

**TROPHIC INTERACTIONS BETWEEN LARVAL GIZZARD  
SHAD AND RESIDENT ZOOPLANKTIVORES  
IN CLAYTOR LAKE, VIRGINIA**

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# TROPHIC INTERACTIONS BETWEEN LARVAL GIZZARD SHAD AND RESIDENT ZOOPLANKTIVORES IN CLAYTOR LAKE, VIRGINIA

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(ABSTRACT)

Anglers unlawfully introduced gizzard shad *Dorosoma cepedianum* into Claytor Lake, Virginia in the late 1980s, apparently with the intention of improving the sportfishery by adding an additional clupeid prey resource. This study examined the trophic interactions between larval shad and resident zooplanktivorous fishes, in an attempt to discover the potential for trophic competition and negative impacts to these fish species. Ichthyoplankton sampling in 1997 and 1998 showed that peak abundances of larval shad overlapped temporally and spatially with both larval *Lepomis* spp. and larval alewife *Alosa pseudoharengus*. Peak larval shad density (0.04-0.06 fish/m<sup>3</sup>) was two to three orders of magnitude less than that reported from other reservoir systems, slightly less than that of larval alewife in Claytor Lake (0.05-0.07 fish/m<sup>3</sup>), and significantly less than that of larval *Lepomis* spp. in Claytor Lake (0.28-0.51 fish/m<sup>3</sup>). Diet overlap values indicated potential resource overlap among all three larval taxa. Diet of larval shad did not overlap with that of either age-0 *Micropterus* spp. or adult alewife. All species of limnetic larvae examined showed feeding preferences for *Diaphanosoma* and copepod nauplii. Crustacean zooplankton densities did not respond negatively to peak larval fish abundances, and never dropped below 250-400 organisms/L. In Claytor Lake, the impact of trophic competition with larval gizzard shad on other zooplanktivores currently appears to be minimized by low densities of larval shad and abundant crustacean zooplankton.

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## INTRODUCTION

The availability of an adequate prey base is often the principal factor limiting predator production in many U.S. reservoirs (Jenkins 1979; Noble 1981). Fisheries managers may therefore manipulate forage-fish populations in an attempt to enhance the growth, survival, and abundance of piscivorous sportfishes (Ney 1981; Noble 1981; DeVries and Stein 1990). Species introductions have been used extensively by managers to modify the forage base in reservoirs on the assumption that a new prey population will benefit the sportfishery (see DeVries and Stein 1990). Unfortunately, many well-intended species introductions have been “games of chance” resulting in unexpected negative consequences (Magnuson 1976); this phenomenon was termed the “Frankenstein effect” by Moyle et al. (1986). Non-native forage fishes are often introduced to expand the existing forage base without full consideration of ecological implications (Kohler et al. 1986). Forage-fish introductions may create an additional prey species population, yet the unexpected trophic disturbance caused by that introduction may outweigh any positive effects related to the increase in prey availability to sportfishes. The expected benefits of an expanded forage base may be short-lived or never realized, due to interactions at various life stages between the introduced forage fish and resident fish species. In lacustrine systems, these interactions are usually trophic in nature, involving predation or competition for a limited food supply at a critical life stage (Ploskey and Jenkins 1982).

A diverse and abundant forage base is necessary to support the variety of sportfish species established in many southeastern reservoirs. The creation of pelagic fisheries in these large, deep reservoirs often results in sportfish populations dependent on clupeid forage fishes because indigenous riverine forage species are unable to expand into new lentic habitats (Kimsey 1957; Shields 1957; Fitz 1968). Therefore, clupeid prey species such as gizzard shad *Dorosoma*

*cepedianum* and alewife *Alosa pseudoharengus* have been widely introduced into reservoirs by fisheries managers. Alternatively, anglers may introduce prey species into reservoirs in an attempt to increase or create a polyspecific forage base. In the late 1980s, one or more anglers illegally introduced gizzard shad into Claytor Lake, Virginia, apparently with the intention of improving the sportfishery by adding an additional prey resource. Prior to this introduction, alewife was the primary pelagic prey species while *Lepomis* spp. were the primary littoral forage (Kohler 1980; Nigro 1980; Kelso 1983; Kohler et al. 1986). Although gizzard shad are the most common and abundant forage fish in many central and southeastern U.S. lakes and reservoirs (Noble 1981), the successful establishment of a prolific gizzard shad population in Claytor Lake may come with some consequence to the existing fishery. Gizzard shad typically account for a high percentage of the total biomass in many southeastern reservoirs (Noble 1981). Jenkins (1970) found that adult gizzard shad might comprise 50-80% of the standing crop in shallow, fertile reservoirs with long growing seasons. Although habitat characteristics of Claytor Lake may differ from those reservoirs studied by Jenkins (1970), several investigators (Jenkins 1957; Kirk and Davies 1985; Guest et al. 1990) have suggested that high populations of gizzard shad may have negative effects on other fish species.

Gizzard shad have long been regarded as “the most efficient biologically of all the forage fishes” (Hubbs 1934), yet an ideal forage species should be not only trophically efficient and prolific, but also should be harmless to other fish species and vulnerable to predation throughout its entire life cycle (Ney 1981). Gizzard shad populations, however, often do not meet these criteria. The availability of gizzard shad as a forage fish often is limited due to the rapid growth of young gizzard shad during their first year. Young gizzard shad frequently grow too fast and too large to be vulnerable as prey for age-0 sportfish (Berry 1957; Noble 1981; Ney and Orth

1986), and adults also may grow too large to be utilized by most adult piscivores (Adams and DeAngelis 1987; Johnson et al. 1988; Hambright et al. 1991). Also, young gizzard shad may directly compete with young-of-year sportfish and other forage fish for zooplankton (Jenkins 1957; Davies et al. 1982; Neuswanger 1983; Kirk and Davies 1985; Guest et al. 1990; DeVries and Stein 1992). In fact, researchers have long suggested that gizzard shad can adversely affect sportfish growth and recruitment through competitive feeding interactions (Jenkins 1957; Smith 1959; Miller 1960; Bodola 1966). The introduction of gizzard shad into Claytor Lake may have resulted in a less than ideal prey population due not only to their limited availability to predators, but also due to their potentially harmful effects on resident fish species through competitive interactions.

