

Trophic Resource Overlap between Age-0 Striped Bass and Largemouth Bass in Smith Mountain Lake, Virginia

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Abstract.—Small body size in fall and low winter survival of fingerling striped bass *Morone saxatilis* stocked into Smith Mountain Lake, Virginia, have been attributed to slow growth during summer months. Although small size at stocking appears to be the primary factor restricting fish prey consumption and rapid growth, trophic competition may also be a contributing factor. We examined the food habits of sympatric populations of age-0 striped bass and largemouth bass *Micropterus salmoides* over the 1994 and 1995 growing seasons to assess temporal and length-related patterns and similarities in trophic resource use. With increasing predator length, food habits for both species shifted from zooplankton to insect and then to fish as the principal prey items over both growing seasons. Except for fish smaller than 50 mm during June and July 1994, diet overlap was insufficient (Schoener's index value <0.60) to suggest trophic competition. Striped bass between 50 and 100 mm long primarily ate aquatic insects and cyprinids, whereas largemouth bass in the same length range ate aquatic and terrestrial insects. Cyprinids were the principal fish prey of striped bass less than 100 mm long, with age-0 alewives *Alosa pseudoharengus* becoming the predominant prey for larger individuals. Darters and age-0 sunfishes constituted the primary fish prey of largemouth bass regardless of body length. Although temporal and length-related segregation by food habitats may be sufficient to minimize trophic overlap, limitations in these resources may cause interspecific competition, especially for smaller individuals. We recommend releasing striped bass at a larger size (>50 mm) and earlier in the growing season to minimize the potential for trophic competition with age-0 largemouth bass immediately after stocking.

Since the early 1800s, the geographical distribution of many freshwater fishes has expanded outside their historical range through intentional and accidental species introductions (Mills et al. 1993; Li and Moyle 1999). Because prey and habitat preferences of introduced fishes may be similar to those of native species, the possibility for substantial overlap and competition for available resources is greater than for coevolved fish assemblages (Li and Moyle 1981). The potential for interspecific competition is particularly high in freshwater impoundments, where native riverine species often cannot successfully colonize pelagic habitats and nonnative fishes are introduced to fill a perceived vacant niche (Timmons et al. 1979; Rainwater and Houser 1982; Kohler et al. 1986). For some species, these interactions may be sufficiently intense to induce population-level responses. This is particularly true for early life stages of piscivores, where limited prey availability often plays a critical role in regulating foraging

success, growth, and consequently survival (Ney and Orth 1986). Therefore, a better understanding of niche relationships among ecologically similar sport fishes in freshwater lakes and reservoirs is important for determining appropriate stocking and management strategies.

Smith Mountain Lake, Virginia, typifies most lakes and reservoirs that support successful sport fisheries for both introduced striped bass *Morone saxatilis* and native largemouth bass *Micropterus salmoides*. The Virginia Department of Game and Inland Fisheries has stocked fingerling striped bass in Smith Mountain Lake annually since 1964, resulting in the development of a trophy fishery. However, survival of striped bass to age 1 has been highly variable (mean = 25%, range = 12–40%) at an average annual stocking density of 300,000 fingerlings (Moore et al. 1991; Sutton 1997). Limited first-year recruitment of striped bass in this system has been attributed to size-selective winter mortality, mediated by differential patterns of growth, prey fish availability, and lipid energy stores between small and large individuals of the same stocked cohort (Sutton and Ney 2001). In nearshore areas containing abundant age-0 largemouth bass, however, the extent to which trophic resource overlap may also limit growth, degree of

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piscivory, and fall body size of juvenile striped bass is unclear.

Although several studies have examined the food habits of age-0 striped bass or largemouth bass in allopatry (e.g., Applegate et al. 1967; Gomez 1970; Richardson 1982; Van Den Avyle et al. 1983; Phillips et al. 1995; Olson 1996), only a single study has compared trophic resource use between sympatric populations of juvenile life stages for these two species. In Lake Texoma, Oklahoma–Texas, Matthews et al. (1992) described and compared food and habitat resource use between age-0 striped bass and largemouth bass over a 6-year period. The authors concluded that the potential for competitive interactions between these species was minimal; however, variability in sampling sites and collection periods among years limits the applicability of their study to other freshwater systems. Because diets of age-0 piscivores are known to shift rapidly (Ney and Orth 1986), a definitive assessment of trophic interactions demands that dietary comparisons are based on sampling programs using standardized spatial and temporal scales.

