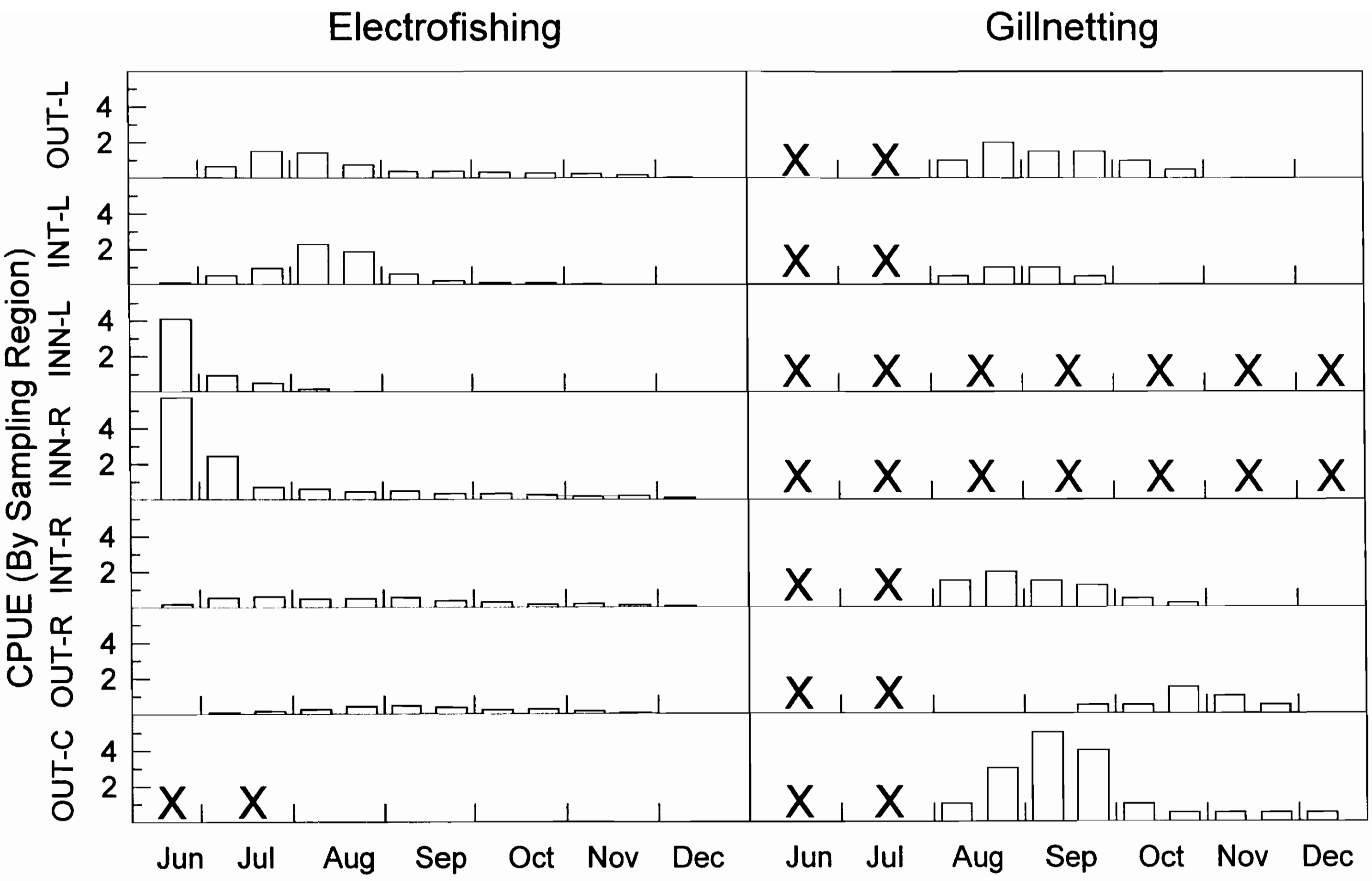


Figure 1.5. Standardized catch-per-unit-effort (CPUE) for age-0 striped bass by gear type (electrofishing = number of fish caught per minute electrofishing; gillnetting = number of fish caught per gillnet night) for each sampling region of the Hales Ford site of the Roanoke River (see Figure 1.2 for location of sampling site transects) over the 1994 growing season; X = no sampling using this gear type during this sampling period.

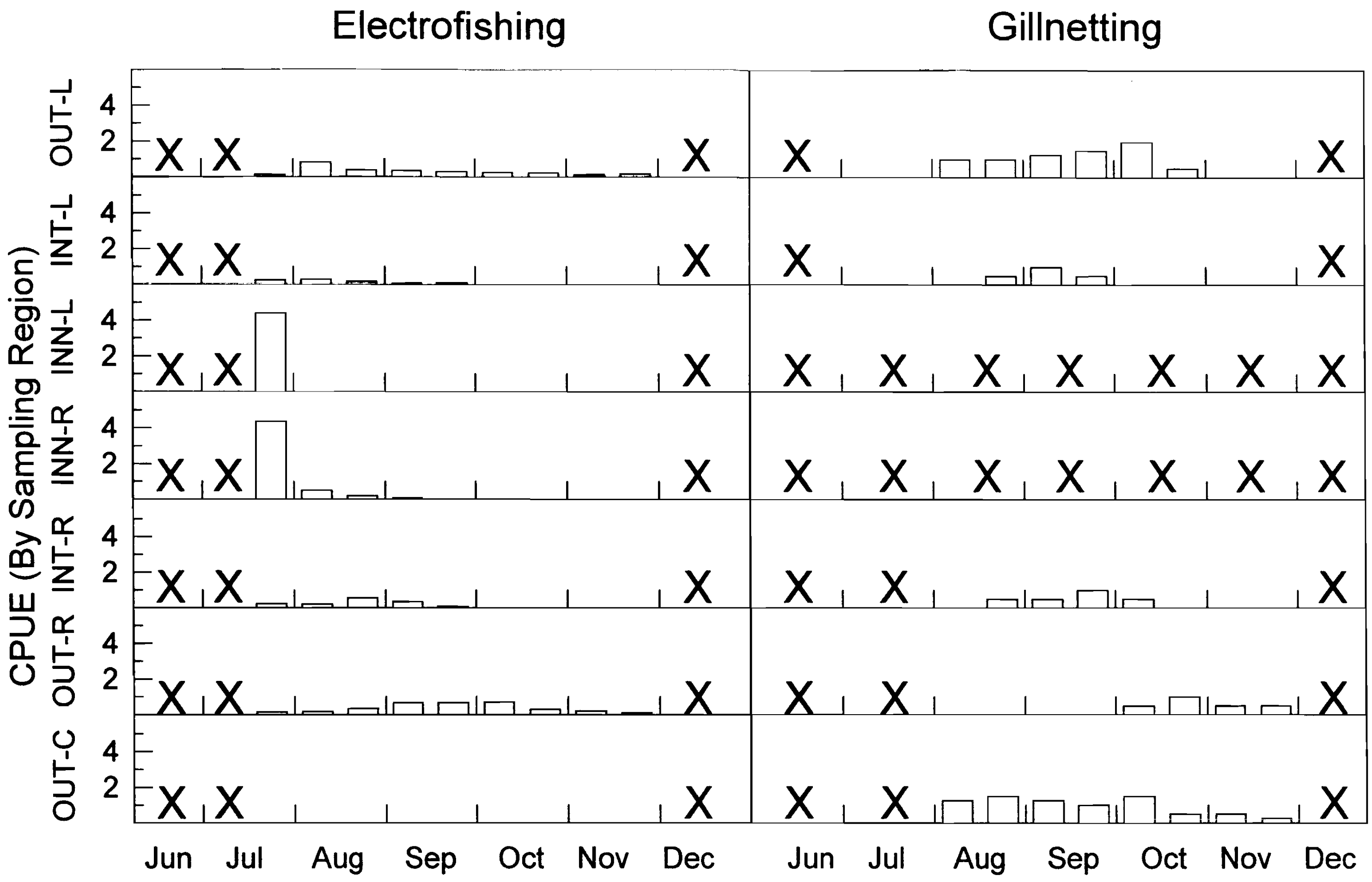


Figure 1.6. Standardized catch-per-unit-effort (CPUE) for age-0 striped bass by gear type (electrofishing = number of fish caught per minute electrofishing; gillnetting = number of fish caught per gillnet night) for each sampling region of the Hales Ford site of the Roanoke River (see Figure 1.2 for location of sampling site transects) over the 1995 growing season; X = no sampling using this gear type during this sampling period.

more thorough description of juvenile striped bass habitat requirements, see Dispersal and Spatial Distribution in the Discussion section), either along the outermost regions of the cove or outside the cove itself (OUT-C; gillnetting only; Figures 1.5 and 1.6).

Although juvenile striped bass stocked at the Penhook state boat ramp exhibited similar patterns of dispersion between 1994 and 1995, these observations differed markedly from those described at the Hales Ford stocking cove. Striped bass at the Penhook cove dispersed rapidly away from the immediate stocking site by the first night post-stocking, and only the outermost region (OUT-R) of this cove exhibited high CPUE during the growing season (both electrofishing and gillnetting; Figures 1.7 and 1.8). A likely explanation for this observation is that OUT-R was the only area that contained suitable habitat (shallow, structureless zones containing a mixture of sand and gravel that graded gradually to deep water) for juvenile striped bass; all other sampling regions were characterized as having combinations of highly-developed shorelines (boat docks and piers), large gravel and cobble substrates, or submerged timber and aquatic vegetation.

Because striped bass CPUE in those regions of both the Hales Ford and Penhook stocking coves from which fish were collected exhibited a temporally declining trend during the 1994 and 1995 growing seasons (both electrofishing and gillnetting; Figures 1.5-1.8), it would appear that juveniles were dispersing from shallow, littoral areas of the stocking coves to deeper, pelagic areas of the main channel. Although this movement appears to have occurred primarily from late summer to mid-fall (gillnetting only; Figures 1.5-1.8), dispersal out of the coves could have begun earlier but undetected because gillnets were not employed until the beginning of August and most were initially set within the

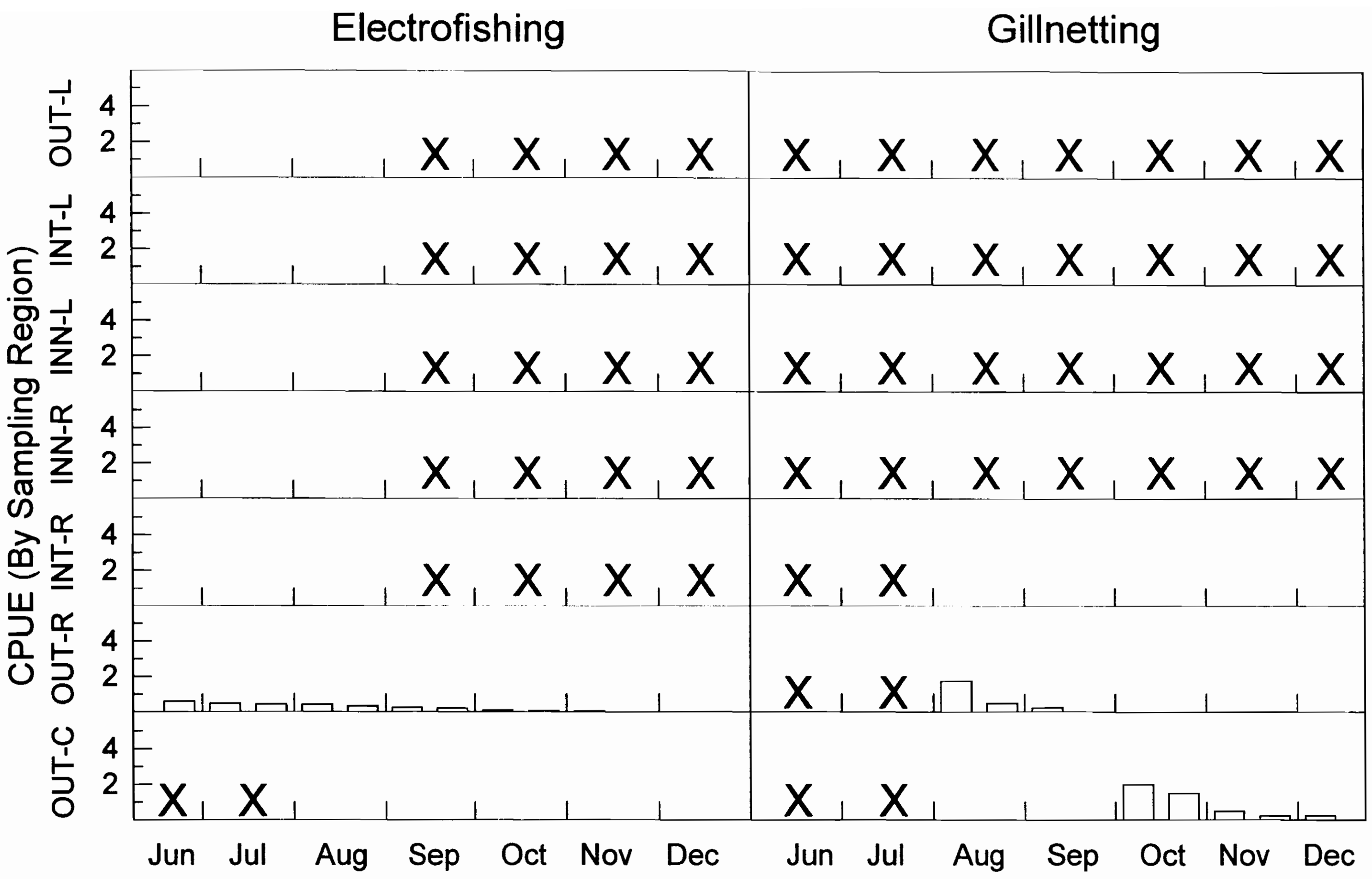


Figure 1.7. Standardized catch-per-unit-effort (CPUE) for age-0 striped bass by gear type (electrofishing = number of fish caught per minute electrofishing; gillnetting = number of fish caught per gillnet night) for each sampling region of the Penhook site of the Blackwater River (see Figure 1.3 for location of sampling site transects) over the 1994 growing season; X = no sampling using this gear type during this sampling period.

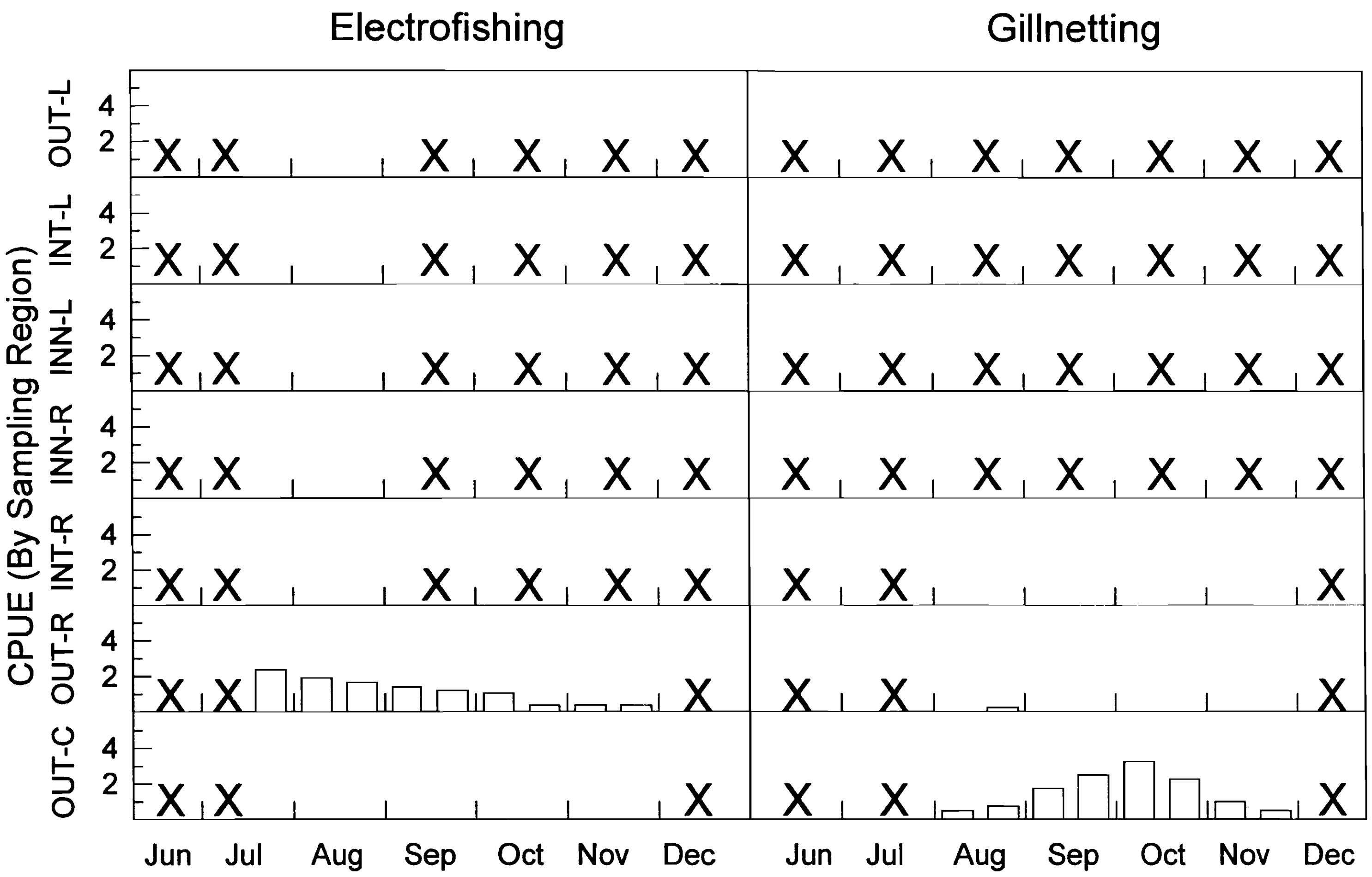


Figure 1.8. Standardized catch-per-unit-effort (CPUE) for age-0 striped bass by gear type (electrofishing = number of fish caught per minute electrofishing; gillnetting = number of fish caught per gillnet night) for each sampling region of the Penhook site of the Blackwater River (see Figure 1.3 for location of sampling site transects) over the 1995 growing season; X = no sampling using this gear type during this sampling period.

stocking coves. By the end of the growing season, juvenile striped bass that had moved out of the coves were distributed widely in Smith Mountain Lake and were captured primarily from the lower s-curve area (LSC) of the Roanoke River arm and Gills Creek confluence (GCC) of the Blackwater River arm to the upper lower lake region (ULL; see Figure 1.1 for exact locations of these areas).

Juvenile striped bass that remained within the stocking coves by the end of the growing season (defined as mid-December in 1994 and the end of November in 1995) were significantly smaller in size range than those captured in pelagic areas of the main channel (90-150 mm TL versus 151-270 mm TL, respectively; $\chi^2 = 42.34$, df = 17, P = 0.001; Figure 1.9) during both sampling years. Juveniles < 150 mm TL were rarely captured outside the stocking coves, even when sampling gears used to collect these fish within the coves (boat electrofishing and 12.7-mm bar mesh gillnets) were used in these regions of the lake. These results indicate that small juvenile striped bass demonstrate fidelity to nearshore habitats and do not disperse away from these areas during the growing season. In contrast, juvenile striped bass > 150 mm TL were never collected from the stocking coves after initial dispersal to deeper, pelagic areas of the lake, and these fish were distributed widely throughout Smith Mountain Lake by the end of the growing season.

First-Year Striped Bass Growth

1994. - Age-0 striped bass in both river arms of Smith Mountain Lake exhibited increases in length and weight, and considerable divergences in size distribution over the 1994 growing season (Figure 1.10). Fingerling striped bass stocked in the Blackwater River on 15 June were slightly larger in length and weight than those stocked in the Roanoke River on 22 June (30-54 mm TL,

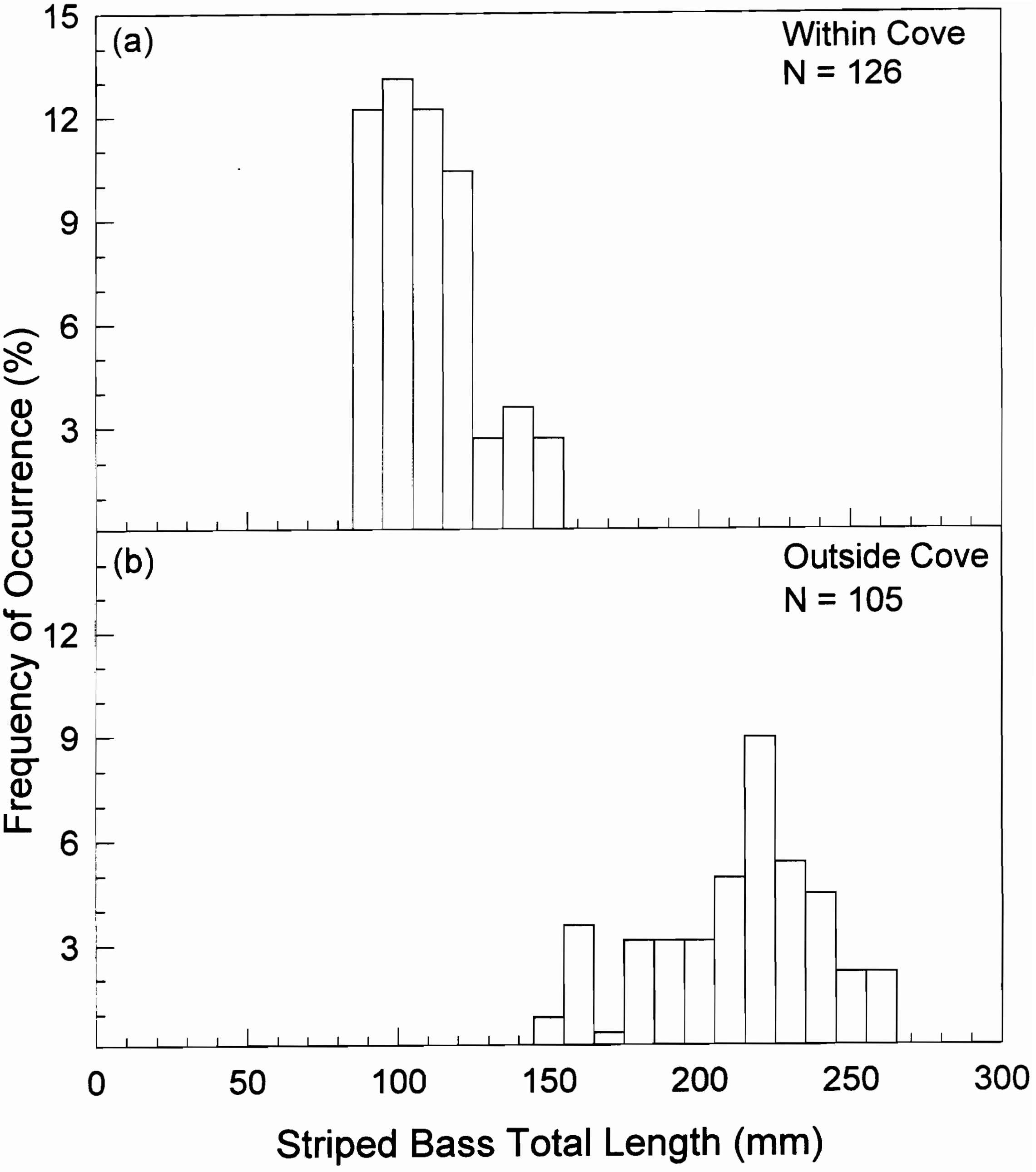


Figure 1.9. Length-frequency distributions of juvenile striped bass collected (a) within and (b) outside Smith Mountain Lake stocking coves (both Roanoke and Blackwater River arms pooled) at the end of the growing season (December 1994 and November 1995).

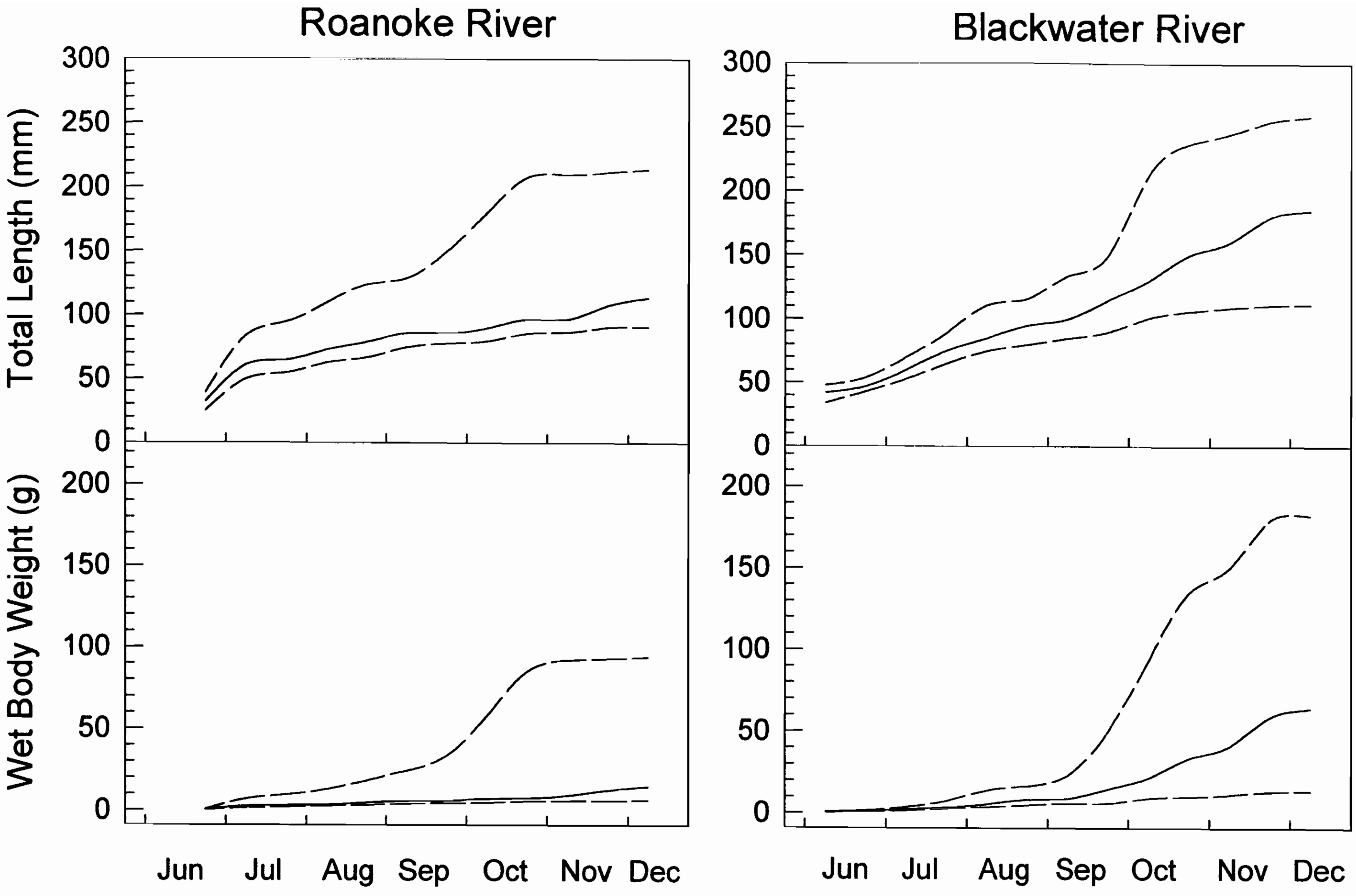


Figure 1.10. Patterns of first-year increases in total length (mm) and body weight (g) for striped bass in the Roanoke and Blackwater River arms of Smith Mountain Lake from stocking until the end of the 1994 growing season. Median total length and body weight are represented by the solid lines and the 10th and 90th percentile ranges are represented by the dashed lines.

0.22-1.53 g versus 24-41 mm TL, 0.10-0.67 g, respectively); however, length and weight distributions at the time of stocking did not differ significantly between river sites (length: $\chi^2 = 7.82$, df = 4, P = 0.10; weight: $\chi^2 = 8.77$, df = 4, P = 0.07). By September, a significant divergence in size had occurred: striped bass in the Roanoke River ranged from 78-150 mm TL (median = 86 mm TL) and 4.1-33.3 g (median = 5.7 g), whereas fish in the Blackwater River ranged from 90-150 mm TL (median = 115 mm TL) and 6.0-33.3 g (median = 14.7 g). Size ranges continued to diverge over the remainder of the growing season and by mid-December, juveniles in the Roanoke River ranged from 91-214 mm TL (median = 114 mm TL) and 6.1-97.2 g (median = 14.5 g), while fish in the Blackwater River arm ranged from 112-259 mm TL (median = 180 mm TL) and 13.6-182.3 g (median = 63.9 g). Although striped bass in the Blackwater River were larger by the end of the growing season in both length and weight, length- and weight-frequency distributions did not differ significantly from those observed in the Roanoke River (length: $\chi^2 = 8.21$, df = 23, P = 0.06; weight: $\chi^2 = 23.19$, df = 23, P = 0.18).

Even though median length of juvenile striped bass was significantly different between river arms, length-frequency distributions were pooled from each site to more closely examine and explain the divergence in size over the growing season because: (1) juvenile striped bass in both river arms displayed similar patterns of size divergence; and (2) length-frequency distributions did not differ significantly between sites. Month-by-month histograms (Figure 1.11) illustrate the development and growth of two different size modes of fish from the same cohort. At the time of stocking in mid-June, juvenile striped bass were relatively uniform in length (24-54 mm TL), with a unimodal distribution that was only slightly positively skewed (Table 1.4). However, length

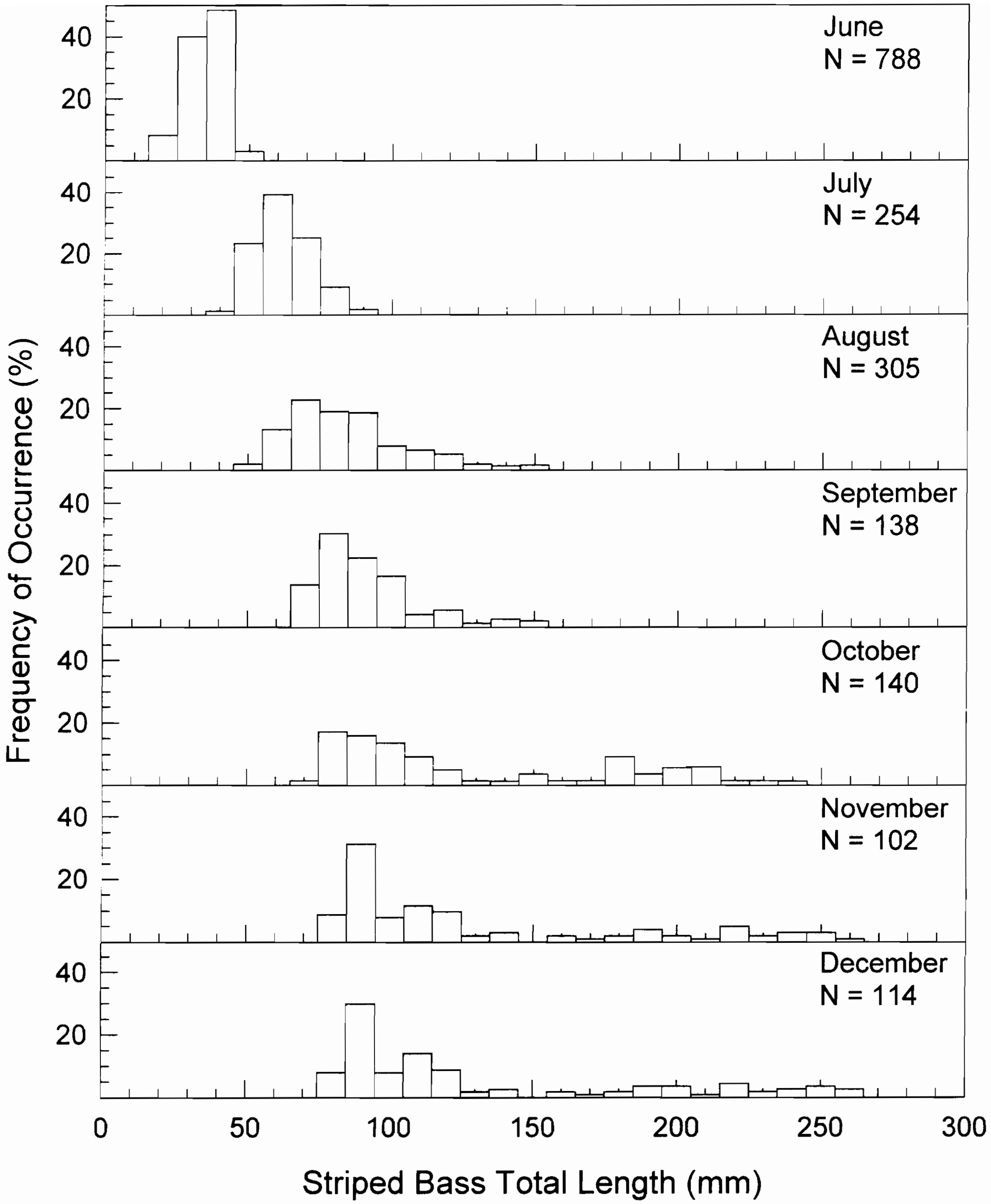


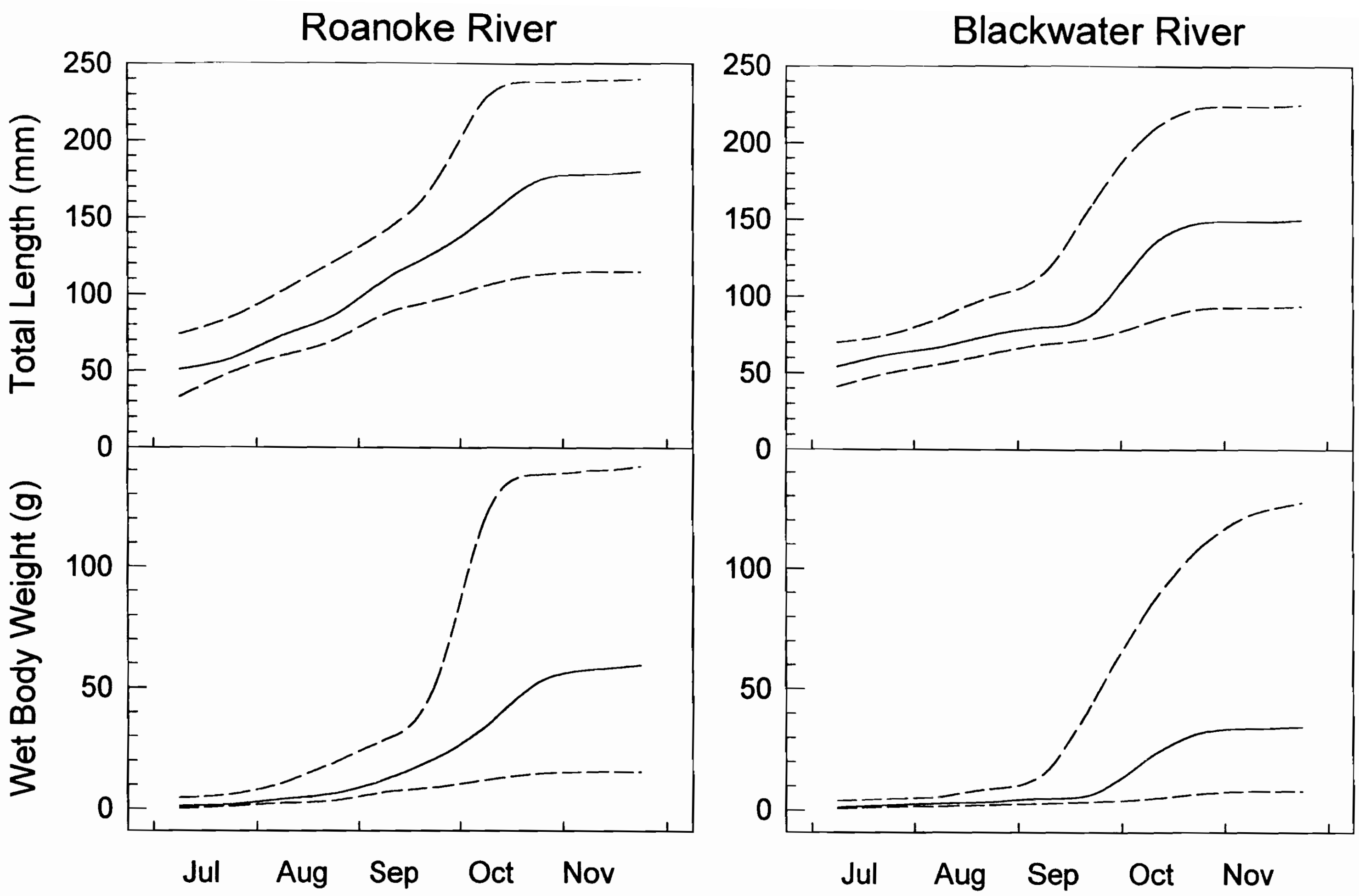
Figure 1.11. Monthly length-frequency distributions of juvenile striped bass in Smith Mountain Lake (both Roanoke and Blackwater River arms pooled) over the 1994 growing season.

Table 1.4. Descriptive statistics for juvenile striped bass length-frequency distributions over the first growing season after stocking (June-December 1994; July-November 1995) and after overwintering (March 1995; April 1996) in Smith Mountain Lake. For each sampling season (1994-95 and 1995-96), length-frequency distributions of juvenile striped bass collected in both the Roanoke and Blackwater River arms were pooled together.

Sampling Season	Sampling Period	N	Median Total Length (mm)	Total Length Range (mm)	Total Length 25th- and 75th-Percentile Range (mm)	Skewness (mm)	Kurtosis (mm)
1994-95	15 Jun	788	40	24 - 54	33 - 43	0.01	0.09
	11-26 Jul	254	66	49 - 99	60 - 74	0.52	0.10
	13-21 Aug	305	84	54 - 157	74 - 97	0.88	0.67
	10-18 Sep	138	93	71 - 153	83 - 103	1.24	0.19
	12-19 Oct	140	100	77 - 240	93 - 169	1.67	-1.10
	09-16 Nov	102	102	84 - 260	94 - 183	2.11	-1.24
	07-15 Dec	114	114	84 - 266	105-261	2.06	-1.38
	15-31 Mar	213	213	97 - 268	230-257	-2.83	10.05
1995-96	12 Jul	905	52	31 - 97	46 - 60	0.59	0.41
	10-18 Aug	267	68	50 - 152	63 - 80	1.66	2.86
	08-16 Sep	203	86	56 - 222	76 - 125	1.12	0.15
	04-14 Oct	164	147	78 - 242	102 - 193	0.33	-1.35
	08-18 Nov	221	162	80 - 261	109 - 219	0.29	-1.51
	01-18 Apr	75	225	128 - 262	213 - 239	-1.65	3.86

distributions diverged considerably over the growing season (Figure 1.11), becoming more kurtotic and positively skewed (Table 1.4); by mid-October, a distinct bimodal distribution was evident (Figure 1.11). Negative kurtosis, an indication of bimodality (Sokal and Rohlf 1981), further supports these results (Table 1.4). The size distribution continued to diverge over the next two months so that by the end of the growing season in mid-December, the median total length of large-mode juveniles (225 mm TL, range 182-266 mm TL) was significantly greater than small-mode fish (94 mm TL, range 84-140 mm TL) from the same stocked cohort (Figure 1.11; Mann-Whitney, $U=595.5$, $P=0.001$). In addition, there were also differences in the proportion of large- and small-mode striped bass collected at the end of the 1994 growing season from each river arm; approximately 63% of large-mode juveniles were collected from Blackwater River sampling sites, whereas 60% of small-mode fish were collected from Roanoke River sampling sites.

1995. - Juvenile striped bass growth patterns in both river arms during the 1995 growing season were similar to those observed in 1994 (Figure 1.12) despite initial differences in size distributions at the time of stocking. Although the range in both length and weight of juvenile striped bass at the time of stocking in mid-July was quite broad (Figure 1.12; Roanoke River: 31-97 mm TL and 0.2-11.1 g; Blackwater River: 38-81 mm TL and 0.5-6.1 g), these distributions were not significantly different (length: $\chi^2=7.83$, $df=5$, $P=0.17$; weight: $\chi^2=9.23$, $df=5$, $P=0.10$). However, juvenile striped bass were significantly larger and had a broader size range at stocking in July 1995 than did fish stocked in June 1994 (Mann-Whitney, $U=8{,}531.0$, $P=0.01$; $\chi^2=29.44$, $df=6$, $P=0.01$). Surprisingly, both medians and ranges in size of fish stocked in July 1995 were significantly less than those observed for fish



Roanoke River

Blackwater River

Figure 1.12. Patterns of first-year increases in total length (mm) and body weight (g) for striped bass in the Roanoke and Blackwater River arms of Smith Mountain Lake from stocking until the end of the 1995 growing season. Median total length and body weight are represented by the solid lines and the 10th and 90th percentile ranges are represented by the dashed lines.

collected by electrofishing in the same areas at the same time during July 1994 (Mann-Whitney, $U=1,164.0$, $P=0.01$; $\chi^2=15.52$, $df=6$, $P=0.01$). Despite these initial differences in size between the two years, juvenile striped bass collected by the end of August 1995 displayed a broader range in size for both the Roanoke ($\chi^2=34.41$, $df=10$, $P<0.001$) and Blackwater ($\chi^2=40.12$, $df=11$, $P<0.001$) River arms than those collected at the same time in 1994.

As in 1994, size ranges of juvenile striped bass over the 1995 growing season diverged considerably from initial stocking distributions. By the end of November, striped bass from the Roanoke River ranged from 115-240 mm TL (median = 180 mm TL) and 15.3-141.9 g (median = 59.4 g), while the size range of juveniles from the Blackwater River was 94-225 mm TL (median = 150 mm TL) and 6.6-127.6 g (median = 34.6 g). In contrast to observed sizes and size distributions in 1994, juvenile striped bass in the Blackwater River were smaller in both length and weight than juveniles in the Roanoke River at the end of the growing season (Figure 1.12). However, length and weight distributions were not significantly different between river arms (length: $\chi^2=24.84$, $df=18$, $P=0.13$; weight: $\chi^2=23.63$, $df=18$, $P=0.17$).

Length-frequency distributions were again pooled from each river arm to examine the size divergence of juvenile striped bass over the 1995 growing season. These month-by-month histograms also portray the development and divergence of two distinct size modes of fish within the same cohort (Figure 1.13). At the time of stocking in mid-July, the length-frequency distribution was unimodal, quite broad (31-97 mm TL), and positively skewed (Table 1.4). During August and September, the length-frequency distribution broadened considerably (Figure 1.13), becoming more positively skewed (Table 1.4). Although the length-frequency distribution flattened and lost its positive

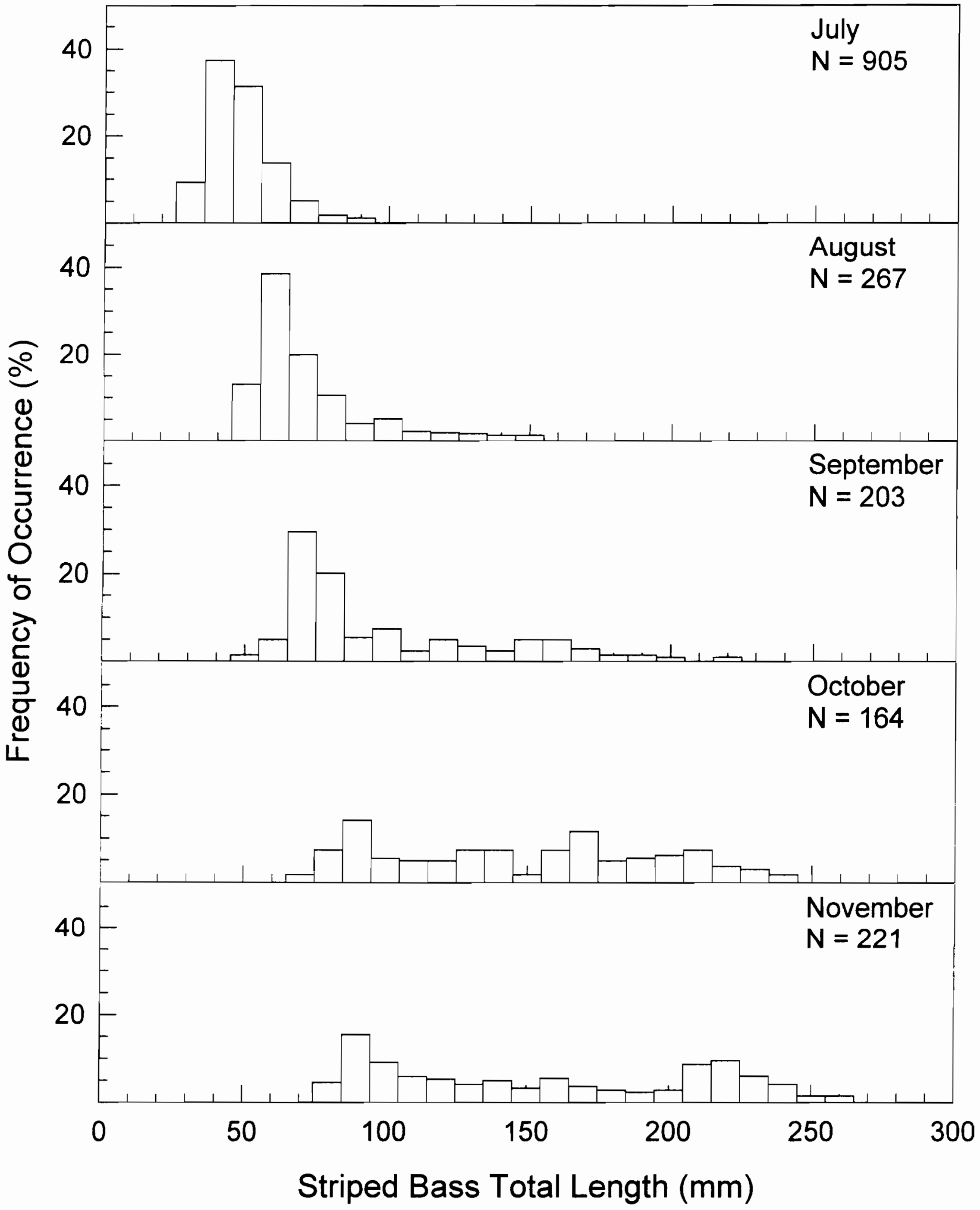


Figure 1.13. Monthly length-frequency distributions of juvenile striped bass in Smith Mountain Lake (both Roanoke and Blackwater River arms pooled) over the 1995 growing season.

skewness by mid-October, a distinct bimodal distribution was evident (Figure 1.13). These two size modes, masked slightly by the continuous nature of the length-frequency distribution, were negatively kurtotic (Table 1.4), further indicating a bimodal size distribution. Divergence between the two size modes continued over the next month; by the end of November, the median total length of large-mode juvenile striped bass (226 mm TL, range 183-261 mm TL) was significantly greater than small-mode juveniles (100 mm TL, range 80-137 mm TL) from the same cohort (Figure 1.13; Mann-Whitney, $U=6,441.5$, $P=0.001$). Although there were again differences in the proportion of large- and small-mode striped bass collected at the end of the 1995 growing season from each river arm, these results were the converse of those observed in 1994; approximately 58% of large-mode juveniles were collected from Roanoke River sampling sites, whereas 55% of small-mode fish were collected from Blackwater River sampling sites.

Overwinter Survival

Observed length-frequency distributions for juvenile striped bass differed markedly between late fall and early spring sampling periods. Although length-frequency distributions for juvenile striped bass were bimodal at the end of both the 1994 and 1995 growing seasons, spring sampling revealed that only a single mode, consisting primarily of fish >150 mm TL, remained in March 1995 and April 1996 (Figure 1.14). Length-frequency distributions and variance in length-frequency distributions in December 1994 (range 84-266 mm TL; 25th- and 75th-percentile range 105-261 mm TL) were significantly greater than in March 1995 (range 97-268 mm TL; 25th- and 75th-percentile range 230-257 mm TL; $\chi^2=70.21$, $df=20$, $P<0.001$; Variance ratio test, $F=2.96$, $P<0.001$).

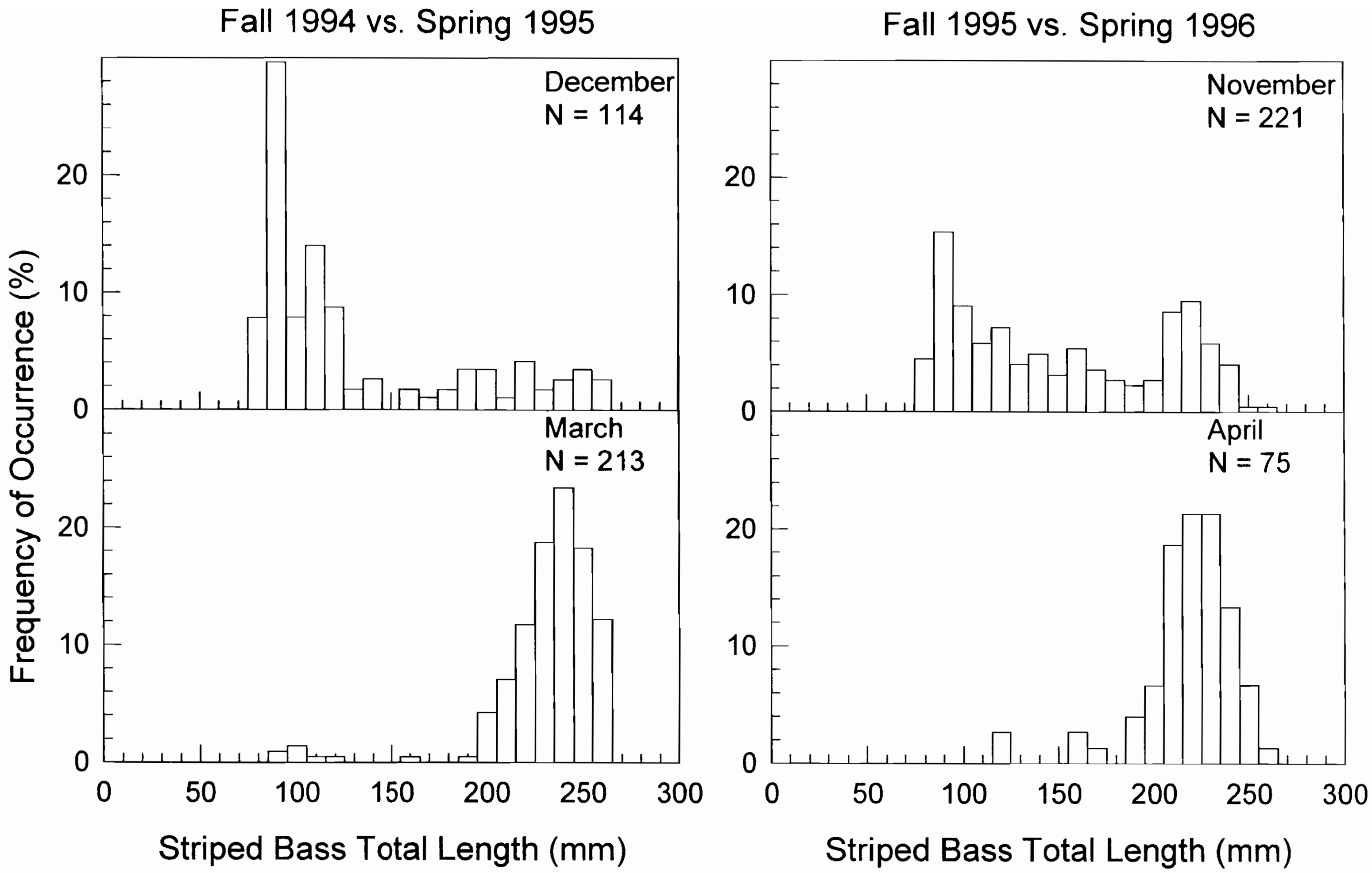


Figure 1.14. Length-frequency distributions of juvenile striped bass before and after overwintering in Smith Mountain Lake during the 1994-95 and 1995-96 sampling seasons (both Roanoke and Blackwater River arms pooled).

Similarly, length-frequency distributions in November 1995 (range 80-261 mm TL; 25th- and 75th-percentile range 109-219 mm TL) were significantly greater than in April 1996 (range 128-262 mm TL; 25th- and 75th-percentile range 213-239 mm TL; $\chi^2 = 42.51$, df = 20, $P < 0.001$; Variance ratio test, $F = 3.18$, $P < 0.001$).

Further evidence for loss of bimodality due to the disappearance of small-mode striped bass over winter comes from measures of skewness and kurtosis. Although spring length-frequency distributions were negatively skewed (a few small-mode fish were collected during these sampling periods), positive kurtosis, indicating a unimodal distribution (Sokal and Rohlf 1981), was observed for both March 1995 and April 1996 (10.05 and 3.86, respectively; Table 1.4). Additionally, small-mode fish (< 150 mm TL) comprised 72.3% and 62.5% of all striped bass collected during late fall sampling in 1994 and 1995, respectively. In sharp contrast, small-mode fish comprised only 3.2% and 2.7% of all striped bass collected during March 1995 and April 1996, respectively. Thus, the transformation from bimodal to unimodal length-frequency distributions between late fall and early spring for juvenile striped bass in Smith Mountain Lake appears to be due to the disappearance of small-mode fish (< 150 mm TL) over the 1994-95 and 1995-96 winters (Figure 1.14).

Food Habits

Striped Bass. - Although food habits for age-0 striped bass were initially dissimilar between sampling years, juveniles exhibited comparable temporal trends in consumed food items for both river arms of Smith Mountain Lake over the remainder of the 1994 and 1995 growing seasons (Figure 1.15). During the first two weeks post-stocking in June 1994, zooplankton (cladocerans and

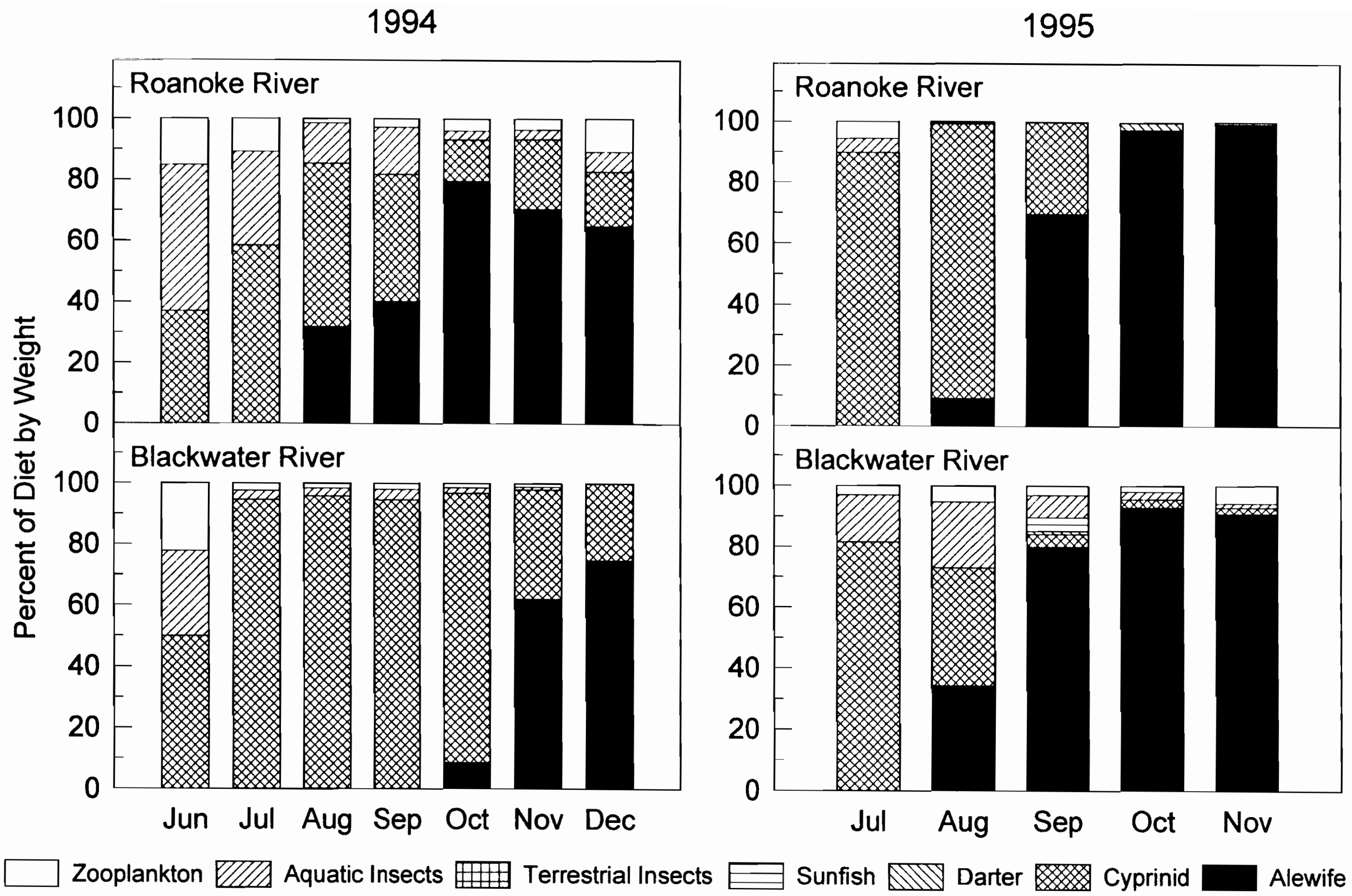


Figure 1.15. Temporal patterns in juvenile striped bass diet composition in the Roanoke and Blackwater River arms of Smith Mountain Lake during the 1994 and 1995 growing seasons.

copepods) and benthic aquatic insects (chironomid larvae and pupae, and ephemeropteran and odonate nymphs) comprised the majority of stomach contents by weight (approximately 60%). In contrast, age-0 cyprinids (mainly *Notropis hudsonius)* were the most important food item by weight (85%) in striped bass stomachs immediately post-stocking in July 1995. Over the remainder of the 1994 and 1995 growing seasons, age-0 fishes were the principal prey items consumed by juveniles in both river arms (Figure 1.15). Age-0 cyprinids comprised the majority of the diet by weight until late September and occurred consistently in the diet throughout the remainder of the growing season months. However, age-0 alewives were the dominant food item consumed by juvenile striped bass during fall months, comprising an increasingly greater percentage of stomach content weight from late September through mid-December 1994 and late August through November 1995. Additionally, age-0 sunfishes (*Lepomis* spp.) and darters (*Etheostoma* spp.) were consumed, albeit infrequently, by juvenile striped bass during both growing seasons.