## **Competitive Interactions between Gizzard Shad and Resident Fishes**

### **Zooplanktivory**

Trophic competition between gizzard shad and other fish species could negate any positive effects related to the increase in prey availability to piscivorous fishes. The potential for resource competition between gizzard shad and resident sportfish and other forage fish is most likely to occur during the larval stages of shad development. While the diets of omnivorous juvenile and adult gizzard shad include detritus, periphyton, phytoplankton, zooplankton, and insects (Kutkuhn 1957; Miller 1960; Bodola 1966; Pierce et al. 1981), the diets of larval gizzard shad (< 30 mm total length, TL) consist primarily of zooplankton (Kutkuhn 1957; Miller 1960; Bodola 1966; Cramer and Marzolf 1970; Barger and Kilambi 1980; Mallin et al. 1985; DeVries et al. 1991). Trophic overlap could result in feeding competition between larval fishes if food resources are limiting. Many investigators have reported that various zooplankters form the primary food of larval bluegill *Lepomis macrochirus* and other *Lepomis* spp. (Kutkuhn 1957; Werner 1969; Siefert 1972; Taylor 1977; Lemly and Dimmick 1982; Mallin et al. 1985). Larval *Micropterus* spp. also feed primarily on zooplankton before switching to a diet of insects (Lemly and Dimmick 1982), and Hirst and DeVries (1994) found larval *Micropterus* spp. to be strictly zooplanktivorous up to 10-15 mm TL. The alewife is also primarily a zooplanktivore throughout its entire life span (Kohler and Ney 1980), indicating the potential for trophic competition between larval gizzard shad and all life stages of alewife.

### **Competition between Gizzard Shad and Sportfish**

Because larval gizzard shad have been shown to sometimes depress zooplankton populations by altering the abundance, species composition, and size structure of zooplankton

assemblages (DeVries et al. 1991; DeVries and Stein 1992), they may affect the availability of food resources to larval sportfish during this critical period of development. Although variable in both timing and intensity, larval gizzard shad may appear weeks before the larvae of most sportfishes (Storck et al. 1978; Beard 1982; Adams and DeAngelis 1987; Miranda and Muncy 1988; DeVries and Stein 1992), and gizzard shad spawning activity may extend for a period of over two months (Tisa and Ney 1991). If larval gizzard shad are able to depress zooplankton populations over an extended period of time, they may affect the feeding, growth, survival, and subsequent recruitment of age-0 sportfish through exploitative competition. Researchers have reported on the detrimental impact of gizzard shad on bluegill populations (Davies et al. 1982; Hill 1983; Mosher 1983; Neuswanger 1983); Jenkins (1957) reported that high densities of gizzard shad (560 kg/ha) reduced the standing crop and condition of sportfish, especially centrarchids, in a small Oklahoma lake. Guest et al. (1990) found that gizzard shad negatively affected white crappie *Pomoxis annularis* by reducing both total number and biomass of age-0 fish in experimental ponds. Studies concerning feeding interactions between larval gizzard shad and *Micropterus* spp. have had somewhat mixed results. Hirst and DeVries (1994) concluded that there was little potential for direct competition between age-0 shad *Dorosoma* spp. and *Micropterus* spp. in large, shallow, eutrophic, Alabama reservoirs due to low diet overlap. Jackson et al. (1990) studied zooplanktivory by young-of-year gizzard shad, threadfin shad *Dorosoma petenense*, and largemouth bass *Micropterus salmoides* in Jordan Lake, North Carolina and determined that low similarity in diets combined with spatial segregation minimized the potential for feeding competition between shad and largemouth bass. Unfortunately, in that study small (< 20 mm TL) gizzard shad and threadfin shad were not separated by species for analysis purposes. Larval gizzard shad may indirectly affect

*Micropterus* spp. by directly competing with and depressing the survival of young-of-year bluegill and other forage fish, altering their availability as prey for piscivorous young-of-year *Micropterus* spp. For example, Kirk and Davies (1985) found that gizzard shad in Alabama ponds, even at low population levels, filtered out enough food items to reduce the survival of small bluegill, eventually leading to recruitment failure of largemouth bass. This interaction between zooplanktivory by larval gizzard shad and eventual recruitment failure of largemouth bass was also cited by DeVries and Stein (1992). The suppression of young-of-year *Lepomis* spp. growth and subsequent survival may have a greater impact on *Micropterus* spp. than any advantage gained from the additional prey source in the form of young-of-year gizzard shad (Storck 1986; Allen et al. 1999).

### **Competition between Gizzard Shad and Alewife**

Prior to gizzard shad introduction into Claytor Lake, the alewife was the primary pelagic forage-fish species in this reservoir. The interactions between alewife and gizzard shad in this system are unknown, but there is potential for direct competition between these two forage species. Negative interactions between alewife and gizzard shad are most likely to occur between larval gizzard shad and all life stages of alewife. Both species exhibit zooplanktivorous feeding habits as larvae, and alewife continue to feed on zooplankton throughout their life. By directly competing with alewife for food resources, gizzard shad may negatively impact the growth and survival of alewife larvae while also reducing food availability to adult alewife. Tisa and Ney (1991) examined the compatibility of alewife and gizzard shad as forage fish in Smith Mountain Lake, Virginia, and concluded that spatial and temporal segregation limited the potential for negative interactions. However, in Smith Mountain Lake these clupeids have



coexisted for over 30 years, and differences in morphometry and water quality between Claytor Lake and Smith Mountain Lake may influence distributional patterns of these fishes. Similar distributional patterns may increase the opportunity for negative interactions between alewife and gizzard shad. Alewives in Claytor Lake were found to be highly size-selective planktivores (Kohler and Ney 1981), and may alter the zooplankton species composition toward smaller forms. The combined effects of zooplanktivory by alewife and larval gizzard shad may also cause adverse impacts upon young-of-year sportfish.