The objectives of this study were to (1) document temporal and length-dependent patterns in food habits of striped bass and largemouth bass during their first year of life and (2) compare temporal and length-dependent patterns in food habits between juvenile striped bass and largemouth bass. To achieve these objectives, we described and compared the diets of sympatric populations of age-0 striped bass and largemouth bass in Smith Mountain Lake, Virginia, to assess patterns in trophic resource use and partitioning over the 1994 and 1995 growing seasons. With an understanding of the food habit requirements and trophic interactions between juveniles of these two species, we then made recommendations regarding the stocking of fingerling striped bass in Smith Mountain Lake and other waters in which largemouth bass are abundant.

Study Area

Smith Mountain Lake is an 8,343-ha impoundment of the Roanoke and Blackwater Rivers in south-central Virginia. This deep storage reservoir was impounded in 1963 and is operated 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 mean depth of 16.8 m, a maximum depth of 63.7 m, and an 805-km shore-

line that is highly dendritic (Simmons and Neff 1969).

The fish assemblage of Smith Mountain Lake comprises 45 native and introduced species. The piscine prey complex consists of cyprinids *Cyprinella* and *Notropis* spp., sunfishes *Lepomis* spp., darters *Etheostoma* spp., and threadfin shad *Dorosoma petenense*, but it is dominated by gizzard shad *D. cepedianum* and alewives *Alosa pseudoharengus*. Principal piscivores include striped bass and largemouth bass. Striped bass have been stocked annually during mid-June or early July on a put-grow-take basis as 35- to 50-mm-long fingerlings, whereas largemouth bass maintain reproducing populations. Other piscivores that contribute to the fishery include walleye *Stizostedion vitreum*, muskellunge *Esox masquinongy*, smallmouth bass *M. dolomieu*, channel catfish *Ictalurus punctatus*, and white and black crappie *Pomoxis annularis* and *P. nigromaculatus*, respectively.

Methods

Field collections.—Age-0 striped bass and largemouth bass were collected from two stocking cove locations in Smith Mountain Lake throughout the 1994 and 1995 growing seasons (see Michaelson et al. 2001 for a description of the stocking sites). Two nights each week from late June through August 1994 and from early July through August 1995, bag seines (10 m long \times 1 m deep, with a bar-mesh size of 3.2 mm) were used to collect fish in shallow, unvegetated areas within each stocking cove. The entire shoreline of both coves was also electrofished by boat, using pulsed direct current two nights each week during the first month after stocking and one night each week thereafter through December 1994 and November 1995. To collect larger age-0 striped bass and largemouth bass in deeper waters, we used experimental monofilament gill nets (50 m long \times 2 m deep, each net consisting of two 25-m panels with bar-mesh sizes of either 12.7 and 19.1 mm, 12.7 and 25.4 mm, or 19.1 and 25.4 mm, five nets of each mesh-size combination) at least one night each week from August through December 1994 and from August through November 1995. Once captured, fish were immediately killed with an overdose of tricaine methanesulfonate and preserved on wet ice. All fish were measured to the nearest 1 mm total length, weighed to the nearest 0.01 g, and frozen for subsequent analysis of their stomach contents.

Food habits.—In the laboratory, stomachs of age-0 striped bass and largemouth bass were re-

moved and fixed in formalin. Diet contents for each fish were examined under magnification with a stereomicroscope, identified to the lowest possible taxon, blotted dry, and weighed to the nearest 0.01 g. Temporal and length-dependent diet patterns for each predator species were examined separately by calculating percent contribution by weight of each diet category for each month of the 1994 and 1995 growing seasons (irrespective of fish length) and for each 10-mm length interval (irrespective of collection month), respectively (Hyslop 1980).

Diet overlap.—Diet overlap was calculated between age-0 striped bass and largemouth bass for each month of the 1994 and 1995 growing seasons and for each 10-mm length interval. To determine the minimum number of stomach samples containing food items necessary to accurately describe diet overlap, we plotted cumulative prey species curves for both species, following the approach described by Brodeur and Pearcy (1984) for each month of both growing seasons and for each length interval. Using Schoener's (1970) overlap index, we determined the potential for interspecific trophic competition as follows:

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

where C_{xy} was the overlap index value, p_{xi} was the proportion of prey type i consumed by species x , p_{yi} was the proportion of prey type i consumed by species y , and n was the total number of prey categories. The Schoener index ranges from 0.0 (no overlap) to 1.0 (complete overlap), with overlap values greater than 0.60 considered to be indicative of significant resource overlap (Zaret and Rand 1971). Wallace (1981) determined that this index, when used with weight percentages, was the most appropriate method for calculating diet overlap when accurate data on prey abundance were unavailable.