Age-0 striped bass in both river arms also demonstrated similar size-dependent shifts in food habits over the 1994 and 1995 growing seasons (Figure 1.16). Although juveniles were piscivorous at all sizes (except for the smallest 10-mm size interval in the Roanoke River 1994 and Blackwater River 1995), stomach contents of striped bass <130 mm TL contained varying amounts of zooplankton, benthic aquatic insects, and age-0 cyprinids (Figure 1.16). For these juveniles, the contribution of age-0 cyprinids to diet composition increased progressively with size. Interestingly, these smaller juveniles in the Roanoke River during 1994 contained greater proportions of invertebrates than those in the Blackwater River over this same time period; in

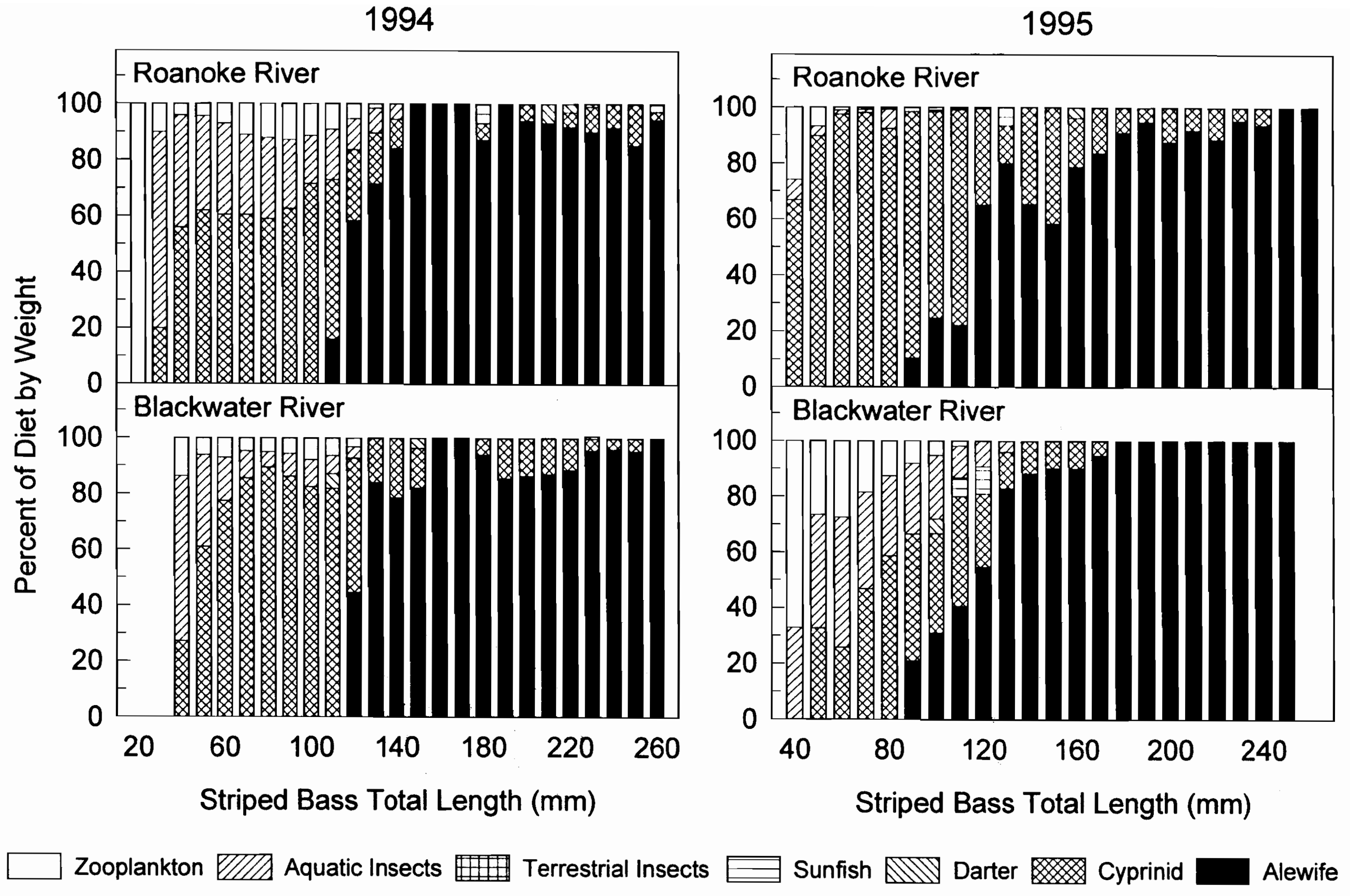


Figure 1.16. Size-dependent patterns in juvenile striped bass diet composition in the Roanoke and Blackwater River arms of Smith Mountain Lake during the 1994 and 1995 growing seasons.

1995, the converse observation was detected (Figure 1.16). For age-0 striped bass >130 mm TL, fishes (age-0 cyprinids, sunfishes, darters, and alewives) totaled greater than 85% of the stomach contents by weight (Figure 1.16). However, age-0 alewives were the dominant dietary component for these larger size classes, comprising at least 80% by weight of consumed fish prey.

Black Basses. - Age-0 black basses (primarily largemouth bass) also exhibited temporal trends in food habits that were similar over the 1994 and 1995 growing seasons in both river arms of Smith Mountain Lake (Figure 1.17). Through September, diets of black basses in both river arms consisted primarily of age-0 fishes (at least 70% for cyprinids, sunfishes, and darters in combination). Additionally, zooplankton (cladocerans and copepods), aquatic insects (chironomid larvae and pupae, ephemeropteran nymphs, and gerrid adults), and terrestrial insects (coleopteran and formicid adults) occurred consistently in black bass stomachs during this time period. Over the remainder of the growing season, age-0 cyprinids became an increasingly smaller component of the diet, while age-0 darters and, to a lesser extent, sunfishes increased in the proportion of stomach content weight (Figure 1.17). Age-0 alewives, although consumed by two largemouth bass in October, were never a significant component of the diet for these juvenile piscivores. From September until the end of the growing season, darters were the dominant prey item by weight consumed by age-0 black basses (Figure 1.17).

Like juvenile striped bass, black basses also demonstrated comparable size-dependent shifts in diet composition over the 1994 and 1995 growing seasons in both river arms of Smith Mountain Lake (Figure 1.18). Although black basses consumed invertebrates until 120 mm TL, the contribution of these prey items decreased with increasing size as juveniles became more piscivorous.

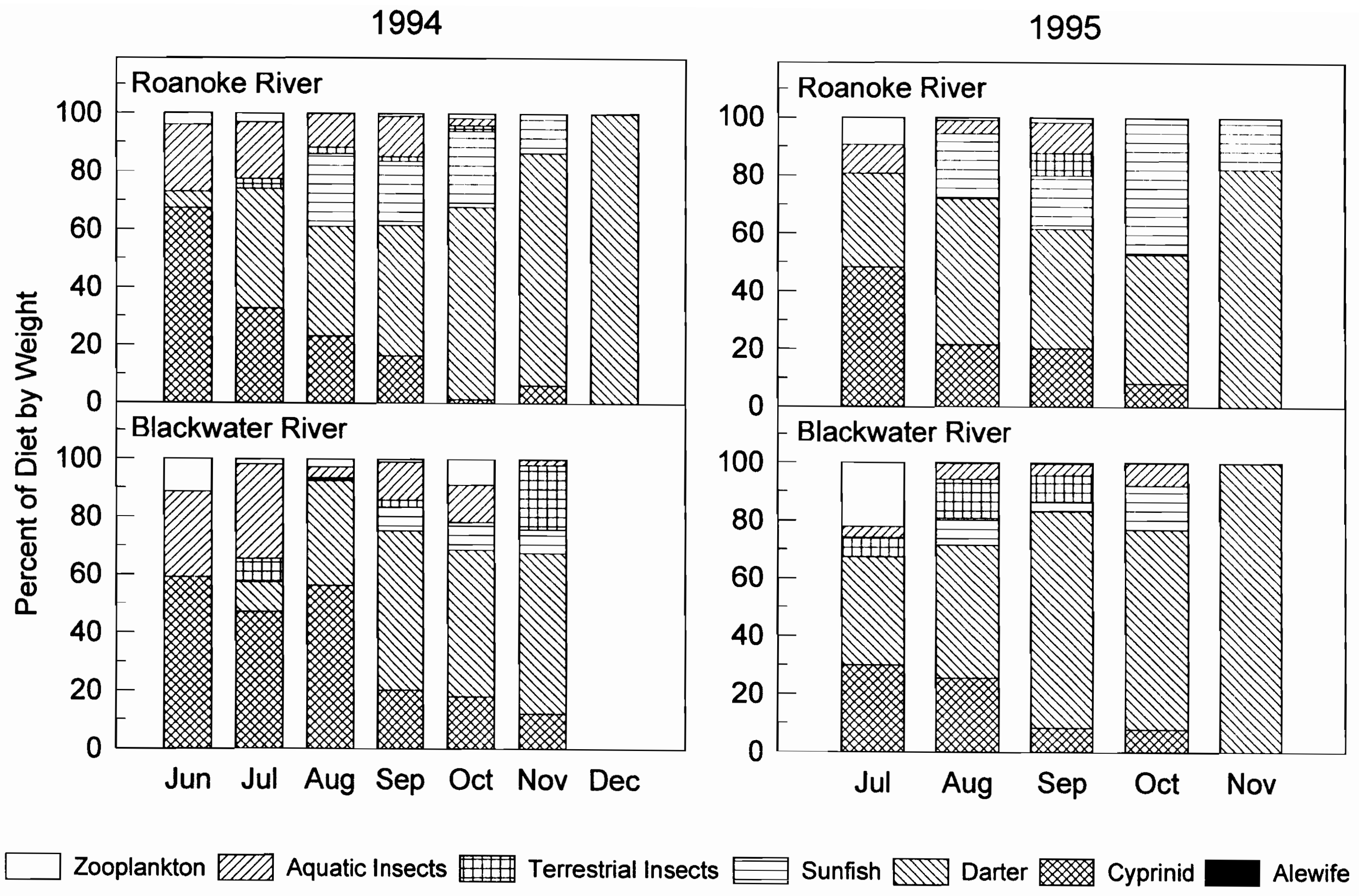


Figure 1.17. Temporal patterns in juvenile black bass diet composition in the Roanoke and Blackwater River arms of Smith Mountain Lake during the 1994 and 1995 growing seasons.

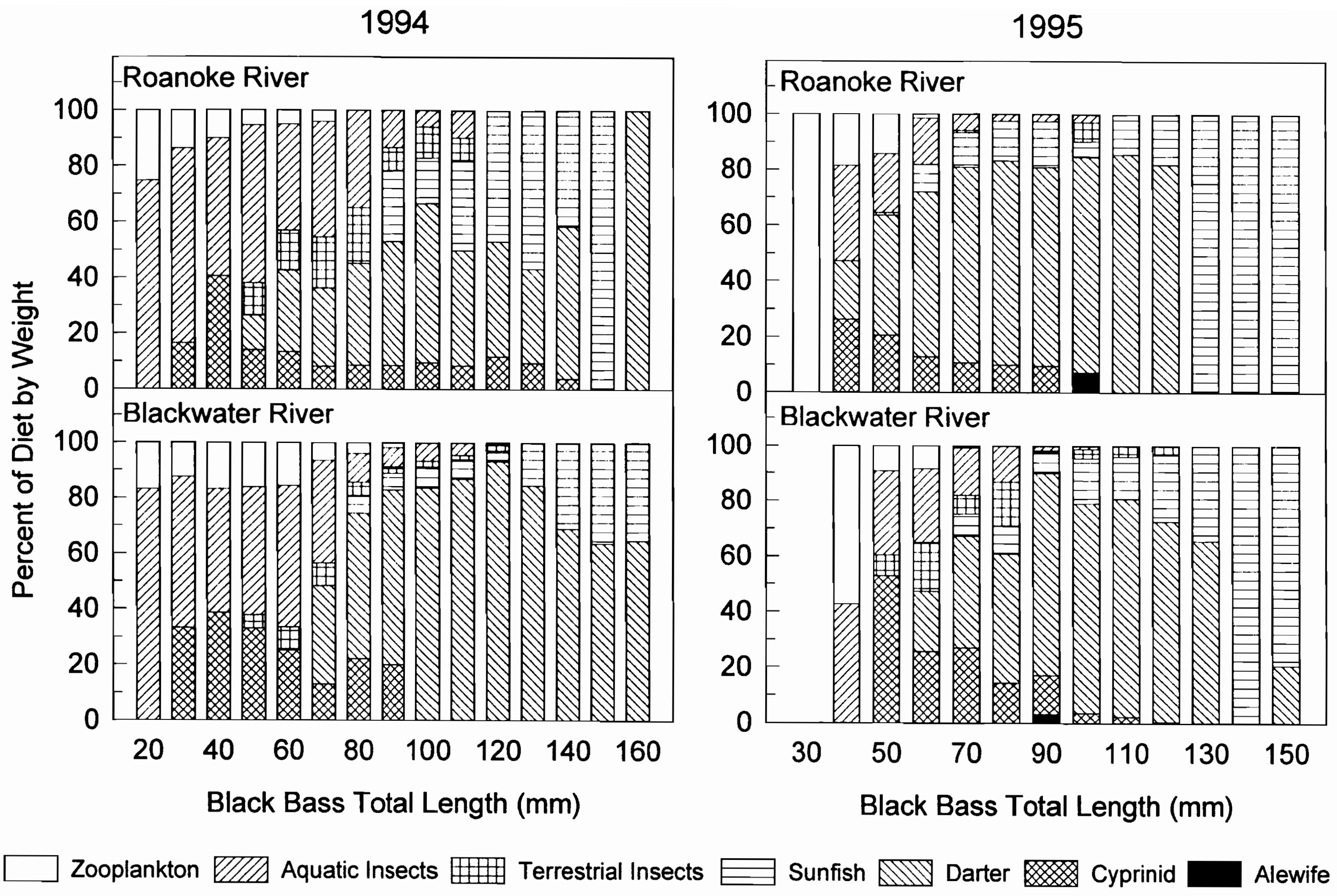


Figure 1.18. Size-dependent patterns in juvenile black bass diet composition in the Roanoke and Blackwater River arms of Smith Mountain Lake during the 1994 and 1995 growing seasons.

For basses <120 mm TL, darters were the dominant fish prey consumed by weight, although age-0 cyprinids, sunfishes, and to a small extent, alewives, also contributed to the stomach contents items (Figure 1.18). Juvenile black basses >120 mm TL were strictly piscivorous; diet contents for these larger size classes consisted primarily of age-0 darters and sunfishes (Figure 1.18).

Diet Overlap

During months in which the minimum number of stomachs necessary to adequately characterize juvenile striped bass and black bass diets were collected, overlap values greater than 0.6 were only detected during June 1994 for both the Roanoke (0.62) and Blackwater (0.87) River arms (Table 1.5). During this month, striped bass and black bass diets consisted of zooplankton (cladocerans), benthic aquatic insects (chironomid larvae and pupae, and ephemeropteran nymphs), and age-0 cyprinids. Throughout the remainder of the summer and early fall for both river arms in 1994 and 1995, diet overlap was insignificant and exhibited a temporally declining trend (Table 1.5) due to increasing divergence in prey items consumed by these two juvenile predators; striped bass consumed primarily aquatic insects (chironomid larvae and pupae, and ephemeropteran nymphs), and age-0 cyprinids and alewives, whereas black bass diet composition primarily consisted of terrestrial insects (coleopteran and formicid adults), and age-0 sunfishes and darters.

Diet overlap was only calculated between juvenile striped bass and black basses that ranged from 40-120 mm TL because the number of predator stomachs necessary to adequately characterize size-dependent differences in diet composition for fish outside this range was less than that determined by cumulative prey species curves (Table 1.6). Evaluation of diet overlap between

Table 1.5. Diet overlap for juvenile striped bass x black bass in Smith Mountain Lake calculated by sampling period and location for both the 1994 and 1995 growing seasons. Only samples that exceeded the minimum number of stomachs necessary to adequately characterize predator diets (as determined by cumulative prey species curves) were used in this analysis.

	1994		1995	
Sampling Period	Roanoke River	Blackwater River	Roanoke River	Blackwater River
Jun	0.62	0.87	-----	-----
Jul	0.57	0.52	0.57	0.22
Aug	0.33	0.60	0.22	0.16
Sep	0.27	0.24	0.21	0.12
Oct	0.06	0.34	0.04	0.13

----- No fish collected during this sampling period.

Table 1.6. Diet overlap for juvenile striped bass x black bass in Smith Mountain Lake calculated by 10-mm size class interval and location for both the 1994 and 1995 growing seasons. Only samples that exceeded the minimum number of stomachs necessary to adequately characterize predator diets (as determined by cumulative prey species curves) were used in this analysis.

	1994		1995	
Size Interval	Roanoke River	Blackwater River	Roanoke River	Blackwater River
20-29	**	-----	**	-----
30-39	**	**	**	-----
40-49	0.77	0.83	0.52	**
50-59	0.44	0.71	0.31	0.69
60-69	0.43	0.48	0.15	0.57
70-79	0.35	0.30	0.12	0.39
80-89	0.26	0.26	0.11	0.24
90-99	0.19	0.26	0.09	0.18
100-109	0.14	0.09	0.08	0.10
110-119	0.12	**	**	0.10
120-129	0.12	**	**	**

** Minimum number of stomachs to adequately characterize predator diets not exceeded.

----- No fish collected during this sampling period.

striped bass and black basses over this size range was most critical because it is at these sizes when both juvenile predators co-occur in nearshore areas and, as a result, have the greatest potential for interspecific competition for food resources. Diet overlap greater than 0.6 was detected only for the 40-mm TL (both Roanoke and Blackwater River arms in 1994) and 50-mm TL (Blackwater River arm only in both 1994 and 1995) size intervals (Table 1.6). Stomachs for these sizes of predators strictly contained zooplankton (cladocerans), benthic aquatic insects (chironomid larvae and pupae, and ephemeropteran nymphs), and age-0 cyprinids. For the remainder of the 10-mm size intervals in both river arms for 1994 and 1995, diet overlap between these two juvenile predators exhibited a declining trend with increasing size (Table 1.6) due to increasing divergence in diet composition (primarily forage-fish prey); larger juvenile striped bass fed on age-0 cyprinids and alewives, whereas larger juvenile black basses consumed age-0 sunfishes and darters.

Predator-Prey Size Relationships

To determine length relationships between consumed fish prey (age-0 cyprinids and alewives) and juvenile striped bass, ingested fish prey TL, as well as fish prey TL to striped bass TL, were each regressed versus striped bass body length. Significant size-dependent trends were detected in linear regression relationships for cyprinid TL to striped bass TL (slope = +0.18, r^2 = 0.31, N=154, P=0.001), alewife TL to striped bass TL (slope = +0.28, r^2 = 0.31, N=217, P=0.001), cyprinid TL to striped bass TL versus striped bass body length (slope = -0.03, r^2 = 0.01, N=154, P=0.001), and alewife TL to striped bass TL versus striped bass body length (slope = -0.05, r^2 = 0.07, N=217, P=0.001). Smaller striped bass (40-120 mm TL) exclusively consumed cyprinids that ranged in size from 9-40 mm TL, whereas large striped bass (175-270 mm TL) primarily ate alewives that ranged from 50-125 mm (Figure 1.19a). Juvenile striped bass ranging in total length from 120-175 mm consumed both cyprinids and alewives. Additionally, consumed age-0 cyprinids ranged from 7-39% of small striped bass TL, while age-0 alewives eaten by large striped bass ranged from 23-52% of predator TL (Figure 1.19b). Although these relationships overlap, alewife TL to striped bass TL was significantly greater than cyprinid TL to striped bass TL (t-test between regression coefficients, $t=3.86$, $P=0.002$). However, a flat or declining trend with increasing striped bass body length was evident for both prey types consumed (Figure 1.19b). For striped bass that fed on cyprinids, a 40- and 120-mm striped bass consumed this prey item, on average, at ratios of 21% and 20% of their TL, respectively, whereas 150- and 270-mm striped bass ate alewives, on average, at ratios of 41% and 35% of their TL, respectively.

Significant size-dependent trends were also detected for the linear regression relationships between of cyprinid body weight to striped bass body weight (slope = +0.01, r^2 = 0.34, $N=154$, $P=0.001$), alewife body weight to striped bass body weight (slope = +0.04, r^2 = 0.31, $N=217$, $P=0.001$), cyprinid body weight to striped bass body weight versus striped bass TL (slope = -0.01, r^2 = 0.03, $N=154$, $P=0.04$), and alewife body weight to striped bass body weight versus striped bass TL (slope = -0.02, r^2 = 0.05, $N=217$, $P=0.001$). Smaller striped bass (40-120 mm TL) exclusively consumed cyprinids that ranged from 0.1-0.5 g, whereas large striped bass (150-270 mm TL) primarily ate alewives that ranged from 2.0-17.5 g (Figure 1.19c). Additionally, consumed age-0 cyprinids ranged from 0.3%-4.0% of small striped bass body weight, while age-0 alewives eaten by large striped bass ranged from

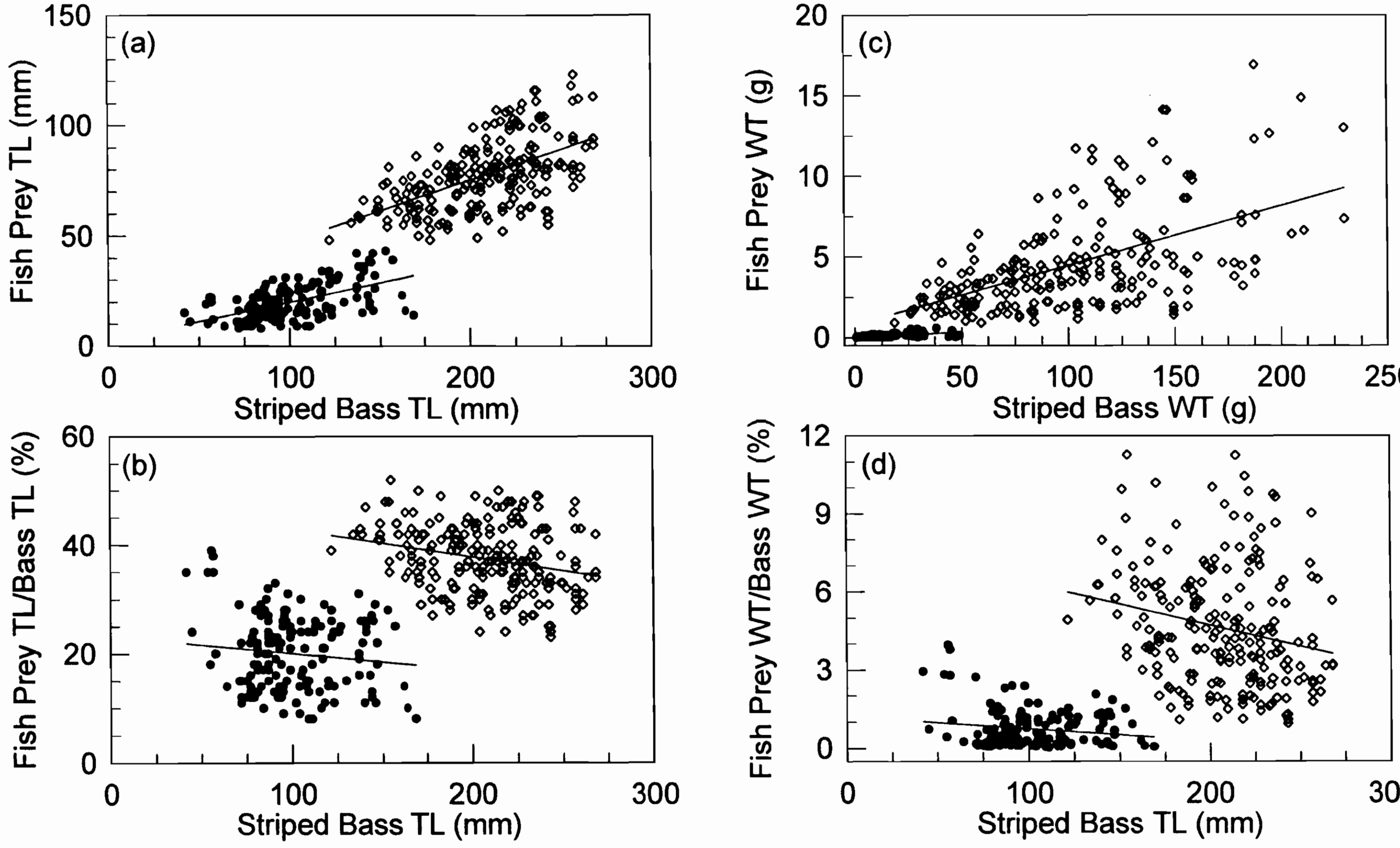


Figure 1.19. Relationships between the size of age-0 cyprinids (solid circles) and alewives (Hollow diamonds) consumed by juvenile striped bass from 1994-96 in Smith Mountain Lake (both the Roanoke and Blackwater River arms combined); (a) fish prey TL versus striped bass TL; (b) fish prey TL to striped bass TL versus striped bass TL; c) fish prey WT versus striped bass WT; (d) fish prey WT to striped bass WT versus striped bass TL (TL = total length; WT = body weight).

2.0%-11.3% of striped bass body weight (Figure 1.19d). Although these relationships overlap, the alewife body weight to striped bass body weight was significantly greater than cyprinid body weight to striped bass body weight (t-test between regression coefficients, $t=3.33$, $P=0.001$). However, once again a declining trend with increasing striped bass body length was evident for both prey types consumed (Figure 1.19d). For striped bass that fed on cyprinids, a 40- and 120-mm striped bass consumed this prey item, on average, at ratios of 1.1% and 0.8% of their body weight, respectively, whereas 150- and 270-mm striped bass ate alewives, on average, at ratios of 5.8% and 3.6% of their body weight, respectively.

Because size-dependent differences in the types and sizes of fish prey consumed by age-0 striped bass were observed, the maximum total lengths of age-0 cyprinids and alewives that could be ingested by progressively increasing 25-mm striped bass size classes (range 25-300 mm TL) were estimated based on the relationship between measured predator gape width and fish prey body depth. Juvenile striped bass consistently consumed age-0 cyprinids that were significantly less than the predicted maximum size (t-test between regression coefficients, $t=3.35$, $P<0.001$; Figure 1.20). Because the size distribution of cyprinids available throughout the growing season (Figure 1.21) was within predator ingestibility limits, juvenile striped bass were not gape limited for this fish prey type. For example, based on ingestibility limitations, a 100-mm striped bass in August could consume age-0 cyprinids as large as 50 mm TL. Although this size was morphologically available at this time (Figure 1.21), 100-mm striped bass consumed cyprinids ranging from 10-30 mm TL, much less than the predicted ingestibility limit (Figure 1.20).

Although sizes of most age-0 alewives consumed by larger juvenile

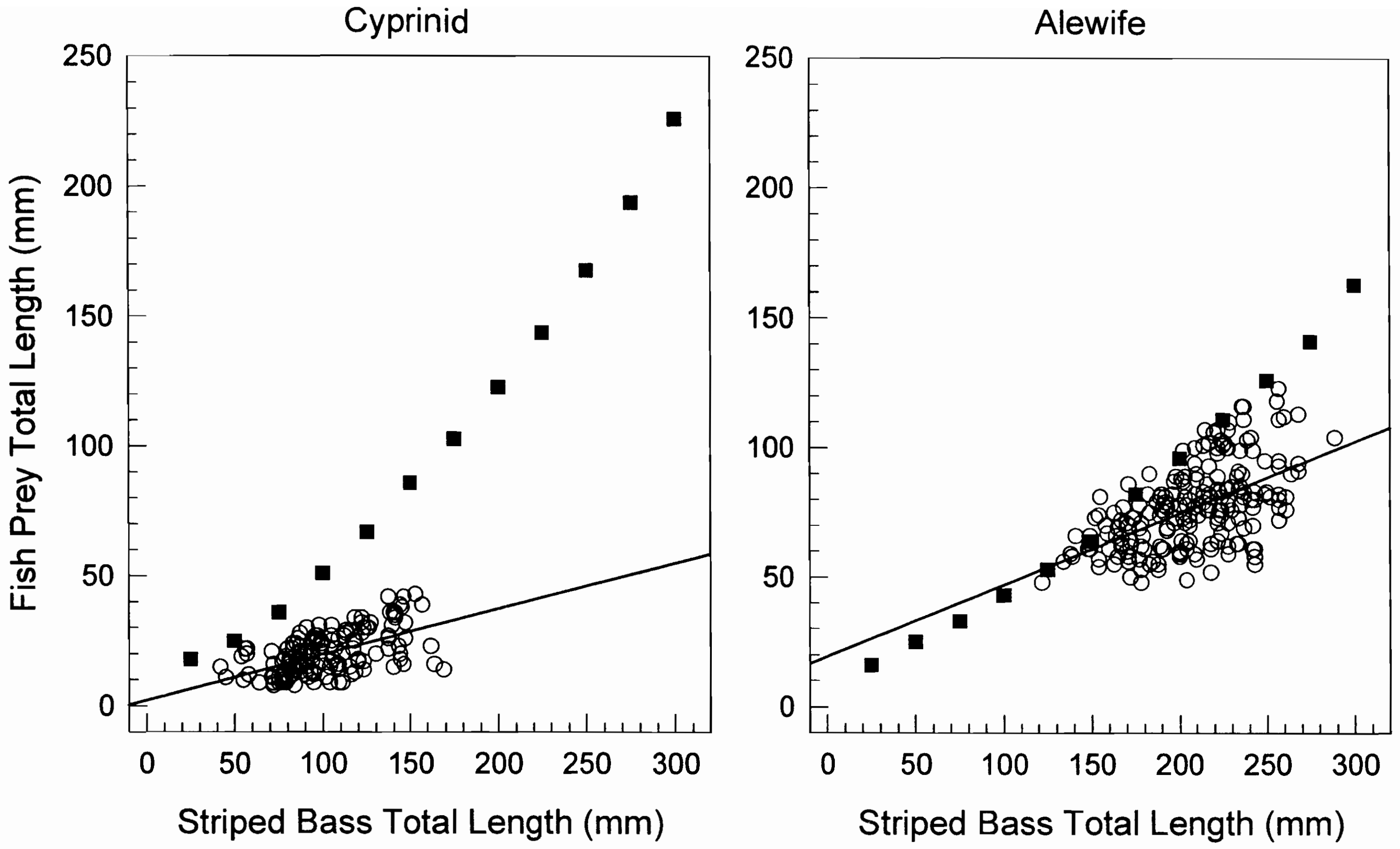


Figure 1.20. Relationships between consumed age-0 cyprinids and alewives TL to juvenile striped bass TL. The solid squares represent the estimated maximum TL of age-0 fish prey that a juvenile striped bass can consume based on the relationship between striped bass gape width and fish prey body depth. The hollow circles for each plot represent the actual sizes of fish prey consumed by juvenile striped bass (TL = total length).

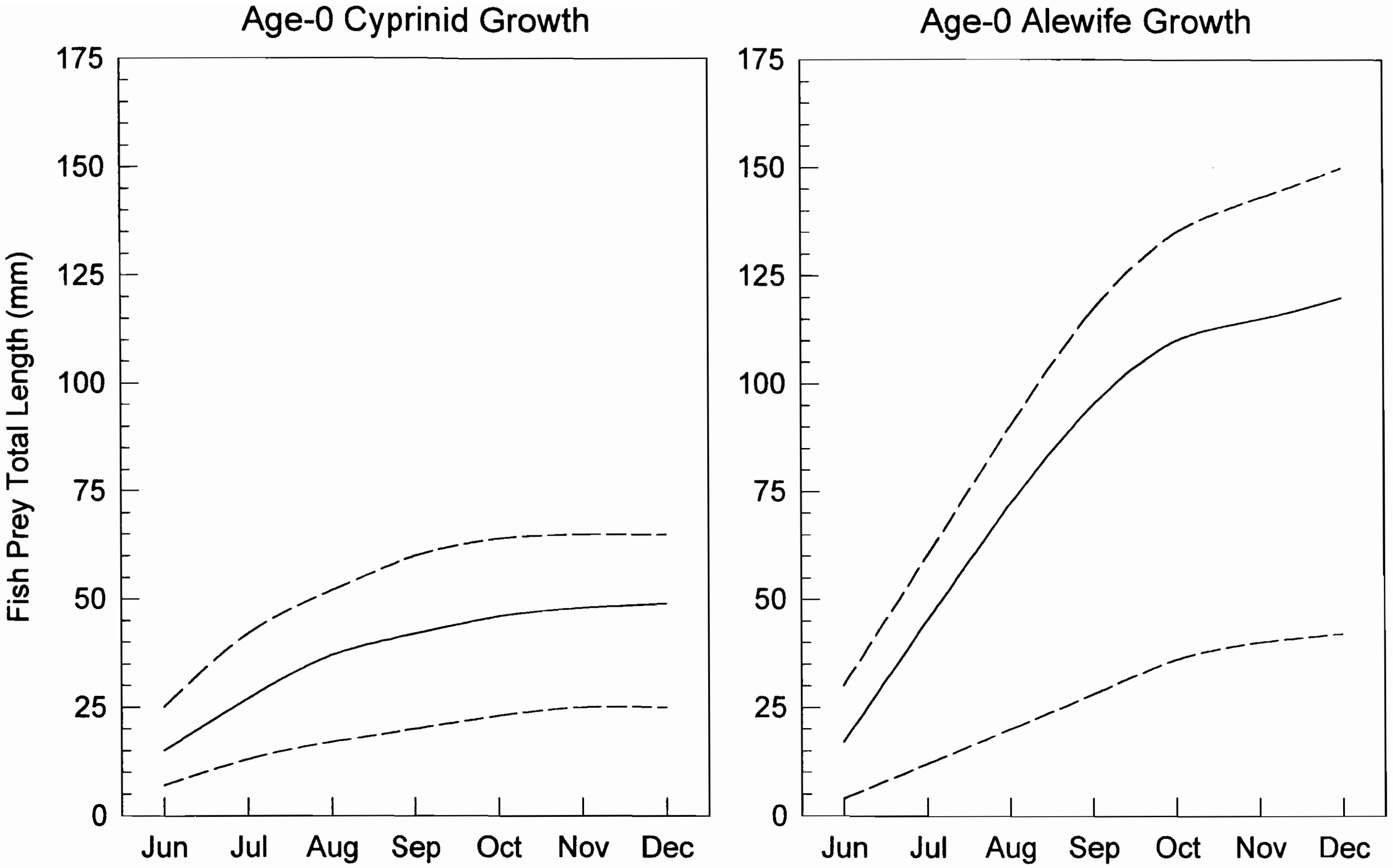


Figure 1.21. Patterns of first-year increases in total lengths (mm) for cyprinids and alewives in Smith Mountain Lake. Median total lengths are represented by the solid lines and the ranges in size distribution are represented by the dashed lines. Cyprinid growth data is from this study and alewife growth data is from Tisa (1988).

striped bass (150-270 mm TL) were less than predicted, a few alewives slightly larger than estimated maximum ingestibility limits were also eaten (Figure 1.20). However, actual sizes of alewives consumed relative to maximum predicted sizes were significantly less (t-test for regression coefficients, $t=3.32$, $P=0.01$). Because age-0 alewives were only consumed by striped bass ≥120 mm TL (Figure 1.20), smaller predators may have been gape limited for this prey type. Based on the prey body depth-predator gape width regression relationship, a 120-mm striped bass could consume age-0 alewives as large as 48 mm TL. Age-0 alewife growth data from Smith Mountain Lake (Tisa 1988) suggests that some ingestible-sized alewives (<48 mm TL) are morphologically available throughout the growing season (Figure 1.21). Further, patterns of age-0 alewife cohort biomass availability to small (<120 mm TL) juvenile striped bass support these results (from Tisa 1988; Figure 1.22). However, only 23% of first-year alewife biomass is available to small striped bass throughout the growing season. In addition, available age-0 alewife biomass for small-mode individuals drops sharply beginning in November and declines throughout the remainder of the growing season, further limiting consumption of this prey fish type. In contrast, alewives provide a continuous supply of forage to large juveniles (>150 mm TL) throughout the growing season. Overall, 67% of the first-year alewife production is within the morphological constraints of larger striped bass during the first season of growth.

Physiological Indices of Health

1994. - Relative condition (K_n; range 76-105), liver-somatic index (LSI; range 0.47-1.40), and lipid index (LI; range 0.08-0.37) for juvenile striped bass in both river arms of Smith Mountain Lake displayed similar temporal patterns

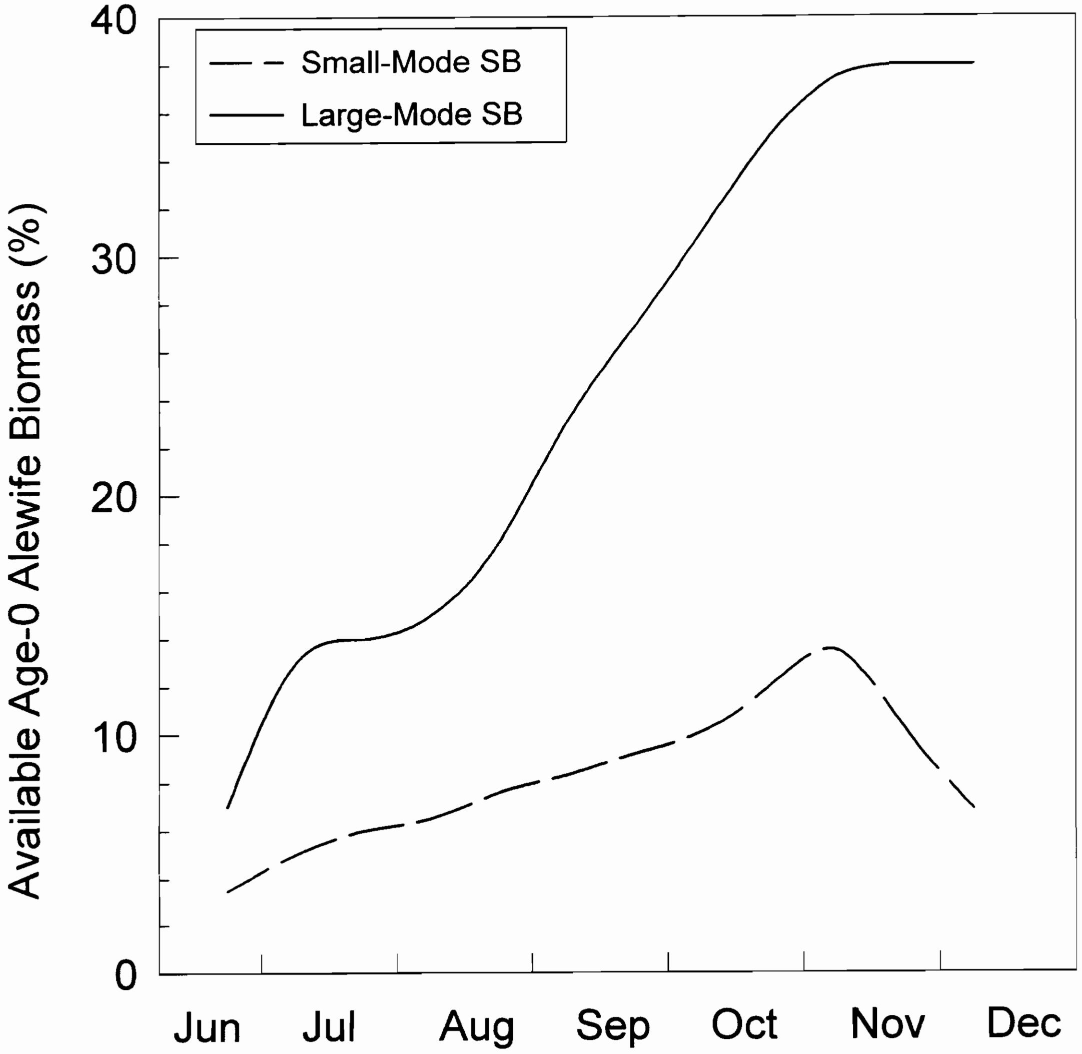


Figure 1.22. Percent of age-0 alewife biomass ingestible by median total length small- and large-mode age-0 striped bass over the growing season in Smith Mountain Lake (data from Tisa 1988).

over the 1994 growing season, while stomach-fullness index (SFI; range 0-2.38) values were highly variable during this period (Figure 1.23). Although median health indice values for striped bass were lowest immediately post-stocking in both river arms, striped bass stocked in the Blackwater River were in significantly better health than juveniles stocked in the Roanoke River (K_n: 89 and 76, respectively, Mann-Whitney, $U=1,383.5$, $P<0.01$; LSI: 0.75 and 0.47, respectively, Mann-Whitney, $U=928.0$, $P<0.01$; LI: 0.15 and 0.08, respectively, Mann-Whitney, $U=1,326.0$, $P<0.01$). However, physiological health of striped bass in both river arms increased progressively over the growing season and, by mid-December, median indice values were greater than at any time during the growing season in both the river arms (K_n: 101 and 105, respectively; LSI: 1.25 and 1.40 respectively; LI: 0.30 and 0.37, respectively). Interestingly, striped bass from the Blackwater River displayed smaller positive increases in these indices from the time of stocking until the end of the growing season ($K_n=113\%$; LSI=226%; LI=247%) than did juveniles in the Roanoke River ($K_n=138\%$; LSI=264%; LI=375%). Despite these differences, median fall values for were significantly greater then median summer values for both the Roanoke (K_n: Kruskal-Wallis, $H=280.0$, $df=6$, $P<0.0001$; LSI: Kruskal-Wallis, $H=250.8$, $df=6$, $P<0.0001$; LI: Kruskal-Wallis, $H=427.9$, $df=6$, $P<0.0001$; Table 1.7) and Blackwater (K_n: Kruskal-Wallis, $H=122.2$, $df=6$, $P<0.0001$; LSI: Kruskal-Wallis, $H=37.1$, $df=6$, $P<0.0001$; LI: Kruskal-Wallis, $H=235.5$, $df=6$, $P<0.0001$; Table 1.7) River arms. Although median SFI values were typically higher during summer months, no significant differences existed among months over the growing season for either the Roanoke (Kruskal-Wallis, $H=10.2$, $df=6$, $P=0.17$; Table 1.7) or Blackwater (Kruskal-Wallis, $H=3.0$, $df=6$ $P=0.23$; Table 1.7) River arms.

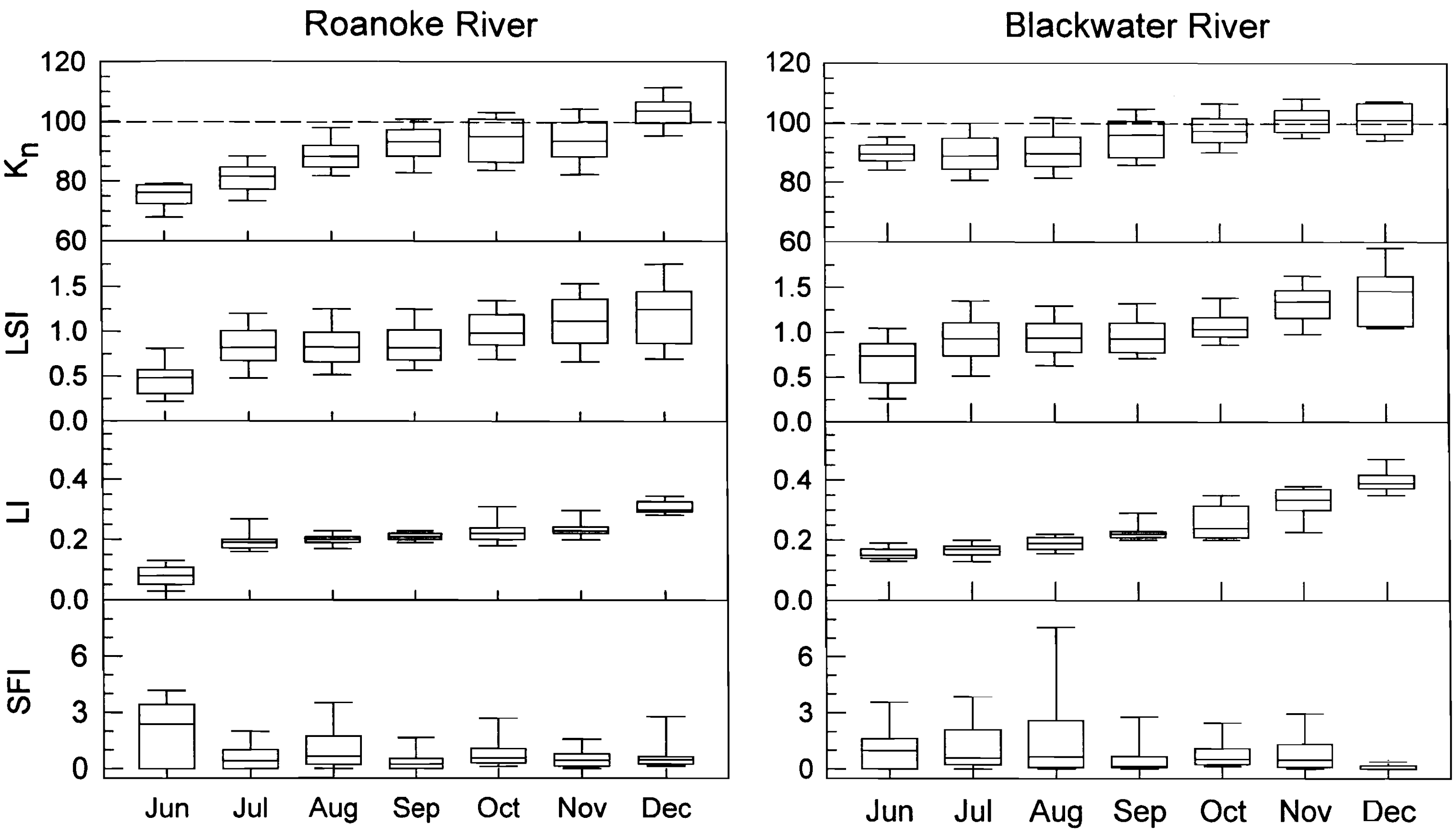


Figure 1.23. Temporal patterns in relative condition (K_n), liver-somatic index (LSI), lipid index (LI), and stomach-fullness index (SFI) for juvenile striped bass in the Roanoke and Blackwater River arms of Smith Mountain Lake during the 1994 growing season. Medians are represented by the lines within each box plot, 75th and 25th percentiles are represented by the upper and lower boundaries of each box plot, respectively, and the 90th and 10th percentiles are represented by the error bars above and below each box plot, respectively. The dashed line at 100 K_n reflects expected condition for a fish of a given size.

Table 1.7. Monthly Dunn's multiple comparisons of differences in physiological indices of well-being (K_n, LSI, LI, SFI) for juvenile striped bass from Figures 1.23 and 1.25. Comparisons that did not differ significantly (P>0.05) share a common subscript.

Sampling Season	Sampling Site	Physiological Index	Multiple Comparison						
1994-95	Roanoke River	K_n	Jun^a	Jul^{ab}	Aug^b	Sep^b	Oct^b	Nov^b	Dec
		LSI	Jun	Jul^a	Aug^a	Sep^a	Oct^b	Nov^b	Dec^b
		LI	Jun	Jul^a	Aug^{ab}	Sep^{bc}	Oct^{cd}	Nov^d	Dec^d
		SFI	Jun	Jul^a	Aug^a	Sep^a	Oct^a	Nov^a	Dec^a
	Blackwater River	K_n	Jun^a	Jul^{ab}	Aug^{ab}	Sep^{bc}	Oct^c	Nov^c	Dec^c
		LSI	Jun	Jul^a	Aug^a	Sep^a	Oct^a	Nov^a	Dec^a
		LI	Jun^a	Jul^a	Aug	Sep^b	Oct^b	Nov^b	Dec^b
		SFI	Jun^a	Jul^a	Aug^a	Sep^a	Oct^a	Nov^a	Dec^a
1995-96	Roanoke River	K_n		Jul^a	Aug^a	Sep^a	Oct^b	Nov^b	
		LSI		Jul^a	Aug^a	Sep^a	Oct^a	Nov	
		LI		Jul	Aug	Sep	Oct^a	Nov^a	
		SFI		Jul	Aug^a	Sep^a	Oct^{ab}	Nov^b	
	Blackwater River	K_n		Jul^a	Aug^{ab}	Sep^{ab}	Oct^b	Nov	
		LSI		Jul^a	Aug^a	Sep^b	Oct^b	Nov^b	
		LI		Jul	Aug	Sep^a	Oct^a	Nov^a	
		SFI		Jul^a	Aug^a	Sep^b	Oct^b	Nov	

Size-specific patterns in K_n, LSI, and LI were observed for juvenile striped bass in both river arms of Smith Mountain Lake, while SFI displayed no distinct trend with striped bass body length (Figure 1.24). Median values for the indices of health were lowest for the smallest size classes in both the Roanoke and Blackwater River arms (K_n: 80 and 90, respectively; LSI: 0.67 and 0.45, respectively; LI: 0.06 and 0.15, respectively). However, indices of health values increased progressively as striped bass increased in size and were significantly higher for the largest size classes (K_n: 108 and 104, respectively; LSI: 1.48 and 1.67, respectively; LI: 0.43 and 0.42, respectively) in both the Roanoke (K_n: Kruskal-Wallis, $H=283.7$, $df=18$, $P<0.0001$; LSI: Kruskal-Wallis, $H=259.3$, $df=18$, $P<0.0001$; LI: Kruskal-Wallis, $H=367.2$, $df=18$, $P<0.0001$; Table 1.8) and Blackwater (K_n: Kruskal-Wallis, $H=366.7$, $df=18$, $P<0.0001$; LSI: Kruskal-Wallis, $H=360.0$, $df=18$, $P<0.0001$; LI: Kruskal-Wallis; $H=205.4$, $df=18$, $P<0.0001$; Table 1.8) River arms. Stomach-fullness index (SFI) was highly variable (Figure 1.24) and no significant differences existed among 10-mm size classes in either the Roanoke (Kruskal-Wallis, $H=6.9$, $df=18$, $P=0.32$; Table 1.8) or Blackwater (Kruskal-Wallis, $H=17.5$, $df=18$, $P=0.31$; Table 1.8) River arms.

1995. - As occurred in 1994, relative condition (K_n; range 89-106), liver-somatic (LSI; range 1.03-1.63), and lipid (LI; range 0.19-0.30) indices of juvenile striped bass in both the Roanoke and Blackwater River arms displayed similar temporal patterns over the growing season, while stomach-fullness index (SFI; range 0-2.62) values were highly variable during this period (Figure 1.25). Although physiological health for juveniles in both river arms was significantly greater in 1995 than 1994 immediately post-stocking (K_n: Mann-Whitney, $U=2,302.5$, $P<0.01$; LSI: Mann-Whitney, $U=2,699.0$, $P<0.01$; LI: Mann-

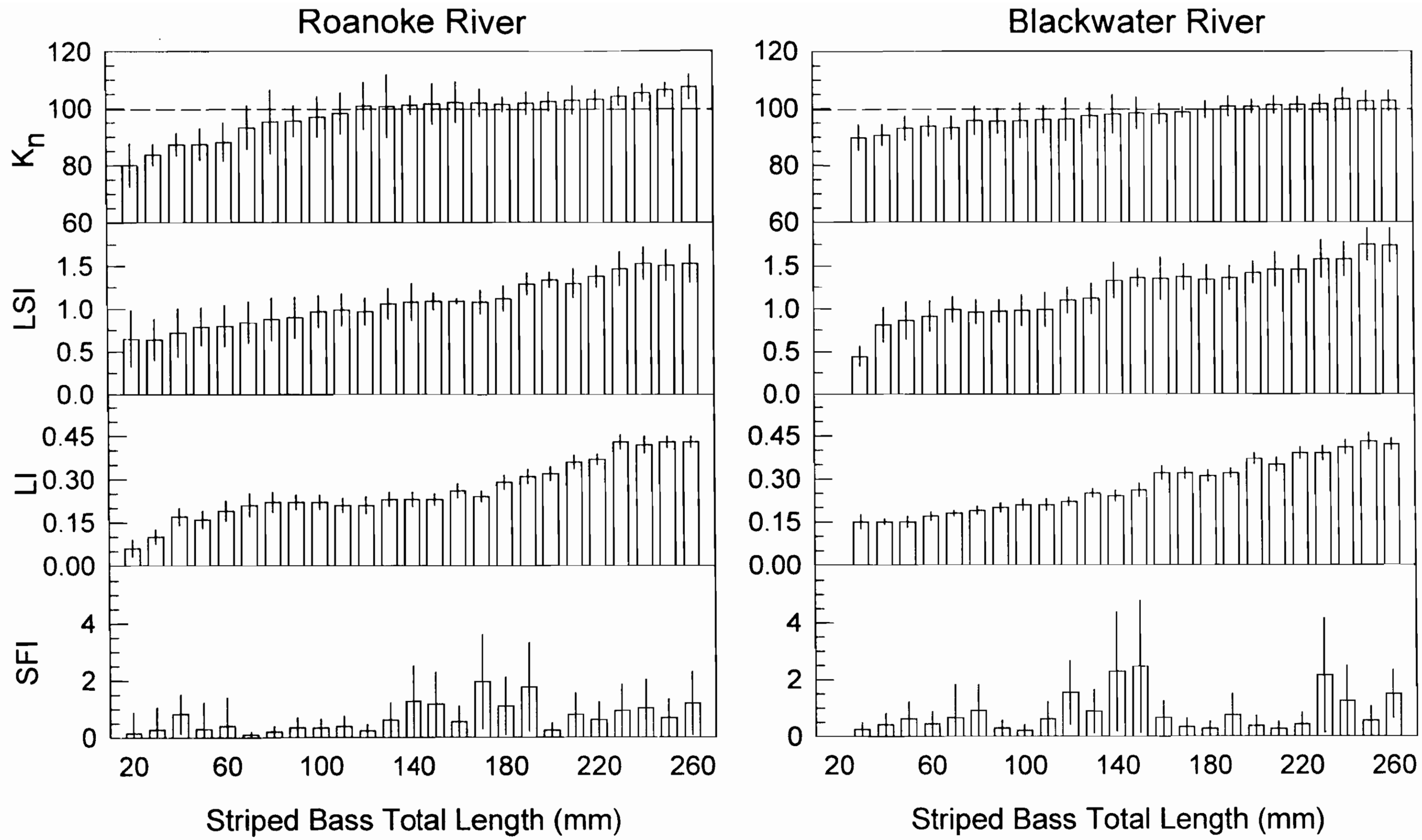


Figure 1.24. Size-dependent patterns in relative condition (K_n), liver-somatic index (LSI), lipid index (LI), and stomach-fullness index (SFI) for juvenile striped bass in the Roanoke and Blackwater River arms of Smith Mountain Lake during the 1994 growing season. Values for each 10-mm size class are the medians and error bars represent the quartile ranges. The dashed line at 100 K_n reflects expected condition for a fish of a given size.

Table 1.8. Dunn's multiple comparisons by 20-mm size class interval of differences in physiological indices of condition (K_n, LSI, LI, SFI) for juvenile striped bass from Figures 1.24 and 1.26. Comparisons that did not differ significantly ($P > 0.05$) share a common subscript.