## Goals and Objectives

This study was undertaken to address the potential negative impact of larval gizzard shad on the abundance and diets of resident zooplanktivorous fishes in Claytor Lake. Results are intended to provide fisheries managers with an important assessment of the impact that gizzard shad have had on the Claytor Lake fishery. In addition, without feedback to anglers concerning the possible negative implications of this and other unauthorized “bait-bucket” stockings, it should be expected that they will only continue to occur. Specifically, this study was designed to evaluate the impacts of zooplanktivory by larval gizzard shad on larval *Lepomis* spp. and young-of-year *Micropterus* spp., the principal sportfish species, and on alewife, the primary pelagic forage fish. Specific objectives were to:

1. Assess the degree of spatial and temporal overlap of gizzard shad and other larval fishes;
2. Describe and compare the diets of larval gizzard shad with those of resident zooplanktivores;
3. Describe the abundance, composition, and distribution of zooplankton relative to the abundance of larval gizzard shad and total ichthyoplankton;
4. Evaluate trophic interactions of larval gizzard shad and age-0 *Micropterus* spp.; and
5. Evaluate trends in biomass and growth of resident *Micropterus* spp. and *Lepomis* spp. populations before and after gizzard shad establishment.

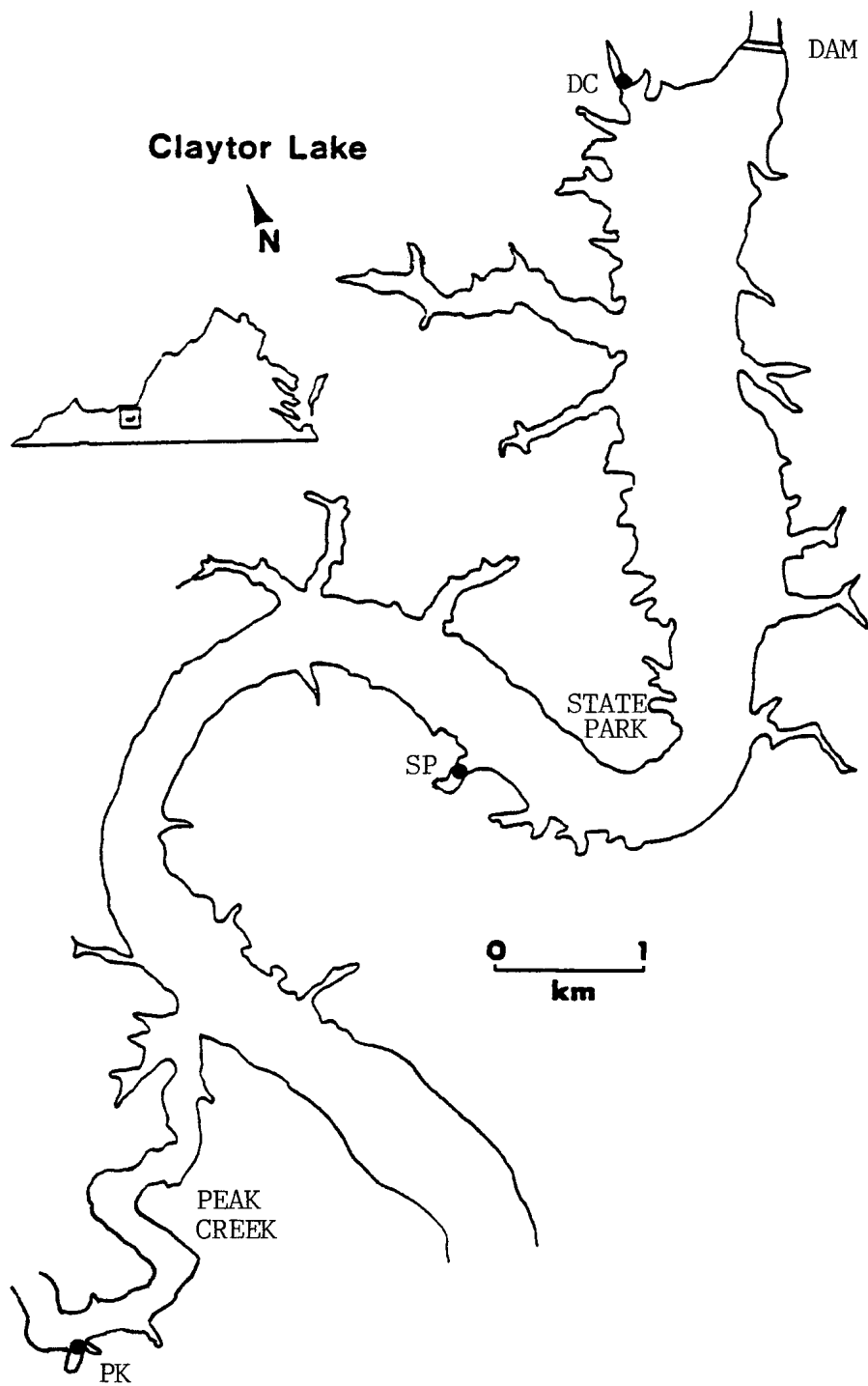
# MATERIALS AND METHODS

## Study Area

Claytor Lake is a mainstream hydroelectric impoundment of the New River in Pulaski County, Virginia (Figure 1). Created by the Appalachian Power Company in 1939, Claytor Lake drains a 3862-km<sup>2</sup> watershed, is 21.7 km long, and has a surface area of 1820 ha at a standard pool elevation of 663 m above mean sea level (Roseberry 1950). Maximum depth is 37.5 m, with a mean depth of 15 m (Kohler et al. 1986). Claytor Lake is distinctly riverine in morphometry, with a mean width of only 451 m and a retention time of approximately 33-63 days (Nigro 1980; DiCenzo 1996). The littoral habitat (< 5 m depth) along approximately 163 km of shoreline in Claytor Lake can be characterized as extremely narrow, rocky, and subject to continual wave action (Kelso 1983). Most littoral habitat suitable for shore-oriented species is found only in shallow coves and along the shoreline extending approximately 12 km upstream from the dam as well as in Peak Creek, Claytor Lake's main tributary (Kelso 1983). An annual water level fluctuation of 1.6 m limits the establishment of rooted aquatic vegetation. Claytor Lake is dimictic (Nigro 1980), and the hypolimnion (> 5 m depth) frequently becomes anoxic during the summer (Boaze 1972). Claytor Lake averaged a total phosphorus concentration of 29.8 ppb, chlorophyll A concentration of 5.4 ppb, and secchi depth of 1.5 m from 1996 to 1998 (Thomas and Johnson 1998). Based on these values, the lake can be characterized as mesotrophic to moderately eutrophic (Carlson 1977; Hart 1981; Reckhow and Chapra 1983).