Results

A total of 3,300 age-0 striped bass and 1,998 age-0 largemouth bass were collected from Smith Mountain Lake for analysis of stomach contents over the 1994 and 1995 growing seasons. Of these fish, 881 (27%) striped bass and 741 (37%) largemouth bass had empty stomachs or contained prey items that could not be identified. Striped bass and largemouth bass ranged in total length from 24 to 266 mm and from 20 to 164 mm, respectively, in

1994 and from 31 to 261 mm and from 34 to 167 mm in total length, respectively, in 1995.

Temporal Food Habits

The temporal patterns in food habits exhibited by age-0 striped bass were similar over the 1994 and 1995 growing seasons (Figure 1). Except for June 1994, zooplankton (primarily cladocerans) and benthic aquatic insects (immature ephemeropterans and dipterans) never constituted more than 25% of the stomach contents by weight, the remainder of the dietary items consisting of fish prey. Over both growing seasons, the contribution of fish prey in diet contents increased progressively for juvenile striped bass (Figure 1). Cyprinids constituted a significant proportion of the diet by weight through August (44% to 86%) and were found consistently in the diet through the remainder of each year. However, age-0 alewives became the predominant prey item by September, and were virtually the sole prey item by November (70% to 94%). During both years, striped bass ate minimal amounts of other fishes such as darters and age-0 sunfish (<4% by weight; Figure 1).

Age-0 largemouth bass also demonstrated similar temporal trends in food habits during both growing seasons (Figure 2). Throughout the year, juvenile largemouth bass were largely piscivorous, with cyprinids and other fishes (darters and age-0 sunfish) accounting for at least two-thirds of the stomach contents by weight. The remainder of age-0 largemouth bass stomach contents consisted of zooplankton (cladocerans and copepods), benthic aquatic insects (immature ephemeropterans and dipterans), and surface insects (hemipterans, as well as terrestrial coleopterans and hymenopterans; Figure 2). Beginning in August 1994 and 1995, cyprinids were an increasingly smaller component of the diet (0% to 33% and 2% to 28% by weight in 1994 and 1995, respectively), while darters and sunfishes were becoming the predominant prey items (48% to 100% by weight). Age-0 alewives were always a negligible component of the diet for juvenile largemouth bass (Figure 2).

Length-Dependent Food Habits

Age-0 striped bass showed similar changes in food habits with body length over the 1994 and 1995 growing seasons (Figure 3). Except for fish 20 mm or smaller in 1994, juvenile striped bass were piscivorous at all lengths. Stomach contents of striped bass smaller than 120 mm were largely zooplankton (primarily cladocerans), benthic aquatic insects (immature ephemeropterans and