Sampling Season	Sampling Site	Physiological Index	Multiple Comparison												
1994-95	Roanoke	K_n	20^{a}	40^{a}	60^{ab}	80^{bc}	100^{bc}	120^{bc}	140^{c}	160^{c}	180^{c}	200^{c}	220^{c}	240^{c}	260^{c}
	River	LSI	20^{a}	40^{a}	60^{abc}	80^{abcd}	100^{bcd}	120^{bcd}	140^{cd}	160^{cd}	180^{d}	200^{e}	220^{e}	240^{e}	260^{e}
		LI	20^{a}	40^{a}	60^{a}	80^{a}	100^{a}	120^{ab}	140^{abc}	160^{abc}	180^{bc}	200^{bc}	220^{c}	240^{d}	260^{d}
		SFI	20^{a}	40^{a}	60^{a}	80^{a}	100^{a}	120^{a}	140^{a}	160^{a}	180^{a}	200^{a}	220^{a}	240^{a}	260^{a}
	Blackwater	K_n	30^{a}	40^{a}	60^{a}	80^{a}	100^{ab}	120^{ab}	140^{ab}	160^{ab}	180^{b}	200^{bc}	220^{bc}	240^{bc}	260^{bc}
	River	LSI	30^{a}	40^{a}	60^{a}	80^{a}	100^{a}	120^{a}	140^{ab}	160^{ab}	180^{ab}	200^{b}	220^{b}	240^{bc}	260^{c}
		LI	30^{a}	40^{a}	60^{a}	80^{a}	100^{ab}	120^{abc}	140^{abc}	160^{abc}	180^{abc}	200^{bc}	220^{c}	240^{c}	260^{c}
		SFI	30^{a}	40^{a}	60^{a}	80^{a}	100^{a}	120^{a}	140^{a}	160^{a}	180^{a}	200^{a}	220^{a}	240^{a}	260^{a}
1995-96	Roanoke	K_n	30	40^{a}	60^{a}	80^{ab}	100^{abc}	120^{abc}	140^{bcd}	160^{cd}	180^{d}	200^{e}	220^{e}	240^{ef}	260^{f}
	River	LSI	30	40	60^{a}	80^{ab}	100^{b}	120^{bc}	140^{c}	160^{cd}	180^{d}	200^{d}	220^{d}	240^{d}	260
		LI	30	40^{a}	60^{a}	80^{a}	100^{a}	120^{a}	140^{ab}	160^{b}	180^{c}	200^{c}	220^{cd}	240^{d}	260^{d}
		SFI	30^{a}	40^{a}	60^{a}	80^{a}	100^{a}	120^{a}	140^{a}	160^{a}	180^{a}	200^{a}	220^{a}	240^{a}	260^{a}
	Blackwater	K_n	30^{a}	40^{a}	60^{a}	80^{ab}	100^{bc}	120^{bc}	140^{cd}	160^{d}	180^{de}	200^{ef}	220^{ef}	240^{f}	250
	River	LSI	30	40^{a}	60^{ab}	80^{abc}	100^{abc}	120^{abc}	140^{bc}	160^{bc}	180^{c}	200	220	240	250
		LI	30	40^{a}	60^{a}	80^{a}	100^{ab}	120^{b}	140^{c}	160^{c}	180^{d}	200^{de}	220^{e}	240^{f}	250^{f}
		SFI	30^{a}	40^{a}	60^{a}	80^{b}	100^{b}	120^{b}	140^{c}	160^{c}	180^{c}	200^{c}	220^{c}	240^{c}	250^{c}

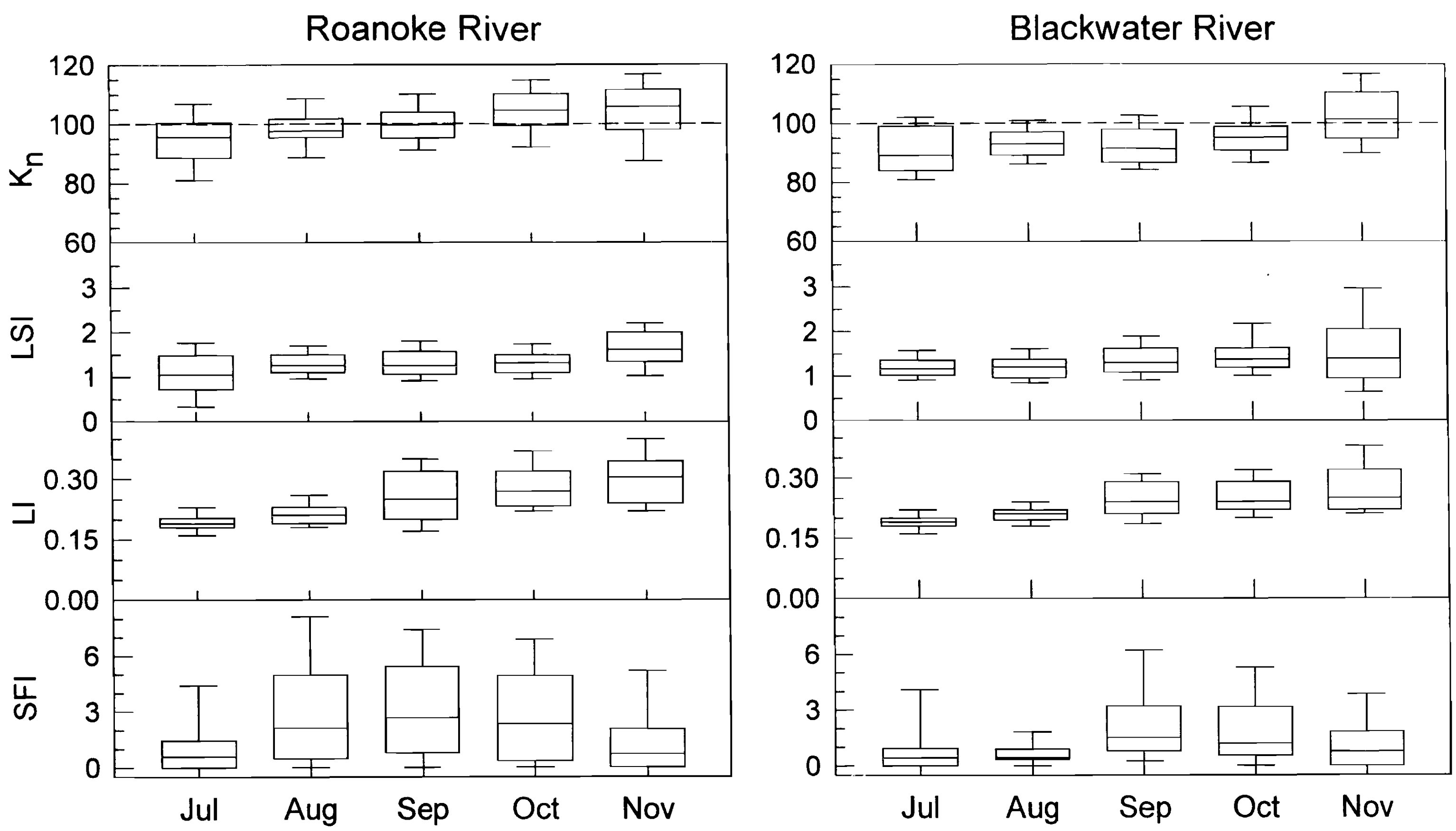


Figure 1.25. Temporal patterns in relative condition (K_n), liver-somatic index (LSI), lipid index (LI), and stomach-fullness index (SFI) for juvenile striped bass in the Roanoke and Blackwater River arms of Smith Mountain Lake during the 1995 growing season. Medians are represented by the lines within each box plot, 75th and 25th percentiles are represented by the upper and lower boundaries of each box plot, respectively, and the 90th and 10th percentiles are represented by the error bars above and below each box plot, respectively. The dashed line at 100 K_n reflects expected condition for a fish of a given size.

Whitney, $U=2{,}803.0$, $P<0.01$), index values were not significantly different between years at the end of the growing season (K_n: Mann-Whitney, $U=136.5$, $P=0.07$; LSI: $U=137.0$, $P=0.07$; LI: Mann-Whitney, $U=135.5$, $P=0.08$). In contrast to 1994, striped bass stocked in the Blackwater River were in similar health to juveniles stocked in the Roanoke River (K_n: 88 and 95, respectively, Mann-Whitney, $U=356.0$, $P=0.13$; LSI: 1.22 and 1.03, respectively, Mann-Whitney, $U=144.5$, $P=0.24$; LI: 0.19 and 0.19, respectively, Mann-Whitney, $U=19.0$, $P>0.17$). In both the Roanoke and Blackwater River arms, median values increased progressively over the growing season and by the end of November were greater than at any time during the growing season (K_n: 106 and 101, respectively; LSI: 1.63 and 1.44, respectively; LI: 0.30 and 0.25, respectively). However, striped bass collected from the Roanoke River displayed greater increases over the growing season ($K_n=111\%$; $LSI=154\%$; $LI=163\%$) than did juveniles in the Blackwater River ($K_n=107\%$; $LSI=119\%$; $LI=132\%$). Despite these differences, median fall values were significantly greater than median summer values for both the Roanoke (K_n: Kruskal-Wallis, $H=84.6$, $df=6$, $P<0.0001$; LSI: Kruskal-Wallis, $H=38.9$, $df=6$, $P<0.0001$; LI: Kruskal-Wallis, $H=162.4$, $df=6$, $P<0.0001$; Table 1.7) and Blackwater (K_n: Kruskal-Wallis, $H=38.5$, $df=6$, $P<0.0001$; LSI: Kruskal-Wallis, $H=141.8$, $df=6$, $P<0.0001$; LI: Kruskal-Wallis, $H=20.7$, $df=6$, $P<0.0001$; Table 1.7) River arms. Although no significant differences existed among median SFI values over the growing season for either the Roanoke (Kruskal-Wallis, $H=10.3$, $df=6$, $P=0.37$; Table 1.7) and Blackwater (Kruskal-Wallis, $H=11.8$, $df=6$, $P=0.33$; Table 1.7) River arms, SFI was typically higher during late summer and early fall (Figure 1.25).

Size-specific patterns in K_n, LSI, and LI were again observed for juvenile striped bass in both river arms, while SFI displayed no distinct trend with striped bass body length (Figure 1.26). Median indices of health were again lowest for the smallest size classes in both the Roanoke and Blackwater River arms (K_n: 82 and 85, respectively; LSI: 0.23 and 0.50, respectively; LI: 0.17 and 0.12, respectively). However, median indices of health values increased progressively with striped bass body length and were significantly greater for the largest size classes (K_n: 110 and 108, respectively; LSI: 2.74 and 2.39, respectively; LI: 0.46 and 0.42, respectively) for both the Roanoke (K_n: Kruskal-Wallis, $H=290.4$, $df=18$, $P<0.0001$; LSI: Kruskal-Wallis, $H=301.1$, $df=18$, $P<0.0001$; LI: Kruskal-Wallis, $H=243.0$, $df=18$, $P<0.0001$; Table 1.8) and Blackwater (K_n: Kruskal-Wallis, $H=328.8$, $df=18$, $P<0.0001$; LSI: Kruskal-Wallis, $H=353.2$, $df=18$, $P<0.0001$; LI: Kruskal-Wallis, $H=363.7$, $df=18$, $P<0.0001$; Table 1.8) River arms. However, SFI was highly variable (Figure 1.26) and no significant differences existed among size class intervals for either the Roanoke (Kruskal-Wallis, $H=12.2$, $df=18$, $P=0.33$; Table 1.8) or Blackwater (Kruskal-Wallis, $H=17.6$, $df=18$, $P=0.24$; Table 1.8) River arms.

Sized-Dependent Seasonal Health Indices. - Measures of health (K_n, LSI, and LI) for large-mode juvenile striped bass (150-270 mm TL) were greater than those observed for small-mode fish (90-120 mm TL) during late fall in both 1994 and 1995 (Figure 1.27). During late November and December 1994, K_n, LSI, and LI for small-mode striped bass were approximately 10%, 33%, and 47% less, respectively, than those observed for large-mode fish. Similarly, K_n, LSI, and LI were approximately 16%, 34%, 39% less, respectively, for small-mode striped bass during November 1995. Differences among these indices for small- versus large-mode striped bass during both fall 1994 and 1995 were significant (K_n: Mann-Whitney, $U=11,905.0$, $P<0.0001$; LSI: Mann-Whitney,

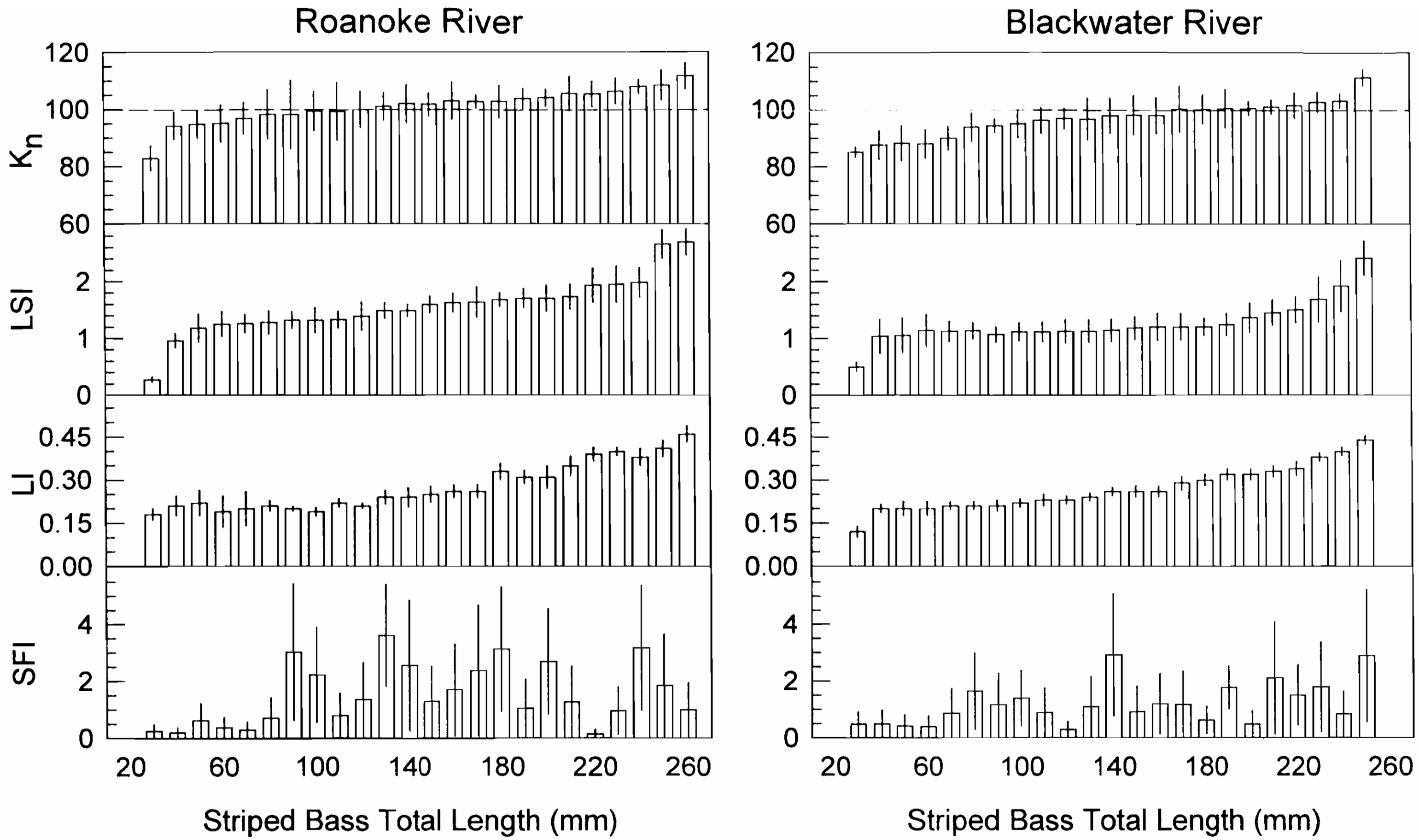


Figure 1.26. Size-dependent patterns in relative condition (K_n), liver-somatic index (LSI), lipid index (LI), and stomach-fullness index (SFI) for juvenile striped bass in the Roanoke and Blackwater River arms of Smith Mountain Lake during the 1995 growing season. Values for each 10-mm size class are the medians and error bars represent the quartile ranges. The dashed line at 100 K_n reflects expected condition for a fish of a given size.

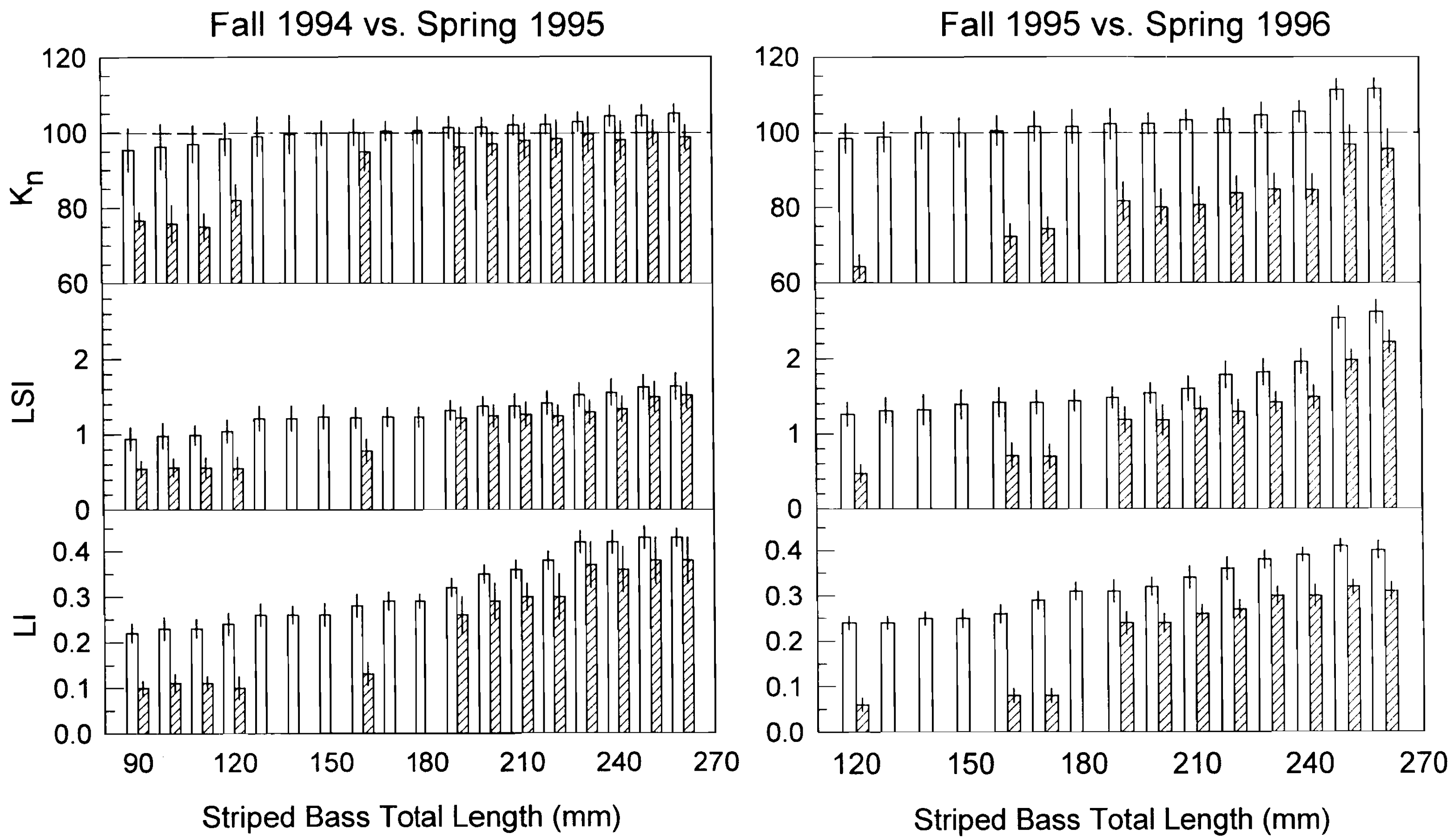


Figure 1.27. Comparison of juvenile striped bass relative condition (K_n), liver-somatic index (LSI), and lipid index (LI), by 10-mm size-class intervals before (fall: unshaded bars) and after (spring; shaded bars) wintering in Smith Mountain Lake during the 1994-95 and 1995-96 sampling seasons (both Roanoke and Blackwater River arms pooled). Values for each 10-mm size class are the medians and error bars represent the quartile ranges. The dashed line at 100 K_n reflects expected condition for a fish of a given size.

$U = 12{,}766.0$, $P < 0.0001$; LI: Mann-Whitney, $U = 2{,}526.5$, $P < 0.0001$).

During spring 1995 and 1996, large-mode striped bass had greater physiological indices of health than small-mode fish of the same cohort (Figure 1.27). Index values for small-mode juveniles were lower during both March 1995 (K_n=-22%, LSI=-54%, LI=-67%) and April 1996 (K_n=-19%, LSI=-58%, LI=-75%) than those observed for large-mode fish. In addition, smaller individuals were thin and emaciated, whereas larger striped bass were plump and appeared to be in good health. These results, particularly differences in lipid index values, suggest that greater overwinter stress and consumption of stored energy reserves were imposed on smaller individuals because median health indice values were significantly less for small- versus large-mode striped bass (K_n: Mann-Whitney, $U = 3{,}865.0$, $P < 0.0001$; LSI: Mann-Whitney, $U = 4{,}015.5$, $P < 0.0001$; LI: Mann-Whitney, $U = 2{,}306.5$, $P < 0.0001$). However, actual differences in index values may have been greater than estimated because only small-mode striped bass that had survived the winter and were collected during spring sampling; small individuals that may have depleted their energy reserves and suffered starvation-induced, overwinter mortality over this period would not have been included in these comparisons.

Although indices of health declined for both small- and large-mode juvenile striped bass between fall and spring sampling for both collection years, small-mode fish suffered considerably greater decreases in health over this period than large-mode fish (Figure 1.27). Over the winter of 1994-95, K_n, LSI, and LI of small-mode juveniles declined by 20%, 44%, and 54%, respectively; in contrast, these indices declined by only 5%, 10%, and 13%, respectively, for large-mode striped bass. Similarly, over the winter of 1995-96, small-mode fish displayed greater decreases in K_n (30%), LSI (55%), and LI (72%) than large-mode striped bass (19%, 21%, and 23%, respectively). Differences in health indices for both small- and large-mode striped bass between fall and spring sampling periods were significantly different (K_n: Mann-Whitney, $U = 5{,}029.5$, $P < 0.0001$; LSI: Mann-Whitney, $U = 5{,}337.5$, $P < 0.0001$, LI: Mann-Whitney, $U = 2{,}743.5$, $P < 0.0001$). Additionally, both small- and large-mode striped bass collected during spring 1996 had suffered significantly greater decreases in physiological indices of health than fish collected during spring 1995 (K_n: Mann-Whitney, $U = 452.0$, $P < 0.01$; LSI: Mann-Whitney, $U = 636.5$, $P < 0.01$; LI: Mann-Whitney, $U = 670.5$, $P < 0.01$), possibly reflecting the greater severity and duration of low temperatures that occurred during the 1995-96 winter.

DISCUSSION

Temporal and size-dependent patterns of spatial distribution and population dynamics of age-0 striped bass post-stocking were examined to determine which factor(s) contribute to the recruitment bottleneck that has been observed in Smith Mountain Lake, Virginia, over the past three decades. These are considered within the context of trophic relationships, in particular forage-fish availability, and physiological indices of health in order to evaluate feeding opportunities and success relative to growth, overwinter survival, and recruitment to age 1 for this juvenile predator.

Dispersal and Spatial Distribution

Although age-0 striped bass exhibited dissimilar patterns of dispersion and spatial distribution between stocking sites in Smith Mountain Lake during the 1994 and 1995 growing seasons, these within-site patterns were similar for each stocking cove between sampling years. Juveniles stocked at the Hales Ford state boat ramp on the Roanoke River arm remained within the immediate vicinity of the stocking site for the first week post-stocking before gradually dispersing to outermost regions of the cove adjacent to the main river channel. In contrast, fingerlings stocked at the Penhook state boat ramp on the Blackwater River arm dispersed rapidly from the immediate stocking site by the first night post-stocking and were only collected along the outermost region of the cove during the remainder of the growing season. However, in both stocking coves, age-0 striped bass were collected primarily from shallow, littoral areas containing a mixture of sand and fine gravel substrate with little physical habitat structure and that graded gradually to deep water. This type of habitat typifies the Hales Ford stocking cove and, not surprisingly, juveniles were collected within this cove throughout the 1994 and 1995 growing seasons. In contrast, the Penhook stocking cove contains primarily large gravel and cobble with an underlying clay substrate, an abundance of physical structure (boat docks, piers, and submerged timber), and a shoreline that grades steeply to deep water. Shallow, gradually-grading shorelines with appropriate substrate types and no physical structure occur only along the outermost region of this cove, which is where juvenile striped bass were collected. Therefore, it appears that the dissimilar patterns of dispersion observed for juvenile striped bass between the Hales Ford and Penhook stocking sites during the 1994 and 1995 growing seasons may be attributed to differences in the availability of suitable habitat between these two coves.

The movement patterns and habitat preferences observed for juvenile striped bass within the stocking coves of Smith Mountain Lake are consistent with studies on this life stage in other systems. In Tennessee reservoirs that are morphometrically similar to Smith Mountain Lake, it has been documented that striped bass <120 mm TL dispersed rapidly away from the immediate stocking vicinity but tended to remain in the general area throughout the growing season as long as shallow, littoral zones containing sand and/or gravel substrate occurred nearby (Van Den Avyle and Higginbotham 1979; Saul 1981; Richardson 1982; Humphreys 1983; Van Den Avyle et al. 1983). Additionally, similar observations have been reported for juvenile striped bass in systems with self-sustaining populations. Matthews et al. (1992) documented that age-0 striped bass <150 mm TL in Lake Texoma, Oklahoma-Texas, preferred shallow shorelines with rock-gravel or sand substrates with little physical habitat structure over those with either coarse gravel or sand/silt substrates.

Additionally, catch rates for estuarine populations of juvenile striped bass were reportedly highest in shallow areas with slow to moderate current and sand or fine gravel substrate, and lowest along steep shorelines riprapped with large boulders in both the Delaware River system (Kernehan et al. 1981) and Potomac River estuary (Setzler-Hamilton et al. 1981) of Chesapeake Bay, the Hudson River, New York (Wells et al. 1991), and the Sacramento-San Joaquin estuary on the California coast (Turner and Chadwick 1972).

Limited dispersal from the stocking coves by juvenile striped bass during summer months may also be attributed to preference for warmer water temperatures in these nearshore areas of Smith Mountain Lake. These shallow regions, where active feeding and growth occur, typically had water temperatures that exceeded 25°C through mid-September in both 1994 and 1995. Results of laboratory experiments on temperature selection and growth of age-0 striped bass match these field observations. Studies by Meldrim and Gift (1971) suggested that the preferred temperature for 80-130 mm TL striped bass is 25°C, while Cox and Coutant (1981) determined that optimal growth temperatures for similar-sized juveniles ranged from 24-26°C. Additionally, Coutant et al. (1984) observed that striped bass ranging from 82-222 mm TL preferred temperatures >26°C in summer. These results support the hypothesis of a thermal niche (Magnuson et al. 1979) for juvenile striped bass that lies in the 24-27°C range. Because these data clearly lie above the 20-24°C range of summer temperatures selected in the field by subadults (Coutant and Carroll 1980) and the 18-22°C range occupied by adults (Schaich and Coutant 1980; Waddle et al. 1980; Cheek et al. 1985), it would appear that striped bass may partition their habitat ontogenetically by age or size class along a thermal gradient. As a result, juvenile striped bass in Smith Mountain Lake may select shallow, littoral areas not only because of habitat preferences, but because temperature regimes in these areas are more optimal for feeding and growth during this life stage.

Despite these habitat and temperature preferences of age-0 striped bass, catch-per-unit-effort (CPUE) for juveniles within both stocking coves gradually declined from late summer through the end of the growing season. Concurrently, CPUE increased in main channel areas of both river arms over this same time period, suggesting that juveniles were dispersing from the stocking sites to deeper, pelagic regions of the lake. For striped bass collected during this time period, significant size-dependent differences were observed within versus outside the stocking coves; fish <150 mm TL were rarely captured outside the stocking coves while fish greater than this size were always collected from main channel areas. Although my sampling design was not sufficiently extensive to statistically analyze these dispersal patterns and quantitatively survey all regions within Smith Mountain Lake in which age-0 striped bass occurred, several hypotheses can be generalized to explain these temporal and size-dependent trends of juvenile striped bass movement.

It is possible that dispersal of hatchery-reared fish is a slow process; these fish might be disoriented initially, requiring time to adapt to the natural environment, before dispersing slowly after several weeks of acclimation. Alternatively, dispersal may take place shortly after release, but the migrants are captured less easily than fish that do not migrate. For example, dispersal of juveniles from shallow, littoral zones of the stocking coves to deeper, pelagic areas of the main channel appears to have begun in late summer. However, dispersal out of the coves could have begun earlier and was not detected because deeper water areas were not sampled with gillnets until August. In the

Potomac River, Setzler-Hamilton et al. (1981) documented that beginning in August and continuing through the fall, age-0 striped bass >100 mm TL were collected with increasing frequency at deeper, downriver stations. In contrast, fish less than this size were collected primarily from shallow, upriver stations during this same time period. Similar observations have also been reported in the Hudson River (McLaren et al. 1988; Wells et al. 1991), the Delaware River system (Kernehan et al. 1981), and Cherokee Reservoir, Tennessee (Saul 1981; Humphreys 1983). Although these studies are consistent with the differential size-dependent dispersion of juvenile striped bass during fall months observed in Smith Mountain Lake, they do not explain why larger juveniles disperse to deeper, offshore areas while smaller individuals remain in shallow, nearshore regions.

In a laboratory study by Coutant et al. (1984), it was observed that 82-222 mm TL striped bass selected water temperatures <25°C during fall. The authors hypothesized that lower temperature preferences during this time period may be a seasonal effect induced by declining photoperiod that lowers thermal preferences independently of thermal acclimation. Although these results suggest that juvenile striped bass prefer cooler water masses during fall months and may actively search for these areas, water temperatures in nearshore regions of Smith Mountain Lake during this time period were also <25°C. As a result, water temperature regimes during fall months alone are not sufficient to explain movement patterns of age-0 striped bass from shallow, littoral zones to deeper, pelagic areas.

A more probable hypothesis to explain size-dependent dispersal patterns is the search for and availability of appropriate-sized food resources. In Smith Mountain Lake, striped bass <100 mm TL collected by electrofishing in nearshore regions were typically caught singly, while larger juveniles that were collected using gillnets from deepwater areas almost always occurred in groups of 3-6 individuals. Although this disparity can perhaps be viewed as a bias associated with using different sampling gears, a more reasonable explanation can be derived by examining food habits and associated foraging behaviors between these different size classes. Small striped bass consumed prey items (invertebrates and age-0 cyprinids) which were abundant and distributed throughout nearshore regions of Smith Mountain Lake. In contrast, larger striped bass were strictly piscivorous, feeding primarily on age-0 alewives, a pelagic schooling species with a highly contagious distribution. In terms of optimal foraging theory (Emlem 1966; MacArthur and Pianka 1966), small juvenile striped bass may utilize a saltatory search mode (cruise between locales and scan upon stopping; O'Brien et al. 1990; Browman and O'Brien 1992) to locate abundant, small prey in nearshore regions, whereas low encounter rates and search for large, schooling prey may cause larger striped bass to become more active in areas where these food resources are encountered (Helfman 1994). Therefore, dispersion of striped bass >150 mm TL to pelagic areas in search of larger food items (i.e. age-0 alewives) and the adoption of an adult-like schooling behavior (Matthews et al. 1988) can be viewed as an adaptive strategy of active search that optimizes the probability of encounter with patchily-distributed forage fish prey. Small striped bass, in contrast, occupy shallow, nearshore areas throughout the growing season and individually search for abundant, ingestible-sized prey items that are located throughout these regions.

The size-dependent differences in juvenile striped bass foraging behaviors and dispersal observed in Smith Mountain Lake are consistent with reports from other impoundments. Humphreys (1983) reported that age-0 striped bass tended to remain in nearshore areas of the stocking vicinity when invertebrates and ingestible-sized threadfin shad were abundant, and moved away from these areas when food resources became limited. In Keystone Reservoir, Oklahoma, larger age-0 striped bass were always collected in small schools and showed a well-defined pattern of migration to downriver sites in search of ingestible-sized age-0 gizzard shad (Mensinger 1970). Higginbotham (1979) reported that larger (>100 mm TL) juvenile striped bass feeding on age-0 threadfin and gizzard shad in Watts Bar Reservoir, Tennessee, also exhibited a schooling tendency. Additionally, Bowles (1975) showed that presence of food reduced the area traveled by striped bass fingerlings held in circular tanks. These observations suggest that size-dependent differences in dispersion may have been due to differences in distribution and ingestibility of available food resources in the stocking coves and main channel areas of Smith Mountain Lake. Growth rates, food habits, and forage-fish availability, which will be discussed in the next section, also support this hypothesis and provide an answer to the size disparity observed between juveniles that disperse to pelagic areas and those that remain in littoral zones near the stocking sites.

In summary, age-0 striped bass exhibited dissimilar patterns of dispersion and spatial distribution from stocking sites in Smith Mountain Lake. This disparity can be attributed to differences in suitable habitat (gently-sloping littoral zones with sand and fine gravel substrate with little or no physical habitat structure immediately adjacent to deep water areas) between these two coves. Lack of dispersal by small juvenile striped bass during the growing season can be attributed to preferred water temperatures (>25°C) during summer months and an abundance of ingestible-sized prey (invertebrates and age-0 cyprinids) in nearshore regions. Movements of larger individuals to main channel areas and adoption of schooling behavior appear to be a result of active search for larger prey items (i.e. age-0 alewives) located in these pelagic regions of Smith Mountain Lake.

First-Year Growth

Progressive increases in total length from the time of stocking through the end of the growing season were observed for age-0 striped bass in both river arms of Smith Mountain Lake. In the Roanoke River, juveniles increased from a median total length of 32 to 114 mm in 1994 and 47 to 180 mm in 1995, while striped bass from the Blackwater River increased from 42 to 180 mm in 1994 and 48 to 150 mm in 1995. Although these observed size increases vary between sites and years, they are consistent with first-year growth estimates observed in other waters. For anadromous populations of striped bass, total length estimates at the end of the first growing season ranged from 76 mm in the Hudson River (Rathjen and Miller 1957; Dey 1981; Wells et al. 1991) to 186 mm in the Choctawatchee River, Florida (Wigfall and Barkuloo 1975). Total length estimates for juvenile striped bass in Chesapeake Bay and its tributaries (Mansueti 1961; Bason 1971; Kernehan et al. 1981; Setzler-Hamilton et al. 1981), Albemarle Sound, North Carolina (Trent 1962), and the Sacramento-San Joaquin River system (Heubach et al. 1961; Turner and Chadwick 1972) were also within this range. Additionally, Humphries and Cumming (1973) observed that fingerlings retained in freshwater hatchery ponds through their first year grew rapidly and reached larger sizes (170 mm TL) than fish from natural waters. Growth studies on age-0 landlocked striped bass have been reported to be much higher than coastal and hatchery-reared juveniles. First-year growth to total lengths >200 mm is common (Stevens 1957; Mensinger 1970; Ware 1970; Erickson et al. 1971; Weaver 1975; Axon 1979; Van Den Avyle and Higginbotham 1979; Saul 1981; Moss and Lawson 1982; Nifong 1982; Richardson 1982; Humphreys 1983), and growth to over 300 mm TL has also been documented (Mensinger 1970; Ware 1970; Erickson et al. 1971; Axon 1979). Although increases in weight over the first growing season of life have not been reported in other studies, it would be reasonable to assume that estimates observed from Smith Mountain Lake would concur with juvenile striped bass in both marine and freshwater systems.

Although striped bass exhibited consistent increases in first-year growth post-stocking, month-by-month length-frequency histograms over the 1994 and 1995 growing seasons illustrate the development of two distinct size modes of fish from the same stocked cohort. Further, contrasting intersite differences in juvenile striped bass growth rates were observed during both sampling years. In 1994, striped bass stocked in the Blackwater River were larger (median = 42 mm TL) than juveniles stocked one week later in the Roanoke River (median = 32 mm TL), while striped bass stocked in the Roanoke River in 1995 were slightly larger (median = 52 mm TL) than juveniles stocked one week later in the Blackwater River (median = 50 mm TL). Despite these initial differences, length-frequency distributions for juvenile striped bass in both river arms during both sampling years diverged over summer months and by October, a distinct bimodal distribution was evident. At the end of the growing season, the initial differences in size between river arms were still evident; striped bass in the Blackwater River were larger (median = 180 mm TL) than juveniles in the Roanoke River (median = 114 mm TL) by mid-December 1994 and striped bass in the Roanoke River were larger (median = 180 mm TL) than juveniles in the Blackwater River (median = 150 mm TL) by the end of November 1995. However, regardless of river site and sampling year, large-mode juveniles (1994: range 186-266 mm TL; 1995: range 183-261 mm TL) were twice as large in length than small-mode fish (1994: 84-140 mm TL; 1995: 80-137 mm TL). In addition, a greater proportion of small- and large-mode striped bass at the end of the 1994 growing season were collected from the Roanoke and Blackwater Rivers, respectively, whereas the converse was observed at the end of the 1995 growing season. Because size at the end of the first growing season has been shown to be a critical determinant of overwinter survival and, ultimately, recruitment to the adult population (see Overwinter Survival), processes influencing both growth rates and the size divergence observed for age-0 striped bass stocked in Smith Mountain Lake will be examined in the next section.

Mechanisms Influencing First-Year Growth Patterns

Growth depensation (divergence in size over time among individuals in the same age class; Keast and Eadie 1985) has been observed for a variety of marine and freshwater fishes. Current hypotheses attribute this phenomenon to: (1) hatching date and nursery site influence on growth rates; (2) stocking of disparate size classes; (3) sex-related differences in growth rates; (4) nonsexual genetic differences in growth rates; (5) influence of food habits and prey availability; and (6) competition for limiting resources. However, all explanations, to some extent, involve food habits and prey availability as a factor that perpetuates and accentuates the size disparity. Because the mechanisms influencing growth depensation in landlocked populations of age-0 striped bass have not been adequately examined, each hypothesis will be considered in terms of its potential contribution to the differential growth and development of bimodality observed for this life stage in Smith Mountain Lake.

Hatching Date and Nursery Site Influence On Growth Rates. - Extended spawning or hatching periods of fish should increase the probability that the environment experienced by individuals of the same year class will differ with hatch date. This has been observed for some fish species that have protracted or disrupted spawning periods, and has been linked to hatching-date-dependent differences in growth (Kramer and Smith 1962; Summerfelt 1975; Thorpe and Morgan 1978; Bailey et al. 1980; Crecco and Savoy 1985; Phillips et al. 1995). For example, studies on largemouth bass have demonstrated that rapidly falling water temperatures during spring disrupted spawning activity, resulting in differences in hatching date between early- and later-spawned progeny. Subsequently, the initial length advantage afforded to early-hatched fish resulted in greater increases in size and a significant size advantage during summer months (Kramer and Smith 1962; Summerfelt 1975; Miller and Storck 1984; Isely and Noble 1987; Phillips et al. 1995). Additionally, larger adult largemouth bass have been observed to spawn earlier than smaller adults (Miranda and Muncy 1987; Goodgame and Miranda 1993). On average, fingerlings from large adults reached swim-up about one week earlier than fingerlings produced by smaller largemouth bass. However, size of larvae at hatching did not differ significantly between small and large adults. Because length increases of the earlier-hatched age-0 largemouth bass were greater during summer months than those of later-hatched fish, the authors believed that length advantages obtained from being spawned earlier resulted from having a longer growing season, and possibly first choice and a wider selection of ingestible-sized prey. Although early spawning was not directly linked to greater progeny survival, their greater lengths and greater length increases during summer months indicate that early-hatched largemouth bass may be recruited to the adult population in greater proportion than later-hatched fish. Therefore, age-0 fish of the same age but hatched on widely-different dates could experience initial differences in size distribution that could affect their food habits and, consequently, growth.

Although striped bass do not naturally reproduce in Smith Mountain Lake, hatching date, duration spent in hatchery ponds, and individual variability in growth rates among striped bass within and among these ponds may have contributed to the observed differences in size distribution at the time of stocking. Further, the relative time at which larvae were introduced to grow-out ponds and subsequently harvested for stocking, coupled with initial variability in size distribution, may have initiated the growth depensation observed in Smith Mountain Lake. As a result, examination of the procedures utilized for spawning and rearing striped bass at Brookneal Hatchery is warranted to determine the plausibility of these factors in terms of their contribution to differential growth of age-0 striped bass prior to stocking, as well as the time at which these fish were introduced to Smith Mountain Lake.

Beginning in mid-April and continuing until mid to late May, running-ripe striped bass broodstock were collected from the Roanoke River and artificially spawned at Brookneal Hatchery. Although the 4-6 wk period in which striped bass were spawned is somewhat protracted, each grow-out pond was stocked with the progeny from 6-8 females and 12-16 males; swim-up larvae that were transferred from spawning tanks to each pond were similar in both age (5- or 6-days-old) and size (3-4 mm TL) at the time of introduction. Striped bass remained in hatchery ponds until the available food supply (zooplankton) began to decline; this occurred approximately 5-6 wk after the ponds had been stocked with swim-up larvae. At this point, fingerlings were harvested from the ponds for stocking in the order that they were initially stocked. For example, swim-up larvae stocked in one pond in mid-April would reach stocking size and begin to depress zooplankton populations earlier than striped bass stocked in a different pond in early May (S. Arthur, VDGIF Brookneal Hatchery, personal communication). Because the duration that striped bass spent in rearing ponds was approximately the same among ponds, and larvae within a pond were the same age and size at the time of introduction, differences in hatching date, initial sizes, and duration of the grow-out period appear to be negligible. However, early-hatched striped bass were ready for removal from hatchery ponds before later-hatched fish. For example, in 1994, age-0 striped bass stocked in the Blackwater River one week earlier than fingerlings stocked in the Roanoke River (15 June versus 22 June, respectively) were also hatched and transferred to grow-out ponds one week earlier (30 April versus 07 May, respectively; S. Arthur, VDGIF Brookneal Hatchery, personal communication). Interestingly, striped bass stocked in the Blackwater River were also larger (median = 42 mm TL) than juveniles stocked in the Roanoke River (median = 32 mm TL). Although individual variability in feeding success and metabolic efficiency among striped bass larvae within the same or different hatchery ponds was not examined in this study, other studies on fingerling striped bass culture in hatchery ponds have indicated that these factors may play a significant role in determining the size distribution at the time of stocking (Harper et al. 1968; Harper and Jarman 1971; Humphries and Cumming 1971, 1973). However, whether individual variability can be attributed to genetic differences (see *Nonsexual Genetic Differences In Growth Rates*) or serendipity (i.e. a good first feeding encounter may promote the chance of a second and so on) cannot be determined at this time. Regardless of the actual source of the initial differences in size distribution, the advantage afforded to fingerling striped bass that have reached a slightly larger size prior to stocking and/or that are stocked one or two weeks earlier in the growing season may allow a wider selection of ingestible-sized prey to be available, particularly forage fish (see *Food Habits And Prey Availability*), which may, in turn, have contributed significantly to the divergence in length-frequency distributions and development of bimodality observed in Smith Mountain Lake during the 1994 and 1995 growing seasons.

Stocking Of Disparate Size Classes. - Fingerling size at stocking can be a critical factor in the success of stocking programs designed to maintain fish populations. However, stocking programs using small predators must be coordinated with the size and abundance of prey available because the narrow size range of prey vulnerable to small predators (Gillen et al. 1981; Ney and Orth 1986). For example, Fielder (1992a) reported that walleyes stocked as fingerlings (36 mm TL) exhibited greater growth rates over summer months than fry (10 mm TL) stocked at the same time in Lake Oahe, South Dakota. The author concluded that the initial length advantage afforded to fingerling walleyes provided this size class with a broader range of ingestible-sized prey throughout summer months, resulting in a larger size by the end of the growing season and a significantly greater contribution to fall young-of-year abundance. In contrast, Serns and Andrews (1991) observed that among three size classes (100 mm, 200 mm, and 300 mm TL) of muskellunge fingerlings stocked in Arrowhead Lake, Wisconsin, 100-mm fish exhibited significantly greater growth over summer months than the other two size classes. The authors attributed the greater growth rate of the smallest size class to an abundance of ingestible-sized age-0 yellow perch, which co-occurred in littoral areas with these small muskellunge fingerlings. Although other studies comparing first-year growth rates of smaller- versus larger-stocked size classes of walleye (Jennings and Phillipp 1992), muskellunge (Hanson et al. 1986; Margenau 1992; Szendrey and Wahl 1996), northern pike (Flickinger and Clark 1978), brown trout (*Salmo trutta*; Garman and Nielsen 1982), striped bass (Dorazio et al. 1991), and hybrid striped bass (*M. saxatilis x M. chrysops*; Yeager 1988) have reported variable results, the consensus was that adequately-sized prey relative to size of predators at the time of stocking was the primary determinant affecting growth rates in these populations.

In Smith Mountain Lake, the divergence in size distribution and development of bimodality observed in 1994 could have been strictly a result of stocking two distinct size classes of age-0 striped bass (Phase I: range 24-51 mm TL; Phase II: range 53-97 mm TL). However, several lines of evidence indicate that this may not be the case. Cage studies conducted immediately post-stocking demonstrated that while Phase I striped bass stocked in mid-June suffered only 1.8% mortality within 48 hours, Phase II fish stocked on 06 and 13 July suffered high initial mortality (99.5% and 51%, respectively; Michaelson 1996). Assuming these post-stocking mortality estimates are representative of actual stocking mortality rates, Phase II fish comprised no more than 3% of the population of age-0 striped bass stocked into Smith Mountain Lake. Examining the bimodal size distribution in mid-December, large-mode fish (>150 mm TL) comprised 28% of age-0 striped bass population. Although the large-mode of fish observed at the end of the growing season probably contained Phase II fish, these differences (3% versus 28%) indicate that Phase I fish probably also contributed to the larger mode. Additionally, microscopic examination of otoliths revealed that only 2% of fish collected during 1994 contained OTC marks (only Phase II fish were marked). Furthermore, both field (Shelton et al. 1979; Timmons et al. 1980) and modeling (DeAngelis and Mattice 1979; DeAngelis and Coutant 1982) studies have demonstrated that bimodal length distributions can develop naturally in populations of age-0 fishes from initial unimodal distributions due to differences in feeding success. Therefore, these lines of evidence indicate that the bimodal distribution observed in mid-December 1994 was primarily a result of divergence in length of Phase I striped bass, probably mediated by size-dependent differences in food habits and forage-fish prey availability (see *Food Habits And Prey Availability*), and not strictly due to stocking of larger Phase II fingerlings.

In contrast to 1994, Phase I and Phase II striped bass in 1995 had overlapping size distributions (range 31-81 mm TL and 45-97 mm TL, respectively) at the time of stocking in July. Additionally, Phase I fingerlings in 1995 had a considerably broader size distribution than Phase I fish in 1994. Because Phase II fish were not OTC marked, it is not possible to directly determine the contribution of this group of fish to the bimodal size distribution observed in mid-November. However, only 7,300 Phase II striped bass were stocked in 1995 (versus 228,800 Phase I fish). Adjusting these numbers using 1995 stocking mortality data from Michaelson (1996; Phase I: 32%; Phase II: 6%), Phase II fish comprised approximately 4% of the age-0 striped bass population immediately post-stocking. In comparison, the proportion of large-mode fish (>150 mm TL) in the age-0 striped bass population at the end of the growing season was 38%. Therefore, it would appear once again that Phase II fish were not the primary cause of bimodality observed in mid-November. A more plausible explanation is that the broad length distribution of Phase I striped bass at the time of stocking, in addition to Phase II fish, continued to diverge over the growing season, probably driven by size-dependent differences in food habits and forage-fish prey availability (see *Food Habits And Prey Availability*).

Sex-Related Differences In Growth Rates. - Numerous studies on reproductively-mature fish populations have demonstrated that sex-related differences in growth rates often exist due to the differential costs associated with the elaboration of gametes (Beckman 1949; Padfield 1951; MacKinnon 1972; Hodgkiss and Mann 1978; Wootton et al. 1978; Diana 1979; Wootton et al. 1980; Diana and Makay 1979; Diana 1983a, 1983b; Diana and Salz 1990; Adams et al. 1992). For example, the ovaries of female threespine sticklebacks (*Gasterosteus aculeatus*) comprise approximately 20% of total body weight, while the testes of males constitute less than 2% of total body weight (Wootton et al. 1978, 1980). In northern pike (*E. lucius*), 6-18 times more energy is deposited in the ovaries by females than in the testes by males (Diana 1983a, 1983b). Because the amount of energy available for both somatic and reproductive tissues is finite, greater energetic expenditures by female fishes after the onset of sexual maturity, which is typically delayed to later ages in female sport fishes in order to increase the probability of a successful breeding event (Wootton 1990), at the expense of somatic growth, result in differential growth rates between sexes.

Although sex-related differences in growth have been observed for reproductively-mature fishes, age-0 striped bass are immature and put no energy into gonad growth. As a consequence, there should be no difference in growth between males and females at this life stage due to lack of reproduction. Diana (1983a) observed that both male and female age-0 northern pike allocated 0% of their energy budget to reproduction and grew at similar rates over the growing season in Lac Ste. Anne, Alberta. Additionally, Shelton et al. (1979) and Timmons et al. (1980) determined that the bimodal length distributions observed for age-0 largemouth bass in West Point Reservoir, Alabama-Georgia, were not caused by sex-related growth differences as both male and female juveniles were equally distributed in the two modes. Similar observances have also been reported for bimodal distributions that developed in hatchery-reared Atlantic salmon (*Salmo salar*; Thorpe 1977; Thorpe and Morgan 1978; Bailey et al. 1980). Although juvenile striped bass were not sexed in this study, it would be reasonable to assume that because these fish were not yet reproductively mature, the divergence in size distribution observed in Smith Mountain Lake could not be attributed to differences in growth between male and female fish.

Nonsexual Genetic Differences In Growth Rates. - Because the genetic contribution of parental broodstock and genotype variability among age-0 striped bass was not examined in this study, it is not possible to positively determine if faster-growing individuals (i.e. large-mode fish) inherited "superior" growth traits from their parents than slower-growing, small-mode fish. However, it would seem reasonable to assume that if male and/or female striped bass parents contained attributes favoring fast growth and/or aggressive feeding behavior, these traits would be passed on to their progeny. Further, the large number of adult striped bass (6-8 females and 12-16 males) used for producing larvae stocked into each hatchery pond make it highly possible that some degree of genotypic variability exists among striped bass within a given pond, resulting in the differential growth rates observed in this study and have been documented in others. For example, Thorpe and Morgan (1978) reported that for bimodal length distributions of hatchery-reared Atlantic salmon, 80-90% of the variation between mean size and proportion of individuals within each size mode were due to genetic factors. Although interfamily variation in the proportion of individuals within each size mode was due to both parents, the male parent was determined to be more influential. In contrast, variation in the mean length of individuals in each size mode was influenced almost entirely by the female parent. Additionally, Thorpe (1977) and Bailey et al. (1980) observed that larger mean length in the upper mode of Atlantic salmon was strongly favored by early-smolting male parents and to a lesser extent by late-smolting female parents; mean length in the upper mode may be related to age at various life stages of both male and female. However, the proportion of individuals in the upper mode was more strongly correlated with the age of female parents; late-smolting and early-maturing female Atlantic salmon tended to produce relatively greater proportions of fish in the upper mode. Although the degree of genetic variability within the age-0 striped bass population is unknown, it is quite possible that differential inheritance of parental genotypes among striped bass larvae favoring disparate growth rates may have contributed to the development of bimodality observed in Smith Mountain Lake.

Food Habits And Prey Availability. - In general, food habits of age-0 striped bass in Smith Mountain Lake agreed with diet data collected for striped bass in other systems. For coastal populations in spawning tributaries and estuaries, juveniles <145 mm TL relied heavily on invertebrate forage (Merriman 1941; Heubach et al. 1961; Markle and Grant 1970; Schaefer 1970; Bason 1971; Boynton et al. 1981). Although age-0 fishes were of minor importance in smaller striped bass diets during the first year, significant utilization of fish by larger juveniles was observed (Merriman 1971; Wigfall and Barkuloo 1975; Boynton et a. 1981). Freshwater hatchery-pond studies have shown that fingerling striped bass consumed primarily copepods and cladocerans at smaller sizes (<60 mm TL), while aquatic insects became more important as fish grew to larger sizes over the duration of the growing season (Sandoz and Johnston 1965; Harper et al. 1968; Harper and Jarman 1971; Humphries and Cumming 1971, 1973). However, utilization of fish prey (larval gizzard shad and cyprinids) was observed only for the largest juveniles (>100 mm TL; Sandoz and Johnston 1965; Logan 1967; Harper et al. 1968; Harper and Jarman 1971; Humphries and Cumming 1973). Similar ontogenetic shifts in food habits have also been observed for reservoir populations of age-0 striped bass; juveniles switched from primarily zooplankton and aquatic insects (chironomid larvae and pupae, and ephemeropteran nymphs) to strictly larval fishes (gizzard shad, threadfin shad, inland silversides (*Menidia beryllina*), brook silversides, and/or cyprinids) at sizes >100 mm TL (Stevens 1957; Gomez 1970; Ware 1970; Weaver 1975; Ricci and Ney 1978; Axon 1979; Higginbotham 1979; Saul 1981; Richardson 1982; Van Den Avyle et al. 1983; Humphreys 1983; Matthews et al. 1992).

Size-dependent differences in diet composition between small- and large-mode juvenile striped bass appears to be the primary factor causing differential growth in Smith Mountain Lake. Small-mode juveniles (<120 mm TL) maintained a mixed diet throughout the growing season, consuming invertebrates (zooplankton and benthic aquatic insects) and age-0 cyprinids. In contrast, large-mode fish (>150 mm TL) were strictly piscivorous, consuming primarily age-0 alewives. Other studies on landlocked striped bass populations have documented that an abundant supply of ingestible-sized, age-0 clupeid prey is critical for rapid growth during the first year of life. Age-0 striped bass in Cherokee (Saul 1981; Humphreys 1983) and Norris (Richardson 1982)

Reservoirs, Tennessee, grew slowly in years when larval gizzard and threadfin shad were not abundant. Humphreys (1983) also reported that age-0 striped bass stocked in July 1981 attained an average total length of only 94 mm by December and that 96% of their diet was composed of invertebrate prey. In 1982, when juvenile striped bass exhibited good growth (>200 mm TL by the end of their first growing season), fish prey (primarily age-0 threadfin shad) comprised the majority of their diet. Axon (1979) documented that first-year growth of one of five year classes of striped bass in Herrington Lake, Kentucky, was poor due to low standing stocks of ingestible-sized gizzard and threadfin shad during that year. Similar reports of size-dependent differences in diet resulting in differential first-year growth of striped bass have also been observed in Santee-Cooper Reservoir, South Carolina (Stevens 1957), Canton Reservoir, Oklahoma (Gomez 1970), Lakes Hollingsworth, Parker, and Hunter, Florida (Ware 1970), and J. Percy Priest Reservoir, Tennessee (Weaver 1975).

Differential growth rates within an age-0 cohort of predatory fishes may result because faster-growing individuals change to the next developmental stage at a point when forage-fish prey are within ingestibility limits. However, slower-growing individuals reach the transition size at a later date and may not be able to successfully make the transition to piscivory because fish prey may be too large for consumption at this time. For example, in Bulls Shoal Lake, Missouri-Arkansas, Aggus and Elliott (1975) observed that age-0 largemouth bass that could begin feeding on larval gizzard shad early in the growing season not only grew rapidly, but these individuals were able to maintain a sufficient length advantage and continue to utilize this forage-fish prey throughout the growing season. In contrast, smaller age-0 largemouth bass that could not completely switch from a diet of invertebrates to larval fish grew slowly, even in the presence of abundant zooplankton and aquatic insect prey, and, over the growing season, had progressively less fish prey available to them because gizzard shad outgrew their ingestibility limits. Several studies have also reported similar observations for populations of age-0 piscivores (Paloheimo and Dickie 1966; Applegate 1967; Popova 1967; Chevalier 1973; Pasch 1975; Rainwater and Houser 1975; Shelton et al. 1979; Timmons et al. 1980; Miller and Storck 1984; Keast and Eadie 1985; McIntyre et al. 1987; Wicker and Johnson 1987; Buijse and Houthuijzen 1992; Phillips et al. 1995). Therefore, larger juvenile striped bass could become piscivorous earlier in the growing season than smaller conspecifics, and, because smaller individuals may not encounter ingestible-sized fish prey when they reach the transition size, they are relegated primarily to an invertebrate diet and grow at a considerably slower rate.