At least 14 fish species and two interspecific hybrids have been intentionally stocked in Claytor Lake since its formation in 1939, representing one of the primary management activities in this lake (Kohler et al. 1986). Certain species, such as threadfin shad, rainbow trout *Oncorhynchus mykiss*, and brown trout *Salmo trutta*, have failed to become established due to

habitat limitations. Others, such as muskellunge *Esox masquinongy*, northern pike *E. lucius*, and tiger musky *E. lucius* X *E. masquinongy*, have failed due to minimal recruitment to the fishery. However, Claytor Lake now supports a diverse fishery of both native and introduced species. Popular sportfish species include largemouth bass, smallmouth bass *Micropterus dolomieu*, spotted bass *M. punctulatus*, white bass *Morone chrysops*, *Lepomis* spp., black and white crappie *Pomoxis* spp., channel catfish *Ictalurus punctatus*, flathead catfish *Pylodictis olivaris*, and walleye *Stizostedion vitreum*, which all reproduce naturally in the lake. Alewife and the recently introduced gizzard shad provide the major forage-fish base. In addition, annual stockings of fingerling striped bass *Morone saxatilis* and hybrid striped bass *M. chrysops* X *M. saxatilis* support a pelagic fishery in Claytor Lake.



**Figure 1.** Map of Claytor Lake, Virginia. Sampling sites for larval fish and zooplankton are indicated (DC = Dam Cove; SP = State Park; PK = Peak Creek).

## Field Collections

Limnetic larval (< 30-mm TL) gizzard shad, alewife, and *Lepomis* spp. were collected throughout the late spring and summer of 1997 and 1998 to determine the temporal distribution, growth, abundance, and diet of these fish species. The timing and intensity of peak larval abundances were specifically identified to assess the potential for interspecific competition based upon the extent of both temporal and spatial overlap among species. Cove (nearshore) and adjacent main channel (offshore) locations at three sites on the lake (Figure 1) were sampled at night on a weekly basis from mid-May to early/mid-August in each year. Cove and main channel locations at each site were sampled separately to evaluate differences in larval abundance in these distinctly different habitats. Sites were chosen to represent the upper lake and main tributary (Peak Creek – PK), middle lake (State Park – SP), and lower lake (Dam – DC). Sampling sites were selected to be representative of cove and main channel habitats in Claytor Lake. Cove habitat is somewhat limited in the lake, and those sites selected were chosen due to their lack of boat docks and other obstacles that would not have allowed enough area required for ichthyoplankton sampling. Additionally, I did not extend my efforts to the extreme uplake regions of the reservoir (uplake of the confluence of Peak Creek). Although evident on Smith Mountain Lake (Tisa 1988), research on large Missouri reservoirs found no consistent density gradients of larval shad based upon spatial location (Michaletz and Gale 1998). In Smith Mountain Lake, larval gizzard shad were almost exclusively limited to fertile, dendritic, uplake regions, while larval alewives were found in more oligotrophic, downlake locations near the dam (Tisa 1988). The high densities of larval gizzard shad found in uplake regions of Smith Mountain Lake were located in a region of the reservoir characterized by extensive coves and

shallow flats favored by spawning gizzard shad. This type of habitat is extremely limited in Claytor Lake, especially in the uplake, riverine sections of the reservoir.

I also collected age-0 *Micropterus* spp. in 1998 from the littoral zone at each of the three sampling sites. Although young *Micropterus* spp. may be spatially segregated from larval clupeids in some reservoir systems (Jackson et al. 1990), Allen and DeVries (1993) found larval gizzard shad inshore and evenly distributed within 50 m of shore in West Point Reservoir, Alabama-Georgia, increasing the potential for interactions with littoral species. I therefore examined the diets of age-0 *Micropterus* spp. to quantify trophic overlap and utilization of larval gizzard shad as food by age-0 *Micropterus* spp. Adult alewives were collected in 1998 to evaluate potential diet overlap and resource competition between these fishes and larval gizzard shad.

I sampled zooplankton in Claytor Lake to relate temporal distribution, abundance, and composition of zooplankton to the abundance and diet composition of larval fishes. These data also were collected to determine whether larval gizzard shad appeared to depress the zooplankton population, or altered the species composition or size structure through selective feeding. I sampled zooplankton concurrently with all limnetic fish sampling.

### **Limnetic Larval Fish**

Larval fish in the limnetic zone (> 5-m deep) were sampled with a neuston net (0.5-m x 1.0-m mouth, 4 m long, 1-mm bar mesh). A 5.5-m johnboat powered by a 60-hp outboard motor and equipped with a Lowrance model X70A (depth-finder and speedometer) was used to tow the net. The Lowrance calculated the speed of the boat, and together with the time traveled per tow and area of the mouth of the net, I was able to estimate volume of water filtered. A flow meter