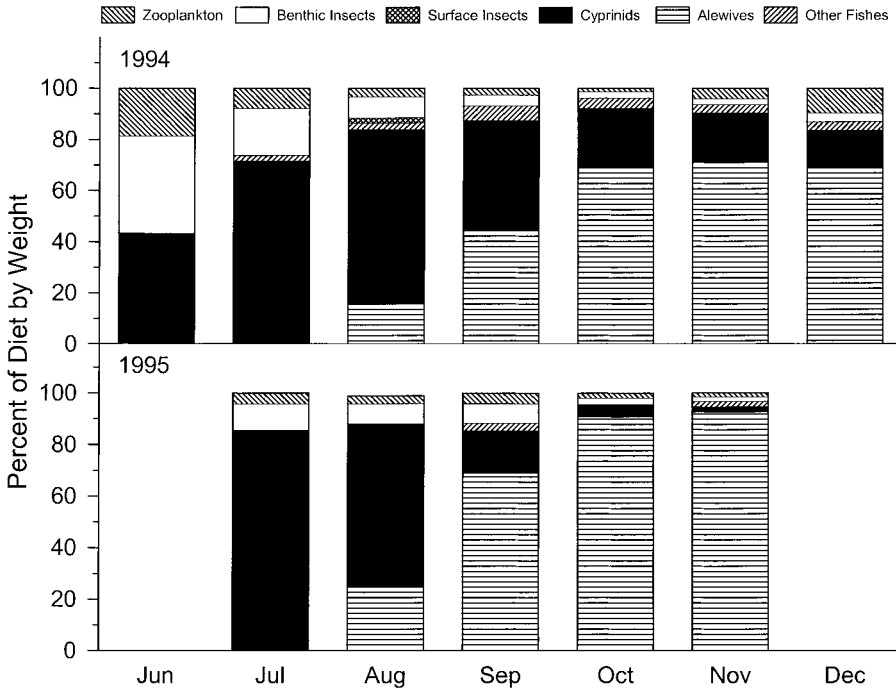


FIGURE 1.—Monthly patterns in age-0 striped bass food habits during the 1994 (top panel) and 1995 (bottom panel) growing seasons in Smith Mountain Lake, Virginia.

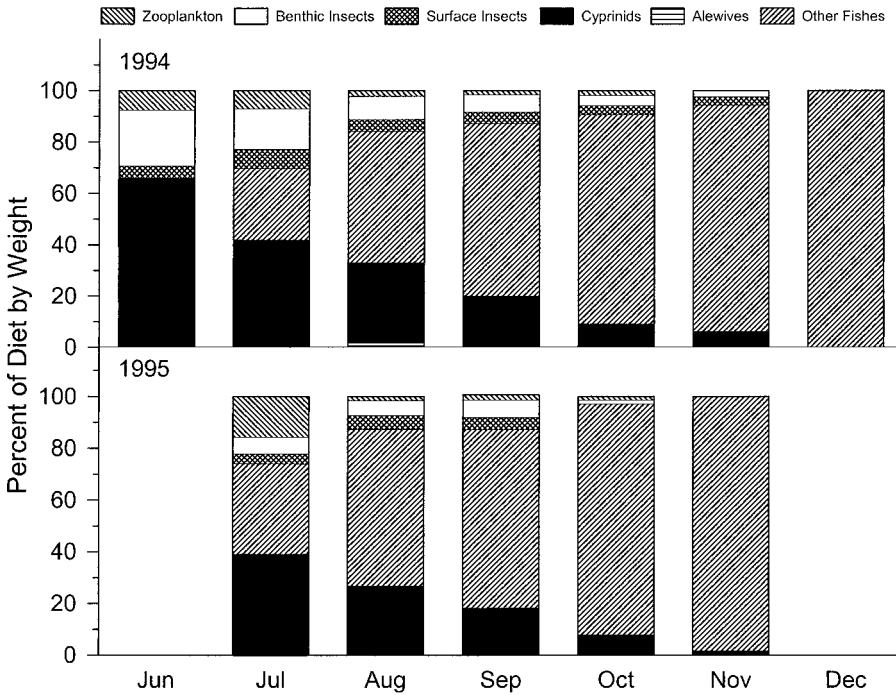


FIGURE 2.—Monthly patterns in age-0 largemouth bass food habits during the 1994 (top panel) and 1995 (bottom panel) growing seasons in Smith Mountain Lake, Virginia.