Differences in the size of fingerling striped bass at stocking and the time of the growing season at stocking, in addition to inter-annual variability between stocking sites, may have also contributed to differences in growth rates observed within the age-0 striped bass cohort. In 1994, fingerlings stocked in the Blackwater River (15 June, median TL = 42 mm) grew at a faster rate than juveniles stocked in the Roanoke River (22 June, median TL = 32 mm). In contrast, striped bass stocked in the Roanoke River in 1995 (12 and 14 July, median TL = 52 mm) grew at a faster rate than fingerlings stocked in the Blackwater River (14 and 20 July, median TL = 50 mm). Because fingerlings that are stocked at a larger size and/or earlier in the growing season will have a wider selection of ingestible-sized prey items available, particularly age-0 forage fishes (Madenjian et al. 1991), these disparities may be strictly a direct result of differences in the size and time at stocking. For example, Van Den

Avyle and Higginbotham (1979) reported that in Watts Bar Reservoir, Tennessee, a strong correlation existed between size and date of stocking, and first-year growth, presumably due to a greater abundance of ingestible-sized forage-fish prey for larger and/or early-stocked fingerling striped bass. In addition, reservoirs are dynamic systems (Hayes et al. 1993; Annett et al. 1996). As a result, feeding conditions, and consequently growth rates, may vary within fish populations on both a temporal and spatial basis; conditions at a particular stocking site one year that favor rapid growth may not the following year. However, because temporal and spatial variability in feeding conditions between stocking sites and river arms was not examined in this study, it is not possible to directly attribute this factor to the observed differences in juvenile striped bass growth rates between years and river sites.

Because differences in diet quality are linked directly to the composition of prey types consumed (Keast and Eadie 1985), it is very likely that the growth divergence observed for age-0 striped bass in Smith Mountain Lake is due to differences in caloric densities among prey items consumed by small- and large-mode fish. Fish prey provides more energy per gram wet weight than aquatic invertebrates (Cummins and Wuycheck 1971; Prus 1975; Penczak et al. 1984; Moore 1988), and among invertebrates, zooplankton provides the least amount of energy per gram wet weight (Cummins and Wuycheck 1971). In addition, assimilation efficiency for fish prey is greater than for invertebrates (Brett and Groves 1979). Although energetic quality and assimilation efficiency of consumed prey items were not evaluated for age-0 striped bass in Smith Mountain Lake, studies on other juvenile piscivores have shown that size-dependent differences in prey types consumed (invertebrates versus fish) resulted in differential growth rates between small and large individuals over the growing season. Keast and Eadie (1985) observed that large-mode largemouth bass in Lake Opinicon, Ontario, which consumed strictly fish prey, had a higher gross energy content in their diet and were able to maintain a greater energy level throughout summer months because of their piscivorous food habits than small-mode fish which consumed primarily zooplankton and aquatic insect prey. The inability of small-mode largemouth bass to switch to piscivory forced this size class to rely completely on lower energetic-quality prey items which, not only resulted in slower growth, but also further restricted their ability to consume larger fish prey. Stahl and Stein (1994) reported that greater efficiency in assimilation and consumption, coupled with high caloric density of fish prey, likely accounted for faster saugeye (*S. vitreum x S. canadense*) growth in Ohio ponds with an abundance of ingestible-sized gizzard shad. Therefore, differences in diet quality, as a consequence of dissimilarities in prey items consumed relative to their availability, appears to have contributed significantly to differential growth within the age-0 striped bass cohort observed in Smith Mountain Lake.

In a laboratory feeding experiment, Miranda and Muncy (1989) determined that for largemouth bass consuming gizzard shad, faster bass growth rates were observed when shad were consumed at sizes greater than 5% of predator body weight. Although larger prey items have lower relative surface-to-volume ratios and evacuate slower in proportion to their size (percent per hour) than smaller prey items (Fange and Grove 1979), Miranda and Muncy (1989) hypothesized that the faster growth rates observed for largemouth bass that consumed larger gizzard shad (>5% of body weight) could be attributed to greater absolute energetic returns relative to the time spent feeding and higher utilization efficiencies for these larger prey items. These results are interesting in that they may further explain differences in growth rates observed between piscivorous small- and large-mode striped bass. In the present study, small-mode striped bass consumed age-0 cyprinids that ranged from 0.3%-4.0% of their body weight, whereas large-mode juveniles consumed age-0 alewives that ranged from 2.0%-11.3% of their body weight. Because the alewife to striped bass body weight ratio lies primarily above 5% while the cyprinid to striped bass body weight ratio lies entirely below this value, it would seem intuitive to assume that large-mode juveniles consuming relatively larger alewives not only gain more energy on an absolute basis, but utilized this prey type more efficiently, resulting in faster growth than small-mode fish consuming relatively smaller, less-energetically profitable cyprinids. However, utilization efficiencies and nutritional content may differ between largemouth bass-gizzard shad and striped bass-cyprinid-alewife; therefore caution must be used when extrapolating bioenergetic relationships among similar fish species (Ney 1993). Nonetheless, these results seem to indicate that differences in the relative weight relationship between forage-fish prey consumed by small- versus large-mode juvenile striped bass may have contributed to the growth depensation observed during the 1994 and 1995 growing seasons in Smith Mountain Lake.

Kerr (1971), using a bioenergetics approach to examine the hypothesis that growth efficiency of predatory fishes may be directly linked to the metabolic costs associated with searching for prey, determined that not only did growth efficiency decrease when prey organisms were small relative to predator size, but that sustained growth required increasingly larger prey items even if they were not abundant. Support for this hypothesis comes from evaluation of physiological indices of health. Although median relative condition (K_n), liver-somatic index (LSI), and lipid index (LI) for all sizes of juvenile striped bass increased progressively over the 1994 and 1995 growing seasons, size-dependent differences in these indices were clearly apparent as large-mode striped bass had significantly higher indice values than small-mode fish. These differences observed for age-0 striped bass in Smith Mountain Lake are consistent with those observed in other systems. In Tennessee reservoirs, striped bass <125 mm TL consistently had lower Fulton-type condition values (0.69-0.91) than larger juveniles (1.08-1.28; Saul 1981; Richardson 1982; Humphreys 1983); in Smith Mountain Lake, relative condition ranged from 80-90 and 104-110 for small- and large-mode fish, respectively. Brown and Murphy (1991a) observed that liver weight (mg/g) of age-0 striped bass increased with body size and attributed this relationship to the greater deposition of surplus energy reserves (glycogen and lipid) in this organ by larger individuals as has been observed in studies of other fishes (MacKinnon 1972; Tyler and Dunn 1976; Heidinger and Crawford 1977; Bulow et al. 1978; Delahunty and de Vlaming 1980; Allen and Wootton 1982; Adams and McLean 1985). Additionally, lipid content, measured in this study as lipid index, was also observed to increase with increasing age-0 striped bass body size (Brown and Murphy 1991a). Similar observations have also been reported for largemouth bass (Isely 1981; Wicker and Johnson 1987; Miranda and Hubbard 1994), smallmouth bass (Oliver et al. 1979), bluegill (Cargnelli and Gross 1997), brook trout (Cunjak 1988), rainbow trout (Li and Brocksen 1977), and Colorado squawfish (*Ptychocheilus lucius*; Thompson et al. 1991). Because deposition of energy stores, in particular lipids, has significant implications for overwintering starvation in age-0 fishes, size-dependent differences in physiological indices of health will be discussed in greater detail later (see Overwinter Survival). Therefore, it would appear that a prolonged diet of small prey items (invertebrates and age-0 cyprinids) for small-mode juvenile striped bass during the first growing season does not provide sufficient surplus energy to sustain growth and physiological health for this size class, whereas consumption of larger fish prey by large-mode individuals supports rapid growth and the deposition of energy stores.

Because significant size-dependent differences in relative condition (K_n) were observed between small- and large-mode striped bass, these results should be viewed with caution as they indicate bias inherent with using this condition-factor approach. As stated by Le Cren (1951), K_n is calculated with the regression coefficient *b* for within subgroups and the adjusted value for y-intercept *a* for the subgroup with the maximum value of *a*. Therefore, comparisons of condition must be limited to subgroups having the same regression coefficient *b*. However, regression coefficients for small-mode juvenile striped bass (<150 mm TL) were lower than large-mode individuals (>150 mm TL) during both sampling years (1994-95: 2.98 versus 3.20, respectively; 1995-96: 2.98 versus 3.33, respectively). The result of these differences was that relative condition values were biased too high for large-mode striped bass and too low for small-mode fish. Thus, when used correctly, K_n can only compare the condition between subgroups as long as they have the same value of *b*. Because of dissimilarities in regression coefficient values between small- and large-mode juvenile striped bass during both sampling years, the use of relative condition as an index to detect size-dependent differences in physiological well-being within the same cohort lead to spurious results.

Although larger age-0 striped bass exhibited greater relative condition, liver-somatic, and lipid indice values than smaller juveniles, size-dependent differences in stomach-fullness index (SFI), a measure of feeding intensity, were not apparent. In theory, one would expect that predators that consumed larger prey (i.e. fish) would have higher SFI values than those feeding on smaller prey (i.e. invertebrates). Humphreys (1983) reported that significant size-dependent differences in SFI during the growing season were detected between small- and large-mode age-0 striped bass in Cherokee Reservoir; SFI averaged 2.4% and 4.0% for small and large juveniles, respectively. A similar observation was also documented for juvenile striped bass collected from Suisun Marsh, California (Herbold 1986). Conversely, Lewis et al. (1974) observed that SFI values were inversely related to body size for age-0 largemouth bass; values averaged 4.0% and 1.5% for small and large fish, respectively. Although no discernable increasing or decreasing trend in SFI with body size was observed for striped bass in this study, several hypothesis can be ventured to explain this phenomenon. Larger juveniles collected using gillnets may have partially regurgitated their diet contents. However, visual evidence of regurgitation was not observed in this study, although it is quite possible that this could have occurred as fish struggled upon entanglement (Ney 1990). Further, loss of stomach contents through the digestive process, which will continue even after death (Eggers 1977), could have contributed to SFI variability as striped bass were not retrieved from gillnets until the morning after these gears were set. Additionally, greater susceptibility of "hungry" fish that were actively seeking prey to electrofishing equipment and gillnets could also have influenced stomach-fullness estimates. Bryan (1974) observed that both arctic char (*Salvelinus alpinus*) and arctic grayling (*Thymallus arcticus*) had lower stomach content levels when taken by angling than by seine and attributed this discrepancy to angling selectivity for hungrier fish. However, the low proportion of empty stomachs observed for age-0 striped bass in this study does not support this hypothesis (see appendix tables A.2a-d). Finally, small striped bass in poor condition may have had higher SFI values than expected because stomach content weights would be greater relative to body weight than those observed for larger individuals in better condition. Regardless of the source for the high variability observed in estimated SFI values, this index was not a useful indicator of feeding intensity for age-0 striped bass in Smith Mountain Lake.

Differing life history characteristics of age-0 piscivores and forage fishes indicate that stocked sportfishes may encounter food deficiencies during the first-year of life (Ney and Orth 1986). Therefore, the inability of striped bass <120 mm TL to make the transition to a strictly fish diet, coupled with the nearly complete lack of age-0 alewife consumption by this size group, suggests that forage-fish prey, particularly age-0 alewives, may be limited in their vulnerability to striped bass during their first growing season. For a successful feeding event to occur, prey must be distributionally, behaviorally, and morphologically available to predators (Ney 1990). Because the magnitude of influence of each of these three components on overall availability varies as a function of the predator, the prey, and the system, limited accessibility of forage-fish prey to juvenile striped bass may be a critical factor regulating food habits, and, consequently, differential growth patterns observed in Smith Mountain Lake.

Since predators will only encounter prey when their spatial distributions overlap, co-occurrence in both space and time is the first requirement necessary for a successful feeding event. In Smith Mountain Lake, spatial distribution of age-0 cyprinids and alewives relative to small- and large-mode striped bass may partially explain the observed differences in food habits. Age-0 cyprinids were numerically abundant in shallow, littoral zones throughout the growing season, but were infrequently observed in pelagic areas of the main channel. In contrast, age-0 alewives, which were frequently observed in littoral zone during summer months (June through September), seemed to be more pelagically oriented, preferring main channel areas of Smith Mountain Lake. Although spatial distributions of cyprinids have not been characterized in other studies, comparable observations for alewives have been reported previously for Smith Mountain Lake (Tisa and Ney 1991) and other freshwater systems (Scott and Crossman 1973; O'Gorman and Schneider 1986). Large-mode striped bass, like alewives, frequented pelagic areas of the main channel; not surprisingly, alewives were the fish prey species identified most frequently in the stomachs of this size group. However, small-mode juveniles, which spatially overlapped with age-0 alewives only during summer months, rarely consumed this fish prey species; cyprinids were primarily identified in the stomach contents of those individuals that consumed fish prey. Therefore, because age-0 alewives did overlap in both space and time with juvenile striped bass in Smith Mountain Lake during summer months, factors in addition to distributional availability must have contributed to the limited utilization of this forage fish species by small-mode individuals.

Spatial and temporal availability of prey alone does not assure utilization by predators. Availability also includes a behavioral component; the predator must recognize the prey as a potential meal and successfully pursue this item. Although numerous studies have observed that juvenile striped bass prefer age-0 clupeid prey fishes (Stevens 1957; Sandoz and Johnston 1965; Logan 1967; Harper et al. 1968; Harper and Jarman 1971; Humphries and Cumming 1971; Wigfall and Barkuloo 1975; Axon 1979; Higginbotham 1979; Saul 1981; Richardson 1982; Humphreys 1983; Van Den Avyle et al. 1983), including alewives in Smith Mountain Lake (Ricci and Ney 1978; Moore 1988), it is possible that the limited consumption of this forage-fish species by small-mode striped bass resulted from a failure to recognize this prey species as a potential food source and/or poor capture success. Small-mode striped bass in the littoral zone fed primarily on invertebrate prey and may not have yet developed a search image for fish prey. As a result, even though small juveniles distributionally overlapped with age-0 alewives that were within their ingestibility limits during summer months, they may not have recognized this prey type as a potential food resource. In addition, even if small-mode striped bass had developed a search image for fish prey, the search mode utilized by this size class in the littoral zone may have further contributed to the limited consumption of age-0 alewife prey. Field collections indicated that small-mode striped bass appeared to search for prey singly, whereas large-mode individuals utilized a schooling search mode. Further, alewives are a schooling species, and this type of behavior is most effective against solitary predators because the school causes the predator to be unable to focus on single targets (Shaw 1978), thereby limiting capture success for individual prey. As a consequence, availability may be limited due to the schooling behavior utilized by alewives which is most likely pronounced for solitary predators, such as small-mode striped bass, that have not coevolved with this forage-fish species.

Analyses of morphological availability and cohort biomass patterns demonstrated that the size distribution of age-0 alewives relative to small-mode juvenile striped bass was a critical factor limiting their ability to utilize this prey resource. Although age-0 alewife growth data from Smith Mountain Lake (Tisa 1988) suggest that ingestible-sized alewives are available to both small- and large-mode striped bass during the growing season, analysis of percent first-year alewife biomass availability on a monthly basis revealed that large-mode striped bass (>150 mm TL) had a substantially greater proportion of alewife prey within their ingestibility limits than small-mode fish (<150 mm TL). Larger striped bass could utilize approximately 67% of total first-year alewife biomass compared to only 23% for small-mode individuals. In addition, ingestible-sized age-0 alewives would only be available to small-mode striped bass until late September because this forage-fish species became pelagic during fall months and, as a result, no longer overlapped spatially with small-mode striped bass. In contrast, age-0 alewives provide a continuous supply of forage to larger-mode juveniles throughout the growing season. Therefore, ingestibility limitations, coupled with temporal dissimilarities in spatial overlap and behavioral constraints in forage-fish prey recognition and capture success, appear to be the primary factors preventing small-mode striped bass from utilizing age-0 alewives during the growing season in Smith Mountain Lake. As a consequence, smaller juveniles are relegated to feeding on a mixed diet of invertebrate and age-0 cyprinid prey that is lower in energetic quality than the strictly alewife diet of larger individuals.

Ingestibility limitations may also explain why juvenile striped bass in Smith Mountain Lake were not observed to consume age-0 gizzard and threadfin shad even though other studies have reported extensive utilization of these forage-fish species (Stevens 1957; Sandoz and Johnston 1965; Logan 1967; Harper et al. 1968; Harper and Jarman 1971; Humphries and Cumming 1971; Wigfall and Barkuloo 1975; Axon 1979; Higginbotham 1979; Saul 1981; Richardson 1982; Humphreys 1983; Van Den Avyle et al. 1983). Tisa (1988) demonstrated that because age-0 gizzard shad grew rapidly during summer months, this forage-fish species was morphologically unavailable to striped bass, including larger-mode juveniles, during their first year of life. Although threadfin shad were not a component of the forage-fish complex during Tisa's study, Humphreys (1983) reported that age-0 threadfin shad often outgrew the ingestibility limits of juvenile striped bass in Cherokee Reservoir. Therefore, results from Tisa (1988) indicate that gizzard shad were not utilized by age-0 striped bass in Smith Mountain Lake because they outgrew the morphological limitations of this piscivore and, as a result, were too large for consumption. Although the growth rate and temporal patterns in size distribution of threadfin shad in Smith Mountain Lake have not been examined, it is possible that this forage-fish species also outgrew the ingestibility limitations of both small- and large-mode striped bass, thereby preventing consumption this prey type.

An interesting result from this study is that for age-0 cyprinids and alewives consumed by small- and large-mode striped bass, respectively, prey TL/predator TL ratios declined with increasing predator size. Perhaps the commonly observed ontogenetic increase in the range and mean size of prey ingested by piscivores has led to the assumption of ontogenetic increases in preferred prey sizes (Nielsen 1980; Knight et al. 1984; Polis 1988). However, Popova (1978) showed that for five freshwater species of piscivorous fishes, mean prey size ingested tended to be closer to the minimum size available; relative prey size was largest at the transition to piscivory (approximately 50% of total length), but tended to decline dramatically as predator size increased, stabilizing at approximately 10%. Similarly, many other studies, including this one, have also demonstrated that piscivorous fishes tend to ingest prey much smaller (20-30% of their total length; Hoogland et al. 1956; Lawrence 1958; Kerby 1979; Gillen et al. 1981; Ott and Malvestuto 1981; Humphreys 1983; Hoyle and Keast 1987; Dennerline 1990; Hambright 1991; Juanes 1994;

Dettmers et al. 1996) than the maximum possible size. These common patterns in predator-prey sizes are likely due to an ontogenetic increase in relative predation success rate (Nursall 1973; Werner 1977; Hoyle and Keast 1987; East and Magnan 1991; Juanes 1994). Because encounter rate is generally assumed to be a positive function of prey size while capture success is assumed to be negatively related to prey size, the resulting vulnerability relationship is typically a convex parabola (Juanes 1994). Greene (1986) has argued that the interaction of differential encounter and capture success rates can lead to perceived predator preference without any active predator choice. Such "passive" foraging tactics can often explain patterns in prey size selectivity as well as optimal foraging models that assume active prey selection (Pastorok 1981; Dunbrack and Dill 1983; Scott and Murdoch 1983; Osenberg and Mittelbach 1989). For example, Hart and Hamrin (1990) suggest that although small fish prey are usually less profitable in terms of energy gained per unit handling time, they are selectively ingested by northern pike because they are "easier to catch". If passive prey selection rather than active predator choice determines the observed selectivity of piscivorous fishes for small prey sizes, peak vulnerabilities at small prey sizes imply that piscivore capture success rates are strongly size-dependent. In addition, prey vulnerability can be reduced through temperature preferences, habitat choice, schooling, and escape responses (Savino and Stein 1982; Coutant et al. 1984; Pitcher and Parrish 1986; Tisa 1988; Christensen and Persson 1993), resulting in piscivores consuming only smaller, more vulnerable prey. Therefore, these factors may, in part, explain the decline in prey size/predator size ratios with increasing predator size observed for age-0 striped bass with piscivorous food habits in Smith Mountain Lake.

Although the size divergence observed for age-0 striped bass is likely a function of food habits and forage-fish prey availability, it does not suggest how the size discrepancy arises initially. The most plausible hypothesis is that the initial differences in total length of fingerlings at the time of stocking was a result of individual variability in feeding success and metabolic efficiency within hatchery ponds. However, whether this individual variability can be attributed directly to genetic differences (i.e. differential inheritance of genotypes favoring faster growth and/or aggressive feeding behavior) or chance (i.e. a good first feeding encounter may promote the chance of a second and so on) cannot be determined at this time. Another mechanism which may contribute to the initial size divergence is that some individuals may accumulate more of the assimilated energy into increases in length at the expense of weight. These individuals would more rapidly obtain a greater length, and because body length, not weight, determines gape width and, consequently, the size of prey that can be ingested (Lawrence 1958; Kerby 1979; Dennerline 1990; Hambright 1991), larger fish could obtain a higher quality diet and possibly gain weight rapidly before the end of the growing season. Comparable late season growth of smaller striped bass would be limited by reduced forage-fish availability as a result of their smaller size. Therefore, there may be alternative growth strategies within a cohort of age-0 predatory fishes, including striped bass.

Competition for limiting resources. - Competitive effects on growth occur when direct and/or indirect interactions between fish cause an unequal distribution of a resource, and resource supply does not meet consumer demand; food and space are the resources that most frequently are unequally distributed and become limited by such interactions (Sale 1979). Dominant fish sequester a disproportionately greater amount of the resource and, consequently, grow faster than they would if the resource was distributed equally among all individuals. The faster growth of the competitively-dominant fish usually enhances their dominance, allowing them to sequester resources even more effectively, and further increases the difference in growth rate. However, competition will exist only when the requirements of two or more individuals for a particular resource exceed the supply of that resource in the location they occupy. For example, when food resources are restricted, large medaka (*Oryzias latipes*) chase small fish away from the food and grow faster, but when this resource is present in excess, large fish have no competitive advantage over smaller fish (Magnuson 1962). Additionally, if demands do not actually exceed food supply, individuals may interfere with one another in their joint efforts at obtaining this resource. For stream salmonid populations, the most dominant individuals maintain and defend feeding stations at locations that are most profitable, so growth rate is correlated with dominance rank (Li and Brocksen 1977; Fausch 1984). Because competitive interactions between fishes in freshwater lentic systems have been shown to significantly influence growth (Werner and Hall 1977; Hanson and Leggett 1985, 1986; Ossenberg et al. 1988), both intraspecific competition between small- and large-mode striped bass and interspecific competition with juvenile black basses may contribute to differential patterns of growth observed in Smith Mountain Lake.

Although intraspecific competition between small- and large-mode age-0 striped bass was not directly quantified, it would appear that prey availability and spatial segregation would preclude intense interactions between these two size groups. Small-mode fish primarily occupied shallow, nearshore zones of Smith Mountain Lake and consumed small, ingestible-sized prey items such as zooplankton, benthic aquatic insects, and age-0 cyprinids. In contrast, large-mode fish were always collected from deeper, pelagic areas of the main channel and consumed almost strictly age-0 alewives. Assuming that size-dependent differences in diet composition and habitat preferences are representative of the entire age-0 striped bass population, it appears that small- and large-mode fish are, in general, limited in their interactions along these niche axes. In addition, because striped bass is a schooling species, it is not likely that aggressive behavior (i.e. interference competition) among small-mode individuals in nearshore areas contributed to differential growth within the age-0 cohort.

Diet overlap analysis indicated competitive interactions could occur between age-0 striped bass and black basses, but only during early summer for fish <60 mm TL. During this time period, food habits of these small predators were most similar, consisting of zooplankton (primarily cladocerans), benthic aquatic insects (chironomid larvae and pupae, and ephemeropteran nymphs), and age-0 cyprinids. Additionally, striped bass and black basses at these sizes were not spatially segregated, as both were numerically abundant in shallow, nearshore zones of both stocking coves. Although similar food resources were utilized by small size classes in these locations, interspecific competition will occur only if resources become limiting, as during crunches in resource availability (Wiens 1977). Because availability of these food resource types was not quantified, these results only suggest that if food resources were to become limiting, these size classes of predators would most likely compete.

In contrast to smaller size classes, juvenile striped bass and black basses >60 mm TL exhibited little diet overlap; striped bass consumed primarily age-0 cyprinids and alewives, while black bass diets contained terrestrial insects, and age-0 sunfishes and darters. Additionally, divergence in habitat use between these two predators with increasing size probably facilitated these differences in diet utilization. Largemouth bass, regardless of size, were collected strictly in nearshore zones, typically areas with submerged timber and/or aquatic vegetation, whereas striped bass became increasingly more pelagic at sizes >100 mm TL. Lack of significant overlap in food and habit use has also been observed between age-0 striped bass and largemouth bass in Lake Texoma (Matthews et al. 1992), age-0 hybrid striped bass and largemouth bass in Sooner Lake, Oklahoma (Gilliland and Clady 1982), and adult striped bass and largemouth bass in Smith Mountain Lake (Moore 1988). Therefore, these results suggest that although the smallest size classes of juvenile striped bass and black basses in nearshore areas may compete for food when these resources become limiting, divergence in diet and habitat use by larger size classes minimizes competitive interactions between these two predators in Smith Mountain Lake.

In summary, although initial differences in the size and time at introduction existed between stocking sites and years, age-0 striped bass exhibited similar consistent increases in size during the 1994 and 1995 growing seasons in Smith Mountain Lake. Further, a distinct bimodal length distribution developed by fall in both years, consisting of large-mode striped bass that were twice as long as small-mode juveniles (>180 mm TL versus <150 mm TL). Although individual variability in growth and behavior among larvae within and among hatchery ponds, time at stocking during the growing season, variability in conditions between stocking sites and river arms, stocking of Phase II fingerlings, and genetic differences in growth cannot be completely discounted as mechanisms contributing to the observed size divergence, hatching date influence, sex-related differences in growth, and trophic competition did not appear to be significant factors influencing first-year growth. However, size-dependent differences in food habits and forage-fish prey availability appear to be the primary factors causing differential growth within the age-0 cohort. Small-mode juveniles maintained a mixed diet of small, lower-energetically profitable prey items throughout the growing season, consuming invertebrates and age-0 cyprinids. In contrast, large-mode fish were strictly piscivorous, consuming primarily larger, more-energetically profitable age-0 alewives. These results are substantiated by observations of prey/predator weight relationships; the ratio of consumed alewife to large-mode striped bass body weight was greater than the ratio of consumed cyprinid to small-mode striped bass body weight. This disparity in food habits and energy content also resulted in significant size-dependent differences in physiological indices of health. Although median relative condition, liver-somatic index, and lipid index for all sizes of age-0 striped bass increased progressively over the 1994 and 1995 growing seasons, size-dependent differences were clearly apparent as large-mode juveniles had significantly higher indice values than small-mode fish. However, stomach-fullness index exhibited no clear temporal or size-dependent trend and was not a useful index for assessing food intensity or prey consumption for juvenile striped bass in Smith Mountain Lake. The inability of small-mode striped bass to make the transition to a strictly fish diet was due to the combined effects of distributional, behavioral, and morphological unavailability of age-0 alewife forage prey. Only a small fraction of the age-0 alewife cohort biomass (approximately 23%) was within the ingestibility limits of small-mode striped bass throughout the growing season. However, even though ingestible-sized age-0 alewives overlapped spatially with small striped bass during summer months, this prey type was not utilized, possibly due to behavioral constraints in prey recognition and/or capture success. Further, once small-mode striped bass had began to become more piscivorous during fall months, age-0 alewives had become pelagic and no longer spatially overlapped with this size class of predator. In contrast, large-mode juveniles were large enough to consume alewife prey from the time they switched to piscivory through the end of the growing season. Therefore, differences in diet quality, as a consequence of dissimilarities in prey items consumed by small- and large-mode striped bass relative to their availability, appears to have contributed significantly to the differential growth and development of bimodality observed within the age-0 striped bass cohort in Smith Mountain Lake during the 1994 and 1995 growing seasons.

Overwinter Survival

Differences in observed length-frequency distributions between late fall and early spring sampling periods for both 1994-95 and 1995-96 suggest that size-dependent overwinter mortality plays a significant role in limiting recruitment of juvenile striped bass to the adult population in Smith Mountain Lake. Length-frequency distributions at the end of the growing season during both sampling years were clearly bimodal, consisting of both small- and large-mode juveniles. In contrast, length-frequency distributions in early spring had become unimodal and were comprised almost entirely of large-mode individuals. Numerous field and laboratory studies have reported that overwinter survival of age-0 fishes is inversely related to length and that the smaller mode of bimodal length distributions tends to experience disproportionately greater overwinter mortality (Forney 1966; Hunt 1969; Chevalier 1973; Aggus and Elliott 1975; Oliver et al. 1979; Shelton et al. 1979; Toneys and Coble 1979; Nielsen 1980; Shuter et al. 1980; Timmons et al. 1980; Toneys and Coble 1980; Isely 1981;

Adams et al. 1982; DeAngelis and Coutant 1982; Cunjak and Power 1987; Post and Prankevicius 1987; Wicker and Johnson 1987; Cunjak 1988; Henderson et al. 1988; Post and Evans 1989; Shuter et al. 1989; Johnson and Evans 1990; Shuter and Post 1990; Johnson and Evans 1991; Thompson et al. 1991; Buijse and Houthuijzen 1992; Miranda and Hubbard 1994; Cargnelli and Gross 1996; Jonas et al. 1996; Cargnelli and Gross 1997; Lyons 1997). The loss of small-mode striped bass from the age-0 cohort in Smith Mountain Lake corroborates these results and can be attributed to size-dependent overwinter mortality.

Winter mortality appears to be caused by depletion of energy reserves and eventual starvation that follows a prolonged period of limited food consumption. The disappearance of small-mode fish demonstrates that to survive through the first winter of life, age-0 striped bass must either accumulate a certain critical amount of energy before winter or feed during this period to partially offset the drain on energy reserves typical of this time of year. Shu'lman (1960) noted that stored lipids frequently constitute the main energy source for winter maintenance but structural proteins may also be used as an energy source as lipid reserves become depleted (Jobling 1980). Niimi (1972) demonstrated that stored lipid and protein were utilized in similar proportions by largemouth bass within the first 20 days of laboratory starvation experiments; after this initial period, protein was utilized at a significantly greater proportion than lipid. Although protein levels were not examined in this study, they may serve as an important source of energy for age-0 striped bass during winter months, particularly after lipid reserves have been depleted. Body lipid content was examined in this study and was observed to increase throughout the growing season for all sizes of juvenile striped bass before declining during winter months. The increase during the latter part of the growing season was likely influenced by decreasing water temperatures, which reportedly prompt fish to accumulate lipids (Shu'lman 1960). At that time, age-0 striped bass appeared to be consuming enough food to maintain metabolism and to build energy reserves, but only juveniles in the larger mode were sequestering enough food to also invest in somatic growth. Reduction in physiological indices of health of juvenile striped bass, in particular lipid content, after the end of the growing season was observed for both small- and large-mode fish. However, the greatest decrease was evident in surviving small-mode juveniles, confirming that a positive relationship exists between fish length and physiological health after the growing season. Not only did small-mode striped bass suffer the greatest percent decreases in physiological health over winter, but they had a lower relative energy reserves (mg/g) than large-mode fish at the end of the growing season. Henderson et al. (1988) observed that the rate of accumulation of lipid reserves in age-0 sand smelt (*Atherina boyeri*) was also size-dependent; larger individuals switched energy input from somatic growth to lipid reserves before winter, while smaller fish directed more energy into somatic growth and maintenance requirements. The authors concluded that the disproportionately greater overwinter mortality observed for smaller smelt was due to depletion of lower accumulated lipid reserves during this stressful period. Similar size-dependent decreases in body lipids and overall physiological health during winter have also been observed for largemouth bass (Toneys and Coble 1979, 1980; Isely 1981; Adams et al. 1982; Wicker and Johnson 1987; Miranda and Hubbard 1994), smallmouth bass (Oliver et al. 1979; Toneys and Coble 1979; Shuter et al. 1980; Cunningham and Shuter 1986), walleye (Kelso 1973), muskellunge (Jonas et al. 1996), brook trout (Toneys and Coble 1980;

Cunjak and Power 1986; Cunjak 1988), green sunfish (*Lepomis cyanellus*; Toneys and Coble 1980), bluegill (Booth and Keast 1986; Cargnelli and Gross 1997), yellow perch (Newsome and Leduc 1975; Toneys and Coble 1979, 1980; Johnson and Evans 1991), white perch (*M. americana*; Johnson and Evans 1991; Johnson and Evans 1996), Colorado squawfish (*Ptychocheilus lucius*; Thompson et al. 1991), gizzard shad (Pierce et al. 1980), and pikeperch (*Stizostedion lucioperca*; Buijse and Houthuijzen 1992).

The physiological mechanism hypothesized to explain size-dependent overwinter mortality is based on metabolic allometry. Smaller fish, with lower absolute energy stores and higher relative metabolic rates (Paloheimo and Dickie 1966; Brett and Groves 1979), would be expected to suffer higher mortality rates during winter after energy stores become exhausted and the fish can no longer meet metabolic demands. Johnson and Evans (1990, 1991, 1996) reported that age-0 white perch that had lost >55% of their stored energy reserves died, regardless of body size, when held at simulated winter temperatures. The authors concluded because a certain proportion of body energy is incorporated in essential tissues and is unavailable for catabolism (Brett and Groves 1979), starved fish at death have exhausted the usable portion of body energy. These results, consistent with the starvation mechanism proposed for other freshwater fishes (Savitz 1971; Shuter et al. 1980), are similar to those observed in this study. Loss of lipid stores over the winter was high for surviving small-mode juveniles (>50%), while large-mode individuals had utilized only 20% of their lipid reserves. Therefore, significantly lower lipid index levels observed for surviving small-mode fish support the hypothesis that size-dependent overwinter mortality may be a result of exhaustion of energy reserves.

Because large-mode striped bass emerged from the overwintering period in better physiological health than surviving small-mode juveniles, the size-dependent differences in health indices observed in spring are probably due to physiological allometry, i.e. positive allometric relationships between body size and energy reserves and negative allometric relationships between body size and metabolic rate (Brett and Groves 1979; Shuter and Post 1990). In adult bluegill populations in Lake Opinicon, Cargnelli and Gross (1997) reported that the relatively greater amounts of lipid energy stored by larger fish before the onset of winter was due to a positive allometric relationship between body size and energy reserves. Additionally, relatively greater depletion of these energy stores by smaller individuals was attributed to the negative allometric between body size and metabolic rate. Because similar observations were made for the age-0 striped bass cohort in Smith Mountain Lake, it would appear that allometric relationships between body size, and energy storage and depletion resulted in the size-dependent differences in physiological health during the overwintering period.

Although liver-somatic and relative condition indices were also lower in spring than fall for both small- and large-mode striped bass, small-mode fish had suffered greater declines in these physiological indices of health than large-mode individuals. However, overwinter declines in relative condition and liver-somatic indices for both small- and large-mode juveniles were not as proportionately large as those observed for lipid index. Because the liver of striped bass is relatively small and glycogen is the primary storage product (Hinton et al. 1972), this organ probably provides short-term supplies of intense energy for activity metabolism, such as pursuit of prey, and does not function as a major winter storage repository as it does in piscivorous fishes in more northern climates (Jensen 1979). In addition, Love (1970) suggested that, with starvation and utilization of lipid reserves, body weight, and consequently body condition, does not decline in proportion to energy losses because water is taken up to compensate for losses in lipid reserves. Similar observations have been reported for other age-0 freshwater fishes (Niimi 1972; Jobling 1980; Toneys and Coble 1980; Isely 1981; Cunningham and Shuter 1986). This phenomenon has been interpreted as reflecting an increase in the relative size of the extracellular space due to lipid loss. Concomitant changes in muscle structure, such as a decline in the cross-sectional area and volume of contractile fibers (Moon 1983; Creach and Serfaty 1974), a decline in the total mitochondrial volume of muscle cells (Moon 1983), and shrinkage of muscle cells with a consequent increase in the extracellular space (Creach and Serfaty 1974; Love 1980), lead to an increase in the relative size of the extracellular space in muscle tissue and an increase in the water content of muscle cells. Therefore, the lower proportional changes in liver-somatic and condition indices relative to lipid index observed for age-0 striped bass in Smith Mountain Lake during winter months can perhaps be attributed to these physiological mechanisms.

It is possible that the observed variation in energy with body size may be due to factors other than physiological allometry. For example, juvenile striped bass may feed during the winter. Additionally, small-mode juveniles may grow at a greater rate during winter months and catch up in total length. However, several studies have documented that age-0 striped bass discontinue feeding after water temperatures have declined below 10°C (Scofield 1931; Vladykov and Wallace 1952; Koo and Ritchie 1973). Because water temperatures in Smith Mountain Lake were below 10°C from the end of November through mid-

March during both sampling years, it is unlikely that juvenile striped bass, regardless of size, were growing during the overwintering period. Further, Spigarelli et al. (1982) reported that brown trout, like other fishes, show a preferential deposition of lipid stores rather than protein (i.e. somatic) growth at low water temperatures. Therefore, it is not likely that the observed variation in energy reserves with body size or disparity in length-frequency distributions between fall and spring sampling was a result of juvenile striped bass growth during winter months.

Another possibility to explain size-dependent variation in energy reserves is that large-mode striped bass may begin feeding earlier in the spring than small-mode juveniles. However, spring sampling began before feeding resumed and the percentage of empty stomachs did not differ between small- and large-mode fish once they began to feed after spring water temperatures increased above 10°C. Greater energy reserves of large-mode juveniles may also be due to behavioral differences associated with body size that are independent of allometric physiology. For example, if large-mode individuals face less predation risk, they may consume more prey items than do smaller individuals, and thus build up greater energy reserves prior to winter irrespective of allometric physiology. In addition, small-mode juveniles in shallow, littoral areas may face greater exposure to predation because they can be prey to smaller predators, including their larger siblings, and are weaker than these larger striped bass, as suggested by the observation that smaller fish deplete their energy reserves at a faster rate. However, age-0 striped bass did not appear to be preyed upon by Smith Mountain Lake predators (Moore 1988; Michaelson 1996), including larger age-0 striped bass, and no size-dependent trends were observed in stomach-fullness index. In conclusion, the observed physiological allometric relationships between metabolic rates and energetics (Paloheimo and Dickie 1966; Brett and Groves 1979; Shuter and Post 1990) appear to be the most likely explanations for the data.

In summary, differences in observed length-frequency distributions between late fall and early spring sampling periods for age-0 striped bass in Smith Mountain Lake appear to confirm that size-dependent overwinter mortality plays a significant role in regulating recruitment to the adult population. Length-frequency distributions were clearly bimodal during fall sampling, consisting of both small- and large-mode fish. However, spring length-frequency distributions had become unimodal and were comprised almost entirely of large-mode juveniles. The loss of small-mode fish over winter months appears to be a result of starvation and exhaustion of energy stores; this size group had less absolute energy stores at the onset of winter and used a significantly greater proportion of these reserves during this period than did large-mode juveniles. Further, surviving small-mode fish collected in spring were extremely emaciated and in poor condition, while large-mode juveniles were deep-bodied, thick, and appeared in good condition. Because large-mode striped bass emerged from the overwintering period in better physiological health than small-mode juveniles, the size-dependent differences in health indices observed in spring are probably due to physiological allometry; positive allometric relationships between body size and energy reserves and negative allometric relationships between body size and metabolic rate. These results confirm the energy linkage with body size that has been postulated to explain why energetic variance may be important for overwinter survival, such as in the relationship between body size and survival in age-0 fishes.

CONCLUSION

Temporal and size-dependent patterns of spatial distribution and food habits, coupled with the seasonality of forage-fish prey abundance and constraints of morphology, explain divergences in growth patterns, overwinter mortality, and, consequently, affect recruitment of stocked fingerling striped bass to age 1 in Smith Mountain Lake. Disparity in patterns of dispersion within stocking sites can be primarily attributed to differences in suitable habitat preferred by juvenile striped bass. Whereas small-mode striped bass (<150 mm TL) remained in littoral, nearshore regions throughout the growing season, large-mode juveniles (>150 mm TL) became pelagic and dispersed widely throughout main channel areas of Smith Mountain Lake. Although differences in dispersion patterns and spatial distribution, coupled with variability in the initial size distribution at stocking, inter-annual variability in conditions between stocking sites and river arms, stocking of larger Phase II fingerlings, and genetic differences in growth cannot be discounted as mechanisms influencing the observed divergence in size distribution over the growing season, hatching date influence, sex-related differences in growth, and intra- and interspecific trophic competition did not appear to contribute to growth depensation within the age-0 cohort. However, this phenomenon can be directly attributed to differences in energy content levels between disparate food habits of small- and large-mode age-0 striped bass. Large-mode juveniles were strictly piscivorous, consuming larger, energetically-more profitable age-0 alewife prey which were morphologically available to this size mode throughout the growing season. In contrast, the inability of small-mode fish to switch completely to piscivory, primarily a consequence of distributional and behavioral constraints which limited the consumption of age-0 alewife prey during the growing season, resulted in prolonged reliance on small, less-energetically profitable food items such as invertebrates and small, age-0 cyprinids. Thus, a primarily invertebrate diet likely stunted growth of striped bass in the smaller mode, and differences in food habits and diet quality between striped bass in the two modes promoted formation of bimodality. In addition, small-mode striped bass accumulated less energy stores prior to the nonfeeding, overwintering period and utilized these reserves at a greater rate during this time than did large-mode juveniles. As a consequence, the unimodal length distribution observed in spring, which consisted almost entirely of large-mode juveniles, suggests that small-mode fish suffered disproportionately greater overwinter mortality as a result of depletion of limited energy reserves and eventual starvation.

From these results, it would appear that stocking age-0 striped bass at a larger size and/or earlier in the growing season should allow juveniles to become piscivorous immediately upon introduction to Smith Mountain Lake. Support for this change in stocking strategy comes from 1994 data; striped bass were stocked in the Blackwater River at a slightly larger size (median = 42 mm TL) and earlier (15 June) than fingerlings stocked in the Roanoke River (median = 32 mm TL, 22 June). Subsequently, juvenile striped bass in the Blackwater River grew at a faster rate and reached a larger size by the end of the growing season than did striped bass stocked in the Roanoke River. Unfortunately, the stocking of larger, Phase II fingerlings (median = 72 mm TL) during 1994 did not result in the desired outcome, in part because of poor hatchery-stocking practices (i.e. high initial stocking mortality due to inadequate time spent acclimating fish to warmer lake water temperatures). However, stocking larger juvenile striped bass should allow them to maintain a length advantage over age-0 alewife prey and utilize this forage species throughout the entire growing season. Faster growth due to consumption of larger, higher caloric density fish prey and, consequently, larger size at the end of the growing season, in addition to greater accumulated energy stores, should allow a larger proportion of the stocked cohort to survive over the first winter of life. Because survival in Smith Mountain Lake after age 1 has been reported, on average, to be significantly greater than at age 0 (40% versus 20%, respectively; Moore 1988), increased survival of age-0 striped bass during the first year of life, particularly during winter months, should alleviate the recruitment bottleneck that has been observed in this system since the creation of this fishery and reduce angler angst by increasing the number of catchable-sized, adult fish.

CHAPTER II

STOCKING STRATEGIES FOR JUVENILE STRIPED BASS IN SMITH MOUNTAIN LAKE: AN INDIVIDUAL-BASED MODEL APPROACH

INTRODUCTION

Although the dynamics of all fish populations depend on the combined effects of recruitment, growth, and mortality (Smith 1988), recruitment is the regulating and most variable component of fish production (Gulland 1982; Sissenwine 1984). As a result, recruitment variability has been identified as the central problem in fishery science and a major contributor to uncertainty in fisheries management (Sissenwine 1984; Rothschild 1986; Cushing 1995). Because the mechanisms governing recruitment operate at the level of the individual and mortality sources that regulate survival are selective, some individuals may be more likely to survive than others based on differences in some phenotypic characteristic (Miller et al. 1988). As a result, understanding the mechanisms controlling cohort recruitment and other population-level responses in relation to individual variability within and among age-0 fish populations, particularly those characteristics important to first-year survival, provides a means by which fisheries managers can enhance fishery production in aquatic ecosystems.

For age-0 fishes, body size appears to be an important variable affecting first-year survival. Most fishes grow 2-3 orders of magnitude in mass during the first few months of life (Werner and Gilliam 1984), and some of the major sources of mortality during this time period, such as predation and starvation, are strongly size dependent (Ricker and Foerster 1948; Gutreuter and Anderson 1985; Rice et al. 1987a; Miller et al. 1988; Luecke et al. 1988; Cushing 1995). In particular, larger fish may exhibit higher survival than smaller individuals of the same cohort (Nielsen 1980; Craig 1982; Post and Prankevicius 1987; Henderson and Cass 1991), and several studies suggest that faster-growing individuals may be favored over slower-growing conspecifics (Forney 1976; Adams et al. 1982; Rosenberg and Haugen 1982; Carline et al. 1986; Rice et al. 1987b). Because growth rate may be a critical determinant of survival, especially when size-dependent mortality is important, relatively small reductions in mean growth rate during the early life stages may cause cohort survival to decrease simply by prolonging the period of vulnerability to mortality sources (Chambers and Leggett 1987; Houde 1987; Pepin 1990). Growth rate variation among individuals within a cohort may also have significant effects as growth rate and size often vary substantially among individuals within a cohort (Paloheimo and Dickie 1966; Aggus and Elliott 1975; Rainwater and Houser 1975; Shelton et al. 1979; Timmons et al. 1980; Miller and Storck 1984; Keast and Eadie 1985; McIntyre et al. 1987; Miranda and Muncy 1987; Wicker and Johnson 1987; Buijse and Houthuijzen 1992; Goodgame and Miranda 1993; Phillips et al. 1995). Consequently, one might expect some individuals to differ markedly from the average fish in response to size-dependent mortality, causing the combined outcome of individual interactions to differ substantially from that for the average individual (Sharp 1987).

One approach to aid the analysis of the factors influencing first-year recruitment mechanisms and variability in abundance of piscivorous fish populations is the use of an individual-based model (IBM; Huston et al. 1988; DeAngelis et al. 1994). An IBM provides a framework within which researchers can conceptualize natural processes, design their research, analyze results, and combine empirical studies and modeling in a synergistic fashion (Van Winkle et al. 1993). Murdoch et al. (1992) demonstrated that individual-based models are, by their nature, predisposed to incorporating the mechanisms that determine a system's dynamic processes and, as a result, in their more detailed form, are highly testable. For that same reason, IBMs lend themselves to a process of progressive removal of particular features, which should facilitate distinguishing the essential mechanisms from those that account for detail rather than major dynamic features. Each individual in a population can be described conceptually by a vector of attributes characterizing the individual's phenotype and location at a given time. Repeated observations on individuals can be differenced to derive rate variables (i.e. growth, feeding, and mortality rates) or integrated to yield cumulative performance (i.e. recruitment and year-class strength). In nature, the consequences of this phenotypic variability can be manifested as differential growth, mortality, and recruitment rates. Mechanisms of phenotypic selection (i.e. size-dependent feeding and mortality) are grounded in differences among individuals, and analysis of the consequences of these differences requires observations at the individual level.

The trend in population models is to include more detail regarding depictions of individual members. Along with the increased phenotypic detail, there has been more frequent inclusion of fundamental processes such as feeding, growth, mortality, and recruitment. The expectation is that these more detailed models will improve the identification of factors responsible for population fluctuations and variability. These factors can, in turn, be used to provide more accurate predictions of population size and structure, and to improve management decisions and strategies.

An individual-based model (IBM) approach has been shown to successfully capture the variation in growth and size-dependent mortality exhibited by several age-0 populations of piscivorous fishes. Adams and DeAngelis (1987) applied an IBM to simulate the influence of environmental factors on the predation and growth of age-0 largemouth bass (*Micropterus salmoides*) feeding on age-0 shad (*Dorosoma* spp.) in a Tennessee reservoir. The authors concluded that age-0 largemouth bass size distribution at the end of the growing season was extremely sensitive to the timing of spawnings of both bass and shad populations and, because overwinter mortality of bass is strongly dependent on the size attained by the end of this period, recruitment of both bass and shad to the adult population depends heavily on the degree of predation. Madenjian (1991), Madenjian and Carpenter (1991), and Madenjian et al. (1996) produced and utilized an IBM for growth and recruitment of age-0 walleyes (*Stizostedion vitreum*) in Oneida Lake, New York, Lake Mendota, Wisconsin, and western Lake Erie. These researchers concluded that size relationships between age-0 walleyes and prey fishes had a tremendous impact on the size distribution, overwinter survival, and recruitment to age 1. Further, Madenjian et al. (1991) used an IBM to investigate the effects of initial size of fingerling walleyes and the timing of stocking on first-year growth and population structure in order to determine what size and time at stocking resulted in the greatest number of age-1 recruits. In addition, Rose and Cowan (1993) have developed an IBM to describe and predict population dynamics of striped bass (*Morone saxatilis*) from spawning through the first year of life in the Potomac River subestuary of Chesapeake Bay. Cowan et al. (1993) have also used this model to test the hypothesis that the high degree of recruitment variability often observed for striped bass can be explained by abiotic and biotic stochasticity, resulting in large changes in growth and mortality rates for early life stages.

The purpose of this study was to evaluate various strategies for stocking fingerling striped bass in Smith Mountain Lake, an 8,343-ha hydroelectric impoundment in southcentral Virginia. An IBM was used because it provided a framework for synthesizing site-specific information and evaluating age-0 striped bass population structure and dynamics based on both biotic and abiotic interactions. Specific objectives, which were investigated through a series of model simulations, were to examine the influence of size at stocking, day of stocking, and stocking density, both singly and in combination, to determine which scenario(s) maximized first-year growth and survival, and, consequently, the number of age-1 recruits. These results, in turn, led to recommendations for management of the VDGIF striped bass stocking program in Smith Mountain Lake. Additionally, perturbations in alewife population dynamics (age-0 alewife cohort density, timing of adult alewife spawning, and age-0 alewife growth and mortality rates), and Smith Mountain Lake water temperature, varied both singly and in combination, were examined to determine the sensitivity and robustness of the IBM for the proposed, "new" versus the existing, "old" stocking strategy.

METHODS

The Potomac River striped bass individual-based model, which served as a precursor to the one I utilized to analyze the influence of different stocking strategies on first-year growth, survival, and recruitment of striped bass in Smith Mountain Lake, was a joint effort among striped bass researchers throughout the United States and individual-based modelers, specifically Dr. Kenneth A. Rose at Oak Ridge National Laboratory in Oak Ridge, Tennessee, and Dr. James H. Cowan at the University of South Alabama in Mobile, Alabama, through the Electric Power Research Institute's COMPMECH Striped Bass Key Species Program. My involvement in the development process of the Smith Mountain Lake striped bass IBM included the following: (1) learning specifically how the Potomac River version of the striped bass IBM operated; (2) determining what information was necessary to make the IBM site-specific for Smith Mountain Lake; (3) two years of field collection, and laboratory and data analysis to understand the dynamics of stocked juvenile striped bass in Smith Mountain Lake; and (4) working with Dr. Rose to incorporate this information into the model so that it not only worked, but also closely mimicked the nature and degree of dynamics and variability observed for age-0 striped bass in Smith Mountain Lake. Once this was determined, the final year was dedicated to running model simulations and analyzing model outputs.

Model Description

The Smith Mountain Lake striped bass IBM is a modified version of the one developed by Rose and Cowan (1993) for the Potomac River, Maryland. The Potomac model consists of an individual-based young-of-the-year (YOY) model coupled to an adult model. The adult model is used to generate the number and length distribution of female spawners each year in order to determine the number of eggs spawned. The growth and mortality of each female's progeny is followed daily as they develop through the egg, yolk-sac larvae, feeding larvae, and juvenile stages during their first year of life. In contrast, the Smith Mountain Lake version of the IBM only utilizes the juvenile component of the YOY model. The adult model was not incorporated into this version because striped bass do not naturally reproduce in this system due to habitat constraints. As a result, the population is maintained strictly through stocking on a put-grow-take basis. Although the egg, yolk-sac larvae, and feeding larvae life stage components of the YOY model are not utilized because striped bass are stocked as larger juveniles, more detail was incorporated into the juvenile life stage of this model such as temporal and size-dependent dynamics in spatial distribution and piscivory. Therefore, the Smith Mountain Lake IBM, which incorporates site-specific data collected from this study and others (Moore 1988; Tisa 1988; Michaelson 1996), is a modified version of the one originally developed for the Potomac River.

The Smith Mountain Lake striped bass IBM begins by specifying input values for fingerling density, size distribution, and Julian date at the time of stocking. After introduction, the model simulates growth and mortality peocesses of juvenile striped bass on a daily basis until 01 May of the next year. These dynamics are represented in two, well-mixed model compartments: the littoral and pelagic zones. Juveniles are introduced into the littoral compartment and begin dispersing to the pelagic compartment after reaching a total length of 150 mm (see Chapter I, Dispersal and Spatial Distribution). The environmental conditions considered in each compartment include temporal dynamics in water temperature and forage-fish prey densities.

Age-0 striped bass were followed day-by-day through growth and mortality processes. Because modeling large numbers of individuals presents logistical problems (i.e. computer memory and computational limitations), the attributes of every individual in the population cannot be tracked feasibly on a day-to-day basis. Although it is possible to develop computer code dimensioned to the number of individuals and to use supercomputers to follow hundreds of thousands of individuals, these alternative programming approaches result in much higher computational costs and inconvenience, and thus more importantly, substantially diminish the general utility of the individual-based simulation approach (Rose et al. 1993). As a result, juvenile striped bass were sampled from the stocked cohort in proportion to their contribution to the total number of surviving individuals. At the beginning of each simulation, the initial value of n_i was computed as T/N for each model individual, where T was the total number of introduced juveniles and N was the total number of model juveniles to be followed. Values of n_i were allowed to vary for all fish and over time; there were always a fixed number of model individuals in each simulation. To reduce computational time, the IBM was run using a resampling algorithm (Rose et al. 1993). A fixed number of randomly-chosen individuals were followed, with each modeled individual representing some number of identical population individuals. As each sampled individual died, a donor individual was replaced with another randomly-selected individual and n_i was reduced to account for daily mortality. Dead individual's attributes were then replaced with those of the donor individual. Differences in model output, when run with and without the resampling algorithm, are negligible (Rose et al. 1993).

Growth, in terms of both length and weight, was based upon a bioenergetics approach where maximum consumption and metabolism were dependent on striped bass body weight and Smith Mountain Lake water temperature. The fraction of maximum consumption realized was set to a fixed value for striped bass feeding on zooplankton and benthic aquatic insects (i.e. invertebrates), and computed dynamically based on encounter rates and capture efficiencies for juveniles consuming fish prey (age-0 cyprinids in the littoral compartment and age-0 alewives in the pelagic compartment; see *Prey Types and Densities* for justification), where encounter rate was determined by forage-fish prey density and capture efficiency was determined by the relationship of encountered fish prey total length relative to striped bass total length. Therefore, daily feeding success of juvenile striped bass, and consequently growth rate, was a function of encounter rate, capture efficiency, maximum consumption, caloric density of forage-fish prey, and metabolism. Because growth rates have a direct influence on the size of an individual and size, in turn, effects survival, predation and starvation mortality were a function of juvenile striped bass length and weight, respectively, and were evaluated each day for each individual.