(General Oceanics model 2030) was mounted at the mouth of the net and also estimated volume of water filtered. I used this estimate to periodically check the accuracy of my original estimate provided by the Lowrance. The neuston net was towed at approximately 1.0-1.3 m/s for 5 min; other researchers (Kilch 1976; Nigro 1980; Cada and Loar 1982; Tisa 1988; Dettmers and Stein 1992; Jackson and Bryant 1993) have sampled larval shad *Dorosoma* spp. and alewife, and found that towing at approximately 1.0-1.8 m/s was an effective speed for capturing these clupeids. Because I was interested in reducing net avoidance by larger larvae, this speed appeared to be the fastest towing speed possible while minimizing the visible pressure wave in front of the net. Each tow filtered 150-195 m<sup>3</sup> of water; 100 m<sup>3</sup> is generally accepted as a minimum sampling volume in freshwater larval fish studies (Kelso and Rutherford 1996). The net was attached to the stern of the boat and towed approximately 18 m behind the boat in a circular pattern, thus keeping the net out of the boat's wake and propwash. Because the neuston net floated and therefore sampled the top 0.5-m of the water column, all sampling for abundance estimates was conducted after dark to take advantage of surface-oriented and more randomly distributed larval fish while minimizing net avoidance (Kelso and Rutherford 1996). The surface-sampling neuston net was chosen instead of other larval nets because of its ease of handling and operation, and because other researchers had found success using the neuston net for collecting larval fishes on similar reservoir systems (Sammons and Bettoli 1998). Although the sampling depth of the neuston net was originally a concern, significant numbers of shad and alewife had previously been sampled at a depth of 1 m in nearby Smith Mountain Lake, Virginia (Tisa 1988), while larval gizzard shad were almost exclusively distributed in the top 1 m of the water column in Kansas reservoirs (Willis 1987). Three replicate tows were made at both nearshore and offshore locations at each of the three sites, equaling 18 tows per sampling night.



I collected samples on approximately ten dates each year between mid-May and early/mid-August for a total of 180 tows per sampling season. Subsurface water temperature (approx. 0.25-m depth) was measured with a handheld thermometer at each site prior to sampling.

In both years, limnetic larval fish samples for stomach content analysis were obtained from the sampling methods just described. However, few larval fish sampled at night in 1997 contained identifiable (or any) food items in their digestive systems. Diet studies involving larval gizzard shad, alewife, and *Lepomis* spp. have presented mixed results concerning diel feeding patterns of these fish (Werner 1969; Barger and Kilambi 1980; Mallin et al. 1985; Dettmers and Stein 1992; Hayward and Hiebert 1993), suggesting that they may not always feed at night. However, through preliminary evening sampling in 1998, I found that many larval fish did feed at dusk. Therefore, in 1998, neuston net samples were also taken at dusk on a weekly basis in conjunction with nighttime tows. These dusk tows were taken exclusively for larval diet samples and were not designed to result in quantitative measures of fish abundance.

For the first two weeks of this study, I fixed larvae in approximately 40% ethanol (V. DiCenzo, VDGIF, and S. Sammons, Tennessee Tech University, personal communications). Unfortunately, this proved to be ineffective as a fixative as specimens exhibited deterioration of tissue and loss of body parts. Aldehyde-based solutions such as formaldehyde are better fixatives for preservation of ichthyoplankton because they immediately combine with tissue proteins and prevent proteins from reacting with other reagents (see Kelso and Rutherford 1996). Samples were therefore fixed in 10% formalin upon capture for the remainder of the study. Larvae were then transferred to 40% ethanol within 24 hrs. Although considerable attention has been given to the effects of preservation on the lengths of young fishes, results have been mixed (see Tisa 1988). Leslie and Moore (1986) reported that changes in body measurements of

freshwater larval fishes associated with fixatives, including formalin and ethanol, were of little or no practical consequence for taxonomy and growth studies. Because measurements of larval fish were taken within 24 to 48 hrs after collection, I assumed the measurements in this study reflected live-state conditions.

### **Littoral Fish**

In 1998, I sampled littoral age-0 *Micropterus* spp. during the day using seines (3 m X 1.3 m, 1.5-mm mesh; 4 m X 1.3 m, 5-mm mesh) and larval dip nets (45-cm mouth diameter, 500- $\mu$ m mesh) for food habit analyses. Two to four seine hauls of approximately 20 m were made parallel to shore in the littoral zone at each site. Larval dip nets were periodically used to sample littoral fishes when larval fish aggregations were visually located in our sample sites. These samples were made both while wading and from the boat. However, this sampling method was neither efficient nor effective in capturing larger (> 20 mm TL) and more mobile age-0 fish. Littoral samples were taken once per week, usually on the same date as limnetic larval tows. Age-0 fish collected for stomach analysis were suffocated in air to prevent regurgitation (Kohler 1980), fixed in 10% formalin, and transferred to 40% ethanol within 24 hrs.

### **Adult Alewife**

The diet composition of planktivorous adult alewife was described to evaluate the potential for competitive feeding interactions between young gizzard shad and other zooplanktivores. Alewives for diet analysis were collected by boat electrofishing and gill net samples taken in a concurrent study (Bonds 2000). These samples were collected once per

month during the summer of 1998. Juvenile and adult fish were suffocated in air to prevent regurgitation (Kohler 1980), and then fixed in 10% formalin.

### **Crustacean Zooplankton**

Crustacean zooplankton was sampled with a Wisconsin-style plankton net (0.2-m mouth diameter, 1.0-m long, 80- $\mu$ m mesh). The net was pulled vertically by hand from 3-m depth to the surface in nearshore and offshore locations at each of the three sampling sites. In 1997, three replicate zooplankton samples were taken at both nearshore and offshore locations at each site concurrently with larval fish samples. As with larval fish sampling, this resulted in 18 tows per night, or approximately 180 tows per sampling season. Once the net was lowered, I waited approximately one minute before retrieving the net to allow zooplankton to redistribute in the water column. Because zooplankton abundance in nearshore and offshore samples collected in 1997 was found not to be statistically different ( $P=0.85$ ), I chose to take only three samples total at each site per week in 1998; one each in the cove, at the mouth of the cove, and in the main lake, for a total of approximately 90 samples. All zooplankton samples were preserved in 4-5% sucrose-formalin (Haney and Hall 1973).