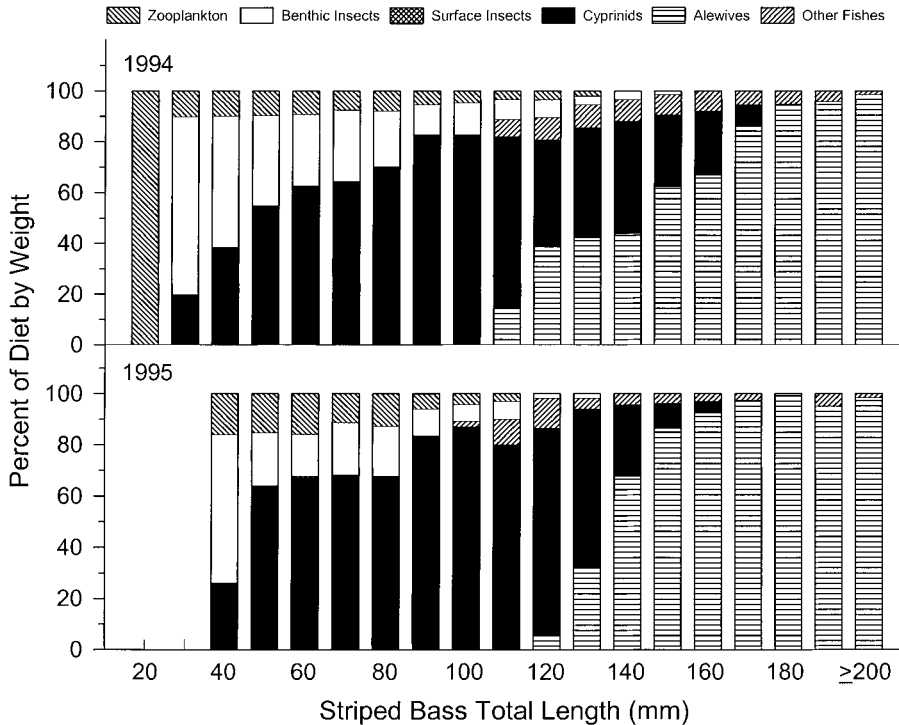


FIGURE 3.—Length-dependent patterns in age-0 striped bass food habits during the 1994 (top panel) and 1995 (bottom panel) growing seasons in Smith Mountain Lake, Virginia. Each bar is represented on the x-axis by the minimum value of its 10-mm length interval (e.g., the 20-mm interval represents fish ranging from 20 to 29 mm in total length).

dipterans), and age-0 cyprinids (Figure 3). The contribution of age-0 cyprinids to the diet increased progressively with length until striped bass exceeded 100 mm. For striped bass from 100 to 150 mm long, fish prey made up more than 90% of the stomach contents. At lengths of 150 mm or greater, striped bass became completely piscivorous; age-0 alewives were the dominant dietary component for these individuals, accounting for at least 84% by weight of all consumed prey items (Figure 3).

Age-0 largemouth bass also exhibited similar changes in food habits with body length over both growing seasons (Figure 4). Except for fish 20 mm or shorter in 1994, largemouth bass were piscivorous at all length intervals. Until largemouth bass were larger than 70 mm, zooplankton (cladocerans and copepods), benthic aquatic insects (immature ephemeropterans and dipterans), and surface insects (hemipterans; terrestrial coleopterans and hymenopterans) made up between 27% and 74% of the stomach contents by weight (Figure 4). However, the contribution of invertebrate prey to the diet decreased with increasing predator length.

Largemouth bass 60 mm and larger ate primarily cyprinids and other fishes (darters and age-0 sunfishes). When larger than 120 mm, largemouth bass were strictly piscivorous; darters and age-0 sunfish were the predominant prey items for these individuals (81% to 100% by weight). Age-0 alewives were always a negligible component of the diet for juvenile largemouth bass (Figure 4).

Diet Overlap

During months in which the minimum number of stomachs required to characterize age-0 striped bass and black bass diets were collected (June through November 1994; July through October 1995), diet overlap values greater than 0.60 were observed only during June and July 1994 (Table 1). Diet overlap values declined progressively over the summer and through the fall months during both 1994 and 1995 as striped bass switched from cyprinid to alewife prey. By October of both years, diet overlap between juvenile striped bass and largemouth bass was negligible (Table 1).

At 10-mm length intervals in which the minimum number of striped bass and largemouth bass