Spatial Scaling. - Two spatial compartments, which were scaled proportionately to their actual, estimated volumes, were used to represent Smith Mountain Lake in the IBM (Figure 2.1). Compartment dimensions were as follows: littoral zone (990 m x 990 m x 2 m deep) and pelagic zone (7,319 m x 7,319 m x 16.8 m deep before 01 October and 9,129 m x 9,129 m x 16.8 m deep afterwards). The pelagic compartment was increased in size after 01 October to simulate dispersal of juvenile striped bass from stocking cove sites to pelagic, main channel areas of Smith Mountain Lake. During the growing season, juvenile striped bass were allowed to occupy either the littoral or pelagic

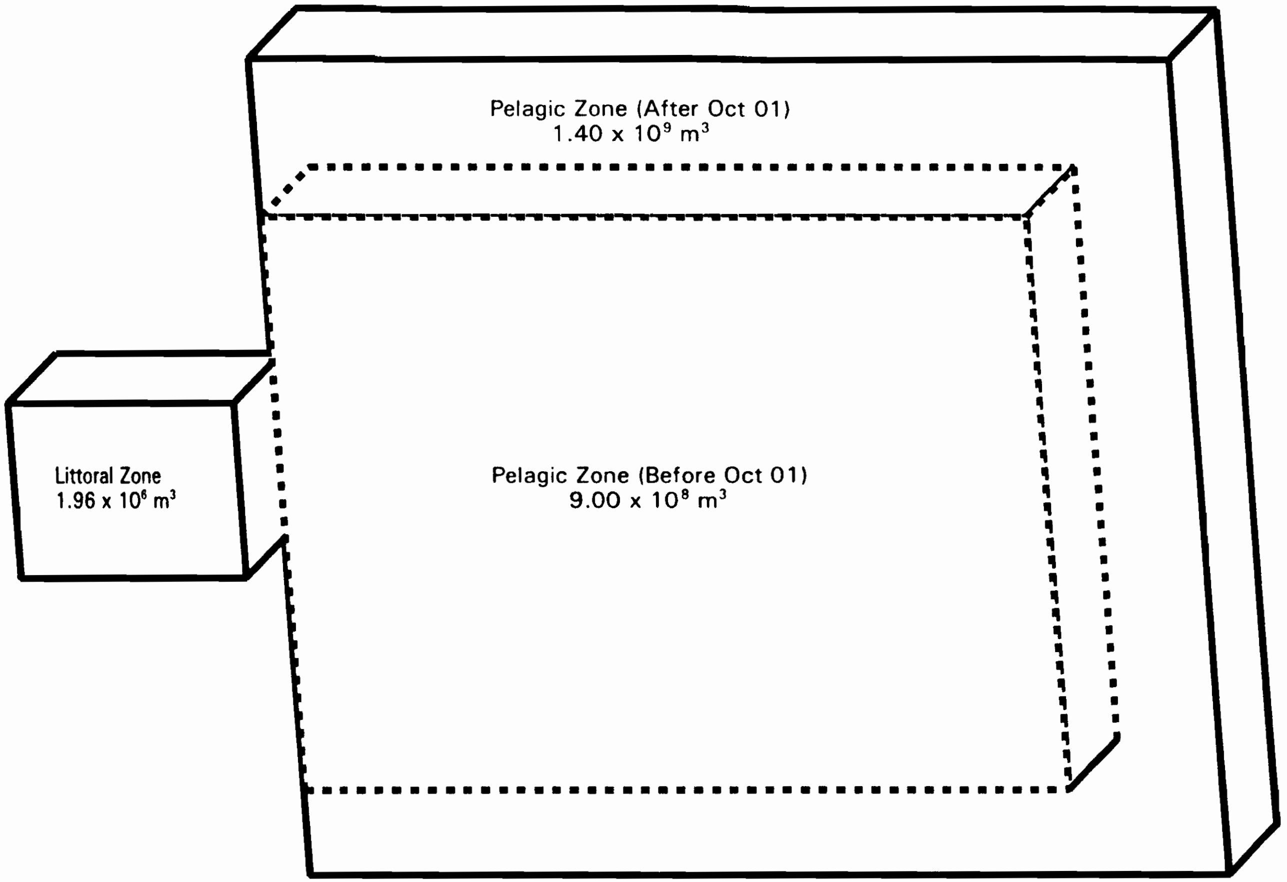


Figure 2.1. Schematic representation and spatial scaling of Smith Mountain Lake model compartments.

compartment depending on their total length (see *Dispersion* for justification).

Daily Water Temperature. - Daily water temperatures in each model compartment were generated from trigonometric functions, in radians, fit to observed average weekly temperatures. The average was based on weekly water temperatures recorded during the 1994-95 and 1995-96 sampling years at a depth of 1 m from both the littoral and pelagic areas of Smith Mountain Lake. Because bi-weekly water temperature estimates were not significantly different between these two areas of Smith Mountain Lake at this depth ($\chi^2 = 20.16$, df = 15, P = 0.11), the temporal temperature regime was assumed to be the same for both model compartments. The equation defining the annual temperature cycle (T; °C) in Smith Mountain Lake, which was modified from Dalton (1987), was:

$$T = 15.94 - 9.07 \cdot \cos(0.0172 \cdot \text{jday}) - 6.10 \cdot \sin(0.0172 \cdot \text{jday}), \qquad (1)$$

where jday was the Julian date and 0.0172 was a conversion factor to transform degrees to radians.

Stocking. - Input parameters, that defined the age-0 striped bass cohort at the time of stocking, were required to run the model and included the following: (1) stocking density (number/m^3); (2) Julian date of introduction; and (3) the median, minimum, and maximum total lengths (mm) which determined the bounds of a normal length-frequency distribution at the time of stocking. These parameters were altered singly and in combination to investigate the effects of density and size of stocked fingerlings, and timing of stocking on subsequent juvenile striped bass growth and mortality (see Stocking Strategies for a more detailed description of simulations performed).

Dispersion. - All fingerling striped bass were introduced into the littoral compartment at the time of stocking. Individuals remained in the littoral compartment until they reached a total length of 150 mm at which point they had a daily probability of 0.2 of moving into the pelagic compartment. Although the dispersal rate of juvenile striped bass from the stocking sites was not quantitatively determined in this study, a daily dispersal probability of 0.2 into the pelagic compartment was chosen because it allowed the length-frequency distribution of juvenile striped bass within and outside the stocking coves to approximate that observed in Smith Mountain Lake at the end of the growing season (see Figure 1.9, Dispersal and Spatial Distribution in Chapter I). After 01 October, the pelagic compartment was expanded to simulate fish dispersing throughout the pelagic, main channel areas of Smith Mountain Lake as observed during the field component of this study. Because large age-0 striped bass (>150 mm TL) were rarely collected within the stocking cove sites (see Figure 1.9), juveniles were not allowed to return to the littoral compartment after dispersing to the pelagic compartment.

Growth. - Simulation of daily food consumption by juvenile striped bass employed a bioenergetics approach based on optimal foraging theory (Emlem 1966; MacArthur and Pianka 1966). Bioenergetics considers the rates of energy intake, and energy transformation losses and uses as functions of the whole organism (Brett and Groves 1979). In the following sections, a brief description of each model component is provided. Rose and Cowan (1993) provide a full description of the logic used in the bioenergetics section of the Potomac River IBM. Unless specifically noted, the Smith Mountain Lake version of the model uses the same equations as Rose and Cowan (1993) to define the foraging and growth of juvenile striped bass.

Site-specific modifications were required to obtain realistic growth rates in the warmer waters of Smith Mountain Lake, relative to the Potomac River. Daily growth in dry weight (W_t; mg) of an individual striped bass, beginning after stocking, was represented with a difference form of a bioenergetics equation:

$$W_t = W_{t-1} + p \cdot C_{max} \cdot K - R_{tot}, \tag{2}$$

where p was the proportion of C_{max} realized, C_{max} was the maximum dry weight consumption rate (mg/d), K was the ratio of forage prey to striped bass caloric density (which accounts for assimilated and nonassimilated wastes), R_{tot} was the total dry weight metabolic rate (mg/d), and t was time (d). The dry weight (W_t), which varied on a day-to-day basis, was converted daily into length (L_t; mm) using the following laboratory-determined relationship for age-0 striped bass (Tuncer 1988):

$$L_t = 9.63 \times W_t^{0.31}. \tag{3}$$

In order for model-simulated growth rates and patterns to parallel those observed in the field, the maximum daily increase in length allowed was 1.5%; individuals adding weight that would convert to greater than a 1.5% increase in length became relatively fat individuals. However, juvenile weight was partially uncoupled from length; length, once established, could only increase or stay the same, whereas weight could also decrease. On days that juveniles lost weight, their lengths were not changed. Following a weight loss, length was increased only after the individual had recovered to the weight predicted by the weight-length relationship.

Maximum Consumption. - Maximum daily consumption (C_{max}) of a juvenile was dependent on its body weight and water temperature. The dependence of C_{max} on temperature was a slowly rising function that reached 1.0 at an optimal temperature and quickly dropped to zero at a maximum temperature for consumption (Hewett and Johnson 1987). The optimal temperature for age-0 striped bass consumption was 25°C (Meldrim and Gift 1971; Cox and Coutant 1981; Coutant et al. 1984), and maximum temperature was near the upper lethal temperature reported for juveniles of this species (35°C: Westin and Rogers 1978; Setzler et al. 1980). In addition, juveniles were not allowed to consume prey items after water temperature declined below 10°C because other studies, including this one, have documented that juvenile striped bass discontinue feeding at this temperature (Scofield 1931; Vladykov and Wallace 1952; Koo and Ritchie 1973).

In order to match model-simulated growth rates of piscivorous striped bass <175 mm TL with those observed from field collections, juveniles were allowed to consume up to twice the fish prey mass that their stomachs would allow, depending on encounter rate and feeding efficiency. As a result, consumed fish prey weight was near C_{max} as striped bass made the transition to piscivory. Because growth rates of model-simulated juvenile striped bass >175 mm TL agreeably matched those estimated from field collections, these individuals were only allowed C_{max} for fish prey. Fish prey mass in the stomach of each individual striped bass (XS_t) was tracked using the following equation:

$$XS_t = XS_{t-1} \cdot E + p \cdot C_{max}, \qquad (4)$$

where E was the daily fraction of consumed fish prey evacuated from the gut (i.e. gastric evacuation rate) and p was as defined previously. Evacuation rate (E) was computed as reported in He and Wurtsbaugh (1993) for adult, piscivorous brown trout (*Salmo trutta*) feeding on fingerling rainbow trout using the following relationship:

$$E = \exp[-0.053 \cdot \exp(0.073 \cdot T)] \cdot 24, \qquad (5)$$

where T was water temperature. On each day, striped bass were allowed to consume fish prey less than $2 \cdot (C_{max}\text{-}XS)$. If all fish prey were digested each day (which was dependent upon fish prey size, predator size, and water temperature), then striped bass would be allowed to consume twice their C_{max} each day. As residual fish prey accumulated in the stomach of an individual striped bass, less new fish prey was allowed for consumption.

Adjustment For Caloric Density. - Caloric density adjustment (K), the ratio of prey to predator caloric density, varied depending on the type of prey consumed by a juvenile striped bass. Average striped bass caloric density was 1143.3 cal/g wet weight (Rogers et al. 1980) and average prey caloric densities were 972.0 cal/g wet weight for zooplankton and benthic aquatic insects, 1123.3 cal/g wet weight for age-0 cyprinids, and 1464.4 cal/g wet weight for age-0 alewives (Moore 1988).

Metabolism. - Metabolic weight loss (R_{tot}) was estimated as the sum of a routine component (R_r), which depended on body weight and water temperature, and an active component, which accounted for periods of activity. The relationship was defined as:

$$R_{tot} = R_r + (ACT - 1) \cdot R_r \cdot FF, \tag{6}$$

where ACT was the activity multiplier of routine metabolism, and FF was the fraction of a day in which metabolism was considered active.

Routine metabolism (R_r), which is a function of striped bass body weight and a Q_{10} water temperature relationship, was determined using the following equations:

$$R_r = 0.076 \cdot W^{0.766} \cdot G(T); \tag{7}$$

$$G(T) = e^{\ln(Q10)/10 \cdot (T/Tr)}, \tag{8}$$

where T was the water temperature and T_r was the reference water temperature for routine metabolism. These equations were derived from Eldridge et al. (1982) for age-0 striped bass and from Moore (1988) for age-1 striped bass. In contrast to the Potomac River model, the reference temperature for routine metabolism (T_r) was increased from 22°C to 25°C to account for the warmer water temperature regime in Smith Mountain Lake relative to the Potomac River. Because Q_{10} values for metabolism vary widely among fish species (1.5-4.9), a value of 1.5 was chosen based on the reported average for age-0 marine fishes at water temperatures ranging from 5 to 30°C (Houde 1989).

The active (or feeding) metabolism multiplier (ACT) was assumed to be constant at 2.0 for juvenile striped bass. This value was chosen because the ratio of feeding to nonfeeding metabolism for 30-80 mm TL white bass ranged from 1.2-2.0 (Wissing and Hasler 1971) and averaged 1.7 for adult fishes (Brett and Groves 1979).

The fraction of the day during which active metabolism occurred (FF) was assumed to be the fraction of day required to achieve realized consumption (C_r), which was defined as:

$$C_r = \sum_{I=1}^{n} B_i \cdot PW_i, \tag{9}$$

where B_i was the number of prey type i eaten and PW_i was the dry weight (mg) per individual of prey type i. If feeding by juveniles during all hours of the day would result in consumption exceeding maximum consumption, I assumed that striped bass achieved maximum consumption and only searched the fraction of the day needed to achieve maximum consumption. Only applying active metabolism to the fraction of the day needed for feeding is realistic, assuming that, on a daily basis, juvenile striped bass expend less energy in nonfeeding compared to feeding activities.

Computation of p. - The proportion of maximum consumption realized by an individual each day was defined as p and was critical for getting model-simulated striped bass growth rates and length-frequency distributions to match those observed from field collections. Computing p involved determining the number of each prey type that was eaten each day. Because zooplankton and benthic aquatic insect densities were not estimated in this study, the value of p was fixed at 0.12 for juveniles feeding on these prey types (lumped together as invertebrates). This value was chosen because it allowed striped bass that consumed strictly invertebrate prey to reach a size range of 90-120 mm TL at the end of the growing season, thereby matching the size range observed for small-mode fish at this time. For striped bass feeding on fish prey, p was based on the number of encounters and probability of capture (CAP). Juveniles got a minimum p equal to 0.3 when feeding on fish resulted in a realized consumption value less than 0.3, which allowed model-simulated length-frequency distributions to match those observed from field collections. Although age-0 striped bass do not feed at water temperatures below 10°C (Scofield 1931; Vladykov and Wallace 1952; Koo and Ritchie 1973), a minimum p equal to 0.12 was given to juveniles at water temperatures <10°C in order to allow model-simulated weight loss and mortality over winter months to match that observed from spring field collections. Rose and Cowan (1993) provide a more detailed description of the logic associated with calculation of the proportion of maximum consumption realized on a daily basis.

Prey Encounters. - Encounters of each striped bass with fish prey were determined stochastically and depended on an individual's mean encounter rate with each fish prey type (age-0 cyprinids or age-0 alewives). The mean number of encounters of a striped bass with a given fish prey type was computed as the product of the volume searched for each prey cohort and the density of each cohort. Search volume was computed as the volume of a cylinder with a radius equal to the reactive distance and height equal to the distance swum at a swimming speed of 0.3 body lengths per second. The actual fish prey cohort(s) (see *Prey Types and Densities* for a more thorough explanation of the different fish prey cohorts) encountered was estimated from a Poisson distribution with a mean equal to the mean number encountered. However, the number of fish prey from a cohort(s) actually encountered and captured was estimated from a binomial distribution, with the number of trials equal to the actual number fish prey encountered and the probability of success equal to the probability of capture.

Prey Capture. - In the model, the proportion of forage-fish prey encountered that were subsequently ingested was the product of the probability of attack, pursuit, capture, and retention (O'Brien 1979). A single capture probability (CAP) term and a prey selection algorithm were used to encompass all of the events between encounter and successful ingestion. Juvenile striped bass capture success for forage fish, which was based on results from Chapter I (see Predator-Prey Size Relationships) declined with increasing prey to predator body length ratio (R) in the following manner:

$$\mathrm{CAP} = \begin{cases} 1 \text{ for } R<0.2 \\ -3.33 \cdot R + 1.66 \text{ for } 0.2<R<0.5 \\ 0 \text{ for } R>0.5. \end{cases} \tag{10}$$

Prey Selection. - Juvenile striped bass consumed the optimal prey type (fish prey) when it was present and switched to less-preferred prey types (invertebrates) when optimal prey were rare or absent. Based on size relationships between predator and prey and whether striped bass occurred in the littoral or pelagic compartment, Smith Mountain Lake striped bass were allowed to select whether they would eat invertebrates and/or forage fish on a daily basis. Based on field-collected data, it was assumed that age-0 striped bass in the littoral compartment would only encounter age-0 cyprinids because age-0 alewives appeared to be behaviorally unavailable when they co-occurred with juvenile striped bass in the littoral zone. However, juvenile striped bass in the pelagic compartment would only encounter age-0 alewife prey. Selection of a prey item by an individual striped bass was based on encounters with fish prey, from the largest to the smallest forage-fish cohort (see *Prey Types and*

Densities for a more thorough explanation of the different fish prey cohorts) available on a particular day, ranked in descending order of preference based on the product of prey dry weight and capture probability (PW·CAP). Forage-fish prey within the ingestibility limits as determined by capture probability (CAP) were consumed, starting with the most preferred, energetically profitable until all eligible prey items had been consumed or until consumption exceeded maximum consumption.

Prey Types and Densities. - Zooplankton and benthic aquatic insects, although utilized by smaller juvenile striped bass, were not explicitly incorporated into the IBM because densities for these prey types were not quantified during the field component of this study. As a result, invertebrate prey were represented only through the proportion of C_{max} realized ($p=0.12$), which remained constant throughout all model simulations for all sizes of juvenile striped bass.

Age-0 cyprinids and alewives were chosen to represent forage fish in the littoral and pelagic compartments, respectively, because they were the primary forage fishes consumed by piscivorous striped bass in Smith Mountain Lake. Both prey types were represented by 10 cohorts which were introduced at subsequent time periods in order to simulate the range in sizes available throughout the growing season as determined in the present study for age-0 cyprinids and by Tisa (1988) for age-0 alewives. Therefore, cyprinids were introduced at 5-d intervals beginning on 10 May and alewives were introduced at 10-d intervals beginning on 20 May (Tables 2.1 and 2.2). Mean total length (TL; mm) of each cohort was represented separately over time and converted to mean wet weight (WT; mg) using the following weight-length regression equations determined in the field component of this study:

Table 2.1. Simulated density (#/m^3) and growth (mm/d) of 10 age-0 cyprinid cohorts in Smith Mountain Lake. A total instantaneous mortality rate (Z) of 0.02/d and 0.01/d was assumed for before and after December 01, respectively. Total length at hatching was assumed to be 5.0 mm.

	Hatch	Initial	Growth			June 25	
Cohort	Date	Density	Before Sept 01	Sept 01 to Dec 01	After Dec 01	Density	Length
1	10 May	0.21	0.35	0.10	0.00	0.10	20.8
2	15 May	0.35	0.35	0.10	0.00	0.18	19.4
3	20 May	0.53	0.30	0.10	0.00	0.30	15.8
4	25 May	0.70	0.30	0.10	0.00	0.54	14.3
5	30 May	0.59	0.25	0.10	0.00	0.39	11.5
6	04 Jun	0.48	0.25	0.10	0.00	0.34	10.3
7	09 Jun	0.39	0.20	0.10	0.00	0.30	8.2
8	14 Jun	0.28	0.15	0.05	0.00	0.24	6.7
9	19 Jun	0.18	0.10	0.05	0.00	0.16	5.6
10	24 Jun	0.11	0.10	0.05	0.00	0.10	5.1

Table 2.2. Simulated density (#/m^3) and growth (mm/d) of 10 age-0 alewife cohorts in Smith Mountain Lake. A total instantaneous mortality rate (Z) of 0.02/d and 0.01/d was assumed for before and after December 01, respectively. Total length at hatching was assumed to be 5.0 mm.

	Hatch	Initial	Growth			August 19	
Cohort	Date	Density	Before Sept 01	Sept 01 to Dec 01	After Dec 01	Density	Length
1	May 20	0.13	1.00	0.30	0.00	0.03	96.0
2	May 30	0.22	0.95	0.30	0.00	0.06	82.0
3	Jun 09	0.33	0.90	0.30	0.00	0.11	68.9
4	Jun 19	0.64	0.85	0.30	0.00	0.25	56.9
5	Jun 29	0.44	0.80	0.30	0.00	0.20	45.8
6	Jul 09	0.31	0.75	0.30	0.00	0.16	35.8
7	Jul 19	0.24	0.75	0.30	0.00	0.15	28.3
8	Jul 29	0.18	0.65	0.30	0.00	0.11	18.7
9	Aug 08	0.11	0.60	0.30	0.00	0.08	11.6
10	Aug 18	0.07	0.55	0.30	0.00	0.06	5.6

$$\text{Cyprinids} \quad WT = 0.000003311 \cdot TL^{3.21} \tag{11}$$

$$\text{Alewives} \quad WT = 0.000005623 \cdot TL^{3.10}. \tag{12}$$

Wet weight was converted to dry weight by using a multiplier of 0.28.

The initial density of each forage fish cohort was based on specifying an initial total year-class density (3.5 cyprinids/m^3 as estimated in this study; 2.2 alewives/m^3 from Tisa 1988) divided among the 10 cohorts such that peak abundance occurred on 25 May for age-0 cyprinids (Jenkins and Burkhead 1993) and 19 June for age-0 alewives (Tisa 1988). Total length of forage fishes at the time of hatching was assumed to be 5 mm and daily growth was based on assigned growth rates as estimated by examining temporal changes in length-frequency distributions in this study (for cyprinids) and Tisa (for alewives; see *Chapter I*).

Because daily mortality rates of cyprinids in Smith Mountain Lake were unknown, densities of both forage-fish prey (numbers/m^3) were reduced daily using a mortality rate of 0.02/d before 01 December and 0.01/d after 01 December as estimated for age-0 alewives by Tisa (1988). However, only age-0 alewife cohort densities were reduced further due to juvenile striped bass consumption. This was not allowed for age-0 cyprinid cohort densities because model-simulated striped bass consumption resulted in the depletion of this prey type from the littoral compartment. Even though age-0 cyprinids were abundant in the littoral zone throughout the 1994 and 1995 growing seasons in Smith Mountain Lake, density estimates for this forage-fish prey type, as determined during the field component of this study, appear to have under-represented their actual, field densities. For example, a 3.18-mm bar mesh beach seine was used to capture cyprinids in the littoral zone of Smith Mountain Lake. Based on the relationship between cyprinid body depth and total length, a beach seine with this mesh size would not be restrictive enough to representatively capture age-0 cyprinids <35 mm TL. As a result, field-determined density estimates for this forage-fish prey that were used in model simulations were too low, which probably contributed significantly to their depletion by juvenile striped bass in model simulations.

Prey Availability. - Prey densities were multiplied by a constant in model simulations to adjust for their availability to juvenile striped bass. Model calibration consisted of trial-and-error adjustment of prey availability factors for invertebrates and forage fishes until model predictions of median total length at the end of the growing season and the beginning of spring were similar to observed values (see Model Calibration and Corroboration). Availability factors were fixed as previously stated for invertebrates (represented as p) and at 0.00065 and 0.0002 for cyprinids and alewives, respectively. Estimation of prey availability factors was necessary to help mimic expected behaviors, such as burrowing of benthic insects, schooling of forage fishes, and prey search by juvenile striped bass.

Mortality. - Mortality of individual striped bass depended on their length and weight. Weight-dependent mortality was based on laboratory data at low food levels without predators (see below) and, therefore, was interpreted as starvation. Length-dependent mortality was based on field data and, therefore, represented predation and other losses.

Individuals died in the simulations if their weight declined below some minimum weight (W_{min}), defined as a fraction (K_{min}) of their expected weight based on their length (W_L):

$$W_{min} = K_{min} \cdot W_L, \tag{13}$$

where W_L was the predicted weight from length (equation 3). For juvenile striped bass, the fraction of expected weight that triggered starvation (K_{min}) was set to 0.5 based on mortality of age-0 smallmouth bass (*Micropterus dolomieu*) and white perch (*M. americana*) at weights 0.4-0.6 of their initial weights in starvation experiments (Shuter et al. 1989; Johnson and Evans 1991, 1996).

Predation mortality consisted of a length-based component and a density-dependent component:

$$P_D = (1 - e^{-Z}) \cdot DDM_t, \tag{14}$$

where P_D is the daily probability of dying, Z is the daily instantaneous length-based mortality rate, and DDM_t is the density-dependent multiplier. If a generated random number from a uniform distribution between 0 and 1 was less than the probability of dying (P_D), the individual was assumed to die.

The length-based component was defined using a nonlinear regression equation fit to reported mortality rates (d^{-1}) of various size ranges of juvenile striped bass (see Figure 7 in Rose and Cowan 1993) from the data of Turner and Chadwick (1972), Polgar (1977), Dey (1981), Logan (1985), Houde (1987), Uphoff (1989), and Dorazio et al. (1991). Instantaneous daily mortality rate (Z; d^{-1}) of juvenile striped bass was defined according to each individual's total length (TL):

$$Z = 0.003 + 0.295e^{-0.075 \cdot TL}. \tag{15}$$

Because first-year survival estimates of stocked age-0 striped bass in Smith Mountain Lake from 1973-96 were correlated with fingerling stocking density ($r^2 = 0.42$; see Figure I.1), model-simulated first-year survival was adjusted to fit this trend using a multiplier for the daily probability of dying for each individual. The multiplier for daily mortality (DDM_t), which was dependent on striped bass density each day (SD_t), used the following sigmoidal function:

$$DDM_t = a + b/(1 + e^{-(SDt - c)/d}), \qquad (16)$$

where a = 0.39, b = 4.45, c = 334,749.33, and d = 138,111.62 (Figure 2.2). These coefficients were estimated by adjusting the model-predicted survival estimates until they mimicked the observed density-dependent survival trend. Although this adjustment in mortality rate does not allow for the same degree of variability observed in the field-collected data set nor does it directly explain how or why density-dependent first-year survival occurs, maintaining first-year survival estimates close to the observed trend allows for the evaluation of various strategies for stocking fingerling striped bass into Smith Mountain Lake, the primary objective of this chapter, and not to explain the density-dependent mortality in the field-collected data.

Stocking Strategies

Various strategies for stocking fingerling striped bass into Smith Mountain Lake were examined via IBM simulations. Baseline stocking conditions, which represented the existing stocking strategy, were 300,000 fingerling striped bass with a median total length of 42 mm (range 35-50 mm total length) introduced on 15 June (day 166); these values were used unless otherwise noted. Four

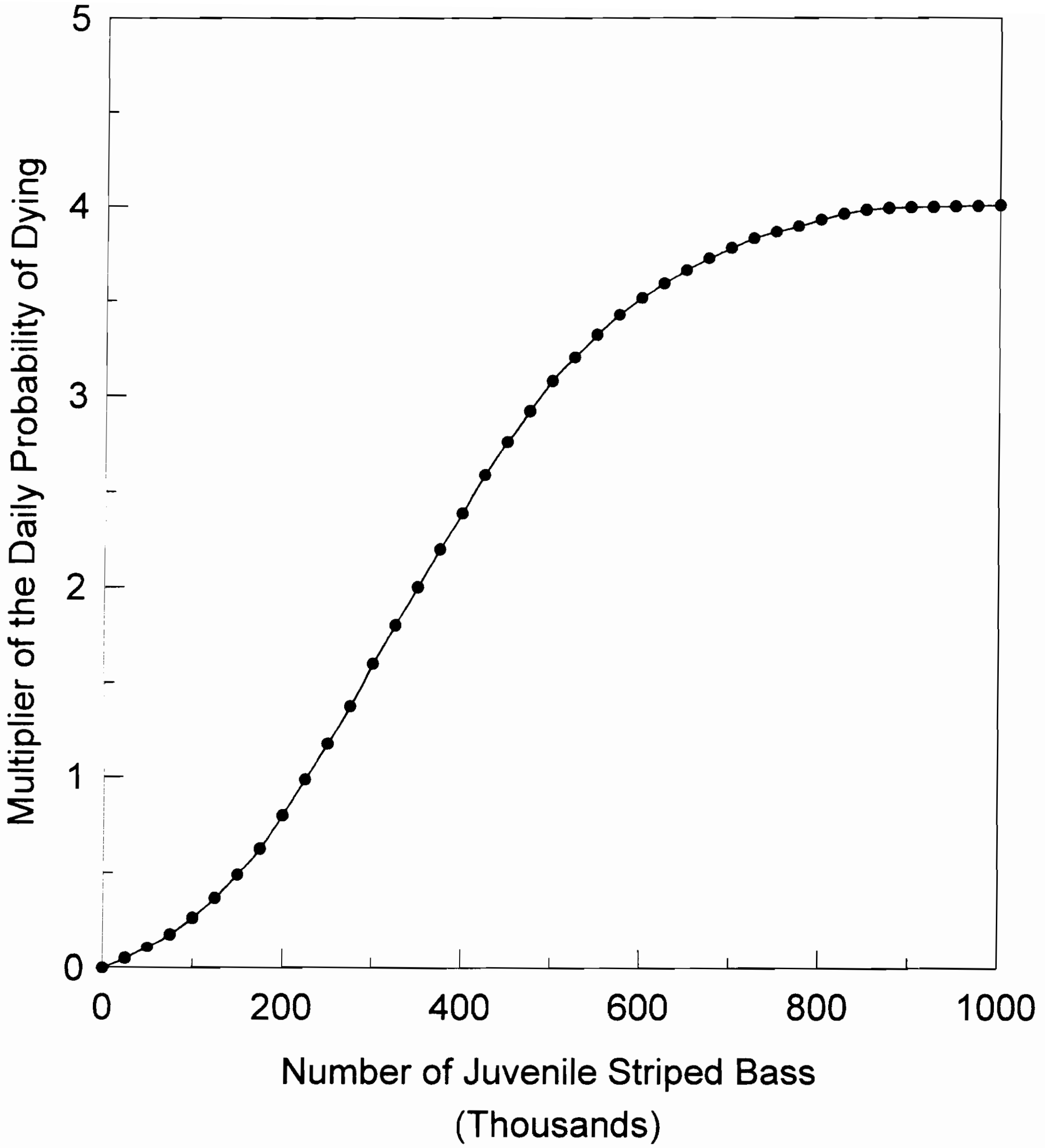


Figure 2.2. Sigmoidal relationship between the multiplier for the daily probability of dying and fingerling striped bass stocking density.

different stocking scenarios were conducted: (1) median total length at stocking was allowed to vary from 22 to 112 mm in 10-mm increments; (2) date of stocking was allowed to range from 18 May (day 138) to 20 July (day 201) in 7-d increments; (3) stocking density was allowed to vary from 100,000 to 1,000,000 fingerlings in 100,000-fingerling increments; and (4) median total length was allowed to vary from 22 to 112 mm in 10-mm increments and date of stocking was allowed to range from 18 May (day 138) to 20 July (day 201) in 7-d increments (Table 2.3). Based on the results of simulations (1)-(4), which were used to formulate the proposed, "new" stocking strategy, fingerling striped bass stocking density was examined again to determine whether the recommended stocking density from simulation (4) remained the same at the proposed fingerling size and date at stocking. As a result, an additional simulation was conducted at these conditions; (5) stocking density was allowed to vary from 100,000 to 1,000,000 fingerlings in 100,000-fingerling increments (Table 2.3). Thus, 10 x 1 or 10 IBM simulation trials were performed for stocking scenarios (1)-(3) and (5), and 10 x 10 or 100 IBM simulation trials were performed for stocking scenario (4).

For every simulation, the shape of the length-frequency distribution of age-0 striped bass was identical to that observed just prior to stocking in Smith Mountain Lake; normal and unimodal with a SD = ±2.74 mm. For example, a cohort of fingerling striped bass stocked at a median total length of 42 mm was normally distributed with a minimum total length of 35 mm and maximum total length of 50 mm. However, the length-frequency distribution at the time of stocking used in each simulation was positioned along the length axis in order to correspond to the selected median total length for that particular simulation.

The number of large-mode striped bass (NLMSB), median total length,

Table 2.3. Simulation scenarios examined using an individual-based model for stocking fingerling striped bass into Smith Mountain Lake.

#	Stocking Simulation Scenarios	Median Total Length At Stocking	Calender Date (Julian Date) At Stocking	Fingerling Density At Stocking
1	Stocking Size	22 to 112 mm (10-mm Increments)	15 June (Day 166) (Constant)	300,000 (Constant)
2	Stocking Date	42 mm (Constant)	18 May (Day 138) to 20 July (Day 201) (7-d Increments)	300,000 (Constant)
3	Stocking Density	42 mm (Constant)	15 June (Day 166) (Constant)	100,000 to 1,000,000 (100,000 Increments)
4	Stocking Size and Date	22 to 112 mm (10-mm Increments)	18 May (Day 138) to 20 July (Day 201) (7-d Increments)	300,000 (Constant)
5	Stocking Size, Date, and Density	52 mm (Constant)	08 June (Day 159) (Constant)	100,000 to 1,000,000 (100,000 Increments)

and first-year survival of the age-0 cohort were recorded at the end of each simulation run (01 May). NLMSB refers to the number of age-1 striped bass recruits on 01 May with a total length >150 mm. This minimum length was chosen because: (1) field results (Chapter I) indicated that age-0 striped bass that do not reach 150 mm total length by the end of the growing season suffer disproportionately greater overwinter mortality than juveniles larger than this length; and (2) individual-based model bioenergetics during winter months did not realistically simulate starvation mortality over this time period as it appears to have occurred in Smith Mountain Lake.

Replicate simulations could be performed that differ only in their random number sequences which, in turn, affect the outcome of stochastic processes such as water temperature regime, fish prey encounters, and striped bass mortality. Because analysis of IBM simulation outputs showed that the average predicted NLMSB and first-year survival among replicate simulations varied less than 8% and that average predicted median total length varied less than 6%, only single simulation results are presented in this chapter.

Sensitivity and Robustness Analysis

Sensitivity analysis was performed on model inputs related to daily Smith Mountain Lake water temperature, and age-0 alewife population density, daily growth and mortality rates, and the timing of adult alewife spawning to determine the extent of their relative influence and to compare their importance on NLMSB, median total length, and first-year survival predictions at the end of the overwintering period under the existing and proposed stocking strategies. Striped bass stocking conditions for each strategy were as follows: (1) existing strategy: 300,000 fingerlings with a median total length of 42 mm (range 35-

50 mm total length) introduced on 15 June (day 166); and (2) proposed strategy: 300,000 fingerlings with a median total length of 52 mm (range 45-60 mm total length) introduced on 08 June (day 159). For this analysis, water temperature and alewife population dynamics were varied singly (Table 2.4) and in combination (Table 2.5) from their baseline values. Combinations represent how these inputs would vary in a linked manner under both warm and cold years. For example, during a warm year, Smith Mountain Lake water temperature would be warmer, prompting adult alewives to spawn earlier in the growing season. Further, age-0 alewives would grow at a faster rate and would be expected to suffer a higher degree of mortality due to intra- and interspecific trophic competition, disease, and predation. In contrast, the converse conditions would be expected during a cold year. To determine sensitivity, the percent relative change from baseline of each of the three prediction variables for both stocking strategies was computed as: $((Y_i - Y_b)/Y_b)\cdot 100$, where Y_i was the predicted model output value for the ith input perturbed and Y_b was the predicted model output value under baseline conditions.

The same results from sensitivity analyses were also used to confirm the robustness of the proposed stocking strategy. For robustness analysis, predicted model output values were compared between the proposed and existing stocking strategies to confirm that the proposed stocking strategy was advantageous under variable conditions in alewife population dynamics and Smith Mountain Lake water temperature regime. However, percent relative change in model predictions was computed in a different manner than for sensitivity analysis simulations. To establish robustness, percent relative change in each of the three prediction variables was computed as: $((Y'_{pi} - Y_{bi})/Y_{bi})\cdot 100$, where Y_{pi} was the predicted model output value for the ith input

Table 2.4. Alewife population dynamics and water temperature perturbation simulations used to compare the sensitivity of the existing versus the proposed fingerling striped bass stocking strategies.

	Alewife Population Dynamics				
Model Simulation	Population Density	Spawning Day Offset	Daily Growth Rate Multiplier	Daily Mortality Rate Multiplier	Daily Water Temp Offset
1. Baseline Conditions	$2.2/m^3$	0	0	0	0
2. Population Density					
a. Density Doubled	$4.4/m^3$	Baseline	Baseline	Baseline	Baseline
b. Density Halved	$1.1/m^3$	Baseline	Baseline	Baseline	Baseline
3. Spawning Day Offset					
a. Two Weeks Earlier	Baseline	- 14 d	Baseline	Baseline	Baseline
b. One Week Earlier	Baseline	- 07 d	Baseline	Baseline	Baseline
c. One Week Later	Baseline	+07 d	Baseline	Baseline	Baseline
d. Two Weeks Later	Baseline	+14 d	Baseline	Baseline	Baseline
4. Daily Growth Rate Multiplier					
a. Slow Growth	Baseline	Baseline	0.75/d	Baseline	Baseline
b. Fast Growth	Baseline	Baseline	1.50/d	Baseline	Baseline
5. Daily Mortality Rate Multiplier					
a. High Mortality	Baseline	Baseline	Baseline	+10.0%/d	Baseline
b. Low Mortality	Baseline	Baseline	Baseline	- 10.0%/d	Baseline
6. Daily Water Temperature Offset					
a. Much Cooler	Baseline	Baseline	Baseline	Baseline	- 4.0°C/d
b. Cooler	Baseline	Baseline	Baseline	Baseline	- 2.0°C/d
c. Warmer	Baseline	Baseline	Baseline	Baseline	+2.0°C/d
d. Much Warmer	Baseline	Baseline	Baseline	Baseline	+4.0°C/d

Table 2.5. Alewife population density and warm and cold year perturbation simulations used to compare the sensitivity of the existing versus the proposed fingerling striped bass stocking strategies.

	Alewife Population Dynamics				
Model Simulation	Population Density	Spawning Day Offset	Daily Growth Rate Multiplier	Daily Mortality Rate Multiplier	Daily Water Temp Offset
1. Baseline Conditions	$2.2/m^3$	0	0	0	0
2. Warm Year					
a. High Density	$4.4/m^3$	- 14 d	1.50/d	+ 10.0%/d	+4.0°C/d
b. Baseline Density	$2.2/m^3$	- 14 d	1.50/d	+ 10.0%/d	+4.0°C/d
c. Low Density	$1.1/m^3$	- 14 d	1.50/d	+ 10.0%/d	+4.0°C/d
3. Cold Year					
a. High Density	$4.4/m^3$	+ 14 d	0.75/d	- 10.0%/d	- 4.0°C/d
b. Baseline Density	$2.2/m^3$	+ 14 d	0.75/d	- 10.0%/d	- 4.0°C/d
c. Low Density	$1.1/m^3$	+ 14 d	0.75/d	- 10.0%/d	- 4.0°C/d

perturbed under the proposed stocking strategy and Y_{bi} was the predicted model output value for the ith input perturbed under the existing stocking strategy.

The magnitudes of variation imposed on model inputs were determined from knowledge about Smith Mountain Lake and other systems (Tables 2.4 and 2.5). Annual water temperature regime was allowed to vary ±2.0°C and ±4.0°C based on data collected during the 1994-95 and 1995-96 sampling seasons from the field component of this study and annual Smith Mountain Lake water temperature records compiled by the VDGIF (M.C. Duval, unpublished data). Variability in the timing of alewife spawning (±7 d, ±14 d) was determined from a previous study on Smith Mountain Lake (Tisa 1988) and reports from Cayuga Lake, New York (Rothschild 1966), Milwaukee Harbor, Lake Michigan (Norden 1967), the Kalamazoo River, Michigan (Edsall 1970), and Claytor Lake, Virginia (Nigro 1980). In addition, the degree of variation in daily growth (0.75/d, 1.50/d) and mortality rate (±10.0%/d) multipliers for age-0 alewives were also based on Tisa's study (1988) and, in addition, observations on growth rates from Claytor Lake (Kohler 1980) and Wautauga Reservoir, Tennessee (Daniel 1984), as well as mortality rates from a small Massachusetts coastal pond (Essig and Cole 1986) and Lake Michigan (Mansfield and Jude 1986). However, estimates for the variability in age-0 alewife density were not based directly on known values. Tisa (1988) observed that the relative abundance of age-0 alewives in Smith Mountain Lake did not vary significantly between 1983 and 1984. Further, year-to-year variations in age-0 alewife density in other systems have not been reported in the literature. Because clupeid populations are characterized by large fluctuations in year-class strength (Lasker 1985) and age-0 alewife cohort density in Smith Mountain Lake, as estimated from hydroaccoustic assessments, has been observed to fluctuate considerably in recent years (M.C. Duval, VDGIF, personal communication), age-0 alewife cohort density was allowed to vary ±200%/m^3 from the estimated baseline value of 2.2/m^3.

MODEL CALIBRATION AND CORROBORATION

Before using the IBM to examine strategies for stocking fingerling striped bass, simulations were calibrated and compared to data from Smith Mountain Lake to examine the model's internal consistency. All calibration and corroboration simulations were performed using data collected from Smith Mountain Lake during the 1994-96 sampling periods, and were run under the existing stocking strategy and baseline conditions for alewife population dynamics and water temperature regime. For model calibrations, one-year simulation runs were used to portray juvenile striped bass fish prey food habits and length relationships between consumed forage-fish prey and juvenile striped bass. Further, multiple, one-year simulation runs, using the actual numbers of fingerling striped bass stocked in Smith Mountain Lake from 1973-96 and the density-dependent daily mortality multiplier (Figure 2.2), were used to mimic density-dependent first-year survival observed for stocked fingerling striped bass. In addition, the efficacy of the model in realistically representing juvenile striped bass growth rates was examined by comparing observed and predicted length-frequency distributions before and after the overwintering period using one-year simulation runs.

Food Habits and Predator-Prey Size Relationships

Model predictions of juvenile striped bass fish prey food habits and size relationships between consumed fish prey total length (TL) relative to juvenile striped bass TL generally agreed with empirical data (Figure 2.3). Observations from field-collected data demonstrated that smaller striped bass (range 40-120 mm TL) exclusively consumed age-0 cyprinids that ranged in size from 9-40 mm

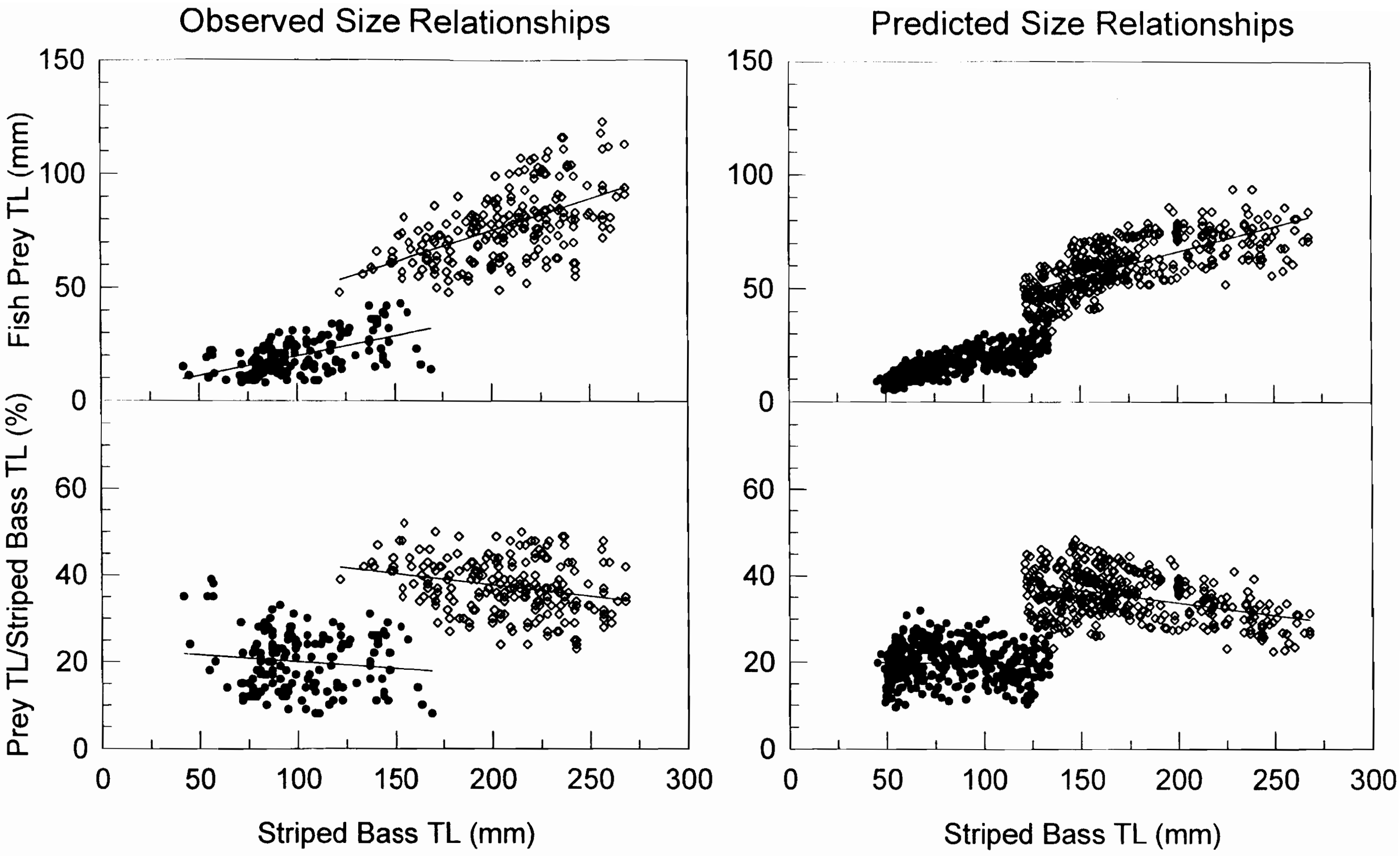


Figure 2.3. Comparison of field-observed and model-predicted size relationships of age-0 cyprinids (solid circles) and alewives (hollow diamonds) consumed by juvenile striped bass. The uppermost plots represent consumed fish prey TL versus striped bass TL and the lowermost plots represent consumed fish prey TL to striped bass TL versus striped bass TL (TL = total length).

TL, whereas larger striped bass (range 150-270 mm TL) primarily ate alewives that ranged in total length from 50-125 mm. Additionally, although the ratio of alewife to striped bass TL (range 23-52%) was, on average, greater than the ratio of cyprinid to striped bass TL (range 7-39%), a declining trend with increasing predator size was clearly evident for both consumed forage fishes. Even though model-simulated predator-prey dynamics were fitted to the above field-collected data and simulation outputs were similar to field observations, IBM predator-prey size relationship predictions were generally less than those estimated from stomach content analysis. For example, age-0 striped bass less than 130 mm total length (TL) consumed primarily age-0 cyprinids that ranged in total length from 6-37 mm, while juvenile striped bass greater than 130 mm TL consumed entirely age-0 alewives that ranged from 40-95 mm total length. Furthermore, a declining trend in the ratio of fish prey to striped bass body length with increasing predator size was apparent for both consumed forage fishes, and the ratio of alewife to striped bass TL was, on average, greater than the ratio of cyprinid to striped bass TL (range 16-49% and 10-32%, respectively), although both ranges were slightly lower than field observations. However, despite these differences in the relative sizes of age-0 cyprinids and alewives consumed by juvenile striped bass, estimates for predicted first-year growth and size distributions of age-0 striped bass were consistent with field observations.

First-Year Survival

Model-simulated first-year survival estimates, using the actual numbers of fingerling striped bass stocked in Smith Mountain Lake from 1973-96, resulted in an inverse relationship that agrees appreciably with the one estimated from fall gillnet surveys (Figure 2.4). For example, at the highest stocking density (809,246 fingerlings), the field-estimated survival rate was 10.2% and the model-predicted survival rate was 11.3%. Likewise, at the lowest stocking density (197,534 fingerlings), the field-estimated survival rate was 39.9% and the model-predicted survival rate was 28.8%. Although the degree of variability in first-year survival was less for predicted than the observed estimates (r^2 = 0.42 for observed versus 0.77 for predicted), the slopes of these relationships were not significantly different (slope = -0.04 versus -0.05, respectively; t-test between regression coefficients, t=3.45, P=0.002).

First-Year Growth

Growth patterns and length-frequency distributions for juvenile striped bass from model simulations during fall and spring were similar to those observed during the 1994-95 and 1995-96 sampling seasons in Smith Mountain Lake (Figure 2.5). Model-simulated striped bass growth resulted in the development of a bimodal distribution by the end of the growing season (15 December) with a range (86-262 mm TL) similar to that observed during December 1994 (84-266 mmTL) and November 1995 (80-261 mm TL). Further, model large-mode striped bass (223 mm TL, range 182-262) were greater than twice as large as small-mode juveniles (93 mm TL, range 86-144 mm TL) from the same stocked cohort at the end of the growing season; similar estimates for large- and small-mode striped bass were also observed in 1994 (225 mm TL, range 182-266 mm TL and 94 mm TL, range 84-140 mm TL, respectively) and 1995 (226 mm TL, range 183-261 mm TL and 100 mm TL, range 80-137 mm TL, respectively). By spring (01 May), the model-predicted

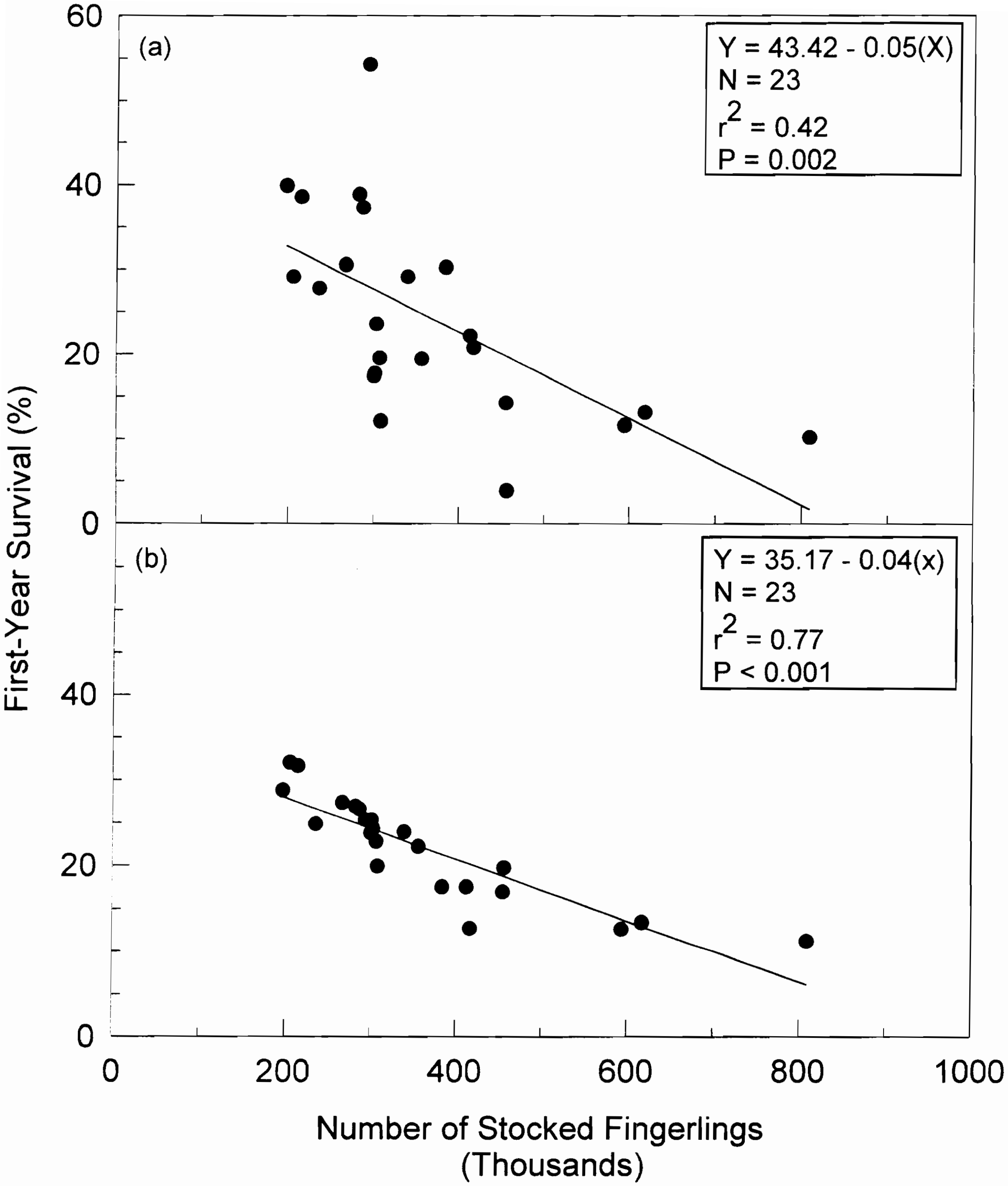


Figure 2.4. Comparison of the relationship between first-year survival and fingerling striped bass stocking density in Smith Mountain Lake, 1973-96, from (a) fall gillnet surveys (observed) and (b) individual-based model simulations (predicted).

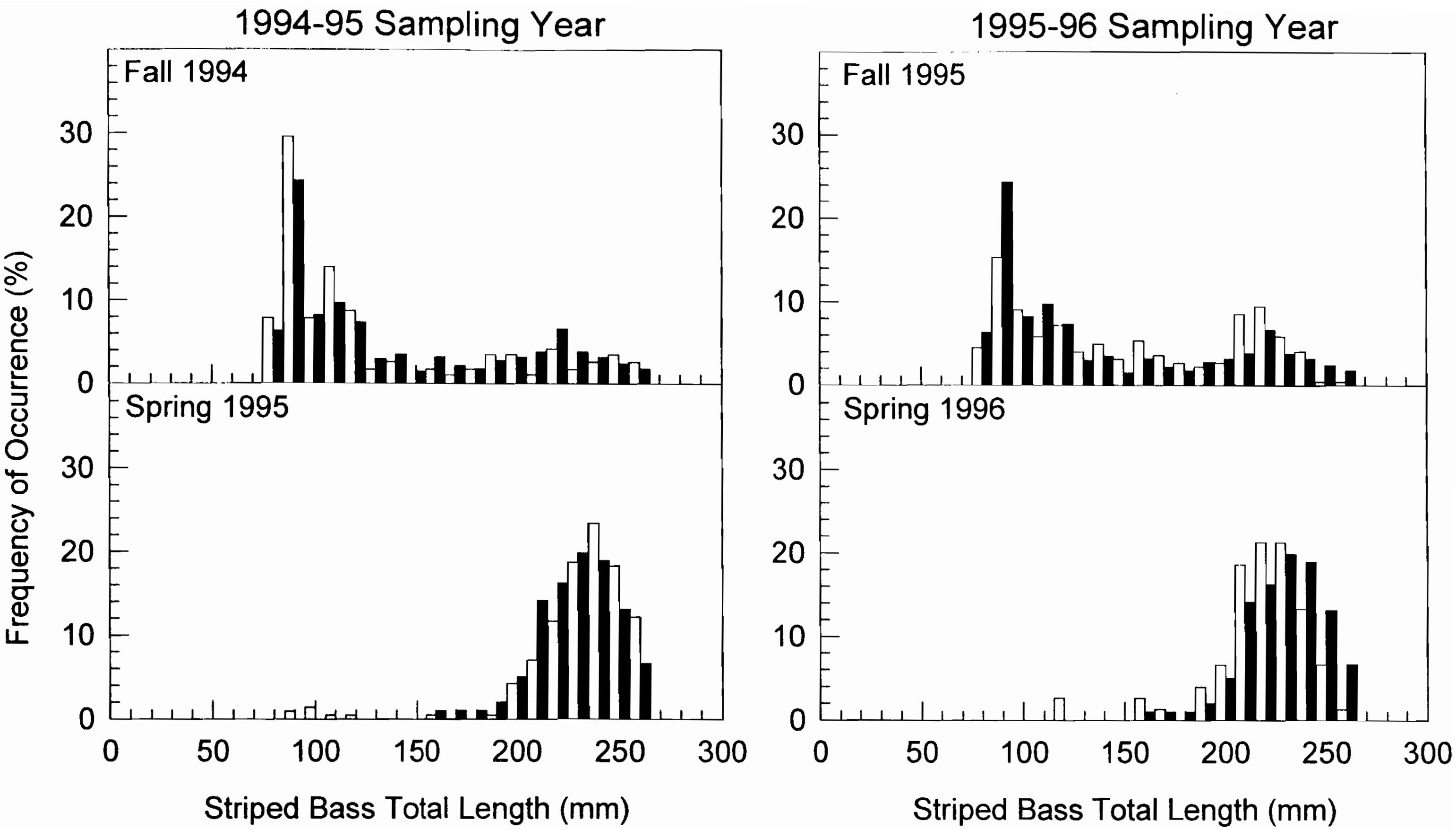


Figure 2.5. Comparison of field-observed (hollow bars) and model-predicted (solid bars) length-frequency distributions of stocked juvenile striped bass before and after the 1994-95 and 1995-96 overwintering periods in Smith Mountain Lake. Observed length-frequency distributions were estimated from field collections in late fall (1994: December; 1995: November) and early spring (1995: March; 1996: April). Predicted length-frequency distributions were estimated from individual-based model simulations in late fall (15 December) and spring (01 May).

striped bass length-frequency distribution had become unimodal as was observed in March 1995 and April 1996. However, the model length-frequency distribution had a narrower range (161-262 mm TL) than observed in 1995 (97-268 mm TL) and 1996 (128-262 mm TL). Despite these slight differences between the field-observed and model-predicted length-frequency distributions, the IBM accurately portrayed the general shape and pattern of first-year growth for juvenile striped bass in Smith Mountain Lake.

RESULTS

Stocking Strategy Simulation

The NLMSB, median total length, and percent first-year survival of the stocked, juvenile striped bass cohort at the end of the simulation period increased with increasing fingerling size at stocking on 15 June (Figure 2.6). Although the greatest increase in the NLMSB occurred when the median total length at stocking was increased from 32 to 42 mm (0 to 64,320 age-1 recruits), a similar increase in the NLMSB also occurred when the median total length at stocking was increased from 42 to 52 mm (64,320 to 126,310 age-1 recruits; +49%). However, stocking fingerling striped bass at median total lengths greater than 52 mm resulted in significantly lower percent increases in NLMSB (< +5% per 10-mm increase in size at stocking). Examination of final median total length and percent first-year survival for juvenile striped bass showed that these output parameters increased from 160 to 256 mm (+38%) and 23.9 to 43.0% (+44%) when the size at stocking on was raised from 42 to 52 mm (Figure 2.6). As was observed for NLMSB, the percent increases in final median total length and first-year survival also declined after a median stocking size of 52 mm total length (< +9% and < +4% per 10-mm increase in the size at stocking, respectively). Therefore, model simulations indicate that a modest increase in the median total length of age-0 striped bass stocked on 15 June in Smith Mountain Lake at a stocking density of 300,000 fingerlings from the current target size of 42 mm to 52 mm should result in the greatest returns in NLMSB, final median total length, and percent first-year survival.