## **Laboratory Analyses**

### **Measurement of Larval Fish**

In the laboratory, larval fish were separated from algae and debris within 24 to 48 hrs after collection. Individual specimens were then identified following the keys developed by Lippson and Moran (1974), Tin (1982), and Wallus et al. (1990). Clupeids were identified to species, while *Lepomis* spp. and *Micropterus* spp. were identified to genus. Larval gizzard shad

and alewife are very similar in appearance, yet there are many diagnostic characteristics. According to Wallus et al. (1990), larval gizzard shad and alewife (< 30 mm TL) essentially differ as follows: 1) preanal length as a percent of SL is greater for gizzard shad than alewife (87% versus 82%, respectively); 2) number of postanal myomeres is fewer for gizzard shad than alewife (4 to 7 versus 5 to 14, respectively); 3) number of dorsal fin rays is fewer for gizzard shad than alewife (10 to 12 versus 15 to 19, respectively); and 4) number of anal fin rays is greater for gizzard shad than alewife (27 to 36 versus 15 to 21, respectively). I found preanal length and postanal myomere counts to be effective for distinguishing larvae less than 15 mm TL, while dorsal and anal fin ray counts were the easiest and most distinct diagnostic characteristics for larvae greater than 15 mm TL. Representative samples of larval fishes were provided to me by other researchers to use as reference samples. (D. DeVries, Auburn University, and S. Sammons, Tennessee Tech University). After identification and sorting, larvae were counted and measured for TL (nearest 0.1 mm) using a dissecting microscope equipped with an ocular micrometer and then transferred to vials containing 40% ethanol.

### **Larval and Juvenile Diet**

Larval and juvenile fish were removed from storage vials within two to six months and examined for stomach contents. Specimens were placed in a petri dish under a dissecting microscope, and stomachs were teased apart using very fine pins. In most instances, as reported by Cramer and Marzolf (1970), I recognized the presence of stomach contents in these fish before dissection due to the thin, transparent stomach wall of small larvae (< 15 mm). For larval gizzard shad and alewife less than 20 mm TL, all food items in the digestive tract were used in analyses because no evident separation existed between stomach and intestine, and few food

items were present in individual fish. In larvae greater than 20 mm TL, analyses included only those food items found in the stomach; the majority of food items found in the intestines of larvae greater than 20 mm TL proved to be unidentifiable due to digestion. Once removed, all prey items from gut contents were identified, counted, and measured for length (nearest 0.01 mm) using the dissecting microscope equipped with an ocular micrometer. Cladocerans were identified to the lowest possible taxonomic classification (family or genus in most cases), and copepods were classified as nauplii, calanoids, or cyclopoids. Insects and fish in juvenile *Micropterus* spp. stomachs were also identified to genus. From each stomach sample, 10 representative specimens from each zooplankton taxon (when present) were measured for length (nearest 0.01 mm) with the ocular micrometer.

In order to provide estimates of zooplankton weight for larval diet analyses, length of zooplankton collected during this study was converted to weight using taxon-specific length-weight regressions developed for equivalent zooplankton taxa by Culver et al. (1985). These regression equations are based on the formula  $W=aL^b$ , where  $a$  and  $b$  are constants, and  $W$  and  $L$  represent weight and length of the organism, respectively (Table 1).

**Table 1.** Taxa and variables used in crustacean zooplankton length-weight regressions.

<b>Taxon Examined</b>	<b>Species Equivalent (Culver et al. 1985)</b>	<b>a (Culver et al. 1985)</b>	<b>b (Culver et al. 1985)</b>	<b>Range in Lengths (mm) (Culver et al. 1985)</b>	<b>Range in Lengths (mm) (N) 1997</b>	<b>Range in Lengths (mm) (N) 1998</b>
<b>Copepods</b>						
Calanoid	<i>Diaptomus siciloides</i>	5.8853	3.8498	0.959-1.176	0.289-1.406 (700)	0.359-1.211 (52)
Cyclopoid	<i>Cyclops vernalis</i>	7.0729	2.5563	0.326-1.086	0.219-1.55 (1631)	0.260-1.328 (767)
	<i>Mesocyclops edax</i>	6.6586	2.8945	0.507-1.050		
	Combined	6.8658	2.7254			
Nauplii	Calanoid nauplii	3.0093	1.7064	0.108-0.342	0.086-0.359 (1694)	0.078-0.336 (805)
	Cyclopoid nauplii	2.5968	1.6349	0.144-0.315		
	Combined	2.8031	1.6707			
<b>Cladocerans</b>						
<i>Bosmina</i>	<i>Bosmina longirostris</i>	17.7369	2.2291	0.217-0.434	0.156-0.453 (982)	0.148-0.414 (472)
Chydoridae	<i>Chydorus sphaericus</i>	14.0793	1.9796	0.219-0.310	0.164-0.813 (32)	0.188-0.820 (30)
Daphnidae	<i>Daphnia retrocurva</i>	3.7847	2.6807	0.398-1.810	0.226-1.445 (545)	0.289-1.484 (148)
Leptodoridae	<i>Leptodora kindtii</i>	1.5605	1.873	2.268-6.804	0.703-7.03 (105)	0.758-7.03 (41)
<i>Diaphanosoma</i>	<i>Diaphanosoma leuchten.</i>	5.0713	1.0456	0.313-0.525	0.234-1.320 (1259)	0.242-1.336 (680)

I analyzed diet composition of fishes to determine trophic overlap and food electivity of larval and juvenile fishes as an indicator of potential interspecific competition. Diet composition was determined as the percent composition by weight, and the percentage of empty stomachs was also noted. Food electivity of major items (>1% of the composite diet by weight) was determined for all zooplanktivorous fish species by applying the linear food selection index developed by Strauss (1979):

$$L = r_i - p_i.$$

In this index,  $r$  = the proportion (%) of food organism in the diet, and  $p$  = the proportion (%) of food organism in the environment. Random feeding will result in an index value of zero. Positive index values ( $0 < L \leq 1$ ) suggest preference for a given food taxa, while negative values ( $-1 \leq L < 0$ ) indicate avoidance, inaccessibility, or lack of preference for a given food taxa.

Size-selective zooplanktivory by larval fishes was evaluated using the techniques employed by Nigro and Ney (1982). Larvae were grouped into 2-mm size groups, and comparisons were made between the size of prey in their diets and the size of prey available in the reservoir. Comparisons were also made between the total length of larval fish and the length of prey items in their diet.