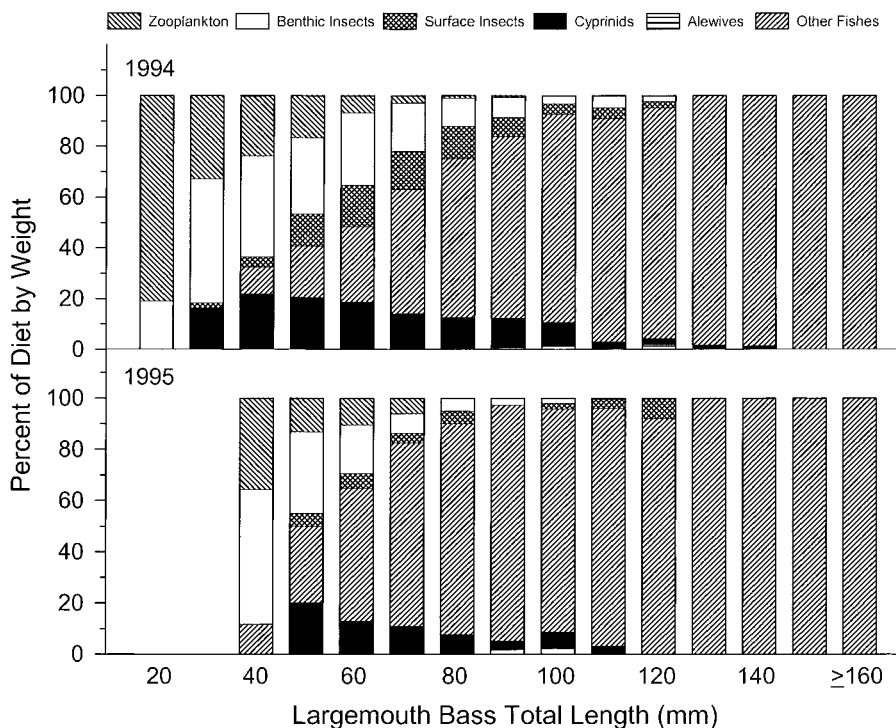


FIGURE 4.—Length-dependent patterns in age-0 largemouth bass food habits during the 1994 (top panel) and 1995 (bottom panel) growing seasons in Smith Mountain Lake, Virginia. As in Figure 3, each bar is represented on the *x*-axis by the minimum value of its 10-mm length interval.

stomachs necessary to describe food habits were collected (1994: 30–140 mm in total length; 1995: 30–130 mm in total length), diet overlap values greater than 0.60 were observed only for fish smaller than 50 mm and 40 mm in 1994 and 1995, respectively (Table 2). Diet overlap values declined progressively with predator length thereafter, as striped bass and largemouth bass switched

to different invertebrate and fish prey types. For juvenile striped bass and largemouth bass larger than 100 mm, diet overlap values were negligible (Table 2).

Discussion

Age-0 striped bass and largemouth bass in Smith Mountain Lake shifted from an invertebrate to a fish diet as they grew throughout the summer, but differences in the specific types of prey consumed by predators larger than 50 mm long minimized trophic overlap. Individuals of both species consumed variable amounts of invertebrate prey in June and July; striped bass ate benthic aquatic insects, whereas largemouth bass maintained a more mixed diet, feeding also on terrestrial and aquatic surface insects. As both species became piscivorous, they targeted different prey fishes: darters and sunfish by largemouth bass, and cyprinids, then alewives, by striped bass. Because length-dependent changes in prey consumption, particularly for fish prey, provide an opportunity for resource partitioning, age-0 striped bass and largemouth bass of piscivorous sizes appear to be trophically compatible in this system.

TABLE 1.—Diet overlap for age-0 striped bass and largemouth bass during each month of the 1994 and 1995 growing seasons in Smith Mountain Lake, Virginia, estimated by means of Schoener's (1970) overlap index.

Month of year	Diet overlap	
	1994	1995
Jun	0.73	1
Jul	0.64	0.50
Aug	0.44	0.34
Sep	0.33	0.25
Oct	0.14	0.06
Nov	0.08	2
Dec	2	1

¹ Fish of at least one of the two species were not collected during this month.

² Too few stomachs were collected to accurately characterize predator diets.

TABLE 2.—Diet overlap for age-0 striped bass and largemouth bass in each 10-mm length interval over the 1994 and 1995 growing seasons in Smith Mountain Lake, Virginia, estimated by means of Schoener's (1970) overlap index.

Length interval (mm)	Diet overlap	
	1994	1995
<30	1	2
30–39	0.80	0.70
40–49	0.67	0.59
50–59	0.52	0.51
60–69	0.46	0.43
70–79	0.33	0.36
80–89	0.26	0.26
90–99	0.23	0.18
100–109	0.12	0.14
110–119	0.06	0.10
120–129	0.06	0.09
130–139	0.05	0.05
140–149	0.03	1
≥150	1	1

¹ Too few stomachs were collected to accurately characterize predator diets.

² Fish of at least one of the two species were not collected in this 10-mm length interval.

For striped bass and largemouth bass smaller than 50 mm, diet overlap values were sufficiently high to indicate the potential for trophic competition. Food habits were similar for predators at these lengths in part because of restrictions associated with feeding on small prey items. Small striped bass and largemouth bass also overlapped in spatial distribution; both species were numerically abundant in nearshore areas early in the growing season (Sutton 1997). Because having available fish prey is a critical requirement for rapid growth of age-0 piscivores during the first year of life (Shelton et al. 1979; Timmons et al. 1980; Keast and Eadie 1985), interspecific competition for invertebrate prey immediately after stocking could impede the transition to piscivory by striped bass, thereby limiting first-year growth, fall body size, and winter survival for some of the age-0 cohort (Gutreuter and Anderson 1985; Ludsins and DeVries 1997; Hurst and Conover 1998; Sutton and Ney 2001).