The NLMSB, final median total length, and percent first-year survival of the stocked, juvenile striped bass cohort declined with increasing date of

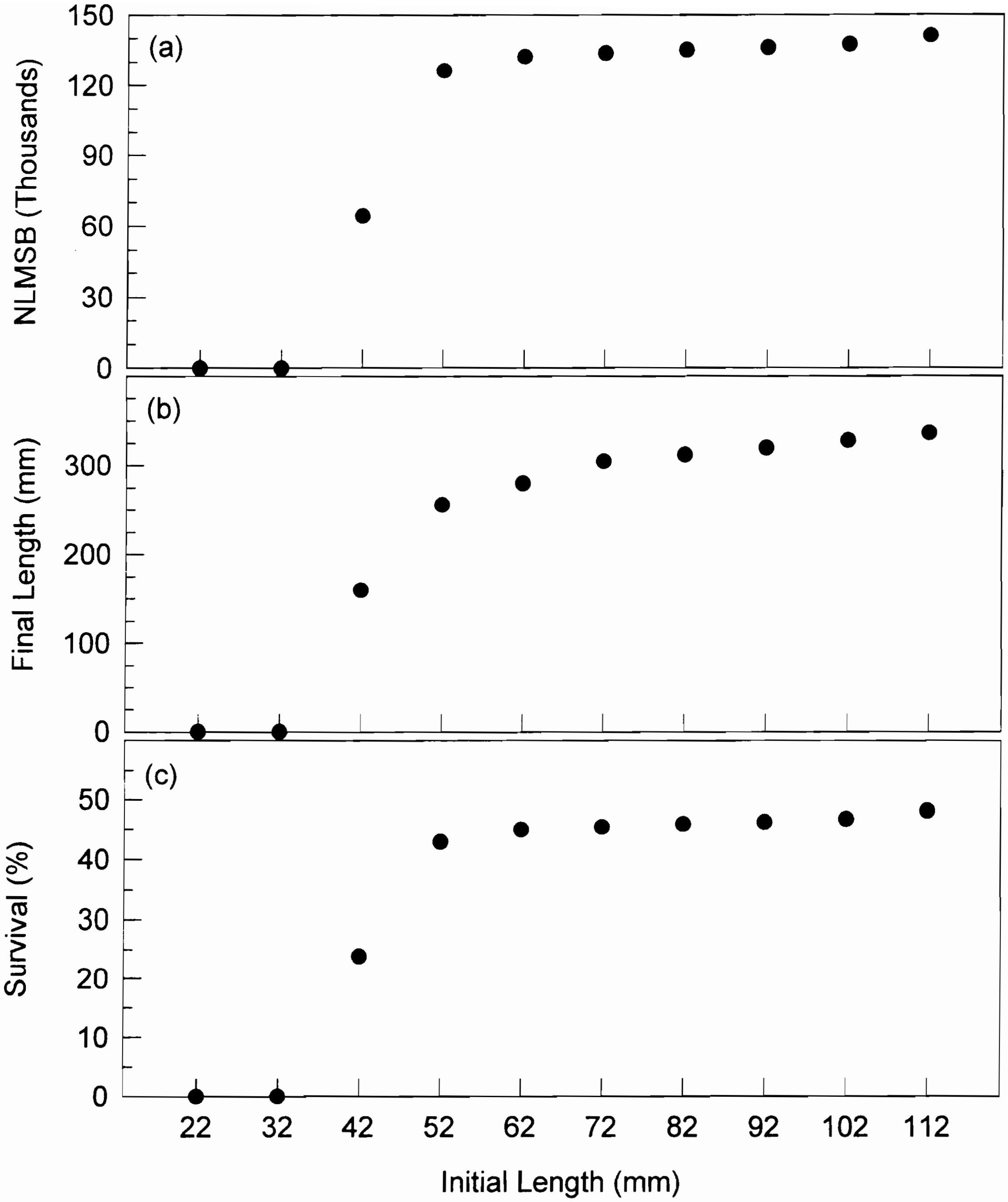


Figure 2.6. Response of (a) number of large-mode striped bass (NLMSB), (b) median total length (Final Length), and c) first-year survival (Survival) of juvenile striped bass on 01 May to median total length of fingerlings at the time of stocking (Initial Length).

stocking (Figure 2.7). Although NLMSB increased from 64,320 to 80,194 age-1 recruits (+20%) when fingerling striped bass were stocked one week earlier (08 June; day 159) than baseline (15 June; day 166), the largest relative increase occurred when stocking was moved two weeks earlier (01 June; day 152) from the baseline stocking date (80,194 to 107,440 age-1 recruits; +25%). Similarly, final median total length and percent first-year survival, which also increased when fingerling striped bass were stocked one week earlier (160 to 172 mm total length (+7%), and 23.9 to 27.3% (+12%), respectively), exhibited the largest relative increases when stocking was moved two weeks earlier from the baseline stocking date (172 to 222 mm total length (+23%), and 27.3 to 37.8% (+28%), respectively). Therefore, it would appear from these model simulation results that stocking juvenile striped bass at a median total length of 42 mm and at a density of 300,000 fingerlings approximately two weeks earlier than they are presently introduced (01 June versus 15 June) would result in the greatest returns in the NLMSB, final median total length, and percent first-year survival.

The NLMSB increased whereas final median total length and first-year survival decreased with increasing density of stocked striped bass (Figure 2.8). Although the NLMSB increased with the number of stocked striped bass (31,853 at 100,000 fingerlings to 85,570 age-1 recruits at 1,000,000 fingerlings), the largest percent increase in age-1 recruits occurred as stocking density was increased to 300,000 fingerlings (+22%), before leveling off after this stocking density (< +6%). Additionally, final median total length and first-year survival also declined most substantially from 200,000 to 300,000 fingerlings (-14% and -21%, respectively) and to a lesser extent after this stocking density (<-3% and <-12%, respectively). Therefore, simulation

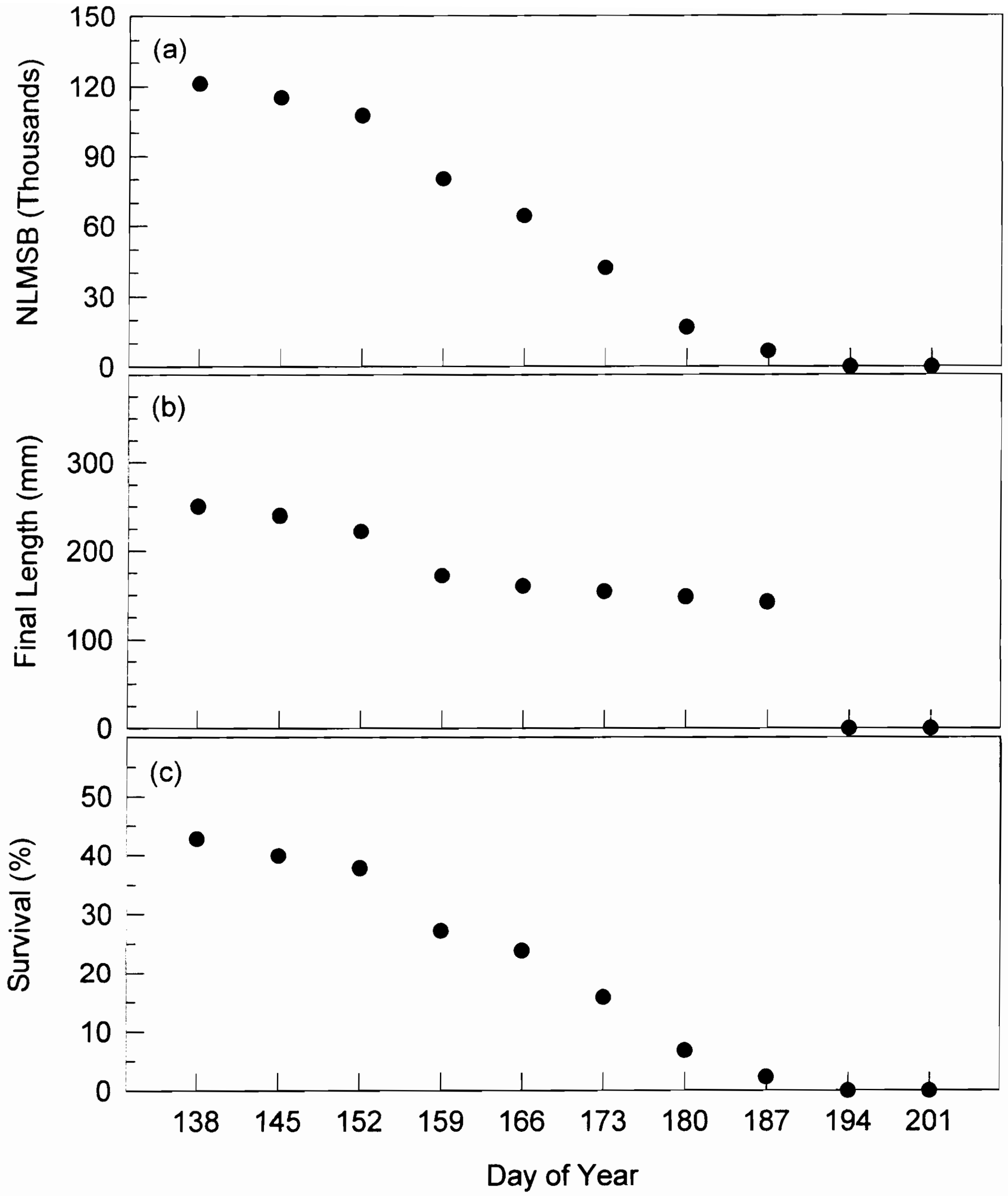


Figure 2.7. Response of (a) number of large-mode striped bass (NLMSB), (b) median total length (Final Length), and c) first-year survival (Survival) of juvenile striped bass on 01 May to Julian date at the time of stocking (Day of Year).

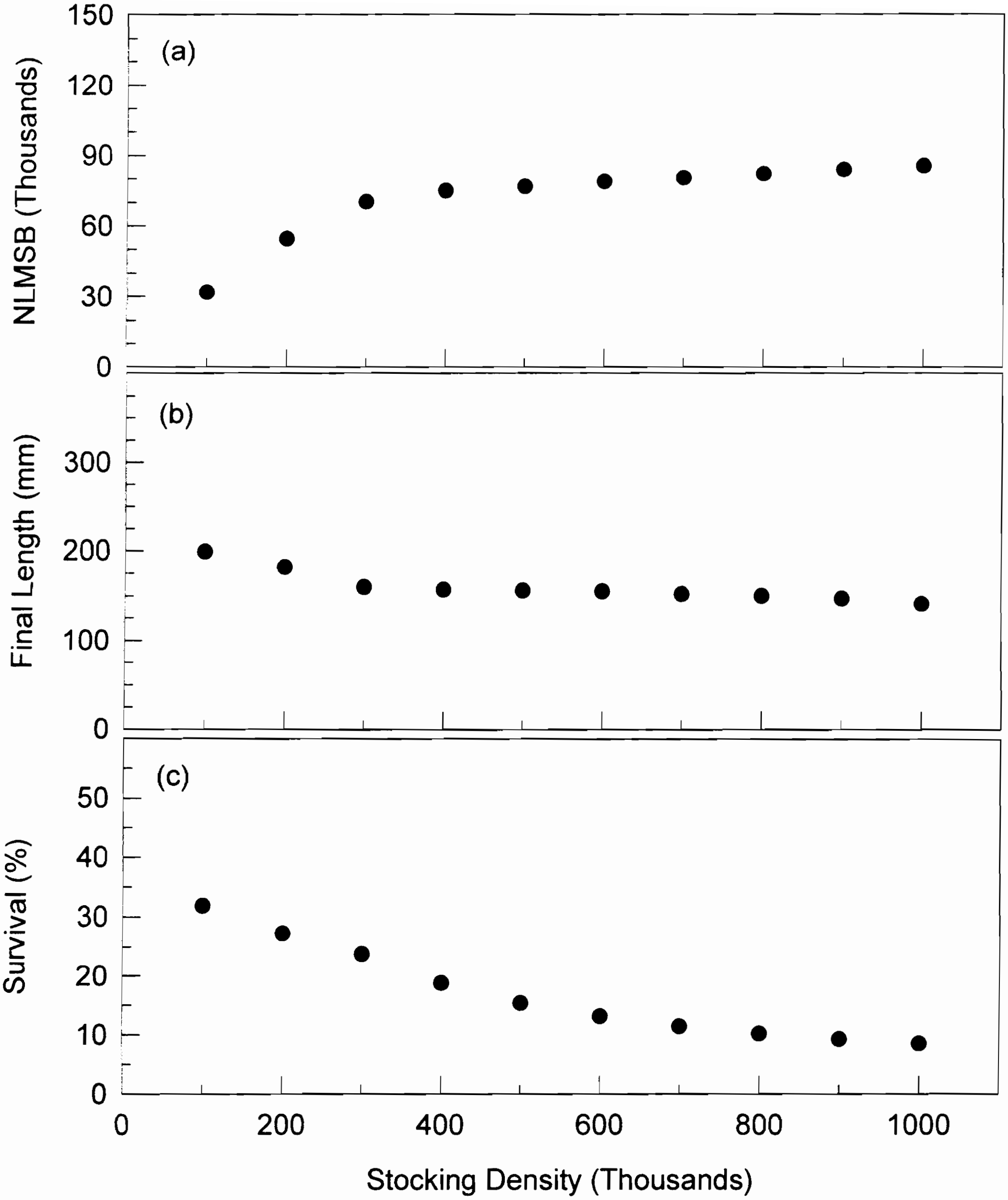


Figure 2.8. Response of (a) number of large-mode striped bass (NLMSB), (b) median total length (Final Length), and c) first-year survival (Survival) of juvenile striped bass on 01 May to density of stocked fingerlings (Stocking Density).

results from the model developed and used in this study do not indicate that incremental increases or decreases in the stocking density from the current level of 300,000 fingerlings will result in greater returns in the NLMSB, final median total length, and percent first-year survival than are now presently realized under the existing stocking scheme.

The combined effects of stocking fingerling striped bass at a larger median total length and earlier in the growing season also resulted in an increase in the NLMSB, final median total length, and percent first-year survival response surfaces (Figure 2.9). These simulations were conducted at a stocking density of 300,000 fingerlings because increasing the number of stocked fish did not have an appreciable effect when varied alone. The NLMSB exhibited a steep gradient, especially with respect to initial median total length of stocked fingerling striped bass (Figure 2.9a). For this output parameter response surface, the greatest percent increase occurred when the median total length at stocking was increased from 42 to 52 mm and as the date of stocking was moved earlier from 15 June (day 166) to 08 June (day 159). A similar result was also observed for the percent first-year survival response surface (Figure 2.9c). Although the final median total length response surface revealed a less distinct trend, median total length gradually increased as both the size of fingerling striped bass at the time of stocking was increased and fingerling striped bass were stocked earlier in the growing season cumulatively (Figure 2.9b). Therefore, it would appear from these IBM simulation results that increasing the median total length of age-0 striped bass at the time of stocking from 42 to 52 mm and stocking these fish in Smith Mountain Lake one week earlier in the growing season (08 June instead of 15 June) should result in the greatest returns in the NLMSB, final median total length, and percent first-year

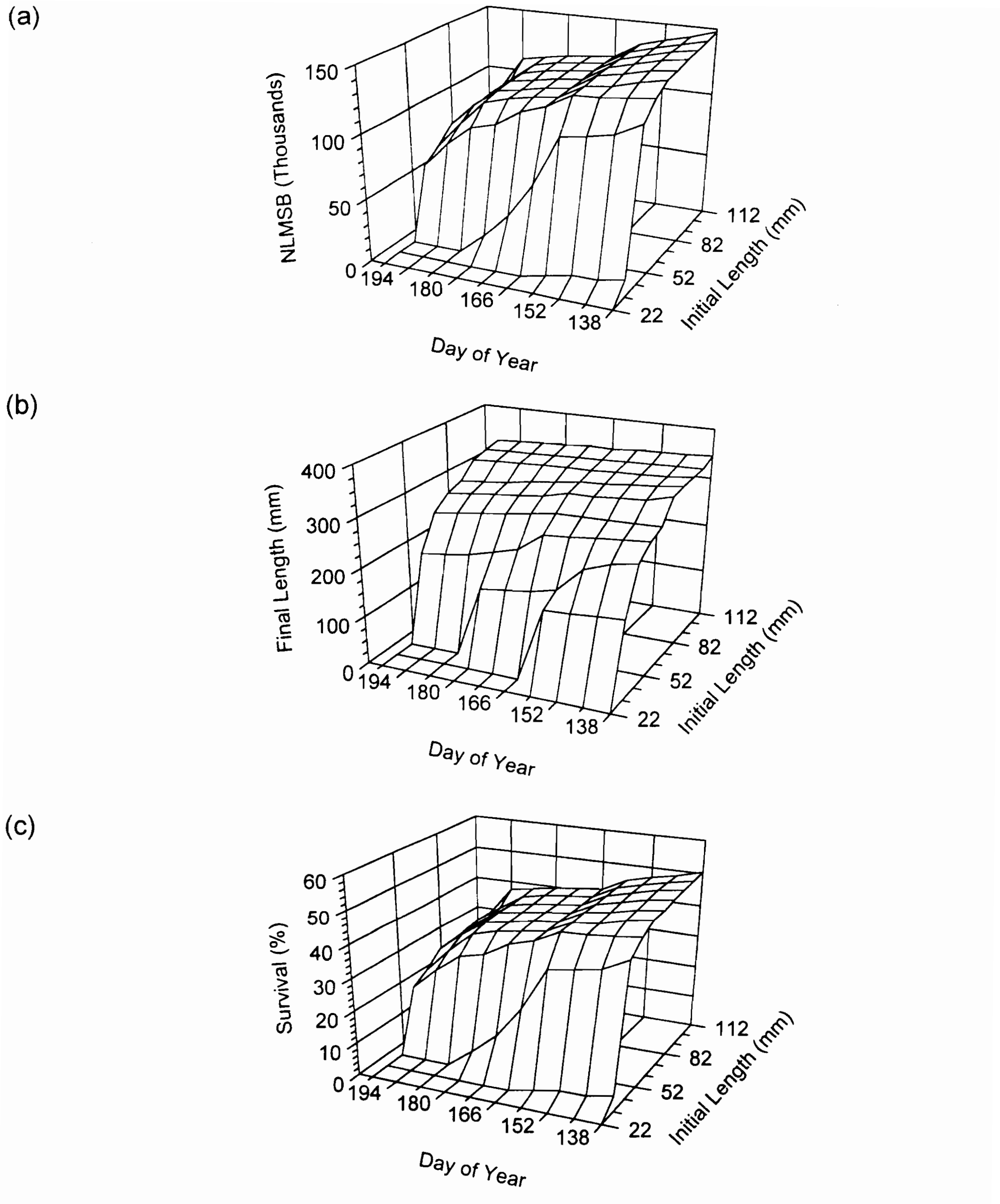


Figure 2.9. Response surfaces for (a) number of large-mode striped bass (NLMSB), (b) median total length (Final Length), and c) first-year survival (Survival) of juvenile striped bass on 01 May to median total length of fingerlings (Initial Length) and Julian date (Day of Year) at the time of stocking.

survival response surfaces at a stocking density of 300,000 fingerlings.

Under the proposed, "new" stocking strategy (52 mm TL and 08 June), the three model outputs exhibited similar trends as those observed at existing stocking conditions when the density of stocked striped bass was increased from 100,000 to 1,000,000 fingerlings (Figure 2.10). Although the NLMSB at the end of the simulation period increased with the number of stocked striped bass (72,650 at 100,000 fingerlings to 175,440 age-1 recruits at 1,000,000 fingerlings), the largest percent increase in age-1 recruits again occurred as stocking density was increased to 300,000 fingerlings (+16%), before declining substantially after this stocking density (< +7%). Additionally, final median total length and first-year survival, which both declined as stocking density was increased from 100,000 to 1,000,000 fingerlings (255 to 235 mm total length and 72.7 to 17.5%, respectively), also declined most substantially from 200,000 to 300,000 fingerlings (-2% and -20%, respectively) and to a lesser extent after this stocking density (<-1% and <-17%, respectively). Therefore, these simulation results do not indicate that at the proposed stocking size and date (52 mm total length and 08 June), a change in stocking density from 300,000 fingerlings will result in greater returns in the NLMSB, final median total length, and percent first-year survival.

Sensitivity and Robustness Analysis

Sensitivity analysis revealed that NLMSB, median total length, and percent first-year survival for juvenile striped bass stocked at the existing and proposed strategies were most strongly influenced by alewife spawning day offset, age-0 alewife daily growth rate multiplier, and daily water temperature

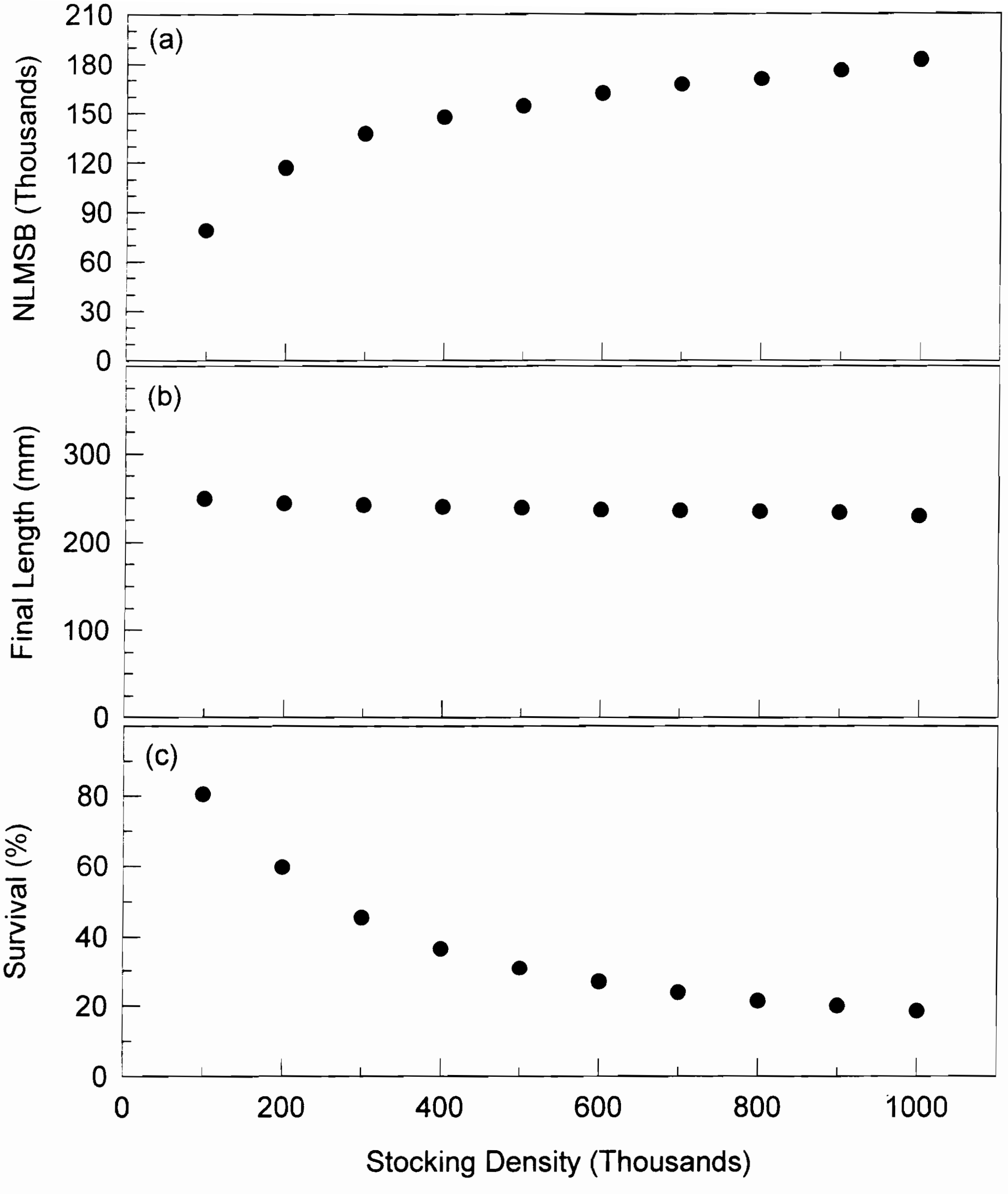


Figure 2.10. Response of (a) number of large-mode striped bass (NLMSB), (b) median total length, and c) first-year survival (Survival) of juvenile striped bass on 01 May to density of stocked fingerlings (Stocking Density) at the proposed stocking size (52 mm TL) and date (08 June).

offset (Figure 2.11). In particular, an alewife spawning day offset of ±14 d, daily growth rate multiplier of 0.75/d and 1.50/d, and daily water temperature offset of ±4°C/d resulted in the largest percent relative changes from baseline conditions for the three model output predictions. In contrast, variations in age-0 alewife cohort density and daily mortality rate multiplier resulted in smaller percent relative changes from baseline for NLMSB, median total length, and percent first-year survival at both stocking strategies (Figure 2.11). Further, for the existing and proposed strategies, perturbations in alewife and water temperature input parameters resulted in greater percent relative changes in NLMSB and first-year survival than for median total length. Although the pattern in percent relative change in the three model outputs was parallel for both stocking strategies, the existing stocking strategy was more sensitive (i.e. had a greater percent relative change from baseline) to parameter perturbations among the three model outputs than the proposed stocking strategy (Figure 2.11).

Sensitivity analysis also indicated that combined perturbations in alewife and water temperature parameter inputs also influenced NLMSB, median total length, and percent first-year survival for fingerling striped bass stocked at the existing and proposed stocking strategy (Figure 2.12). During warm year simulations, NLMSB, median total length, and first-year survival exhibited percent relative decreases from baseline values at both stocking strategies (Figure 2.12). In addition, the percent relative change from baseline for the three output parameters increased during simulated warm years as age-0 alewife density was reduced from $4.4/m^3$ to $1.1/m^3$ at the existing and proposed stocking strategies. For cold year simulations, the NLMSB, median total length, and first-year survival exhibited percent relative increases from

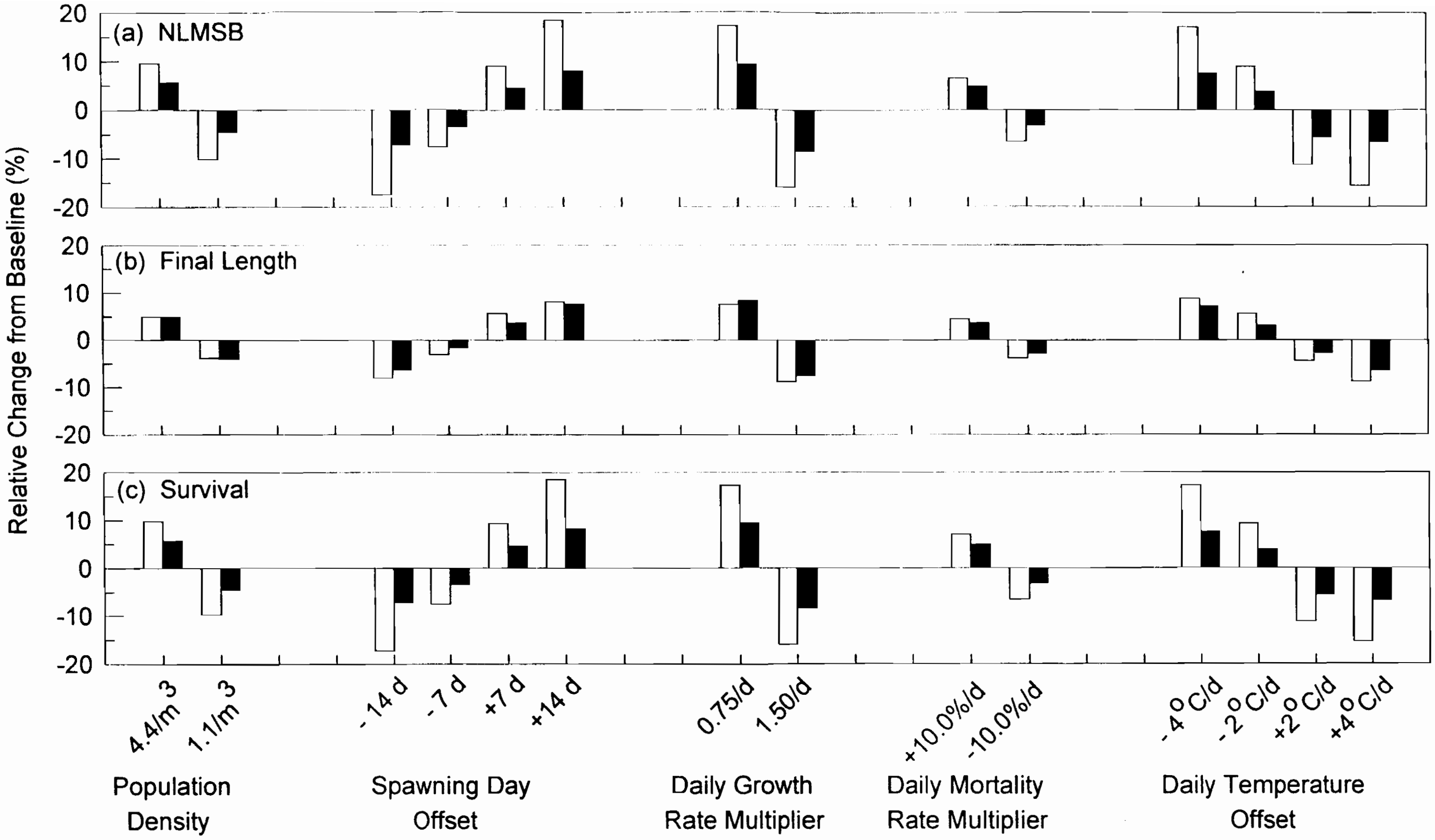


Figure 2.11. Comparison of sensitivities for (a) number of large-mode striped bass (NLMSB), (b) median total length (Final Length; mm), and c) first-year survival (Survival; %) of juvenile striped bass at the end of the overwintering period stocked at the existing (hollow bars) and proposed (solid bars) strategies from baseline conditions to perturbations in alewife population dynamics and Smith Mountain Lake water temperature regime varied individually. For details on sensitivity analysis, see *Methods: Sensitivity and Robustness Analysis*.

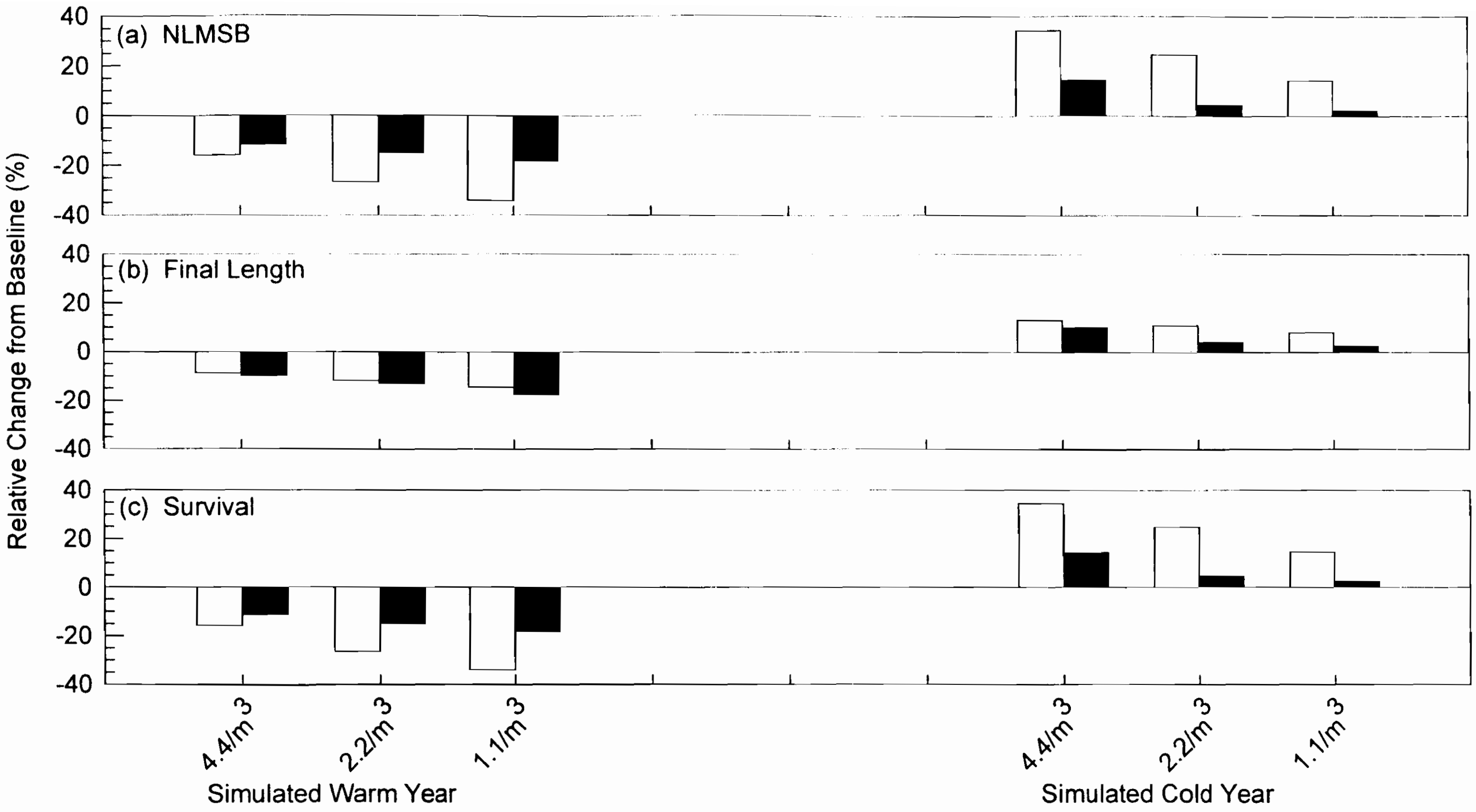


Figure 2.12. Comparison of sensitivities for (a) number of large-mode striped bass (NLMSB), (b) median total length (Final Length; mm), and c) first-year survival (Survival; %) of juvenile striped bass at the end of the overwintering period stocked at the existing (hollow bars) and proposed (solid bars) strategies from baseline conditions to perturbations in age-0 alewife population density during simulated warm and cold years. For details on sensitivity analysis, see *Methods: Sensitivity and Robustness Analysis.*

baseline values at both stocking scenarios (Figure 2.12). Further, the percent relative change from baseline for the three output parameters decreased during simulated cold years as age-0 alewife density was reduced from 4.4/m^3 to 1.1/m^3 at the existing and proposed stocking strategies. Although the observed percent relative change was greater for NLMSB and percent first-year survival than for median total length at both stocking strategies, the pattern was identical for the existing and proposed stocking strategies. However, the existing stocking strategy was more sensitive (i.e. had a greater percent relative change from baseline) to combined parameter perturbations among the three model outputs than the proposed stocking strategy (Figure 2.12).

Comparison of NLMSB, median total length, and percent first-year survival between the existing and proposed stocking strategies revealed that despite perturbations in the alewife and water temperature input parameters, both singly and combined, the proposed stocking strategy consistently resulted in percent relative increases in all three model outputs (Table 2.6). For model inputs varied singly, the greatest percent relative increases in the proposed over the existing strategy were observed for NLMSB and first-year survival outputs (range +96.8% to +145.6% and 96.9% to 145.2%, respectively; Table 2.6). Median total length also increased, albeit to a lesser extent (range +53.8% to +60.6%), than the other two model outputs. In addition, lower age-0 alewife density, early alewife spawning, faster age-0 alewife growth, lower age-0 alewife mortality, and warmer water temperatures resulted in the greatest percent relative increases in model outputs when these input parameters were varied singly for the proposed over the existing stocking strategy. When model inputs were varied concurrently, the greatest percent relative increases in the proposed over the existing strategy were also observed for NLMSB and first-

Table 2.6. Percent relative increases in the number of large-mode striped bass (NLMSB), median total length (Length), and first-year survival (Survival) at the end of the overwintering period for the proposed versus the existing fingerling striped bass stocking strategies to perturbations in age-0 alewife population dynamics and Smith Mountain Lake water temperature varied singly and in combination. For details on simulation conditions used to examine robustness analysis, see *Methods: Sensitivity and Robustness Analysis*.

Model Simulation	Parameter Variation	NLMSB	Length	Survival
Baseline Conditions	-----	+118.4	+57.5%	+118.7
Population Density				
Density Doubled	4.4/m^3	+110.4	+57.1%	+110.2
Density Halved	1.1/m^3	+131.8	+57.1%	+131.6
Spawning Day Offset				
Two Weeks Earlier	- 14 d	+145.6	+60.5%	+145.2
One Week Earlier	- 07 d	+128.2	+60.0%	+128.3
One Week Later	+07 d	+109.0	+54.4%	+109.0
Two Weeks Later	+14 d	+96.8%	+56.6%	+96.9%
Daily Growth Rt Multiplier				
Slow Growth	0.75/d	+103.6	+58.7%	+104.0
Fast Growth	1.50/d	+127.4	+59.6%	+138.3
Daily Mortality Rt Multiplier				
High Mortality	+10.0%/d	+114.6	+56.3%	+114.4
Low Mortality	- 10.0%/d	+126.0	+59.1%	+126.5
Daily Water Temp Offset				
Much Cooler	- 4°C/d	+100.4	+55.2%	+100.4
Cooler	- 2°C/d	+108.0	+53.8%	+107.7
Warmer	+2°C/d	+137.0	+60.1%	+137.4
Much Warmer	+4°C/d	+141.4	+61.6%	+141.0
Simulated Warm Year				
High Density	4.4/m^3	+129.9	+55.5%	+130.6
Baseline Density	2.2/m^3	+153.0	+55.3%	+153.5
Low Density	1.1/m^3	+170.5	+51.8%	+170.9
Simulated Cold Year				
High Density	4.4/m^3	+85.7%	+53.0%	+85.8%
Baseline Density	2.2/m^3	+88.5%	+49.1%	+88.7%
Low Density	1.1/m^3	+95.5%	+48.9%	+95.5%

year survival outputs (range +85.7% to +170.5% and +85.8% to 170.9%), while median total length also increased to a lesser extent (range +48.9% to +55.5%; Table 2.6). Further, low age-0 alewife density during warm years and high age-0 alewife density during cold years resulted in the largest and smallest percent relative changes (+170.5% and +85.7%, respectively) among the three model outputs for the proposed over the existing stocking strategy. Therefore, these results indicate not only that the proposed stocking strategy results in greater returns in NLMSB, median total length, and percent first-year survival over the existing stocking strategy regardless of input perturbation, but that the percent relative change remains the same magnitude (i.e. is robust) under fluctuations in alewife population parameters and Smith Mountain Lake water temperature regime.

DISCUSSION

Individual-based model simulation results clearly demonstrated that stocking juvenile striped bass into Smith Mountain Lake at a slightly larger size (52 mm total length) and one week earlier in the growing season (08 June), while maintaining the current annual stocking density at 300,000 fingerlings, resulted in the largest percent increases in median size, first-year survival, and number of age-1 recruits. Based on the life-history characteristics and factors regulating recruitment of this stocked sport fish in Smith Mountain Lake identified in *Chapter I*, these increases would arise in response to greater feeding opportunities afforded to stocked fingerlings. For example, juvenile striped bass stocked at a larger size and earlier in the growing season would have a greater initial length advantage over age-0 forage-fish prey, in particular age-0 alewives. Further, calculations from model simulations indicate that a greater proportion of the age-0 alewife cohort biomass would be morphologically available during the growing season to juveniles stocked at the proposed than the existing strategy (68% versus 21%, respectively). As a consequence, larger and/or earlier stocked fingerling striped bass will be able to maintain a higher degree of piscivory, grow at a faster rate, and reach a larger size by the end of the growing season. Because larger individuals tend to accumulate greater absolute energy stores and have lower relative weight-dependent metabolic rates than smaller conspecifics (Paloheimo and Dickie 1966; Brett and Groves 1979; Oliver et al. 1979; Shuter et al. 1980), increasing the size of juvenile striped bass by the end of the growing season will allow a considerable increase in the overwinter survival of the age-0 cohort; consequently, the success of striped bass stocking program will be increased in Smith Mountain Lake.

The close agreement of model simulation results with empirical data does not necessarily mean that the mechanisms in the model are the sole explanation for the age-0 striped bass cohort growth, survival, and recruitment trends observed in Smith Mountain Lake. Conditions in aquatic ecosystems are more complex, and somewhat different mechanisms can interact, resulting in similar outcomes. For example, model-simulated mortality was primarily a result of disproportionately lower overwinter survival for juvenile striped bass <150 mm total length; individuals that did not reach this size by the end of their first growing season were not allowed to survive the winter. Because studies on other age-0 sport fishes have reported that individuals that do not reach some critical size prior to the onset of the overwintering period suffer disproportionately greater starvation-induced overwinter mortality (Forney 1976; Adams et al. 1982; Carline et al. 1986), the critical size designated for juvenile striped bass in Smith Mountain Lake has a sound biological basis. As reported in *Chapter I*, juvenile striped bass smaller than 150 mm total length were rarely collected during the 1995 and 1996 spring sampling periods. Based on size distribution and physiological indices of health data, it would appear that the inability of these smaller individuals to store sufficient energy reserves prior to the overwintering period, coupled with their relatively higher weight-dependent metabolic rates (Paloheimo and Dickie 1966; Brett and Groves 1979; Oliver et al. 1979; Shuter et al. 1980), resulted in disproportionately greater overwinter mortality for small- versus large-mode striped bass. However, whether small juveniles in Smith Mountain Lake actually reached the starvation point or other sources of mortality (i.e. disease, parasitism, predation) removed these fish first is not entirely clear. Nonetheless, any mechanism by which age-0 fishes are rapidly lost from the population due to causes directly or indirectly related to a loss in body weight should produce behaviors similar to those observed in the model simulations; the precise mechanism by which individuals are lost should not affect these results.

Although the highest mortality for fish populations typically occurs shortly after hatching when larvae are numerous and most vulnerable (Rice et al. 1993), these simulation results suggest that mortality processes for older life stages, such as size-dependent overwinter starvation, can also have a substantial impact on recruitment to age 1. Further, sensitivity analyses revealed that biotic and abiotic factors influencing the size relationship between age-0 striped bass and their forage-fish prey can influence the recruitment process through their effects on growth during the first year of life. For example, water temperature not only alters the timing of alewife spawning relative to the time that fingerling striped bass are introduced, but it also impacts age-0 alewife growth rates. These will, in turn, influence forage-fish prey morphological availability, growth of age-0 striped bass, and ultimately, the size distribution of the stocked striped bass cohort at the end of the first growing season. Because population structure appears to be a major determinant regulating recruitment of striped bass to the adult stock in Smith Mountain Lake, environmental factors such as water temperature, which influence prey fish population dynamics, can be a greater factor regulating year-class strength later during the first year of life than has been assumed for other naturally-reproducing populations of fishes (Sale 1990).

The Smith Mountain Lake version of the IBM projects juvenile striped bass growth and survival as a function of the size distribution of fingerling striped bass at the time of stocking, the day of year at introduction, fingerling stocking density, water temperature regime, and population dynamics of forage-fish prey species. However, the success of the striped bass stocking program may also depend on biological factors not explicitly incorporated within the model utilized for this study; these factors include availability of prey types such as invertebrates and other forage fishes, genetic variability inherent within the stocked age-0 striped bass cohort, and variation in the physiological health of striped bass fingerlings at the time of stocking and throughout the growing season. Further, the age-0 cyprinid component of the model did not allow for the realistic characterization of predator-prey dynamics in the littoral compartment; the best available field-collected data regarding age-0 cyprinid growth and density resulted in the depletion of this prey type by juvenile striped bass. Because age-0 cyprinids were highly abundant in nearshore regions of Smith Mountain Lake throughout the growing season, it is unlikely that juvenile striped bass could completely exhaust this prey resource. Support for this assumption comes from the relationship between cyprinid body depth and total length relative to beach seine mesh size used to estimate density of this forage-prey type during the field component of this study; a beach seine with 3.18-mm bar mesh would not be restrictive enough to representatively capture age-0 cyprinids <35 mm TL, resulting in density estimates that were likely lower than actual densities in the littoral zone of Smith Mountain Lake. As a result of this bias in density estimation, age-0 cyprinids, which were consumed in the littoral compartment, were not allowed to be removed from the population in order to allow the model to accurately portray first-year growth of striped bass post-stocking. Because of these limitations, the model could not be used, in its present form, to identify the specific sources and mechanisms involved in the development of density-dependent mortality or examine alternative hypotheses which may potentially explain this phenomenon. These hypotheses include, but are not restricted to: (1) size-selective predation exerted on juvenile striped bass during vulnerable periods, such as winter months, by larger piscivores which may only become a significant source of mortality at unusually high stocking densities or during particularly adverse climatic conditions; (2) the influence of stress on the physiological well-being of juvenile striped bass during transportation from grow-out facilities to Smith Mountain Lake; (3) an artifact of using different sampling gears to collect juvenile striped bass over both spatial and temporal scales; (4) movement of smaller juvenile striped bass into the pelagic zone to avoid predators, resulting in a mismatch in the size relationship with forage-fish prey; and (5) density-dependent growth of juvenile striped bass in the littoral zone before they disperse to pelagic areas of Smith Mountain Lake. As more specific information becomes available regarding the effects of these factors, in particular age-0 cyprinid dynamics, on juvenile striped bass growth, survival, and recruitment, these data can be incorporated within the model and used to identify the specific mechanisms resulting in the recruitment bottleneck observed in Smith Mountain Lake.

A significant limitation of the IBM used in this study resulted from the utilization of the density-dependent daily mortality rate multiplier, calibrated to empirical data, that operated throughout the first year of life to mimic the observed relationship between fingerling striped bass stocking density and first-year survival. Although model density estimates at the end of the simulation period increased as the number of stocked fingerlings was increased, one would expect to see a decline in the number of age-1 recruits at higher densities, particularly as densities were increased above 300,000 fingerlings. A reasonable explanation for the observed model-simulated results is that the density-dependent mortality multiplier did not allow for the same degree of variability observed in the empirical data. Further, because striped bass have not been stocked at densities greater than 400,000 fingerlings since the early 1980s, and only twice at densities greater than this during the late 1970s, a high degree of uncertainty exists as to how striped bass populations would respond if stocking densities were increased above the current level of 300,000 fingerlings. For example, because the support capacity for striped bass in Smith Mountain Lake is unknown, it is possible that sustaining high fingerling striped bass stocking densities over a several year period could result in a recruitment bottleneck for older age classes due to competition for forage-fish prey, such as alewives. Further, it is also unknown how other sport fishes, such as largemouth bass, smallmouth bass, walleye, and muskellunge, and forage fish populations in Smith Mountain Lake would respond to an increase in the number of adult striped bass. As a result, striped bass stocking densities in Smith Mountain Lake should not be increased above 300,000 fingerlings until the relationship between forage fish supply and sport fish demand has been adequately addressed in this reservoir system.

The individual-based model presented in this chapter could be also used to predict, prior to the onset of the growing season, the size, survival, and number of recruits at age 1 for the stocked striped bass cohort should biotic and/or abiotic conditions change in Smith Mountain Lake. Although the proposed stocking strategy is robust to variability in alewife population dynamics and water temperature regime, it is possible that the limnological and ecological status of Smith Mountain Lake could become altered in the future due to reservoir aging, watershed perturbation, and/or exotic species introductions (Kimmel and Groeger 1986). As a result, utilization of the IBM used in this study may become important in the future should changes in the Smith Mountain Lake system occur at some point in time. However, for this to occur, some prediction of population abundances, growth schedules, and mortality rates of age-0 forage fishes would be necessary in order to make predictions, with some degree of certainty, before the start of the growing season. Monitoring of spring water temperatures and sampling of forage-fish larvae prior to the stocking of juvenile striped bass, as well as how much year-to-year variation to expect in growth and mortality rates of other age-0 forage fishes, such as cyprinids, would be useful in this regard. The results of IBM simulations, coupled with field-collected data, could then be used to determine the most appropriate size, time, and/or fingerling density at the time of stocking for a particular year based on the given conditions. In addition, IBMs like the one presented in this chapter may also be useful in helping to determine the limits on the ability of fisheries managers to predict cohort population response in regards to variations in abiotic and biotic processes because they incorporate the uncertainty inherent in the mechanisms determining growth, survival, and, consequently, recruitment. Although these results may only provide "bounds" on the ability to accurately predict year-class variability in response to environmental stochasticity, little more could be expected even from models which perfectly summarize and document the recruitment process.

Cowan et al. (1993), utilizing an IBM developed by Rose and Cowan (1993), investigated the influence of both abiotic and biotic factors on the recruitment of age-0 striped bass in the Potomac River, Maryland. Although their model followed the fates of individual fish in a naturally-reproducing population, it was not originally designed to examine the effects of different stocking strategies and harvest regimes on the striped bass fishery. The IBM presented here could be incorporated into a more detailed model of the Smith Mountain Lake striped bass fishery, or modified to simulate another landlocked striped bass fishery, to be used as a predictive tool by fisheries managers to evaluate the effects of stocking and harvest policies on long-term population dynamics and sustainable yield. Such a model would describe the entire striped bass recruitment sequence from the time of stocking as fingerlings through the adult life stage. However, more detailed information on the striped bass fishery would be needed to further develop and apply a more elaborate IBM to the Smith Mountain Lake striped bass population.

In summary, based on the IBM simulations presented in this chapter, length of the growing season and age-0 forage-fish availability, which is directly related to the size relationship between predator and prey, set the potential for growth of the stocked striped bass cohort in Smith Mountain Lake. Because age-0 striped bass growth and size reached by the onset of the first overwintering period are regulated primarily by the size of forage-fish prey relative to juvenile striped bass size throughout the course of the growing season, stocking juveniles at a slightly larger size (52 mm TL) and earlier in the growing season (08 June), while maintaining the current stocking level of 300,000 fingerlings, were the most reasonable and sound means by which to enhance stocking success in this system taking into account year-to-year variation in alewife population dynamics and water temperature regime. If prey fish were too large to be vulnerable to predation (i.e. not within ingestibility limits), such as when fingerling striped bass were stocked at a smaller size and/or later in the growing season, then age-0 striped bass growth would be relatively slow because lower energetic-quality invertebrate prey would primarily comprise the diet. As a consequence, juveniles would reach a smaller size by the end of the growing season and suffer a higher degree of overwinter mortality. In contrast, if prey fish were vulnerable to predation throughout the growing season, such as when fingerling striped bass were stocked at a larger size and/or earlier in the growing season, then juvenile striped bass would be able to maintain a greater degree of piscivory and exhibit faster growth, resulting in a larger size reached by the end of the growing season and increasing the probability of surviving during winter months. Therefore, the relationship between forage-fish prey and juvenile striped bass size, as mediated by size and/or day at introduction, has a significant influence on stocking success for striped bass in Smith Mountain Lake.

CONCLUSION

The individual-based model presented in this chapter has been used to evaluate different strategies for stocking fingerling striped bass into Smith Mountain Lake. Similar analyses would also be appropriate for other freshwater systems and applicable to other species of age-0 piscivorous fishes, assuming that relevant site- and species-specific information has been incorporated into the model. Because the model is relatively complex, it more accurately describes predator-prey dynamics by taking into account size-dependent spatial overlap and the size relationships of individual predators relative to the size of encountered prey. As a result, the IBM approach represents a significant innovation for exploring stocking strategies for piscivorous fishes in temperate, freshwater systems. The model has been shown to accurately portray the influence of variability resulting from individual differences in body size on first-year striped bass growth and survival, both critical determinants of successful stocking programs. Further, the proposed fingerling striped bass stocking strategy is robust to variability in alewife population dynamics and water temperature regime that might be observed on an annual basis in Smith Mountain Lake. As a result of these attributes, the IBM approach not only appears well suited to evaluate management plans for stocking juvenile striped bass, but other juvenile piscivorous fishes as well.

SUMMARY

1. Age-0 striped bass exhibited dissimilar patterns of dispersion and spatial distribution between Smith Mountain Lake stocking cove sites in both 1994 and 1995. Juveniles stocked in the Hales Ford cove remained within the immediate vicinity of the stocking site for the first week post-stocking before gradually dispersing to outermost regions of the cove. In contrast, fingerlings stocked in the Penhook cove dispersed rapidly from the immediate stocking site by the first night post-stocking and were only collected along the outermost region of the cove during the remainder of the growing season. This disparity was attributed to differences in habitat availability between these two coves.

2. Size-dependent differences in dispersal patterns and spatial distribution for age-0 striped bass appear to be a result of water temperature preferences and the search for appropriate-sized food resources. Lack of dispersal by small juveniles (<150 mm TL) from stocking cove sites during the growing season was due to a preference for warmer water temperatures (>25°C) and an abundance of ingestible-sized prey items (invertebrates and age-0 cyprinids) in nearshore areas. In contrast, movements of larger individuals (>150 mm TL) to deeper, pelagic areas of the main channel was in response to a preference for cooler water temperatures and active search for larger, schooling prey items (age-0 alewives).

3. Progressive increases in total length from the time of stocking through the end of the growing season were observed for the age-0 striped bass cohort in both river arms of Smith Mountain Lake during both sampling years. In the

Roanoke River arm, juveniles increased from a median total length of 32 to 114 mm in 1994 and 47 to 180 mm in 1995, while striped bass from the Blackwater River arm increased from 42 to 180 mm in 1994 and 48 to 150 mm in 1995. Further, a distinct bimodal length distribution developed by fall during both 1994 and 1995; this distribution consisted of large-mode striped bass (>180 mm TL) that were greater than twice as long as small-mode juveniles (<140 mm TL).

4. Several factors were examined to identify those causing growth depensation. Individual variability in growth and behavior among larval striped bass within and among hatchery ponds, time at stocking during the growing season, variability in conditions between stocking sites and river arms, and genetic differences in growth rate could not be discounted as mechanisms causing the dissimilar patterns of growth observed within the age-0 striped bass cohort. However, hatching date influence, stocking of Phase II fingerlings, sex-related differences in growth rates (males versus females), and trophic competition with juvenile black basses in littoral areas of Smith Mountain Lake did not appear to be significant factors influencing first-year growth.

5. Size-dependent differences in food habits and diet quality appear to be the primary factors influencing differential growth within the age-0 striped bass cohort. Small-mode juveniles (<120 mm TL) maintained a mixed diet of small prey items, consuming primarily invertebrates (zooplankton and aquatic benthic insects) and small age-0 cyprinids. In contrast, large-mode fish (>150 mm TL) were strictly piscivorous, consuming almost entirely age-0 alewives. Differences in diet quality, as a consequence of dissimilarities in prey types

consumed, seem to have contributed to growth depensation because: (1) fish prey provides more energy per gram wet weight and is assimilated with greater efficiency than invertebrate prey items; and (2) the ratio of consumed alewife to large-mode striped bass body weight was greater than the consumed cyprinid to small-mode striped bass body weight, resulting in greater gains in energy per unit time spent feeding.

6. The disparity in food habits and diet quality also resulted in significant size-dependent differences in physiological indices of health. Relative condition, liver-somatic index, and lipid index values increased progressively over the growing season for all sizes of striped bass; however, size-dependent differences in these indices were clearly apparent as large-mode juveniles had significantly higher values than small-mode fish. Stomach-fullness index exhibited no clear temporal or size-dependent trend and was not a useful metric for assessing feeding intensity for juvenile striped bass.

7. The inability of small-mode age-0 striped bass to make the transition to a strictly fish diet was due to the unavailability of age-0 alewife prey on a distributional, behavioral, and morphological basis. This forage-fish prey rapidly outgrew the ingestibility limits of small-mode striped bass; only 23% of the total first-year alewife cohort biomass was available to small-mode fish throughout the growing season. Further, when small-mode striped bass did co-occur spatially with age-0 alewives early in the growing season and were also large enough to consume this forage-fish prey species, they did not appear to have developed a search image for fish prey or were not successful in capturing age-0 alewives due to their prey search behavior. In contrast, large-mode juveniles

could utilize approximately 67% of the total first-year alewife cohort biomass and this prey type provided a continuous supply of forage for this size group throughout the the growing season. Additionally, gizzard and threadfin shad, forage-fish species utilized by juvenile striped bass in other freshwater impoundments were not utilized by age-0 striped bass in Smith Mountain Lake because it appears that they are not within the ingestibility limits of this juvenile piscivore.