Diet overlap between fish species was calculated using Schoener's (1970) index based on the mean percent composition by weight, or the "mean of the volume (weight) percentages" as described by Wallace (1981). Percent composition by weight of gut contents was determined for each prey category and individual fish examined. Mean percent composition by weight for the fish species in question was then calculated for each prey category. Schoener's index is one of

the most popular and simplest measures of resource overlap, requires few assumptions, and is often used to screen for potentially important trophic interactions (Hurlbert 1978; Petraitis 1979):

$$C_{xy} = 1 - 0.5(\Sigma|p_{xi} - p_{yi}|).$$

In this index,  $p_{xi}$  is the proportion of food item  $i$  used by species  $x$ , and  $p_{yi}$  is the proportion of item  $i$  used by species  $y$ . Index values range from 0 to 1, with an index value greater than 0.5 to 0.6 generally considered indicative of resource overlap and potential competition.

### **Crustacean Zooplankton**

In the laboratory, field samples were stirred and mixed, and one 20-ml random subsample from each field sample was taken with a pipette; field samples were approximately 200 ml each. These subsamples were removed and stored in vials within 24 to 48 hrs after collection. The contents of each vial were then stirred, and the first of three random aliquots was taken with a large-bore Hensen-Stempel pipette (1 ml). After each 1-ml aliquot was analyzed, I returned it to the vial before the next aliquot was taken to maintain the sample at its original volume. Each 1-ml aliquot was then placed in a Sedgewick-Rafter counting cell (1 ml), and all individuals were identified and counted using a dissecting microscope. Cladocerans were identified to the lowest possible taxonomic classification (family or genus in most cases), and copepods were classified as nauplii, calanoids, or cyclopoids. Also, from each replicate subsample, the first 10 random specimens from each taxon were measured for TL (nearest 0.01 mm) with an ocular micrometer.



The mean number of individuals identified and counted from each of the three replicate 1-ml aliquots was used for density calculations.

## Statistical Analysis

Parametric statistical procedures were employed throughout this study to analyze the various data sets. Most comparisons of larval fish and zooplankton abundance were analyzed using repeated-measures analysis of variance (ANOVA) procedures (SAS Institute 1990; Maceina et al. 1994); all tests were performed at a significance level of  $\alpha=0.05$ . Comparisons of larval fish species abundance between nearshore and offshore locations were made using a single-factor ANOVA. Regression analyses were used to describe relationships between length of zooplankton and date, and length of fish and size of *Diaphanosoma* consumed. Tukey's multiple comparisons (Sokal and Rohlf 1995) were used to identify peak larval fish densities and to evaluate the response of zooplankton abundance to these peaks; all tests were again performed at a significance level of  $\alpha=0.05$ . Abundance data were transformed before statistical analyses to normalize them. Common transformations, including  $\log_{10}(\text{catch}+1)$ ,  $\log_e(\text{catch}+1)$ , and square root( $\text{catch}+0.5$ ), were compared using the Shapiro-Wilk test. This procedure tests for normality of the residuals, and therefore can be used to determine which transformation best normalizes the data. The transformation  $\log_{10}(\text{catch}+1)$  proved to be the most appropriate. Conversion of variates into logarithms is the most common form of transformation, and frequency distributions skewed to the right are often made more normal by transformation to logarithm scale (Sokal and Rohlf 1995). Also, in many cases logarithm transformations remove heteroscedasticity and cause sample variances to become independent of their means, both important assumptions of analysis of variance (Sokal and Rohlf 1995). Because my count data often included zeros, the transformation  $\log_{10}(\text{catch}+1)$  was also used to avoid the problem of computing the logarithm of zero.

# RESULTS

## Larval Distribution

Spatial and temporal distributions of larval shad, alewife, and *Lepomis* spp. were described to evaluate the potential for resource overlap. Limnetic larval fish samples during both 1997 and 1998 consisted primarily of these three species. While these fish all co-occurred at each of the three sampling sites on the reservoir, larval yellow perch, walleye, and *Micropterus* spp. were also collected incidentally in low numbers (< 5 each, per year). Larvae were collected at both cove and main channel locations at each site. In 1997, cove (nearshore) versus main channel (offshore) densities of each larval taxon did not differ significantly (Table 2), with a single exception: the nearshore abundance of *Lepomis* spp. at site PK was significantly higher than the offshore abundance ( $P=0.023$ ). Because eight of the nine abundance comparisons (3 species x 3 sites) did not differ between nearshore and offshore locations, I combined these data to eliminate intra-site comparisons and raise statistical power. This resulted in six replicates per site per date rather than three replicates per site per location per date. Cove and main channel locations were also sampled in 1998 for a total of six replicates per site per date. I disregarded intra-site comparisons and combined replicate data as in 1997 based on the assumption that no significant differences existed between the two locations. Densities of larval fishes were expressed as  $\#/1000\text{m}^3$ . Because larval densities in this study were often low, this extrapolation allowed for comparisons of whole number values.

### Distribution in 1997

Sampling for larval fishes began on May 20, but no fish were captured. Larvae were first collected on May 28. All larvae collected on this date, consisting of several larval clupeids

(N~10), were unidentifiable to the species level due to tissue deterioration. Concerns with preservation techniques were discussed previously, and new preservation techniques were employed by the next sampling date. It is likely that the majority of these larvae were alewife, based on their abundance the following sampling date. Gizzard shad, alewife, and *Lepomis* spp. were present in most samples by June 10. Lengths of limnetic fish collected during 1997 ranged from 5.5-17.9 mm for gizzard shad, 5.5-26.1 mm for alewife, and 4.6-27.8 mm for *Lepomis* spp. Total lengths of all three species increased in my collections throughout the summer ( $P < 0.01$ ) (Table 3). All three species followed the same general trends in abundance throughout the season, although alewives were generally more abundant than the other two species earlier in the sampling season (Figure 2). Peaks in abundance for all species appeared to occur during the same two-week period. Peaks occurred during the weeks of June 25 and July 1, after which abundances declined steadily the remainder of the summer; densities of all species reached zero by the middle of August. This pattern of larval abundance held true for all three sampling sites, except for a lack of a significant *Lepomis* spp. peak at site PK witnessed at the other two sites (Figure 3).