After juvenile striped bass and largemouth bass reached piscivorous sizes, they exhibited little trophic overlap; divergence in habitat use with increasing body length most likely facilitated these differences in diet utilization. Largemouth bass, irrespective of length, were always collected in nearshore areas with submerged timber or aquatic macrophytes. In contrast, striped bass became increasingly pelagic when longer than 75 mm (Sut-

ton 1997). Our results are corroborated by other studies that have documented low habitat overlap between larger individuals of these species (Gilliland and Clady 1984; Matthews et al. 1992). Interspecific habitat segregation precludes interference competition and will minimize exploitative competition to the extent that potential food resources are habitat-specific (Werner and Hall 1977; Scott and Angermeier 1998), which is the case for age-0 striped bass and largemouth bass in Smith Mountain Lake. Offshore movement of striped bass coincided with their dietary switch to pelagic alewives, whereas piscivorous largemouth bass fed almost exclusively on littoral fishes.

Differences in foraging behavior by striped bass and largemouth bass larger than 50 mm may also have played a role in minimizing trophic resource overlap. Striped bass exhibit an active search-and-pursuit schooling behavior that is adapted for locating patchily distributed, schooling prey such as clupeids (Mensing 1971; Matthews et al. 1988). In contrast, largemouth bass are solitary and are more likely to use a sit-and-wait strategy, especially when they are associated with submerged structure (Winter 1977; Ward and Neumann 1998). This foraging mode is effective for capturing structure-seeking species, such as sunfish, or for fishes that lack rapid acceleration rates, such as darters (Hobson 1979).

The trophic resource use and patterns observed for age-0 striped bass and largemouth bass in Smith Mountain Lake are similar to the results of dietary studies reported for these species in other lentic systems. Richardson (1982) reported that striped bass in Norris Reservoir, Tennessee, ate zooplankton and aquatic insects until they reached 125 mm. Fish prey (*Dorosoma* spp.) were not eaten until juveniles exceeded 120 mm, but became increasingly more important in the diet as striped bass grew longer. Olson (1996) reported that largemouth bass shorter than 100 mm fed primarily on aquatic insects, but the contribution of insects to their diet declined with increasing fish length. At larger sizes, largemouth bass were completely piscivorous and fed on age-0 bluegill *Lepomis macrochirus*. Other studies have also reported that the contribution of invertebrates to the diet of juvenile striped bass and largemouth bass declined, whereas the importance of fish prey (typically age-0 clupeids and centrarchids for striped bass and largemouth bass, respectively) increased progressively over the growing season (Applegate et al. 1967; Gomez 1970; Van Den Avyle et al. 1983; Mat-

thews et al. 1992; Ward and Neumann 1998; Long and Fisher 2000).

Given the results of this study, we recommend stocking striped bass fingerlings at a larger size and earlier in the growing season in systems that support native, age-0 largemouth bass. Using an individual-based model, Sutton et al. (2000) determined that stocking striped bass in Smith Mountain Lake in early June at a median length of 52 mm (rather than in mid-June at a median length of 42 mm) resulted in the largest percentage increases in first-year growth and recruitment. These increases were largely attributed to greater feeding opportunities for striped bass on fish prey, particularly alewives, throughout the entire first growing season. In addition, this stocking strategy should minimize the potential for interspecific trophic competition because food habits and habitat use of striped bass and largemouth bass diverge considerably after they reach lengths of 50 mm. Support for this recommendation is derived from field and modeling evaluations showing that stocking larger fingerling piscivores often translates to greater first-year growth and survival (Madenjian et al. 1991; Stahl et al. 1996; Donovan et al. 1997). However, we suggest applying this stocking strategy cautiously to other lakes and reservoirs, considering the inherent intersystem differences in reproductive periodicity, food-web structure, hydrological regime, or the physicochemical environment. Regardless of the extent of these differences, gaining a better understanding of the ecological relationships among and within populations of age-0 piscivores will allow implementation of appropriate stocking and management strategies that will enhance reservoir sport fisheries.

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