8. The total length of age-0 cyprinids and alewives relative to small- and large-mode striped bass total length, respectively, declined with increasing predator size. These observations suggest that even though small fish prey are usually less profitable in terms of energy gained per unit handling time, they may be selectively ingested by predators because they are easier to catch, resulting in piscivore capture success rates that are strongly size dependent. Additionally, temperature preferences, habitat choice, schooling, and escape responses may also reduce prey fish vulnerability to predators, resulting in the consumption of small, vulnerable individuals.

9. Differences in length-frequency distributions of juvenile striped bass between late fall and early spring sampling periods appears to confirm that size-dependent overwinter mortality plays a significant role in regulating recruitment to age 1. Length-frequency distributions were clearly bimodal during fall sampling, consisting of both small- and large-mode fish. In contrast, spring sampling revealed that length-frequency distributions had become unimodal and was comprised almost entirely of large-mode juveniles.

10. The loss of small-mode juvenile striped bass over winter months appears to be a result of starvation and exhaustion of energy stores because this size group had less absolute energy stores at the onset of winter and used a significantly greater proportion of these reserves during this period than did large-mode individuals. Further, surviving small-mode fish collected in spring were extremely emaciated and in poor condition, while large-mode juveniles were deep-bodied, thick, and appeared in good condition.

11. Because large-mode striped bass emerged from the overwintering period in better physiological health than small-mode juveniles, the size-dependent differences in health indices observed in spring are probably due to physiological allometry: positive allometric relationships between body size and energy reserves and negative allometric relationships between body size and metabolic rate. These results confirm the energy linkage with body size that has been postulated to explain why energetic variance may be important for overwinter survival, such as in the relationship between body size and survival in age-0 fishes.

12. The above site-specific, field-collected data were incorporated into a modified individual-based model (IBM) to evaluate the influence of size distribution at stocking, day of year at introduction, and stocking density, singly and in combination, to determine which scenario(s) maximized first-year growth, survival, and number of age-1 striped bass recruits in Smith Mountain Lake. Based on model simulation results, stocking juvenile striped bass at a median total length 10 mm larger (52 mm) and approximately one week earlier in the growing season (08 June), while maintaining the current stocking density at

300,000 fingerlings, would result in the greatest percent returns in the number of age-1 recruits (140,470 individuals), median total length (252 mm), and first-year survival (46.8%) by the beginning of the following growing season (01 May).

13. Sensitivity analysis revealed that alewife spawning day offset, age-0 alewife growth rate multiplier, and Smith Mountain Lake water temperature offset resulted in the largest relative increases from baseline conditions for the number of age-1 recruits (3.8% to 9.3%), median total length (3.1% to 8.3%), and first-year survival (3.8% to 9.4%) at the end of the simulation period for both the existing and proposed stocking strategies. In contrast, variations in age-0 alewife density and daily mortality rate multiplier resulted in smaller relative changes from baseline conditions for the number of age-1 recruits (4.8% to 5.6%), median total length (3.6% to 4.8%), and first-year survival (4.9% to 5.6%) for both stocking strategies. Although the number of age-1 recruits and first-year survival were more sensitive (i.e. had a greater percent relative change from baseline) than median total length to perturbations in alewife and water temperature input parameters, the existing stocking strategy was more sensitive to parameter perturbations among all three model outputs than the proposed stocking strategy.

14. Sensitivity analysis also demonstrated that variations in age-0 alewife density during simulated warm and cold years also had an influence on the number of age-1 recruits, median total length, and first-year survival for fingerling striped bass stocked at the existing and proposed stocking strategies. During warm year simulations, output parameters exhibited percent relative

decreases from baseline values (-9.9% to -18.3%) at both stocking strategies. In addition, the percent relative change from baseline for the three output parameters increased during simulated warm years as age-0 alewife density was reduced from $4.4/m^3$ to $1.1/m^3$. The converse was observed for cold year simulations (+2.4% to +14.3%). However, the existing stocking strategy was more sensitive (i.e. had a greater percent relative change from baseline) to combined parameter perturbations among the three output parameter values than the proposed stocking strategy.

15. Based on sensitivity analysis results, the proposed stocking strategy resulted in much greater marginal returns in terms of first-year growth (+53.8% to +61.6%), survival (+96.8% to +145.2%), and the number of age-1 recruits (+96.8% to +145.6%) than the existing stocking strategy when alewife and water temperature parameter inputs were varied singly and in combination. Further, the percent relative change for the proposed over the existing stocking strategy remained the same magnitude (i.e. is robust) under fluctuations in alewife population parameters and Smith Mountain Lake water temperature regime.

MANAGEMENT IMPLICATIONS

Fisheries managers must consider factors regulating first-year growth, survival, and recruitment to age 1 for fingerling piscivores that are stocked on an annual, put-grow-take basis when formulating hatchery production and management strategies. Results of this study indicate that size at stocking and day of year at introduction for fingerling striped bass are the most critical factors affecting recruitment success in Smith Mountain Lake. During a typical year, age-0 striped bass are stocked at a median total length of 42 mm in mid to late June. As a result, most juveniles are too small relative to forage-fish prey to make the complete transition to piscivory and are relegated to a mixed, low-quality diet of invertebrates and small age-0 cyprinids during their first growing season. The slower growth afforded to most of the age-0 cohort, coupled with their lower accumulated energy reserves and higher relative weight-dependent metabolic rates, results in disproportionately greater size-dependent, starvation-induced mortality during the non-feeding, overwinter period. Only those juveniles which grow large enough to begin feeding on age-0 alewives and can continue to utilize this prey resource throughout the growing season reach a sufficient size (>150 mm total length) and amass adequate energy stores to survive the critical overwintering period. Therefore, behavioral and morphological invulnerability of age-0 alewives to striped bass during periods when these two species spatially overlap in Smith Mountain Lake can be remedied by stocking this juvenile piscivore at a larger size (52 mm TL) and earlier in the growing season (08 June) while maintaining the current stocking density of 300,000 fingerlings. Results of individual-based model simulations indicate that this proposed stocking strategy will allow juvenile striped bass to make the transition to piscivory earlier in the growing season and, as a result, utilize a higher caloric density prey source (alewives) throughout the growing season, thereby accelerating first-year growth rates and increasing the probability of surviving over the winter.

Modification of the VDGIF striped bass fingerling culture program to accommodate the recommended stocking regime might be accomplished in a number of ways. For example, striped bass eggs could be obtained and hatched earlier, either by collecting wild broodstock from sections of the Roanoke River downstream of the Brookneal Hatchery or by maintaining captive broodstock onsite at the Brookneal Hatchery. Alternatively, striped bass eggs could be obtained later, and larvae could be reared indoors in heated raceways and/or circular tanks and fed high daily rations of artificial feeds in order to get them to a larger size by the recommended stocking date. Currently, running-ripe striped bass from Kerr Reservoir are collected from the Roanoke River adjacent to Brookneal Hatchery from mid-April to early May (S. Arthur, VDGIF Brookneal Hatchery, personal communication). However, striped bass eggs could potentially be made available approximately 2-3 wk earlier by collecting spawning adults from downstream locations of the Roanoke River or Kerr Reservoir, instead of waiting for fish to move upstream near the Brookneal Hatchery facility. Conversely, adult striped bass broodstock could be maintained onsite year-round. Although this option would most likely result in a significant increase in hatchery-production costs, particularly in the short term as holding facilities would have to be designed and constructed (S. Arthur, VDGIF Brookneal Hatchery, personal communication), the high degree of control over egg availability, size of fingerlings at the time of stocking, and day of year at introduction may far outweigh the increase in operating costs. However, regardless of the culture method eventually adopted and utilized, practical constraints on the rearing and maintenance of striped bass, as well as the advantages and disadvantages of each technique, must be considered within the specified goals and objectives of the VDGIF stocking program in relation to their budgetary limitations. Because additional considerations not included in this analysis, such as costs (time, effort, and capital), could affect the feasibility of different rearing and stocking schemes, implementation of these strategies would require a detailed consideration of these constraints.

Although fingerling stocking density has been identified in a previous study as the primary factor regulating first-year survival of striped bass in Smith Mountain Lake (Moore 1988), field observations and model simulation results do not indicate that fingerling density post-stocking plays as significant a role as previously thought. However, it is possible that density-dependent mechanisms may have an influence on larval striped bass growth rates during the rearing process in hatchery ponds. For example, in 1994, striped bass stocked at the Penhook site were reared in grow-out ponds at a lower density than fish stocked at the Hales Ford site (140,342 versus 160,105 fingerlings, respectively). In addition, the median total length and size distribution of fingerlings stocked at the Penhook site was greater (42 mm, range 30-54 mm) than those stocked at the Hales Ford site (32 mm, 24-41 mm). Although pond size and productivity may have contributed to these growth differences (S. Arthur, VDGIF Brookneal Hatchery, personal communication), it would seem reasonable to assume that age-0 striped bass stocked at the Hales Ford site became food limited during the rearing process, resulting in slower growth rates and, as a consequence, were smaller in size than fish stocked at the Penhook site. Therefore, rearing larval striped bass at lower densities and/or augmenting the prey base with artificial pellet feeds after zooplankton densities have been reduced may alleviate the potential for density-dependent mechanisms during the rearing process.

Location of stocking sites, as well as the size and date at which fingerling striped bass are stocked, can also be used to maximize forage fish availability. Stocking striped bass at a larger size and earlier in the growing season may allow this juvenile predator to begin to utilize age-0 gizzard and threadfin shad, forage-fish species which under the current stocking regime are not utilized by striped bass during their first-year of life due to morphological constraints. Because densities of shad species are greatest in the upper tributary arms of Smith Mountain Lake, while alewives are most numerous in the mid and lower lake regions, stocking fingerling striped bass in both of these areas should ensure good growth and survival for at least some portion of the cohort even in the event that one clupeid species should suffer reproductive failure or produce a weak year class. Juvenile striped bass can tolerate warmer water temperatures than adults (Meldrim and Gift 1971; Coutant and Carroll 1980; Schaich and Coutant 1980; Waddle et al. 1980; Cox and Coutant 1981; Coutant et al. 1984; Cheek et al. 1985); therefore, the thermal regime of the upper lake should not pose any significant problems in terms of their thermal tolerance. Although predation by littoral piscivores (i.e. largemouth bass) in the upper lake could potentially impact age-0 striped bass survival, the ability of larger stocked fingerlings to consume forage-fish prey earlier in life should accelerate their growth rates, thereby minimizing predation mortality. Further, largemouth bass do not selectively prey on juvenile striped bass when these two species spatially overlap (Michaelson 1996). Therefore, sites in the upper tributary arms, as well as additional locations in downlake areas of Smith

Mountain Lake, should be identified in terms of appropriate habitat availability (shallow, littoral areas containing a mixture of sand and fine gravel substrate with little physical habitat structure that grade gradually to deeper water), accessibility, and forage-fish productivity for stocking of fingerling striped bass.

Finally, in addition to providing a means to evaluate striped bass stocking strategies in Smith Mountain Lake, utilization of the individual-based model used in this study provides a useful tool for VDGIF fisheries managers to predict recruitment dynamics of stocked striped bass prior to introduction in a given year or in the face of changing limnological and ecological conditions in Smith Mountain Lake. Further, the juvenile model could be coupled to an adult model to evaluate the effects of stocking and harvest policies on long-term population dynamics and sustainable yield; such a model would describe the entire striped bass recruitment sequence from the time of stocking as fingerlings through the adult life stage. However, more detailed information on the striped bass fishery and Smith Mountain prey base would be needed to further develop and apply a more elaborate model to the Smith Mountain Lake striped bass fishery. Therefore, fall gillnet surveys should continue each year and catch-per-unit-effort of age-1 striped bass should be used as an index to monitor success of the stocking program. Survival rates of stocked fingerlings and probable future densities of harvestable adults should also continue to be estimated using the method described by Moore (1988). Monitoring of clupeid populations should also be continued and intensified, particularly for alewives on which no reliable estimates for population density and dynamics exist at the present time. Population dynamics and biotic interactions of threadfin shad with other forage fishes should also be assessed as recent density trends have indicated that in years of high age-0 threadfin shad cohorts, year-class strength of age-0 alewives is lower that in years of poor threadfin shad recruitment (M.C. Duval, VDGIF, personal communication). Cyprinid densities should also be monitored as this prey fish type plays a critical link in the transition to piscivory for juvenile striped bass. Therefore, by incorporating and utilizing these data within an individual-based model approach, more efficient and sound management can occur for the Smith Mountain Lake striped bass fishery.

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* C.W. Kerfoot and A.H. Sih, editors. Predation: direct and indirect effects on aquatic communities. University of New England Press, Hanover, New Hampshire.

Adams, S.M., and R.B. McLean. 1985. Estimation of largemouth bass, *Micropterus salmoides* Lacépède, growth using the liver somatic index and physiological variables. Journal of Fish Biology 26:111-126.

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

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

Anderson, R.O., and R.M. Neumann. 1996. Length, weight, and associated structural indices. Pages 447-482 *in* B.R. Murphy and D.W. Willis, editors. Fisheries techniques, 2nd edition. American Fisheries Society, Bethesda, Maryland.

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

Applegate, R.L., J.W. Mullen, and D.I. Morais. 1967. Food and growth of six centrarchids from shoreline areas of Bull Shoals Reservoir. Proceedings of the Annual Conference Southeastern Association of Game and Fish Commissioners 20:469-482.

Axon, J.R. 1979. An evaluation of striped bass introductions in Herrington Lake. Kentucky Department of Fish and Wildlife Resources, Fisheries Bulletin 63.

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

Bailey, J.K., R.L. Saunders, and M.I. Buzeta. 1980. Influence of parental smolt age and sea age on growth and smolting and hatchery-reared Atlantic salmon. Canadian Journal of Fisheries and Aquatic Sciences 37:1379-1386.

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

Bason, W.H. 1971. Ecology and early life history of striped bass, *Morone saxatilis*, in the Delaware Estuary. Ichthyological Associates Bulletin 4. Middletown, Delaware.

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

Booth, D.J., and J.A. Keast. 1986. Growth energy partitioning by juvenile bluegill sunfish, *Lepomis macrochirus* Rafinesque. Journal of Fish Biology 28:37-45.

Boreman, J., and R.J. Klauda. 1988. Distributions of early life stages of striped bass in the Hudson River Estuary, 1974-1979. American Fisheries Society Monograph 4:53-58.

Bowen, S.H. 1996. Quantitative description of the diet. Pages 513-532 *in* B.R. Murphy and D.W. Willis, editors. Fisheries techniques, 2nd edition. American Fisheries Society, Bethesda, Maryland.

Bowles, R.R. 1975. Effects of water velocity on activity patterns of juvenile striped bass. Proceedings of the Annual Conference Southeastern Association of Game and Fish Commissioners 29:142-151.

Boynton, W.B., T.T. Polgar, and H.H. Zion. 1981. Importance of juvenile striped bass food habits in the Potomac estuary. Transactions of the American Fisheries Society 110:56-63.

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

Brodeur, R.S., and W.G. Pearcy. 1984. Food habits and dietary overlap of some shelf rockfishes (Genus *Sebastes*) from the Northeastern Pacific coast. Fisheries Bulletin 82:269-293.

Browman, H.I., and W.J. O'Brien. 1992. The ontogeny of search behavior in the white crappie, *Pomoxis annularis*. Environmental Biology of Fishes 34:181-195.

Brown, M.L., and B.R. Murphy. 1991a. Relationship of relative weight (W_r) to proximate composition of juvenile striped bass and hybrid striped bass. Transactions of the American Fisheries Society 120:509-518.

Brown, M.L., and B.R. Murphy. 1991b. Standard weights (W_s) for striped bass, white bass, and hybrid striped bass. North American Journal of Fisheries Management 11:451-467.

Bryan, J.E. 1974. Hunger and the capture of grayling and char. Journal of the Fisheries Research Board of Canada 31:1945-1951.

Buijse, A.D., and R.P. Houthuijzen. 1992. Piscivory, growth, and size-selective mortality of age-0 pikeperch (*Stizostedion lucioperca*). Canadian Journal of Fisheries and Aquatic Sciences 49:894-902.

Bulak, J.S., J.S. Crane, D.H. Secor, and J.M. Dean. 1997. Recruitment dynamics of striped bass in the Santee-Cooper system, South Carolina. Transactions of the American Fisheries Society 126:133-143.

Bulow, F.J., C.B. Colburn, Jr., and C.S. Cobb. 1978. Comparisons of two bluegill populations by means of the RNA-DNA ratio and liver-somatic index. Transactions of the American Fisheries Society 107:799-803.

Busacker, G.P., I.A. Adelman, and E.M. Goolish. 1990. Pages 363-387 *in* C.B. Schreck and P.B. Moyle, editors. Methods for fish biology. American Fisheries Society, Bethesda, Maryland.

Cargnelli, L.M., and M.R. Gross. 1996. The temporal dimension in fish recruitment: birth date, body size and size-dependent survival in a sunfish (bluegill: *Lepomis macrochirus*). Canadian Journal of Fisheries and Aquatic Sciences 53:360-367.

Cargnelli, L.M., and M.R. Gross. 1997. Fish energetics: larger individuals emerge from winter in better condition. Transactions of the American Fisheries Society 126:153-156.

Carline, R.F., R.A. Stein, and L.M. Riley. 1986. Effects of size at stocking, season, largemouth bass predation, and forage abundance on survival of tiger muskellunge. American Fisheries Society Special Publication 15:151-167.

Chadwick, H.K. 1966. Variation in the growth of young striped bass (*Roccus saxatilis*) in the Sacramento-San Joaquin system. California Fish and Game, Inland Fisheries Administration Report 66-11.

Chambers, R.C., and W.C. Leggett. 1987. Size and age at metamorphosis in marine fishes: an analysis of laboratory-reared winter flounder (*Pseudopleuronectes americanus*) with a review of variation in other species. Canadian Journal of Fisheries and Aquatic Sciences 44:1936-1947.

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

Chesney, E.J. 1993. A model of survival and growth of striped bass larvae *Morone saxatilis* in the Potomac River, 1987. Marine Ecology Progress Series 92:15-25.

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

Christensen, B., and L. Persson. 1993. Species-specific antipredatory behaviours: effects on prey choice in different habitats. Behavioral Ecology and Sociobiology 32:1-9.

Clark, M.E., and K.A. Rose. 1997a. An individual-based modeling analysis of management strategies for enhancing brook trout populations in southern Appalachian streams. North American Journal of Fisheries Management 17:54-76.

Clark, M.E., and K.A. Rose. 1997b. Factors affecting competitive dominance of rainbow trout over brook trout in southern Appalachian streams: implications of an individual-based model. Transactions of the American Fisheries Society 126:1-20.

Clark, M.E., and K.A. Rose. 1997c. Individual-based model of stream-resident rainbow trout and brook char: model description, corroboration, and effects of sympatry and spawning season duration. Ecological Modelling 94:157-175.

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.

Coutant, C.C., K.L. Zachman, D.K. Cox, and B.L. Pearman. 1984. Temperature selection by juvenile striped bass in laboratory and field. Transactions of the American Fisheries Society 113:666-671.

Cowan, J.H., Jr., K.A. Rose, E.S. Rutherford, and E.D. Houde. 1993. Individual-based model of young-of-the-year striped bass population dynamics. II. Factors affecting recruitment in the Potomac River, Maryland. Transactions of the American Fisheries Society 122:439-458.

Cox, D.K., and C.C. Coutant. 1981. Growth dynamics of juvenile striped bass as functions of temperature and ration. Transactions of the American Fisheries Society 110:226-238.

Craig, J.F. 1982. Population dynamics of Windermere perch. Report of the Freshwater Biological Association 50:49-59.

Crance, J.H. 1984. Habitat suitability index models and instream flow suitability curves: inland stocks of striped bass. U.S. Department of the Interior, FWS/OBS-82/10.85, Washington, D.C.

Creach, Y., and A. Serfaty. 1974. Starvation and refeeding of carp (*Cyprinus carpio* L.) Journal of Physiology 68:245-260.

Crecco, V.A., and T.F. Savoy. 1985. Effects of biotic and abiotic factors on growth and relative survival of young American shad, *Alosa sapidissma*, in the Connecticut River. Canadian Journal of Fisheries and Aquatic Sciences 42:1640-1648.

Cummins, K.W., and J.C. Wuycheck. 1971. Calorific equivalents for investigations in ecological energetics. Mitteilungen Internationale Vereinigung für Theoreische und Angewandte Limnologie 18:1-158.

Cunjak, R.A. 1988. Physiological consequences of overwintering in streams: the cost of acclimatization? Canadian Journal of Fisheries and Aquatic Sciences 45:443-452.

Cunjak, R.A., and G. Power. 1986. Seasonal changes in the physiology of brook trout, *Salvelinus fontinalis* (Mitchill), in a sub-Arctic river system. Journal of Fish Biology 29:279-288.

Cunningham, G.L., and B.J. Shuter. 1986. Interaction of low pH and starvation on body weight and composition of young-of-the-year smallmouth bass (*Micropterus dolomieui*). Canadian Journal of Fisheries and Aquatic Sciences 43:869-876.

Cushing, D. 1995. Population production and regulation in the sea: a fisheries perspective. Cambridge University Press, Cambridge, Great Britain.

Dalton, P.D. 1987. Ecology of bay anchovy (*Anchoa mitchilli*) eggs and larvae in the mid-Chesapeake Bay. Master's thesis. University of Maryland, College Park.

Daniel, K.L. 1984. Food habits, age and growth, and forage value of the alewife in Wautauga Reservoir, Tennessee. Master's thesis. University of Tennessee, Knoxville.

DeAngelis, D.L., and C.C. Coutant. 1982. Genesis of bimodal size distributions in species cohorts. Transactions of the American Fisheries Society 111:384-388.

DeAngelis, D.L., L. Godbout, and B.J. Shuter. 1991. An individual-based approach to predicting density-dependent dynamics in smallmouth bass populations. Ecological Modeling 57:91-115.

DeAngelis, D.L., and J.S. Mattice. 1979. Implications of a partial-differential-equation cohort model. Mathematical Biosciences 47:271-285.

DeAngelis, D.L., K.A. Rose, and M.A. Huston. 1994. Individual-oriented approaches to modeling ecological populations and communities. Pages 390-410 *in* S.A. Levin, editor. Frontiers in mathematical biology. Lecture notes in biomathematics, Volume 100. Springer-Verlag, Berlin, Germany.

DeAngelis, D.L., B.J. Shuter, M.S. Ridgway, and M. Scheffer. 1993. Modeling growth and survival in an age-0 fish cohort. Transactions of the American Fisheries Society 122:927-941.

Delahunty, G., and V.L. de Vlaming. 1980. Seasonal relationships of ovary weight, liver weight and fat stores with body weight in the goldfish, *Carassius auratus* (L.). Journal of Fish Biology 16:5-13.

Dennerline, D.E. 1990. Prey sizes utilized by hybrid and striped bass: implications for assessing prey availability. Master's thesis. University of Georgia, Athens.

Dettmers, J.M., D.R. DeVries, and R.A. Stein. 1996. Reservoir biomanipulation: quantifying piscivore effects and prey productivity across multiple trophic levels. Transactions of the American Fisheries Society 125:491-504.

Dey, W.P. 1981. Mortality and growth of young-of-year striped bass in the Hudson River estuary. Transactions of the American Fisheries Society 110:151-157.

Diana, J.S. 1979. The feeding pattern and daily ration of a top carnivore, the northern pike (*Esox lucius*). Canadian Journal of Zoology 57:2121-2127.

Diana, J.S. 1983a. An energy budget for northern pike (*Esox lucius*). Canadian Journal of Zoology 61:1968-1975.

Diana, J.S. 1983b. Growth, maturation, and production of northern pike in three Michigan lakes. Transactions of the American Fisheries Society 112:38-46.

Diana, J.S., and W.C. Mackay. 1979. Timing and magnitude of energy deposition and loss in the body, liver, and gonads of northern pike (*Esox lucius*). Journal of the Fisheries Research Board of Canada 36:481-487.

Diana, J.S., and R. Salz. 1990. Energy storage, growth, and maturation of yellow perch from different locations of Saginaw Bay, Michigan. Transactions of the American Fisheries Society 119:976-984.

Dobush, G.R., C.D. Ankney, and D.G. Krementz. 1985. The effect of apparatus, extraction time, and solvent type on lipid extractions in snow geese. Canadian Journal of Zoology 63:1917-1930.

Dorazio, R.M., B.M. Florence, and C.M. Wooley. 1991. Stocking of hatchery-reared striped bass in the Patuxent River, Maryland: survival, relative abundance, and cost-effectiveness. North American Journal of Fisheries Management 11:435-442.

Dunbrak, R.L., and L.M. Dill. 1983. A model of size dependent surface feeding in a stream dwelling salmonid. Environmental Biology of Fishes 8:41-54.

Duval, M.C. 1996. Virginia Department of Game and Inland Fisheries large impoundment management report: Smith Mountain Lake 1993-1995. Virginia Department of Game and Inland Fisheries, Richmond.

East, P., and P. Magnan. 1991. Some factors regulating piscivory in brook trout, *Salvelinus fontinalis*, in lakes of the Laurentian Shield. Canadian Journal of Fisheries and Aquatic Sciences 48:1735-1743.

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.

Eggers, D.M. 1977. Factors in interpreting data obtained by diel sampling of fish stomachs. Journal of the Fisheries Research Board of Canada 34:290-293.

Eldridge, M.B., J.A. Whipple, and M.J. Bowers. 1982. Bioenergetics and growth of striped bass embryos and larvae. U.S. National Marine Fisheries Service Fishery Bulletin 80:461-474.

Emlem, J.M. 1966. The role of time and energy in food preference. American Naturalist 100:611-617.

Erickson, K.E., J. Harper, G.C. Mensinger, and D. Hicks. 1971. Status and artificial reproduction of striped bass from Keystone Reservoir, Oklahoma. Proceedings of the Annual Conference Southeastern Association of Game and Fish Commissioners 25:513-522.

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.

Fange, R., and D. Grove. 1979. Digestion. Pages 162-260 *in* W.S. Hoar, D.J. Randall, and J.R. Brett, editors. Fish physiology, volume 8. Academic Press, New York.

Fausch, K.D. 1984. Profitable stream positions for salmonids relating specific growth rate to net energy gain. Canadian Journal of Zoology 62:441-451.

Fielder, D.G. 1992a. Evaluation of stocking walleye fry and fingerlings and factors affecting their success in Lower Lake Oahe, South Dakota. North American Journal of Fisheries Management 12:336-345.

Fielder, D.G. 1992b. Relationship between walleye fingerling stocking density and recruitment in lower Lake Oahe, South Dakota. North American Journal of Fisheries Management 12:346-352.

Flickinger, S.A., and J.H. Clark. 1981. Management evaluation of stocked northern pike in Colorado's small irrigation reservoirs. American Fisheries Society Special Publication 11:284-291.

Forney, J.L. 1966. Factors affecting first-year growth of walleyes in Oneida Lake, New York. New York Fish and Game Journal 13:146-167.

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

Forney, J.L. 1980. Evolution of a management strategy for the walleye in Oneida Lake, New York. New York Fish and Game Journal 27:105-141.

Fulton, T.W. 1904. The rate of growth of fishes. Fisheries Board of Scotland Annual Report 22 (part 3): 141-241, Edinburgh.

Garman, G.C., and L.A. Nielsen. 1982. Piscivory by stocked brown trout (*Salmo trutta*) and its impacts on the nongame fish community of Bottom Creek, Virginia. Canadian Journal of Fisheries and Aquatic Sciences 39:862-869.

Gibbons, J.D. 1985. Nonparametric methods for quantitative analysis, 2nd edition. American Sciences Press, Inc, Columbus, Ohio.

Gillen, A.L., R.A. Stein, and R.F. Carline. 1981. Predation by pellet-reared tiger muskellunge on minnows and bluegills in experimental systems. Transactions of the American Fisheries Society 110:197-209.

Gilliland, E.R., and M.D. Clady. 1982. Diet overlap of striped bass x white bass hybrids and largemouth bass in Sooner Lake, Oklahoma. Proceedings of the Annual Conference Southeastern Association of Fish and Wildlife Agencies 35:317-330.

Gomez, R. 1970. Food habits of young-of-the-year striped bass, *Roccus saxatilis* (Walbaum), in Canton Reservoir. Proceedings of the Oklahoma Academy of Sciences 50:79-83.

Goodgame, L.S., and L.E. Miranda. 1993. Early growth and survival of age-0 largemouth bass in relation to parental size and swim-up time. Transactions of the American Fisheries Society 122:131-138.

Greene, C.H. 1986. Patterns of prey selection: implications of predator foraging tactics. American Naturalist 128:824-839.

Groves, T.D.D. 1970. Body composition changes during growth of young sockeye salmon, *Oncorhynchus nerka*, in freshwater. Journal of the Fisheries Research Board of Canada 27:929-942.

Gulland, J.A. 1982. Why do fish numbers vary? Theoretical Population Biology 97:69-75.

Gutreuter, S.J., and R.O. Anderson. 1985. Importance of body size to the recruitment process in largemouth bass. Transactions of the American Fisheries Society 114:317-327.

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

Hanson, J.M., and W.C. Leggett. 1985. Experimental and field evidence for inter- and intraspecific competition in two freshwater fishes. Canadian Journal of Fisheries and Aquatic Sciences 42:280-286.

Hanson, J.M., and W.C. Leggett. 1986. Effect of competition between two freshwater fishes on prey consumption and abundance. Canadian Journal of Fisheries and Aquatic Sciences 43:1363-1372.

Harper, J.L., and R. Jarman. 1971. Investigation of striped bass, *Morone saxatilis* (Walbaum), culture in Oklahoma. Proceedings of the Annual Conference Southeastern Association of Game and Fish Commissioners 25:501-512.

Harper, J.L., R. Jarman, and J.T. Yacovino. 1968. Food habits of young striped bass *Roccus saxatilis* (Walbaum), in culture ponds. Proceedings of the Annual Conference Southeastern Association of Game and Fish Commissioners 22:373-380.

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

Hart, P., and S.F. Hamrin. 1988. Pike as a selective predator. Effects of prey size, availability, cover and pike jaw dimensions. Oikos 51:220-226.

Hayes, D.B., W.W. Taylor, and E.L. Mills. 1993. Natural lakes and large impoundments. Pages 493-515 *in* C.C. Kohler and W.A. Hubert, editors. Inland fisheries management in North America. American Fisheries Society, Bethesda, Maryland.

He, E., and W.A. Wurtsbaugh. 1993. An empirical model of gastric evacuation rates for fish and an analysis of digestion in piscivorous brown trout. Transactions of the American Fisheries Society 122:717-730.

Heidinger, R.C., and S.D. Crawford. 1977. Effect of temperature and feeding rate on the liver-somatic index of the largemouth bass, *Micropterus salmoides*. Journal of the Fisheries Research Board of Canada 34:633-638.

Helfman, G.S. 1994. Adaptive variability and mode choice in foraging fishes. Pages 3-17 *in* D.J. Stouder, K.L. Fresh, and R.J. Feller, editors. Theory and application in fish feeding ecology. University of South Carolina Press, Columbia.

Henderson, M.A., and A.J. Cass. 1991. Effect of smolt size on smolt-to-adult survival for Chilco Lake sockeye salmon (*Oncorhynchus nerka*). Canadian Journal of Fisheries and Aquatic Sciences 48:988-994.

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

Herbold, B. 1986. An alternative to the fullness index. Pages 315-320 *in* C.A. Simenstad and G.M. Cailliet, editors. Contemporary studies on fish feeding: the proceedings of Gutshop '84. Dr. W. Junk Publishers, The Hague, Netherlands.

Heubach, W., R.J. Toth, and A.M. McCready. 1963. Food of young-of-the-year striped bass (*Roccus saxatilis*) in the Sacramento-San Joaquin River system. California Fish and Game 49:224-239.

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

Higginbotham, B. 1979. Growth, food habits, maturation, and distribution of the striped bass (*Morone saxatilis*) in Watts Bar Reservoir, Tennessee. Master's thesis. Tennessee Technological University, Cookeville.

Hinton, D.E., R.L. Snipes, and M.W. Kendall. 1972. Morphology and enzyme histochemistry in the liver of largemouth bass (*Micropterus salmoides*). Journal of the Fisheries Research Board of Canada 29:531-534.

Hodgkiss, I.J., and H.S.H. Mann. 1978. Reproductive biology of *Sarotherodon mossambicus* (Cichlidae) in Plover Creek Reservoir, Hong Kong. Environmental Biology of Fishes 3:287-292.

Hoogland, R., D. Morris, and N. Tinbergen. 1956. The spines of sticklebacks (*Gasterosteus* and *Pygosteus*) as means of defence against predators (*Perca* and *Esox*). Behavior 10:205-236.

Houde, E.D. 1987. Fish early life history dynamics and recruitment variability. American Fisheries Society Symposium 2:17-29.

Hoyle, J.A., and A. Keast. 1987. The effect of prey morphology and size on handling time in a piscivore, the largemouth bass (*Micropterus salmoides*). Canadian Journal of Zoology 65:1972-1977.

Hume, J.M.B., and E.A. Parkinson. 1987. Effect of stocking density on the survival, growth, and dispersal of steelhead trout fry (*Salmo gairdneri*). Canadian Journal of Fisheries and Aquatic Sciences 44:271-281.

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.

Humphries, E.T., and K.B. Cumming. 1971. Food habits and feeding selectivity of striped bass fingerlings in culture ponds. Proceedings of the Annual Conference Southeastern Association of Game and Fish Commissioners 25:522-536.

Humphries, E.T., and K.B. Cumming. 1973. An evaluation of striped bass fingerling culture. Transactions of the American Fisheries Society 102:13-20.

Hunt, R.L. 1969. Overwinter survival of wild fingerling brook trout in Lawrence Creek, Wisconsin. Journal of the Fisheries Research Board of Canada 26:1473-1483.

Huston, M., D. DeAngelis, and W. Post. 1988. New computer models unify ecological theory. BioScience 38:682-691.

Hyslop, E.J. 1980. Stomach content analysis - a review of methods and their application. Journal of Fish Biology 17:411-429.

Iles, T.D., and R.J. Wood. 1965. The fat/water relationship in north sea herring (*Clupea harengus*), and its possible significance. Journal of the Marine Biological Association of the United Kingdom 45:353-366.

Isely, J.J. 1981. Effects of water temperature and energy reserves on overwinter mortality in young-of-the-year largemouth bass (*Micropterus salmoides*). Master's thesis. Southern Illinois University, Carbondale.

Isely, J.J., and R.L. Noble. 1987. Use of daily otolith rings to interpret development of length distributions of young largemouth bass. Pages 475-481 *in* R.C. Summerfelt and G.E. Hall, editors. Age and growth of fish. Iowa State University Press, Ames.

Jenkins, R.E., and N.M. Burkhead. 1993. Freshwater fishes of Virginia. 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, D.C.

Jenkins, R.M., and D.I. Morais. 1978. Predator-prey relations in the predator-stocking-evaluation reservoirs. Proceedings of the Annual Conference Southeastern Association of Fish and Wildlife Agencies 33:692-702.

Jennings, M.J., and D.P. Phillipp. 1992. Use of allozyme markers to evaluate walleye stocking success. North American Journal of Fisheries Management 12:285-290.

Jensen, A.J. 1979. Energy content analysis from weight and liver index measurements of immature pollock (*Pollachius virens*). Journal of the Fisheries Research Board of Canada 36:1207-1213.

Jobling, M. 1980. Effects of starvation on proximate chemical composition and energy utilization of plaice, *Pleuronectes platessa* L. Journal of Fish Biology 17:325-334.

Johnson, T.B., and D.O. Evans. 1990. Size dependent winter mortality of young-of-year white perch: climate warming and invasion of the Laurentian Great Lakes. Transactions of the American Fisheries Society 119:301-313.

Johnson, T.B., and D.O. Evans. 1991. Behavior, energetics, and associated mortality of young-of-the-year white perch (*Morone americana*) and yellow perch (*Perca flavescens*) under simulated winter conditions. Canadian Journal of Fisheries and Aquatic Sciences 48:672-680.

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

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

Johnson, D.H., G.L. Krapu, K.J. Reinecke, and D.G. Jorde. 1985. An evaluation of condition indices for birds. Journal of Wildlife Management 49:569-575.

Johnson, D.H., and R.E. Stewart. 1973. Racial composition of migrant populations of sandhill cranes in the northern plains states. Wilson Bulletin 85:148-162.

Jonas, J.L., C.E. Kraft, and T.L. Margenau. 1996. Assessment of seasonal changes in energy density and condition in age-0 and age-1 muskellunge. Transactions of the American Fisheries Society 125:203-210.

Juanes, F. 1994. What determines prey size selectivity in piscivorous fishes? Pages 79-100 *in* D.J. Stouder, K.L. Fresh, and R.J. Fuller, editors. Theory and application in fish feeding ecology. University of South Carolina Press, Columbia.

Keast, A. 1968. Feeding of some Great Lakes fishes at low temperature. Journal of the Fisheries Research Board of Canada 25:1199-1218.

Keast, A., and J. Eadie. 1984. Growth in the first summer of life: a comparison of nine co-occurring fish species. Canadian Journal of Zoology 62:1242-1250.

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

Keith, W.E., and S.W. Barkley. 1971. Predation on stocked rainbow trout by chain pickerel and largemouth bass in Lake Ouachita, Arkansas. Proceedings of the Annual Conference Southeastern Association of Game and Fish Commissioners 24:401-407.

Kelso, J.R.M. 1973. Seasonal energy changes in walleye and their diet in West Blue Lake Manitoba. Transactions of the American Fisheries Society 102:363-368.

Kerby, J.H. 1979. Morphometric characters of two Morone hybrids. Proceedings of the Annual Conference Southeastern Association of Fish and Wildlife Agencies 33:344-352.

Kernehan, R.J., M.R. Hendrick, and R.E. Smith. 1981. Early life history of striped bass in the Chesapeake and Delaware Canal and vicinity. Transactions of the American Fisheries Society 110:137-150.

Kerr, S.R. 1971. Prediction of fish growth efficiency in nature. Journal of the Fisheries Research Board of Canada 28:809-814.

Kimmel, B.L., and A.W. Groeger. 1986. Limnological and ecological changes associated with reservoir aging. Pages 103-109 *in* G.E. Hall and M.J. Van Den Avyle, editors. Reservoir fisheries management: strategies for the 80's. American Fisheries Society, Bethesda, Maryland.

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. 1982. Suitability of alewife as a pelagic forage fish for southeastern reservoirs. Proceedings of the Annual Conference Southeastern Association of Fish and Wildlife Agencies 34:137-150.

Koo, T.S.Y., and D.E. Ritchie, Jr. 1973. Growth of juvenile striped bass, *Morone saxatilis*, as determined by tagging and recapture. Pages 124-125 *in* A.L. Pacheco, editor. Proceedings of a workshop on egg, larval, and juvenile stages of fish in Atlantic Coast estuaries. U.S. National Marine Fisheries Service, Middle Atlantic Coastal Fisheries Center, Technical Publication 1, Highlands, New Jersey.

Kramer, R.H., and L.L. Smith, Jr. 1962. Formation of year-classes in largemouth bass. Transactions of the American Fisheries Society 91:29-41.

Krebs, J.R. 1978. Optimal foraging: decision rules for predators. Pages 23-63 *in* J.R. Krebs and N.B. Davies, editors. Behavioral ecology: an evolutionary approach. Sinauer, Sunderland, Massachusetts.

Krummrich, J.T., and R.C. Heidinger. 1973. Vulnerability of channel catfish to largemouth bass predation. The Progressive Fish-Culturist 35:173-175.

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

Lasker, R. 1985. What limits clupeoid production? Canadian Journal of Fisheries and Aquatic Sciences 42(Supplement 1):31-38.

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

Le Cren, E.D. 1951. The length-weight relationship and seasonal cycle in gonad weight and condition in the perch (*Perca flavescens*). Journal of Animal Ecology 20:201-219.

Lewis, W.M., R. Heidinger, W. Kirk, W. Chapman, and D. Johnson. 1974. Food intake of the largemouth bass. Transactions of the American Fisheries Society 103:277-280.

Li, H.W., and R.W. Brocksen. 1977. Approaches to the analysis of energetic costs of interspecific competition for space by rainbow trout. Journal of Fish Biology 11:329-341.

Logan, H.J. 1967. Comparison of growth and survival rates of striped bass and striped bass x white bass hybrids under controlled environments. Proceedings of the Annual Conference Southeastern Association of Game and Fish Commissioners 21:260-263.

Love, R.M. 1970. The chemical biology of fishes. Volume 1. Academic Press, New York.

Love, R.M. 1980. The chemical biology of fishes. Volume 2. Academic Press, New York.

Luecke, C., J.A. Rice, L.B. Crowder, S.F. Yeo, and F.P. Binkowski. 1990. Recruitment mechanisms of bloater in Lake Michigan: an analysis of the predatory gauntlet. Canadian Journal of Fisheries and Aquatic Sciences 47:524-532.

Lyons, L. 1997. Influence of winter starvation on the distribution of smallmouth bass among Wisconsin streams: a bioenergetics modeling assessment. Transactions of the American Fisheries Society 126:157-162.

MacArthur, R.H., and E.R. Pianka. 1966. On optimal use of a patchy environment. American Naturalist 100:603-609.

MacKinnon, J.C. 1972. Summer storage of energy and its use for winter metabolism and gonad maturation in American plaice (*Hippoglossoides platessoides*). Journal of the Fisheries Research Board of Canada 29:1749-1759.

Madenjian, C.P. 1991. Limits to growth of young-of-the-year walleye (*Stizostedion vitreum vitreum*): an individual-based model perspective. Canadian Journal of Fisheries and Aquatic Sciences 48:1492-1499.

Madenjian, C.P., and S.R. Carpenter. 1991. Individual-based model for growth of young-of-the-year walleye: a piece of the recruitment puzzle. Ecological Applications 1:268-279.

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

Madenjian, C.P., J.T. Tyson, R.L. Knight. M.W. Kershner, and M.J. Hansen. 1996. First-year growth, recruitment, and maturity of walleyes in western Lake Erie. Transactions of the American Fisheries Society 125:821-830.

Magnuson, J.J. 1962. An analysis of aggressive behavior, growth and competition for food and space of medaka. Canadian Journal of Zoology 40:313-363.

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

Manooch, C.S., III. 1973. Food habits of yearling and adult striped bass, *Morone saxatilis* (Walbaum), from Albemarle Sound, North Carolina. Chesapeake Science 14:73-86.

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.

Mansueti, R.J. 1971. Age, growth, and movements of the striped bass, *Roccus saxatilis*, taken in size selective fishing gear in Maryland. Chesapeake Science 2:9-36.

Margenau, T.L. 1992. Survival and cost-effectiveness of stocked fall fingerling and spring yearling muskellunge in Wisconsin. North American Journal of Fisheries Management 12:484-493.

Markle, D.F., and G.C. Grant. 1970. The summer food habits of young-of-the-year striped bass in three Virginia rivers. Chesapeake Science 11:50-54.

Martin, F.D., D.A. Wright, J.C. Means, and E.M. Setzler-Hamilton. 1985. The importance of food supply to nutritional state of larval striped bass in the Potomac River estuary. Transactions of the American Fisheries Society 114:137-145.

Matthews, W.J., F.P. Gelwick, and J.J. Hoover. 1992. Food and habitat use by juveniles of species of *Micropterus* and *Morone* in a southwestern reservoir. Transactions of the American Fisheries Society 121:54-66.

Matthews, W.J., L.G. Hill, D.R. Edds, J.J. Hoover, and T.G. Heger. 1988. Trophic ecology of striped bass, *Morone saxatilis*, in a freshwater reservoir (Lake Texoma, U.S.A). Journal of Fish Biology 33:273-288.

McGovern, J.C., and J.E. Olney. 1988. Potential predation by fish and invertebrates on early life history stages of striped bass in the Pamunkey River, Virginia. Transactions of the American Fisheries Society 117:152-161.

McIntyre, D.B., F.J. Ward, and G.M. Swanson. 1987. Factors affecting cannibalism by pond-reared juvenile walleyes. The Progressive-Fish Culturist 49:264-269.

McLaren, J.B., J.R. Young, T.B. Hoff, I.R. Savidge, and W.L. Kirk. 1988. Feasibility of supplementary stocking of age-0 striped bass in the Hudson River. American Fisheries Society Monograph 4:286-291.

Meldrim, J.W., and J.J. Gift. 1971. Temperature preference, avoidance and shock experiments with estuarine fishes. Bulletin 7, Ichthyological Associates, Ithaca, New York.

Mensinger, G.C. 1970. Observations on the striped bass, *Morone saxatilis*, in Keystone Reservoir, Oklahoma. Proceedings of the Southeastern Association of Game and Fish Commissioners 24:447-463.

Merriman, D. 1941. Studies on the striped bass, *Roccus saxatilis*, of the Atlantic Coast. U.S. Fish and Wildlife Service Bulletin 50:1-77.

Michaelson, D.P. 1996. The impacts of stocking stress and largemouth bass predation on the survivorship of stocked juvenile striped bass in Smith Mountain Lake, Virginia. Master's thesis. Virginia Polytechnic Institute and State University, Blacksburg.

Miller, S.J., and T. Storck. 1984. Temporal spawning distribution of largemouth bass and young-of-year growth, determined from daily otolith rings. Transactions of the American Fisheries Society 113:571-578.

Miller, T.J., L.B. Crowder, J.A. Rice, and E.A. Marschall. 1988. Larval size and recruitment mechanisms in fishes: toward a conceptual framework. Canadian Journal of Fisheries and Aquatic Sciences 45:1657-1670.

Minton, J.W., and R.B. McLean. 1982. Measurements of growth and consumption of sauger (*Stizostedion canadense*): implication for fish energetics studies. Canadian Journal of Fisheries and Aquatic Sciences 39:1396-1403.

Miranda, L.E., and W.D. Hubbard. 1994a. Length-dependent winter survival and lipid composition of age-0 largemouth bass in Bay Springs Reservoir, Mississippi. Transactions of the American Fisheries Society 123:80-87.

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

Miranda, L.E., and R.J. Muncy. 1987. Recruitment of young-of-year largemouth bass in relation to size structure of parental stock. North American Journal of Fisheries Management 7:131-137.

Miranda, L.E., and R.J. Muncy. 1989. Bioenergetic values of shads and sunfishes as prey for largemouth bass. Proceedings of the Annual Conference Southeastern Association of Fish and Wildlife Agencies 43:153-163.

Moon, T.W. 1983. Changes in tissue ion contents and ultrastructure of food-deprived immature American eel, *Anguilla rostrata* (Le Sueur). Canadian Journal of Zoology 61:812-821.

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.

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

Morton, J.M., R.L. Kirkpatrick, and M.R. Vaughan. 1990. Changes in body composition of American black ducks wintering in Chincoteague, Virginia. The Condor 92:598-605.

Moss, L.J., and C.S. Lawson. 1982. Evaluation of striped bass and hybrid striped bass stockings in eight Alabama public fishing lakes. Proceedings of the Annual Conference Southeastern Association of Game and Fish Commissioners 36:33-41.

Murdoch, W.W., E. McCauley, R.M. Nisbet, W.S.C. Gurney, and A.M. de Roos. 1992. Individual-based models: combining testability and generality. Pages 18-34 *in* D.L. DeAngelis and L.J. Gross, editors. Individual-based models and approaches in ecology: populations, communities, and ecosystems. Routledge, Chapman and Hall, NewYork.

Murphy, B.R., D.W. Willis, and T.A. Springer. 1991. The relative weight index in fisheries management: status and needs. Fisheries 16(2):30-38.

Newsome, G.E., and G. Leduc. 1975. Seasonal changes in fat content in the yellow perch (*Perca flavescens*) of two Laurentian lakes. Journal of the Fisheries Research Board of Canada 32:2214-2221.

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

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

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

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

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.

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

Nifong, S.C. 1982. Growth and food habits of adult striped bass in Cherokee Reservoir, Tennessee. Master's Thesis. University of Tennessee, Knoxville.

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 history accommodations of landlocked alewives to a southern range extension. Transactions of the American Fisheries Society 111:559-569.

Niimi, A.J. 1972. Changes in the proximate composition of largemouth bass (*Micropterus salmoides*) with starvation. Canadian Journal of Zoology 50:815-819.

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. 1967. Age, growth, and fecundity of the alewife, *Alosa pseudoharengus* (Wilson), in Lake Michigan. Transactions of the American Fisheries Society 96:387-393.

Nursall, J.R. 1973. Some behavioral interactions of spottail shiners (*Notropis hudsonius*), yellow perch (*Perca flavescens*), and northern pike (*Esox lucius*). Journal of the Fisheries Research Board of Canada 30:1161-1178.

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

O'Brien, W.J. 1979. The predator-prey interaction of planktivorous fish and zooplankton. American Scientist 67:572-581.

O'Brien, W.J., H.I. Browman, and B.I. Evans. 1990. Search strategies of foraging animals. American Scientist 78:152-160.

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.

Oliver, J.D., G.F. Holeton, and K.E. Chua. 1979. Overwinter mortality of fingerling smallmouth bass in relation to size, relative energy stores, and environmental temperature. Transactions of the American Fisheries Society 108:130-136.

Osenberg, C.W., and G.G. Mittelbach. 1989. Effects of body size on the predator-prey interaction between pumpkinseed sunfish and gastropods. Ecological Monographs 59:405-432.

Osenberg, C.W., E.E. Werner, G.G. Mittelbach, and D.J. Hall. 1988. Growth patterns in bluegill (*Lepomis macrochirus*) and pumpkinseed (*L. gibbosus*) sunfish: environmental variation and the importance of ontogenetic niche shifts. Canadian Journal of Fisheries and Aquatic Sciences 45:17-26.

Ott, R.A., Jr., and S.P. Malvestuto. 1981. The striped bass x white bass hybrid in West Point Reservoir. Proceedings of the Annual Conference Southeastern Association of Fish and Wildlife Agencies 35:641-646.

Owen, M., and W.A. Cook. 1977. Variations in body weight, wing length and condition of mallards (*Anas platyrhynchos*) and their relationship to environmental changes. Journal of Zoology, London 183:377-385.

Pace, M.L., S.B. Baines, H. Cyr, and J.A. Downing. 1993. Relationships among early life stages of *Morone americana* and *Morone saxatilis* from long-term monitoring of the Hudson River estuary. Canadian Journal of Fisheries and Aquatic Sciences 50:1976-1985.

Padfield, J.H., Jr. 1951. Age and growth differentiation between the sexes of the largemouth bass *Micropterus salmoides*. Journal of the Tennessee Academy of Science 26:42-54.

Paloheimo, J.E., and L.M. Dickie. 1966b. Food and growth in fishes. III. Relations among food, body size, and growth efficiency. Journal of the Fisheries Research Board of Canada 23:1209-1248.

Pasch, R.W. 1975. Some relationships between food habits and growth of largemouth bass in Lake Blackshear, Georgia. Proceedings of the Annual Conference Southeastern Association of Game and Fish Commissioners 28:307-321.

Pastorok, R.A. 1981. Prey vulnerability and size selection by *Chaoborus* larvae. Ecology 62:1311-1324.

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

Pepin, P. 1990. Predation and starvation of larval fish: a numerical experiment of size- and growth-dependent survival. Biology and Oceanography 6:23-44.

Phillips, J.M., J.R. Jackson, and R.L. Noble. 1995. Hatching date influence on age-specific diet and growth of age-0 largemouth bass. Transactions of the American Fisheries Society 124:370-379.

Pierce, R.J., T.E. Wissing, J.G. Jaworski, R.N. Givens, and B.A. Megrey. 1980. Energy storage and utilization patterns of gizzard shad in Acton Lake, Ohio. Transactions of the American Fisheries Society 109:611-616.

Pirie, W.R., and W.A. Hubert. 1977. Assumptions in statistical analysis. Transactions of the American Fisheries Society 99:440-443.

Pitcher, T.J, and J.K. Parrish. 1986. Functions of shoaling behaviour in teleosts. Pages 363-440 *in* T.J. Pitcher, editor. Behavior of teleost fishes. Chapman & Hall, London, England.

Polgar, T.T. 1977. Striped bass ichthyoplankton abundance, mortality, and production estimates for the Potomac River population. Pages 110-126 *in* W. Van Winkle, editor. Proceedings of the conference on assessing the effects of power-plant induced mortality on fish populations. Pergamon Press, New York.

Polgar, T.T. 1982. Factors affecting recruitment of Potomac River striped bass and the resulting implications for management. Pages 427-442 *in* V.S. Kennedy, editor. Estuarine comparisons. Academic Press, New York.

Polis, G. 1988. Exploitation competition and the evolution of interference, cannibalism, and intraguild predation in age/size structured populations. Page 185-202 *in* B. Ebenman and L. Persson, editors. Size-structured populations. Springer-Verlag, New York.

Popova, O.A. 1967. The "predator-prey" relationship among fish. Page 359-376 *in* S.D. Gerking, editor. The biological basis of freshwater fish production. Blackwell Scientific Publications, Oxford, England.

Popova, O.A. 1978. The role of predaceous fish in ecosystems. Pages 215-249 *in* S.D. Gerking, editor. Ecology of freshwater fish production. John Wiley & Sons, New York.

Post, J.R., and D.O. Evans. 1989. Size-dependent overwinter mortality of young-of-the-year yellow perch (*Perca flavescens*): laboratory, in situ enclosure, and field experiments. Canadian Journal of Fisheries and Aquatic Sciences 46:1958-1968.

Post, J.R., and A.B. Prankevicius. 1987. Size-selective mortality in young-of-the-year yellow perch (*Perca flavescens*): evidence from otolith microstructure. Canadian Journal of Fisheries and Aquatic Sciences 44:1840-1847.

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

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

Rainwater, W.C., and A. Houser. 1975. Relation of physical and biological variables to black bass crops. Pages 306-309 *in* R.H. Stroud and H. Clepper, editors. Black bass biology and management. Sport Fishing Institute, Washington, D.C.

Rathjen, W.F., and L.C. Miller. 1957. Aspects of the early life history of the striped bass (*Roccus saxatilis*) in the Hudson River. New York Fish and Game Journal 4:43-60.

Reznick, D.N., and B. Braun. 1987. Fat cycling in the mosquitofish (*Gambusia affinis*): fat storage as a reproductive advantage. Oecologia 73:401-413.

Ricci, E.D., and J.J. Ney. 1978. A food habit study of young-of-the-year largemouth bass and striped bass from Smith Mountain Lake. Independent study report. Department of Fisheries and Wildlife Sciences, Virginia Polytechnic Institute and State University, Blacksburg.

Rice, J.A., L.B. Crowder, and F.P. Binkowski. 1987a. Evaluating potential sources of mortality for larval bloater (*Coregonus hoyi*): starvation and vulnerability to predation. Canadian Journal of Fisheries and Aquatic Sciences 44:467-472.

Rice, J.A., L.B. Crowder, and M.E. Holey. 1987b. Exploration of mechanisms regulating larval survival in Lake Michigan Bloater: a recruitment analysis based on characteristics of individual larvae. Transactions of the American Fisheries Society 116:703-718.

Rice, J.A., T.J. Miller, K.A. Rose, L.B. Crowder, E.A. Marschall, A.S. Trebitz, and D.L. DeAngelis. 1993. Growth rate variation and larval survival: inferences from an individual-based size-dependent predation model. Canadian Journal of Fisheries and Aquatic Sciences 50:133-142.

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., and R.E. Foerster. 1948. Computation of fish production. Bulletin of the Bingham Oceanography Collection, Yale University 11(4):173-211.

Rogers, B.A., D.T. Westin, and S.B. Saila. 1980. Development of techniques and methodology for the laboratory culture of striped bass, *Morone saxatilis* (Walbaum). U.S. Environmental Protection Agency, EPA-600/3-80-000, Cincinnati, Ohio.

Rose, K.A., S.W. Christensen, and D.L. DeAngelis. 1993. Individual-based modeling in populations with high mortality: a new method based on following a fixed number of model individuals. Ecological Modeling 68:273-292.

Rose, K.A., and J.H. Cowan, Jr. 1993. Individual-based model of young-of-the-year striped bass population dynamics. I. Model description and baseline simulations. Transactions of the American Fisheries Society 122:415-438.

Rosenberg, A.A., and A.S. Haugen. 1982. Individual growth and size-selective mortality of larval turbot reared in enclosures. Marine Biology 72:73-77.

Rothschild, B.J. 1966. Observations on the alewife (*Alosa pseudoharengus*) in Cayuga Lake. New York Fish and Game Journal 13:188-195.

Rothschild, B.J. 1986. Dynamics of marine fish populations. Harvard University Press, Cambridge, Massachusetts.

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

Rulifson, R.A., and C.S. Manooch III. 1990. Recruitment of juvenile striped bass in the Roanoke River, North Carolina, as related to reservoir discharge. North American Journal of Fisheries Management 10:397-407.

Rutherford, E.S., and E.D. Houde. 1995. The influence of temperature on cohort-specific growth, survival, and recruitment of striped bass *Morone saxatilis* larvae in Chesapeake Bay. U.S. National Marine Fisheries Service Fishery Bulletin 93:315-322.

Sale, P.F. 1979. Habitat partitioning and competition in fish communities. Page 323-330 *in* R.H. Stroud and H. Clepper, editors. Predator-prey systems in fisheries management. Sport Fishing Institute, Washington, D.C.

Sale, P.F. 1990. Recruitment of marine species: is the bandwagon rolling in the right direction? Trends in Ecology and Evolution 5:25-27.

Sandoz, O., and K.H. Johnston. 1965. Culture of striped bass, *Roccus saxatilis* (Walbaum). Proceedings of the Annual Conference Southeastern Association of Game and Fish Commissioners 19:390-394.

Santucci, V.J., and D.H. Wahl. 1993. Factors influencing survival and growth of stocked walleye (*Stizostedion vitreum*) in a centrarchid-dominated impoundment. Canadian Journal of Fisheries and Aquatic Sciences 50:1548-1558.

Saul, B.M. 1981. Food habits and growth of young-of-year striped bass in Cherokee Reservoir, Tennessee. Master's thesis. University of Tennessee, Knoxville.

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

Savitz, J. 1971. Effects of starvation on body protein utilization of bluegill sunfish (*Lepomis macrochirus*) with a calculation of caloric requirements. Transactions of the American Fisheries Society 100:18-21.

Schaefer, R.H. 1970. Feeding habits of striped bass from the surf waters of long island. New York Fish and Game Journal 17:1-17.

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

Schmidt-Nielsen, K. 1979. Animal physiology, 2nd edition. Cambridge University Press, Cambridge, United Kingdom.

Schoener, T.W. 1970. Non-synchronous spatial overlap of lizards in patchy habitats. Ecology 51:408-418.

Scofield, E.C. 1931. The life history of the striped bass. California Division of Fish and Game Fisheries Bulletin 29:26-60.

Scott, M.A., and W.W. Murdoch. 1983. Selective predation by the backswimmer, *Notonecta*. Limnology and Oceanography 28:352-366.

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

Scruggs, G.D. 1957. Reproduction of resident striped bass in Santee-Cooper reservoir, South Carolina. Transactions of the American Fisheries Society 85:144-159.

Secor, D.H., J.M. Dean, and E.H. Laban. 1991a. Manual for otolith removal and preparation for microstructural examination. Belle W. Baruch Institute for Marine Biology and Coastal Research Technical Publication 1991-01.

Secor, D.H., and E.D. Houde. 1995. Temperature effects on the timing of striped bass egg production, larval viability, and recruitment potential in the Patuxent River (Chesapeake Bay). Estuaries 16:527-544.

Secor, D.H., M.G. White, and J.M. Dean. 1991b. Immersion marking of larval and juvenile hatchery-produced striped bass with oxytetracycline. Transactions of the American Fisheries Society 120:261-266.

Serns, S.L. 1982. Relation of temperature and population density to first-year recruitment and growth of smallmouth bass in a Wisconsin lake. Transactions of the American Fisheries Society 111:570-574.

Serns, S.L., and L.M. Andrews. 1986. Comparative survival and growth of three sizes of muskellunge fingerlings stocked in four northern Wisconsin lakes. American Fisheries Society Special Publication 15:229-237.

Setzler-Hamilton, E.M., J.A. Boynton, J.A. Mihursky, T.T. Polgar, and K.V. Wood. 1981. Spatial and temporal distribution of striped bass eggs, larvae, and juveniles in the Potomac estuary. Transactions of the American Fisheries Society 110:121-136.

Setzler, E.M., W.R. Boynton, K.V. Wood, H.H. Zion, L. Lubbers, N.K. Mountford, P. Frere, L. Tucker, and J.A. Mihursky. 1980. Synopsis of biological data on striped bass, *Morone saxatilis* (Walbaum). NOAA (National Oceanic and Atmospheric Administration) Technical Report NMFS (National Marine Fisheries Service) Circular 433.

Setzler-Hamilton, E.M., D.A. Wright, F.D. Martin, C.V. Millsaps, and S.I. Whitlow. 1987. Analysis of nutritional condition and its use in predicting striped bass recruitment: field studies. American Fisheries Society Symposium 2:115-128.

Sharp, G.D. 1987. Averaging the way to inadequate information in a varying world. American Institute if Fisheries Research Biologists Briefs 16:3-4.

Shaw, E. 1978. Schooling fishes. American Scientist 66:166-175.

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

Shu'lman, G.E. 1960. Dynamics of the fat content of the body of fish. Russian Review of Biology 49:209-222.

Shuter, B.J., P.E. Ihssen, D.L. Wales, and E.J. Snucins. 1989. The effects of temperature, pH, and water hardness on winter starvation of young-of-the-year smallmouth bass, *Micropterus dolomieui* Lacépède. Journal of Fish Biology 35:765-780.

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

Shuter, B.J., and J.R. Post. 1990. Climate, population viability, and the zoogeography of temperate fishes. Transactions of the American Fisheries Society 119:314-336.

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

Sissenwine, M.P. 1984. Why do fish populations vary? Pages 59-94 *in* R.M. May, editor. Exploitation of marine communities. Springer-Verlig, Berlin, Germany.

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

Smith, E.P. 1985. Statistical comparison of weighted overlap measures. Transactions of the American Fisheries Society 114:250-257.

Smith, T.D. 1988. Stock assessment methods: the first fifty years. Pages 1-33 *in* J.A. Gulland, editor. Fish population dynamics. John Wiley & Sons, Chichester, England.

Spigarelli, S.A., M.M. Thomes, and W. Prepejchal. 1982. Feeding, growth, and fat deposition by brown trout in constant and fluctuating temperatures. Transactions of the American Fisheries Society 111:199-209.

Sokal, R.R., and F.J. Rohlf. 1981. Biometry, 2nd edition. Freeman and Company, New York.

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

Stahl, T.P., and R.A. Stein. 1994. Influence of larval gizzard shad (*Dorosoma cepedianum*) density on piscivory and growth of young-of-year saugeye (*Stizostedion vitreum* x *S. canadense*). Canadian Journal of Fisheries and Aquatic Sciences 51:1993-2002.

Stein, R.A., R.F. Carline, and R.S. Hayward. 1981. Largemouth bass predation on tiger muskellunge. Transactions of the American Fisheries Society 110:604-612.

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

Stevens, R.E. 1967a. A final report on the use of hormones to ovulate striped bass. Proceedings of the Annual Conference Southeastern Association of Game and Fish Commissioners 18(1964):525-538.

Stevens, R.E. 1967b. The striped bass of the Santee-Cooper Reservoir. Proceedings of the Annual Conference Southeastern Association of Game and Fish Commissioners 11:253-264.

Strange, R.J., and J.C. Pelton. 1987. Nutrient content of clupeid forage fishes. Transactions of the American Fisheries Society 116:60-66.

Summerfelt, R.C. 1975. Relationship between weather and year-class strength of largemouth bass. Pages 166-174 *in* R.H. Stroud and H. Clepper, editors. Black bass biology and management. Sport Fishing Institute, Washington, D.C.

Szendrey, T.A, and D.H. Wahl. 1996. Size-specific survival and growth of stocked muskellunge: effects of predation and prey availability. North American Journal of Fisheries Management 16:395-402.

Thompson, J.M., E.P. Bergersen, C.A. Carlson, and L.R. Kaeding. 1991. Role of size, condition, and lipid content in the overwinter survival of age-0 Colorado squawfish. Transactions of the American Fisheries Society 120:346-353.

Thorpe, J.E. 1977. Bimodal distribution of length of juvenile Atlantic salmon under artificial rearing conditions. Journal of Fish Biology 11:174-184.

Thorpe, J.E., and R.I.G. Morgan. 1978. Parental influence on growth rate, smolting rate and survival in hatchery-reared juvenile Atlantic salmon. Journal of Fish Biology 13:549-556.

Timmons, T.J., W.L. Shelton, and W.D. Davies. 1980. Differential growth of largemouth bass in West Point Reservoir, Alabama-Georgia. Transactions of the American Fisheries Society 109:176-186.

Tisa, M.S. 1988. Compatibility and complementarity of alewife and gizzard shad in Smith Mountain Lake, Virginia. Doctoral dissertation. Virginia Polytechnic Institute and State University, Blacksburg.

Tisa, M.S., and J.J. Ney. 1991. Compatibility of alewives and gizzard shad as reservoir forage fish. Transactions of the American Fisheries Society 120:157-165.

Toneys, M.L., and D.W. Coble. 1979. Size-related first winter mortality of freshwater fishes. Transactions of the American Fisheries Society 108:415-419.

Toneys, M.L., and D.W. Coble. 1980. Mortality, hematocrit, osmolality, electrolyte regulation, and fat depletion of young-of-the-year freshwater fishes under simulated winter conditions. Canadian Journal of Fisheries and Aquatic Sciences 37:225-232.

Trent, W.L. 1962. Growth and abundance of young-of-year striped bass, *Roccus saxatilis* (Walbaum), in Albemarle Sound, North Carolina. Master's thesis. North Carolina State University, Raleigh.

Tuncer, H. 1988. Growth, survival, and energetics of larval and juvenile striped bass (*Morone saxatilis*) and its white bass hybrid (*M. saxatilis* x *M. chrysops*). Master's thesis. University of Maryland, College Park.

Turner, J.L., and H.K. Chadwick. 1972. Distribution and abundance of young-of-the-year striped bass, *Morone saxatilis*, in relation to river flow in the Sacramento-San Joaquin estuary. Transactions of the American Fisheries Society 101:442-452.

Tyler, A.V., and R.S. Dunn. 1976. Ration, growth, and measures of somatic and organ condition in relation to meal frequency in winter flounder, *Pseudopleuronectes americanus*, with hypotheses regarding population homeostasis. Journal of the Fisheries Research Board of Canada 33:63-75.

Ulanowicz, R.E., and T.T. Polgar. 1980. Influence of anadromous spawning behavior and optimal environmental conditions upon striped bass *Morone saxatilis* year-class success. Canadian Journal of Fisheries and Aquatic Sciences 37:143-154.

Uphoff, J.J., Jr. 1989. Environmental effects on survival of eggs, larvae, and juveniles of striped bass in the Choptank River, Maryland. Transactions of the American Fisheries Society 118:251-263.

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 of the Southeastern Association of Fish and Wildlife Agencies. 33:361-370.

Van Den Avyle, M.J., B.J. Higginbotham, B.T. James, and F.J. Bulow. 1983. Habitat preferences and food habits of young-of-the-year striped bass, white bass, and yellow bass in Watts Bar Reservoir, Tennessee. North American Journal of Fisheries Management 3:163-170.

Van Winkle, W., K.A. Rose, and R.C. Chambers. 1993. Individual-based approach to fish population dynamics: an overview. Transactions of the American Fisheries Society 122:397-403.

Van Winkle, W., K.A. Rose, K.O. Winemiller, D.L. DeAngelis, S.W. Christensen, R.G. Otto, and B.J. Shuter. 1993. Linking life history theory, environmental setting, and individual-based modeling to compare responses of different fish species to environmental change. Transactions of the American Fisheries Society 122:459-466.

Vladykov, V.D., and D.H. Wallace. 1952. Studies of the striped bass, *Roccus saxatilis* (Walbaum), with special reference to the Chesapeake Bay region during 1936-1938. Bulletin of the Bingham Oceanography Collection, Yale University 14:132-177.

Waddle, H.R., C.C. Coutant, and J.L. Wilson. 1980. Summer habitat selection by striped bass, *Morone saxatilis*, in Cherokee Reservoir, Tennessee, 1977. Oak Ridge National Laboratory, ORNL/TM-6927, Oak Ridge, Tennessee.

Wahl, D.H., and R.A. Stein. 1989. Comparative vulnerability of three esocids to largemouth bass (*Micropterus salmoides*) predation. Canadian Journal of Fisheries and Aquatic Sciences 46:2095-2103.

Wallace, R.K., Jr. 1981. An assessment of diet-overlap indexes. Transactions of the American Fisheries Society 110:72-76.

Wallin, J., M.J. Van Den Avyle, and M.C. Griffin. 1993. Reproduction, recruitment, and habitat requirements of striped bass in the Savannah River. Annual Project Completion Report F52, University of Georgia, Athens.

Ware, F.J. 1970. Some early life history of Florida's inland striped bass, *Morone saxatilis*. Proceedings of the Annual Conference Southeastern Association of Game and Fish Commissioners 24:439-447.

Weatherly, A.H., and H.S. Gill. 1981. Recovery growth following periods of restricted rations and starvation in rainbow trout *Salmo gairdneri* Richardson. Journal of Fish Biology 18:195-208.

Weaver, O.R. 1975. A study of the striped bass, *Morone saxatilis*, In J. Percy Priest Reservoir, Tennessee. Master's thesis. Tennessee Technological University, Cookeville.

Wege, G.J., and R.O. Anderson. 1978. Relative weight (W_r): a new index of condition for largemouth bass. Pages 79-91 *in* G.D. Novinger and J.G. Dillard, editors. New approaches to the management of small impoundments. American Fisheries Society, North Central Division, Special Publication 5, Bethesda, Maryland.

Wells, A.W., D.M. Randall, D.J. Dunning, and J.R. Young. 1991. Dispersal of young-of-the-year hatchery striped bass in the Hudson River. North American Journal of Fisheries Management 11:381-392.

Werner, E.E. 1977. Species packing and niche complementarity in three sunfishes. American Naturalist 111:553-578.

Werner, E.E., and J.F. Gilliam. 1984. The ontogenetic niche and species interactions in size-structured populations. Annual Review of Ecology and Systematics 15:393-426.

Werner, E.E., and D.J. Hall. 1977. Competition and habitat shift in two sunfishes Centrarchidae). Ecology 58:869-876.

Westin, D.T., and B.A. Rogers. 1978. Synopsis of biological data on striped bass, *Morone saxatilis* (Walbaum) 1972. University of Rhode Island, Marine Technical Report 67, Kingston.

White, M.G., III. 1989. Fingerling densities produced by a spawning population of striped bass in the Santee-Cooper reservoir, South Carolina. Proceedings of the Annual Conference Southeastern Association of Fish and Wildlife Agencies 42(1988):44-50.

Wicker, A.M., and W.E. Johnson. 1987. Relationships among fat content, condition factor, and first-year survival of Florida largemouth bass. Transactions of the American Fisheries Society 116:264-271.

Wiens, J.A. 1977. On competition and variable environments. American Scientist 65:590-597.

Wigfall, M., and J.M. Barkuloo. 1975. A preliminary report on the abundance and biology of stocked striped bass in the Choctawhatchee River system, Florida. Proceedings of the Annual Conference Southeastern Association of Game and Fish Commissioners 29:152-161.

Wissing, T.E., and A.D. Hasler. 1971. Effects of swimming activity and food intake on the respiration of young-of-the-year white bass, *Morone chrysops*. Transactions of the American Fisheries Society 100:537-543.

Wootton, R.J. 1990. Ecology of teleost fishes. Chapman and Hall, London, United Kingdom.

Wootton, R.J., J.R.M. Allen, and S.J. Cole. 1980. Energetics of the annual reproductive cycle in female sticklebacks, *Gasterosteus aculeatus* L. Journal of Fish Biology 17:387-394.

Wootton, R.J., G.W. Evans, and L. Mills. 1878. Annual cycle in female three-spined sticklebacks (*Gasterosteus aculeatus* L.) from an upland and lowland population. Journal of Fish Biology 12:331-343.

Yeager, D.M. 1988. Evaluation of phase I and phase II hybrid striped bass in the Escambia River, Florida. Proceedings of the Annual Conference Southeastern Association of Fish and Wildlife Agencies 41:41-47.

Zar, J.H. 1984. Biostatistical analysis, 2nd edition. Prentice Hall, New Jersey.

Zaret, T.M., and A.S. Rand. 1971. Competition in tropical stream fishes: support of the competitive exclusion principle. Ecology 52:336-342.

APPENDIX TABLES

Table A.1a. Percent of total food weight contributed by different types of prey consumed by juvenile striped bass in the Roanoke River of Smith Mountain Lake, 1994-95. Zooplankton - Clad (Cladoceran), Cope (Copepod); Aquatic Insects - Baet (Baetid mayfly nymphs), Chir (Chironomid midge larvae), Anis (Anisoptera - dragonfly naiads); Fish - Cyp (Cyprinidae - shiners), Ale (alewife), Sun (sunfish), Dart (darters), UnID (unidentified fish).

Sampling	Stomachs		Zooplankton		Aquatic Insects			Fish				
Period	N	Empty (%)	Clad	Cope	Baet	Chir	Anis	Cyp	Ale	Sun	Dart	UnID
15-30 Jun	52	35	15.14	0.00	18.51	29.32	0.00	31.63	0.00	0.00	0.00	5.40
01-15 Jul	137	48	9.11	2.44	14.57	25.90	0.00	47.06	0.00	0.00	0.00	0.92
16-31 Jul	111	31	8.00	2.66	17.67	13.00	0.00	54.67	0.00	0.00	0.00	4.00
01-15 Aug	93	14	3.48	0.70	12.38	13.49	0.00	69.40	0.00	0.00	0.00	0.56
16-31 Aug	71	31	0.90	0.40	8.94	4.32	0.00	53.41	32.03	0.00	0.00	0.00
01-15 Sep	48	44	0.32	0.49	5.54	1.14	0.00	53.09	37.30	0.00	0.00	2.12
16-30 Sep	37	22	0.52	2.24	2.02	7.56	5.76	40.90	40.33	0.00	0.00	0.67
01-15 Oct	66	6	0.68	1.62	1.56	0.38	0.00	7.68	85.68	2.40	0.00	0.00
16-31 Oct	34	12	1.57	2.35	2.44	0.44	0.00	10.72	79.70	0.00	0.00	2.78
01-15 Nov	53	23	0.45	3.10	1.68	0.52	0.90	19.69	70.67	0.00	0.00	2.99
16-30 Nov	28	21	1.89	3.67	3.15	1.58	0.00	26.50	63.21	0.00	0.00	0.00
01-15 Dec	7	0	6.06	4.61	3.50	3.03	0.00	15.15	65.15	0.00	0.00	2.50
15-31 Mar	125	76	0.00	0.00	0.00	0.00	0.00	12.04	84.25	2.05	1.66	0.00

Table A.1b. Percent of total food weight contributed by different types of prey consumed by juvenile striped bass in the Blackwater River of Smith Mountain Lake, 1994-95. Zooplankton - Clad (Cladoceran), Cope (Copepod); Aquatic Insects - Baet (Baetid mayfly nymphs), Chir (Chironomid midge larvae), Anis (Anisoptera - dragonfly naiads); Fish - Cyp (Cyprinidae - shiners), Ale (alewife), Sun (sunfish), Dart (darter), UnID (unidentified fish).

Sampling	Stomachs		Zooplankton		Aquatic Insects			Fish				
Period	N	Empty (%)	Clad	Cope	Baet	Chir	Anis	Cyp	Ale	Sun	Dart	UnID
15-30 Jun	58	34	22.09	0.00	11.63	16.28	0.00	48.84	0.00	0.00	0.00	1.16
01-15 Jul	80	20	9.95	3.41	5.90	9.83	0.00	70.25	0.00	0.00	0.00	0.66
16-31 Jul	63	21	2.16	0.16	1.57	1.42	0.00	93.71	0.00	0.00	0.00	0.98
01-15 Aug	86	24	2.19	0.13	1.71	1.29	0.00	93.80	0.00	0.00	0.00	0.88
16-31 Aug	55	22	1.41	0.08	1.82	0.82	0.00	95.87	0.00	0.00	0.00	0.00
01-15 Sep	32	22	5.50	0.50	3.00	1.50	0.00	89.50	0.00	0.00	0.00	0.00
16-30 Sep	21	14	1.57	0.31	1.89	1.57	0.00	93.40	0.00	0.00	0.00	1.26
01-15 Oct	25	4	0.30	0.36	0.18	0.12	0.00	68.12	30.92	0.00	0.00	0.00
16-31 Oct	15	0	0.30	0.98	1.59	0.16	0.00	88.22	8.75	0.00	0.00	0.00
01-15 Nov	16	12	0.79	0.18	1.00	0.00	0.00	35.90	62.13	0.00	0.00	0.00
16-30 Nov	6	33	0.00	0.00	0.00	0.00	0.00	32.11	67.89	0.00	0.00	0.00
01-15 Dec	5	60	0.00	0.00	0.00	0.00	0.00	25.15	74.85	0.00	0.00	0.00
15-31 Mar	113	67	0.00	0.00	0.00	0.00	0.00	18.16	81.84	0.00	0.00	0.00

Table A.1c. Percent of total food weight contributed by different types of prey consumed by juvenile striped bass in the Roanoke River of Smith Mountain Lake, 1995-96. Zooplankton - Clad (Cladoceran), Cope (Copepod): Aquatic Insects - Baet (Baetid mayfly nymphs), Chir (Chironomid midge larvae), Anis (Anisoptera - dragonfly naiads); Fish - Cyp (Cyprinidae - shiners), Ale (alewife), Sun (sunfish), Dart (darters), UnID (unidentified fish).

Sampling	Stomachs		Zooplankton		Aquatic Insects			Fish				
Period	N	Empty (%)	Clad	Cope	Baet	Chir	Anis	Cyp	Ale	Sun	Dart	UnID
16-30 Jul	64	27	5.43	0.00	3.10	1.55	0.00	89.52	0.00	0.00	0.00	0.40
01-15 Aug	74	9	0.00	0.00	0.56	0.06	0.00	86.18	13.20	0.00	0.00	0.00
16-31 Aug	35	29	0.00	0.00	0.58	0.00	0.00	90.01	9.41	0.00	0.00	0.00
01-15 Sep	17	18	0.00	0.15	1.36	0.08	0.00	25.50	72.91	0.00	0.00	0.00
16-30 Sep	42	14	0.06	0.00	0.02	0.00	0.00	29.35	69.92	0.00	0.00	0.65
01-15 Oct	26	12	0.00	0.00	0.05	0.00	0.00	3.84	96.11	0.00	0.00	0.00
16-31 Oct	29	31	0.00	0.00	0.00	0.00	0.00	0.23	97.50	0.00	2.27	0.00
01-15 Nov	22	23	0.89	0.00	0.00	0.00	0.00	0.00	96.55	2.56	0.00	0.00
16-30 Nov	22	45	0.00	0.00	0.00	0.00	0.00	0.00	99.23	0.00	0.00	0.77
15-31 Mar	8	75	0.00	0.00	0.00	0.00	0.00	0.00	100	0.00	0.00	0.00
01-15 Apr	26	92	0.00	0.00	0.00	0.00	0.00	0.00	100	0.00	0.00	0.00

Table A.1d. Percent of total food weight contributed by different types of prey consumed by juvenile striped bass in the Blackwater River of Smith Mountain Lake, 1995-96. Zooplankton - Clad (Cladoceran), Cope (Copepod); Aquatic Insects - Baet (Baetid mayfly nymphs), Chir (Chironomid midge larvae), Anis (Anisoptera - dragonfly naiads); Fish - Cyp (Cyprinidae - shiners), Ale (alewife), Sun (sunfish), Dart (darters), UnID (unidentified fish).

Sampling	Stomachs		Zooplankton		Aquatic Insects			Fish				
Period	N	Empty (%)	Clad	Cope	Baet	Chir	Anis	Cyp	Ale	Sun	Dart	UnID
16-30 Jul	64	34	2.98	0.00	5.97	8.46	1.49	80.73	0.00	0.00	0.00	0.37
01-15 Aug	92	22	3.58	0.17	6.64	1.70	0.00	41.57	46.34	0.00	0.00	0.00
16-31 Aug	66	8	4.19	0.97	16.13	3.22	2.26	38.22	34.52	0.00	0.00	0.49
01-15 Sep	66	5	8.01	5.92	18.12	2.79	0.00	7.90	57.26	0.00	0.00	0.00
16-30 Sep	78	6	2.71	0.22	5.95	1.43	0.00	3.31	80.09	4.42	1.02	0.85
01-15 Oct	53	21	0.17	0.00	0.83	0.06	0.00	12.50	85.71	0.00	0.00	0.73
16-31 Oct	57	14	1.76	0.00	0.00	2.55	0.00	2.61	93.08	0.00	0.00	0.00
01-15 Nov	52	35	2.89	0.00	0.00	1.09	0.00	2.45	91.30	1.87	0.00	0.40
16-30 Nov	38	32	5.64	0.00	0.00	1.42	0.00	1.97	90.97	0.00	0.00	0.00
15-31 Mar	6	83	0.00	0.00	0.00	0.00	0.00	0.00	100	0.00	0.00	0.00
01-15 Apr	35	80	0.00	0.00	0.00	0.00	0.00	0.00	100	0.00	0.00	0.00

Table A.2a. Percent of total food weight by different types of prey consumed by juvenile striped bass in the Roanoke River of Smith Mountain Lake, 1994-95. Zooplankton - Clad (Cladoceran), Cope (Copepod); Aquatic Insects - Baet (Baetid mayfly nymphs), Chir (Chironomid midge larvae), Anis (Anisoptera - dragonfly naiads); Fish - Cyp (Cyprinidae - shiners), Ale (alewife), Sun (sunfish), Dart (darters), UnID (unidentified fish).

	Stomachs		Zooplankton		Aquatic Insects			Fish				
Length (mm)	N	Empty (%)	Clad	Cope	Baet	Chir	Anis	Cyp	Ale	Sun	Dart	UnID
20	4	25	100	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
30	49	32	10.00	0.00	33.34	36.67	0.00	19.99	0.00	0.00	0.00	0.00
40	32	56	4.00	0.00	24.00	16.00	0.00	54.67	0.00	0.00	0.00	1.33
50	65	25	3.03	1.21	18.94	14.70	0.00	62.12	0.00	0.00	0.00	0.00
60	130	22	3.82	3.12	17.18	15.35	0.00	60.21	0.00	0.00	0.00	0.32
70	131	35	3.46	7.43	15.09	13.45	0.00	60.57	0.00	0.00	0.00	0.00
80	119	39	5.86	6.18	17.35	10.54	0.94	59.13	0.00	0.00	0.00	0.00
90	82	22	4.73	7.89	14.86	8.28	1.48	61.33	0.00	0.00	0.00	1.43
100	30	27	3.30	7.85	10.39	6.73	0.00	71.73	0.00	0.00	0.00	0.00
110	36	22	1.41	7.51	9.32	6.04	2.59	56.50	16.18	0.00	0.00	0.45
120	29	24	0.98	4.22	5.52	4.55	0.98	25.25	58.50	0.00	0.00	0.00
130	6	17	0.00	1.49	3.57	2.24	2.99	18.07	71.64	0.00	0.00	0.00
140	5	0	0.00	0.00	5.45	0.00	0.00	10.15	84.25	0.00	0.00	0.15
150	6	33	0.00	0.00	0.00	0.00	0.00	0.00	100	0.00	0.00	0.00
160	2	50	0.00	0.00	0.00	0.00	0.00	0.00	100	0.00	0.00	0.00
170	2	0	0.00	0.00	0.00	0.00	0.00	0.00	100	0.00	0.00	0.00
180	10	10	0.00	0.00	0.00	0.00	0.00	5.21	87.34	6.85	0.00	0.60
190	5	20	0.00	0.00	0.00	0.00	0.00	0.00	100	0.00	0.00	0.00
200	10	40	0.00	0.00	0.00	0.00	0.00	5.04	94.21	0.00	0.00	0.75
210	5	0	0.00	0.00	0.00	0.00	0.00	0.00	93.39	0.00	6.61	0.00
220	14	43	0.00	0.00	0.00	0.00	0.00	5.32	91.80	0.00	2.81	0.07
230	23	74	0.00	0.00	0.00	0.00	0.00	8.54	90.08	0.00	0.88	0.50
240	29	86	0.00	0.00	0.00	0.00	0.00	8.37	91.63	0.00	0.00	0.00
250	23	70	0.00	0.00	0.00	0.00	0.00	14.75	85.25	0.00	0.00	0.00
260	15	67	0.00	0.00	0.00	0.00	0.00	2.92	94.47	2.61	0.00	0.00

Table A.2b. Percent of total food weight by different types of prey consumed by juvenile striped bass in the Blackwater River of Smith Mountain Lake, 1994-95. Zooplankton - Clad (Cladoceran), Cope (Copepod); Aquatic Insects - Baet (Baetid mayfly nymphs), Chir (Chironomid midge larvae), Anis (Anisoptera - dragonfly naiads); Fish - Cyp (Cyprinidae - shiners), Ale (alewife), Sun (sunfish), Dart (darters), UnID (unidentified fish).

	Stomachs		Zooplankton		Aquatic Insects			Fish				
Length (mm)	N	Empty (%)	Clad	Cope	Baet	Chir	Anis	Cyp	Ale	Sun	Dart	UnID
40	48	42	13.51	0.00	29.73	29.43	0.00	27.03	0.00	0.00	0.00	0.30
50	64	29	5.37	0.67	18.12	14.76	0.00	61.08	0.00	0.00	0.00	0.00
60	48	14	3.00	3.93	7.72	7.82	0.00	76.11	0.00	0.00	0.00	1.42
70	46	24	2.26	2.26	5.30	4.51	0.00	85.62	0.00	0.00	0.00	0.05
80	67	21	3.65	1.21	3.31	2.15	0.00	88.47	0.00	0.00	0.00	1.21
90	76	24	3.24	2.14	4.25	3.95	0.00	85.55	0.00	0.00	0.00	0.87
100	44	20	3.63	3.98	4.92	4.87	0.00	82.18	0.00	0.00	0.00	0.42
110	19	11	2.34	3.87	4.74	1.77	0.00	82.07	0.00	0.00	5.21	0.00
120	10	20	1.46	1.50	3.13	1.04	0.00	48.12	44.75	0.00	0.00	0.00
130	3	33	0.00	0.00	0.00	0.00	0.00	14.05	84.19	0.00	0.00	1.76
140	4	0	0.00	0.00	0.00	0.00	0.00	20.58	78.75	0.00	0.00	0.67
150	4	0	0.00	0.00	0.17	0.00	0.00	12.12	82.20	0.00	3.52	2.16
160	3	67	0.00	0.00	0.00	0.00	0.00	0.00	100	0.00	0.00	0.00
170	1	0	0.00	0.00	0.00	0.00	0.00	0.00	100	0.00	0.00	0.00
180	4	0	0.00	0.00	0.00	0.00	0.00	5.46	94.11	0.00	0.00	0.43
190	6	17	0.00	0.00	0.00	0.00	0.00	14.35	85.65	0.00	0.00	0.00
200	10	60	0.00	0.00	0.00	0.00	0.00	13.24	86.53	0.00	0.00	0.23
210	19	58	0.00	0.00	0.00	0.00	0.00	12.50	87.19	0.00	0.00	0.31
220	18	67	0.00	0.00	0.00	0.00	0.00	11.28	88.72	0.00	0.00	0.00
230	21	29	0.00	0.00	0.00	0.00	0.00	4.16	95.84	0.00	0.88	0.00
240	25	68	0.00	0.00	0.00	0.00	0.00	3.76	96.24	0.00	0.00	0.00
250	20	60	0.00	0.00	0.00	0.00	0.00	2.76	95.42	0.00	0.00	1.82
260	15	67	0.00	0.00	0.00	0.00	0.00	0.00	100	0.00	0.00	0.00

Table A.2c. Percent of total food weight by different types of prey consumed by juvenile striped bass in the Roanoke River of Smith Mountain Lake, 1995-96. Zooplankton - Clad (Cladoceran), Cope (Copepod); Aquatic Insects - Baet (Baetid mayfly nymphs), Chir (Chironomid midge larvae), Anis (Anisoptera - dragonfly naiads); Fish - Cyp (Cyprinidae - shiners), Ale (alewife), Sun (sunfish), Dart (darters), UnID (unidentified fish).

	Stomachs		Zooplankton		Aquatic Insects			Fish				
Length (mm)	N	Empty (%)	Clad	Cope	Baet	Chir	Anis	Cyp	Ale	Sun	Dart	UnID
40	22	18	25.74	0.00	5.15	2.20	0.00	66.91	0.00	0.00	0.00	0.00
50	36	27	6.64	0.00	2.21	1.33	0.00	89.50	0.00	0.00	0.00	0.32
60	47	12	0.87	0.00	1.39	0.07	0.00	97.03	0.00	0.00	0.00	0.64
70	31	13	0.67	0.00	1.12	0.00	0.00	96.72	0.00	0.00	0.00	1.49
80	22	26	0.59	0.00	6.26	0.59	0.00	92.34	0.00	0.00	0.00	0.22
90	16	19	1.34	0.00	0.00	0.00	0.00	88.10	10.56	0.00	0.00	0.00
100	18	17	0.84	0.00	0.60	0.00	0.00	72.56	24.89	0.00	0.00	1.11
110	12	25	0.50	0.00	0.00	0.31	0.00	76.40	22.31	0.00	0.00	0.48
120	15	27	0.00	0.00	0.49	0.00	0.00	34.15	65.36	0.00	0.00	0.00
130	10	10	0.00	0.00	0.00	0.00	0.00	12.43	80.18	6.43	0.00	0.96
140	10	36	0.00	0.00	0.00	0.00	0.00	34.34	65.66	0.00	0.00	0.00
150	11	25	0.00	0.00	0.00	0.00	0.00	39.80	58.66	0.00	0.00	1.54
160	20	20	0.00	0.00	0.00	0.00	0.00	15.98	79.83	0.00	3.62	0.57
170	15	25	0.00	0.00	0.00	0.00	0.00	13.31	83.87	0.00	0.00	2.82
180	4	20	0.00	0.00	0.00	0.00	0.00	8.85	91.15	0.00	0.00	0.00
190	9	44	0.00	0.00	0.00	0.00	0.00	4.11	94.88	0.00	0.00	1.01
200	11	36	0.00	0.00	0.00	0.00	0.00	10.39	87.83	0.00	0.00	1.78
210	15	47	0.00	0.00	0.00	0.00	0.00	7.81	91.97	0.00	0.00	0.22
220	16	56	0.00	0.00	0.00	0.00	0.00	11.29	88.71	0.00	0.00	0.00
230	12	75	0.00	0.00	0.00	0.00	0.00	4.52	95.48	0.00	0.00	0.00
240	7	71	0.00	0.00	0.00	0.00	0.00	5.99	94.01	0.00	0.00	0.00
250	4	25	0.00	0.00	0.00	0.00	0.00	0.00	100	0.00	0.00	0.00
260	2	50	0.00	0.00	0.00	0.00	0.00	0.00	100	0.00	0.00	0.00

Table A.2d. Percent of total food weight by different types of prey consumed by juvenile striped bass in the Blackwater River of Smith Mountain Lake, 1995-96. Zooplankton - Clad (Cladoceran), Cope (Copepod); Aquatic Insects - Baet (Baetid mayfly nymphs), Chir (Chironomid midge larvae), Anis (Anisoptera - dragonfly naiads); Fish - Cyp (Cyprinidae - shiners), Ale (alewife), Sun (sunfish), Dart (darters), UnID (unidentified fish).

	Stomachs		Zooplankton		Aquatic Insects			Fish				
Length (mm)	N	Empty (%)	Clad	Cope	Baet	Chir	Anis	Cyp	Ale	Sun	Dart	UnID
40	5	60	67.00	0.00	0.00	33.00	0.00	0.00	0.00	0.00	0.00	0.00
50	52	17	26.00	0.41	31.02	9.80	0.00	32.77	0.00	0.00	0.00	0.00
60	116	16	26.62	0.63	36.22	9.39	1.25	25.47	0.00	0.00	0.00	0.42
70	99	11	11.71	6.52	27.87	6.60	0.44	46.02	0.00	0.00	0.00	0.84
80	65	10	8.46	3.89	22.74	5.16	0.00	56.87	0.00	0.00	0.00	2.88
90	47	6	7.86	0.00	20.76	4.71	0.00	45.29	21.13	0.00	0.00	0.25
100	27	0	5.02	0.00	10.41	12.45	0.00	35.39	31.03	0.00	5.34	0.36
110	18	11	1.65	0.00	0.00	11.52	0.00	38.22	40.66	6.66	0.00	1.29
120	18	44	0.00	0.00	0.00	9.19	0.00	25.43	54.81	9.70	0.00	0.87
130	10	20	0.00	0.00	0.00	3.81	0.00	12.90	83.06	0.00	0.00	0.23
140	9	66	0.00	0.00	0.00	0.00	0.00	10.92	88.36	0.00	0.00	0.72
150	10	40	0.00	0.00	0.00	0.00	0.00	8.32	90.32	0.00	0.00	1.36
160	10	30	0.00	0.00	0.00	0.00	0.00	9.75	90.25	0.00	0.00	0.00
170	10	40	0.00	0.00	0.00	0.00	0.00	5.06	94.94	0.00	0.00	0.00
180	11	45	0.00	0.00	0.00	0.00	0.00	0.00	100	0.00	0.00	0.00
190	8	25	0.00	0.00	0.00	0.00	0.00	0.00	100	0.00	0.00	0.00
200	9	33	0.00	0.00	0.00	0.00	0.00	0.00	100	0.00	0.00	0.00
210	30	63	0.00	0.00	0.00	0.00	0.00	0.00	100	0.00	0.00	0.00
220	21	67	0.00	0.00	0.00	0.00	0.00	0.00	100	0.00	0.00	0.00
230	19	53	0.00	0.00	0.00	0.00	0.00	0.00	100	0.00	0.00	0.00
240	11	82	0.00	0.00	0.00	0.00	0.00	0.00	100	0.00	0.00	0.00
250	2	0	0.00	0.00	0.00	0.00	0.00	0.00	100	0.00	0.00	0.00

Table A.3a. Percent of total food weight contributed by different types of prey consumed by juvenile black bass (largemouth and smallmouth bass) in the Roanoke River of Smith Mountain Lake, 1994-95. Zooplankton - Cld (Cladoceran), Cop (Copepod); Aquatic Insects - Bae (Baetid mayfly nymphs), Chr (Chironomid midge larvae), Ans (Anisoptera - dragonfly naiads), Ger (Gerridae - water striders); Terrestrial Insects - For (Formicidae - ants), Col (Coleoptera - beetles); Fish - Cyp (Cyprinidae - shiners), Ale (alewife), Sun (sunfish), Dar (darters), UID (unidentified fish); Emp = empty.

	Stomachs		Zooplankton		Insects						Fish				
Sampling Period	N	Emp (%)	Cld	Cop	Bae	Chr	Ans	For	Ger	Col	Cyp	Ale	Sun	Dar	UID
15-30 Jun	41	66	3.85	0.00	3.85	19.23	0.00	0.00	0.00	0.00	65.38	0.00	0.00	5.61	2.08
01-15 Jul	24	29	1.85	0.00	7.41	9.26	0.00	0.00	1.85	0.00	50.00	0.00	0.00	29.63	0.00
16-31 Jul	75	39	2.49	0.50	13.93	4.98	0.00	3.48	0.50	0.00	32.83	0.00	0.00	41.29	0.00
01-15 Aug	38	29	4.07	0.58	13.37	4.07	0.00	0.58	4.07	1.16	20.35	0.00	0.00	50.90	0.85
16-31 Aug	46	43	0.00	0.00	7.73	3.31	0.00	0.55	0.55	1.66	21.05	0.00	25.00	37.93	2.22
01-15 Sep	36	50	0.00	0.00	3.96	0.30	0.00	0.91	1.22	0.61	32.02	0.00	14.02	46.96	0.00
16-30 Sep	32	22	0.96	0.00	8.68	1.93	0.00	1.61	3.22	0.00	16.62	0.00	22.05	44.93	0.00
01-15 Oct	14	21	0.00	0.00	4.36	0.79	0.00	0.00	0.40	0.00	1.99	0.00	34.32	58.14	0.00
16-31 Oct	28	39	1.00	0.50	1.00	0.50	0.00	0.00	1.00	2.01	1.53	0.00	26.13	66.33	0.00
01-15 Nov	6	50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	5.22	0.00	13.48	80.15	1.15
16-30 Nov	4	75	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	100	0.00
01-15 Dec	2	50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	100	0.00
15-31 Mar	0	0	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Table A.3b. Percent of total food weight contributed by different types of prey consumed by juvenile black bass (largemouth and smallmouth bass) in the Blackwater River of Smith Mountain Lake, 1994-95. Zooplankton - Cld (Cladoceran), Cop (Copepod); Aquatic Insects - Bae (Baetid mayfly nymphs), Chr (Chironomid midge larvae), Ans (Anisoptera - dragonfly naiads), Ger (Gerridae - water striders); Terrestrial Insects - For (Formicidae - ants), Col (Coleoptera -beetles); Fish - Cyp (Cyprinidae - shiners), Ale (alewife), Sun (sunfish), Dar (darters), UID (unidentified fish); Emp = empty.

	Stomachs		Zooplankton		Insects						Fish				
Sampling Period	N	Emp (%)	Cld	Cop	Bae	Chr	Ans	For	Ger	Col	Cyp	Ale	Sun	Dar	UID
15-30 Jun	64	55	11.11	0.00	7.56	12.56	0.00	0.00	9.51	0.00	57.00	0.00	0.00	0.00	2.26
01-15 Jul	30	40	3.70	0.00	7.70	13.11	0.00	0.00	9.70	9.22	48.15	0.00	0.00	6.77	1.65
16-31 Jul	59	46	1.69	0.00	11.86	13.56	0.00	0.00	7.24	8.02	46.49	0.00	0.00	10.29	0.85
01-15 Aug	56	21	0.58	0.00	1.74	0.39	0.00	0.19	2.32	1.54	51.93	0.00	0.00	40.54	0.77
16-31 Aug	31	19	2.55	0.00	3.18	0.32	0.00	0.96	0.32	0.00	56.37	0.00	0.00	36.30	0.00
01-15 Sep	33	24	3.00	0.00	15.02	3.00	0.00	2.62	2.96	1.12	18.73	0.00	10.11	43.44	0.00
16-30 Sep	39	23	0.91	0.00	10.99	0.72	0.00	1.62	1.44	0.72	20.32	0.00	8.21	55.07	0.00
01-15 Oct	10	30	0.25	0.00	0.70	0.24	0.00	0.00	0.47	0.00	21.54	0.00	8.55	66.25	0.00
16-31 Oct	17	24	8.80	0.00	12.00	0.80	0.00	0.00	0.00	0.00	16.54	0.00	9.63	50.63	1.60
01-15 Nov	8	12	0.00	0.00	1.23	9.62	0.00	0.00	0.00	2.22	23.20	0.00	8.22	55.51	0.00
16-30 Nov	8	50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	5.00	14.67	0.00	7.16	73.17	0.00
01-15 Dec	0	0	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
15-31 Mar	0	0	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Table A.3c. Percent of total food weight contributed by different types of prey consumed by juvenile black bass (largemouth and smallmouth bass) in the Roanoke River of Smith Mountain Lake, 1995-96. Zooplankton - Cld (Cladoceran), Cop (Copepod); Aquatic Insects - Bae (Baetid mayfly nymphs), Chr (Chironomid midge larvae), Ans (Anisoptera - dragonfly naiads), Ger (Gerridae - water striders); Terrestrial Insects - For (Formicidae - ants), Col (Coleoptera - beetles); Fish - Cyp (Cyprinidae - shiners), Ale (alewife), Sun (sunfish), Dar (darters), UID (unidentified fish); Emp = empty.

	Stomachs		Zooplankton		Insects						Fish				
Sampling Period	N	Emp (%)	Cld	Cop	Bae	Chr	Ans	For	Ger	Col	Cyp	Ale	Sun	Dar	UID
16-31 Jul	110	45	9.28	0.00	1.43	7.86	0.00	0.00	0.71	0.00	47.86	0.00	0.00	32.34	0.52
01-15 Aug	80	30	2.62	0.00	1.31	0.00	0.00	0.00	0.66	1.31	32.86	0.00	11.15	50.09	0.00
16-31 Aug	65	46	0.22	0.00	2.19	1.32	0.66	0.00	1.10	0.00	21.71	0.00	22.37	50.43	0.00
01-15 Sep	42	40	0.28	0.00	1.96	0.00	1.96	0.00	1.40	0.00	22.35	0.00	31.28	40.77	0.00
16-30 Sep	27	52	0.00	0.00	8.98	1.17	1.56	7.81	0.39	0.00	20.42	0.00	18.39	41.28	0.00
01-15 Oct	10	70	3.14	0.00	2.79	0.00	0.00	0.00	0.00	0.00	5.23	0.00	16.72	71.26	0.86
16-31 Oct	7	71	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	7.26	0.00	47.04	44.70	0.00
01-15 Nov	4	50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	7.38	0.00	27.98	64.64	0.00
16-30 Nov	1	0	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	17.67	82.33	0.00
15-31 Mar	0	0	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
01-15 Apr	0	0	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Table A.3d. Percent of total food weight contributed by different types of prey consumed by juvenile black bass (largemouth and smallmouth bass) in the Blackwater River of Smith Mountain Lake, 1995-96. Zooplankton - Cld (Cladoceran), Cop (Copepod); Aquatic Insects - Bae (Baetid mayfly nymphs), Chr (Chironomid midge larvae), Ans (Anisoptera - dragonfly naiads), Ger (Gerridae - water striders); Terrestrial Insects - For (Formicidae - ants), Col (Coleoptera - beetles); Fish - Cyp (Cyprinidae - shiners), Ale (alewife), Sun (sunfish), Dar (darters), UID (unidentified fish); Emp = empty.

	Stomachs		Zooplankton		Insects						Fish				
Sampling Period	N	Emp (%)	Cld	Cop	Bae	Chr	Ans	For	Ger	Col	Cyp	Ale	Sun	Dar	UID
16-31 Jul	63	30	4.40	17.59	2.64	1.17	0.00	2.93	0.00	3.81	27.56	0.00	0.00	37.36	2.54
01-15 Aug	51	27	0.71	0.00	8.90	0.23	0.46	1.14	0.68	0.23	27.85	6.85	0.00	52.95	0.00
16-31 Aug	60	13	0.12	0.00	2.17	0.48	0.48	9.49	6.29	0.00	25.54	0.00	9.28	46.15	0.00
01-15 Sep	41	24	0.46	0.00	6.78	0.92	0.00	0.00	0.00	0.23	22.41	0.00	12.19	57.01	0.00
16-30 Sep	47	23	0.26	0.00	3.89	0.09	0.00	9.16	0.00	0.18	8.38	0.00	3.11	74.93	0.00
01-15 Oct	26	35	1.31	0.00	1.15	0.00	0.00	0.00	0.00	0.00	11.49	0.00	28.08	57.97	0.00
16-31 Oct	5	60	0.00	0.00	0.00	7.69	0.00	0.00	0.00	0.00	7.93	0.00	15.32	69.06	0.00
01-15 Nov	6	83	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	100	0.00
16-30 Nov	4	75	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	100	0.00
15-31 Mar	0	0	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
01-15 Apr	0	0	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Table A.4a. Percent of total food weight contributed by different types of prey consumed by juvenile black bass (largemouth and smallmouth bass) in the Roanoke River of Smith Mountain Lake, 1994-95. Zooplankton - Cld (Cladoceran), Cop (Copepod); Aquatic Insects - Bae (Baetid mayfly nymphs), Chr (Chironomid midge larvae), Ans (Anisoptera - dragonfly naiads), Ger (Gerridae - water striders); Terrestrial Insects - For (Formicidae - ants), Col (Coleoptera - beetles); Fish - Cyp (Cyprinidae - shiners), Ale (alewife), Sun (sunfish), Dar (darters), UID (unidentified fish); Emp = empty.

	Stomachs		Zooplankton		Insects						Fish				
Length (mm)	N	Emp (%)	Cld	Cop	Bae	Chr	Ans	For	Ger	Col	Cyp	Ale	Sun	Dar	UID
20	16	73	25.00	0.00	25.00	50.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
30	18	65	13.45	0.00	20.66	49.22	0.00	0.00	0.00	0.00	16.67	0.00	0.00	0.00	0.00
40	48	46	9.26	0.70	15.96	33.33	0.00	0.00	0.00	0.00	40.55	0.00	0.00	0.00	0.20
50	62	40	5.22	0.00	12.46	26.09	0.00	11.74	17.97	0.00	13.91	0.00	0.00	12.30	0.31
60	48	40	4.84	0.00	11.05	17.91	0.00	10.24	9.01	4.16	12.41	0.00	0.00	29.28	1.10
70	48	37	3.94	0.00	9.42	17.70	0.00	15.78	14.22	2.59	8.38	0.00	0.00	27.97	0.00
80	26	35	0.00	0.00	7.13	17.52	0.00	12.85	10.04	7.15	8.24	0.00	0.00	36.56	0.51
90	21	33	0.00	0.00	5.44	3.15	1.05	7.32	3.68	1.05	8.45	0.00	25.13	44.43	0.30
100	21	43	0.00	0.00	3.33	1.16	0.00	6.67	1.33	4.50	9.21	0.00	16.24	57.00	0.56
110	17	29	0.00	0.00	3.11	0.57	0.00	5.98	5.95	2.02	8.51	0.00	32.37	41.41	0.08
120	11	36	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	11.97	0.00	46.77	41.26	0.00
130	3	0	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	7.56	0.00	56.50	33.89	2.05
140	5	40	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	4.08	0.00	41.31	54.61	0.00
150	1	0	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	100	0.00	0.00
160	1	0	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	100	0.00

Table A.4b. Percent of total food weight contributed by different types of prey consumed by juvenile black bass (largemouth and smallmouth bass) in the Blackwater River of Smith Mountain Lake, 1994-95. Zooplankton - Cld (Cladoceran), Cop (Copepod); Aquatic Insects - Bae (Baetid mayfly nymphs), Chr (Chironomid midge larvae), Ans (Anisoptera - dragonfly naiads), Ger (Gerridae - water striders); Terrestrial Insects - For (Formicidae - ants), Col (Coleoptera - beetles); Fish - Cyp (Cyprinidae - shiners), Ale (alewife), Sun (sunfish), Dar (darters), UID (unidentified fish); Emp = empty.

	Stomachs		Zooplankton		Insects						Fish				
Length (mm)	N	Emp (%)	Cld	Cop	Bae	Chr	Ans	For	Ger	Col	Cyp	Ale	Sun	Dar	UID
20	12	55	16.67	0.00	33.33	50.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
30	45	57	12.22	0.00	21.11	27.78	0.00	0.00	5.56	0.00	33.12	0.00	0.00	0.00	0.21
40	51	50	13.89	2.78	19.44	22.22	0.00	0.00	2.78	0.00	38.24	0.00	0.00	0.00	0.65
50	48	34	13.16	2.74	19.82	22.41	0.00	2.26	4.01	2.41	31.77	0.00	0.00	0.00	1.42
60	46	24	12.02	3.42	22.43	21.67	1.47	4.15	5.45	4.11	25.20	0.00	0.00	0.00	0.08
70	45	24	5.12	1.22	14.54	18.73	0.00	4.50	3.73	3.78	13.08	0.00	0.00	35.30	0.00
80	33	12	2.83	0.94	8.75	0.47	0.00	2.83	1.25	2.26	21.42	0.00	6.04	52.50	0.71
90	31	26	1.20	0.48	6.42	0.35	0.00	1.29	0.22	1.00	18.44	0.00	6.04	63.00	1.56
100	15	27	0.00	0.00	4.79	0.56	0.00	0.56	1.21	1.54	0.00	0.00	7.54	83.80	0.00
110	12	33	0.00	0.00	1.84	1.69	0.00	1.00	0.87	1.16	0.00	0.00	6.48	86.24	0.72
120	6	50	0.00	0.00	0.00	0.00	0.00	0.25	0.75	2.32	0.00	0.00	3.31	90.53	2.84
130	3	33	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	15.34	84.16	0.50
140	2	0	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	30.89	69.11	0.00
150	2	0	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	36.14	62.58	1.28
160	4	25	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	35.13	64.87	0.00

Table A.4c. Percent of total food weight contributedby different types of prey consumed by juvenile black bass (largemouth and smallmouth bass) in the Roanoke River of Smith Mountain Lake, 1995-96. Zooplankton - Cld (Cladoceran), Cop (Copepod); Aquatic Insects - Bae (Baetid mayfly nymphs), Chr (Chironomid midge larvae), Ans (Anisoptera - dragonfly naiads), Ger (Gerridae - water striders); Terrestrial Insects - For (Formicidae - ants), Col (Coleoptera - beetles); Fish - Cyp (Cyprinidae - shiners), Ale (alewife), Sun (sunfish), Dar (darters), UID (unidentified fish); Emp = empty.

	Stomachs		Zooplankton		Insects						Fish				
Length (mm)	N	Emp (%)	Cld	Cop	Bae	Chr	Ans	For	Ger	Col	Cyp	Ale	Sun	Dar	UID
30	4	75	100	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
40	24	65	18.42	0.00	17.89	10.53	0.00	0.00	5.79	0.00	25.17	0.00	0.00	21.05	1.15
50	65	81	14.22	0.00	10.78	6.48	0.00	0.00	3.86	0.86	20.24	0.00	0.00	43.11	0.45
60	75	27	1.38	0.00	10.14	2.30	1.84	0.00	2.30	0.00	12.30	0.00	9.89	59.14	0.71
70	52	25	0.00	0.00	3.69	0.68	0.00	0.00	1.37	0.82	9.51	0.00	12.40	70.11	1.42
80	37	44	0.00	0.00	1.62	0.00	0.00	0.00	0.81	0.00	8.87	0.00	14.23	73.31	1.16
90	25	28	0.00	0.00	1.79	0.00	0.67	0.00	0.00	0.00	8.50	0.00	16.42	71.37	1.25
100	26	42	0.00	0.00	0.34	0.00	2.40	6.85	0.00	0.00	0.00	7.40	5.60	77.19	0.22
110	17	88	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	14.29	84.58	1.13
120	9	67	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	17.95	81.28	0.77
130	2	50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	100	0.00	0.00
140	2	0	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	100	0.00	0.00
150	7	86	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	100	0.00	0.00

Table A.4d. Percent of total food weight contributed by different types of prey consumed by juvenile black bass (largemouth and smallmouth bass) in the Blackwater River of Smith Mountain Lake, 1995-96. Zooplankton - Cld (Cladoceran), Cop (Copepod); Aquatic Insects - Bae (Baetid mayfly nymphs), Chr (Chironomid midge larvae), Ans (Anisoptera - dragonfly naiads), Ger (Gerridae - water striders); Terrestrial Insects - For (Formicidae - ants), Col (Coleoptera - beetles); Fish - Cyp (Cyprinidae - shiners), Ale (alewife), Sun (sunfish), Dar (darters), UID (unidentified fish); Emp = empty.

	Stomachs		Zooplankton		Insects						Fish				
Length (mm)	N	Emp (%)	Cld	Cop	Bae	Chr	Ans	For	Ger	Col	Cyp	Ale	Sun	Dar	UID
40	10	50	57.14	0.00	28.57	14.29	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
50	48	15	9.05	0.00	21.05	5.89	3.37	5.89	0.00	1.68	53.07	0.00	0.00	0.00	0.00
60	49	8	5.84	2.41	21.73	2.41	0.80	14.08	1.60	3.62	25.75	0.00	0.00	21.76	0.00
70	41	22	0.62	0.00	11.18	0.62	0.00	5.59	5.28	1.24	25.90	0.00	8.07	40.38	1.12
80	32	12	0.00	0.00	8.60	0.32	0.00	14.97	4.14	0.96	12.80	0.00	9.87	46.68	1.66
90	19	16	0.00	0.00	0.77	0.77	0.00	0.51	0.00	0.00	11.89	3.34	7.71	73.02	1.99
100	32	44	0.00	0.00	1.10	0.00	0.00	3.29	0.00	0.00	2.35	0.00	16.35	75.58	1.33
110	37	46	0.00	0.00	0.00	0.00	0.00	3.82	0.00	0.00	1.57	0.00	15.17	78.59	0.85
120	14	36	0.00	0.00	0.00	0.00	0.00	3.22	0.00	0.00	0.00	0.00	24.04	72.19	0.55
130	11	45	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	34.23	65.77	0.00
140	6	83	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	100	0.00	0.00
150	4	25	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	79.25	20.75	0.00

VITA

Trent Michael Sutton was born on May 20, 1969, in Kalamazoo, Michigan. He spent his formative years in the sticks of Coloma, Michigan, where he developed a fond interest for wild critters, in particular those wet and slimy. Following graduation from Coloma High School in 1987, he enrolled at Michigan State University, and graduated with honor in June 1991 with a Bachelor of Science degree in Fisheries and Wildlife. In August 1991, he began graduate research studies at Michigan Technological University, focusing on the feeding ecology of larval lampreys, and received a Master of Science degree in Aquatic Ecology in June 1993. After a brief one month hiatus from academia, he entered the doctoral program in the Department of Fisheries and Wildlife Sciences in August 1993 at Virginia Polytechnic Institute and State University, where his research focused on examining factors affecting recruitment of stocked fingerling striped bass in Smith Mountain Lake, Virginia. During his tenure at VPI&SU, he served as president of the Virginia Tech Chapter of the American Fisheries Society and received the Society's Skinner Memorial Award. Prior to completing his doctoral dissertation in December 1997, he accepted an offer to return to his home state as an assistant professor of fisheries biology and director of fisheries research and culture for the Aquatic Research Laboratory at Lake Superior State University in Sault Sainte Marie.

Trent Michael Sutton