Larval gizzard shad were first collected in neuston net samples in early June of 1997 (Figure 2) as water temperatures reached 20° C. Total catch of larval shad for all sites combined from June 3 to August 13 was 228 fish. After larval shad first appeared on June 3, catch remained low during the next two sampling dates. Total catch and corresponding mean density in the reservoir increased during the period from June 25 to July 1, with the highest density of 41.0 fish/1000m<sup>3</sup> recorded on July 1; water temperature on this date was 26.5° C. After mid-July, larval shad density declined and remained low (<5.0/1000m<sup>3</sup>) until larvae were no longer collected on or after August 5.

Larval alewives were also first identified in neuston net samples in early June of 1997 (Figure 2) as water temperatures approached 20° C. Total catch of larval alewife from June 3 to August 13 was 568 fish. As noted, several unidentifiable larval clupeids (N~10), likely alewife, were collected in late May. The first confirmed appearance of larval alewife in my samples also corresponded with the first visual peak in larval alewife density (50.3/1000m<sup>3</sup>). Catch declined through mid-June, yet peaked again on June 25 (65.3/1000m<sup>3</sup>) with water temperature at 27.6° C. After this peak, catch steadily declined until larvae were no longer collected on or after August 5.

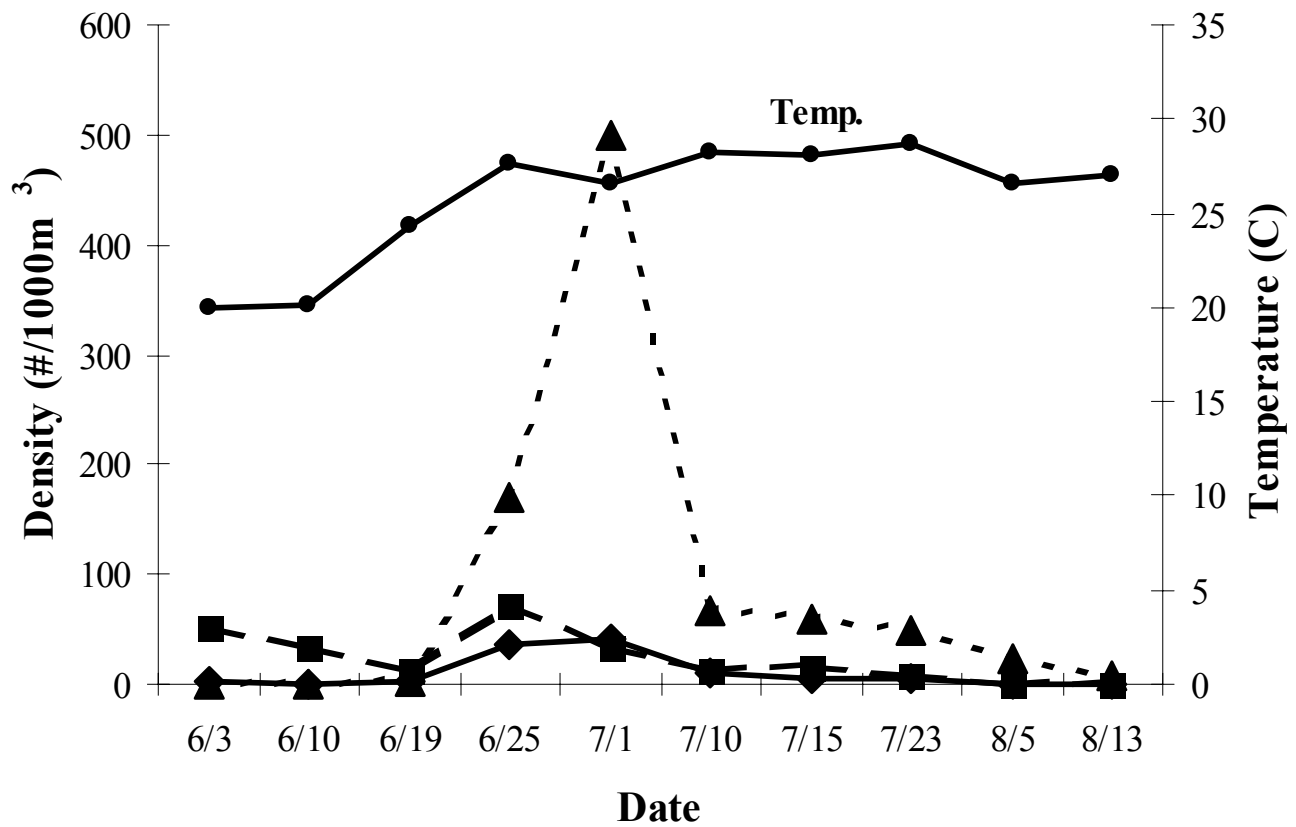
Larval *Lepomis* spp. were also first collected in neuston net samples in early June of 1997. Water temperature at this time was slightly above 20° C. Catch during the first three sampling dates was relatively low compared to the other two species (Figure 2). Although less abundant early in the sampling season, total catch of larval *Lepomis* spp. from June 10 to August 13 was 2,117 fish. Overall, *Lepomis* spp. densities were more than twice those of both clupeids combined. After larval *Lepomis* spp. first appeared on June 10 (0.4/1000m<sup>3</sup>), density also remained low during the next sampling date (3.0/1000m<sup>3</sup>). Density then increased substantially on June 25 (138.5/1000m<sup>3</sup>) and peaked on July 1 at 513.8/1000m<sup>3</sup> when water temperature was at 26.5° C. After this peak, larval *Lepomis* spp. density declined steadily until the last sampling date of August 13.

**Table 2.** Comparisons of larval fish abundances between nearshore and offshore locations during 1997. Results are from analysis of variance for  $\log_{10}(\text{catch}+1)$  transformed data.

Site	Gizzard Shad			Alewife			<i>Lepomis</i> spp.		
	df	F	P	df	F	P	df	F	P
<b>PK</b>	52	3.71	0.060	52	0.02	0.90	52	5.47	0.023
<b>SP</b>	53	0.38	0.54	53	2.14	0.15	53	0.52	0.47
<b>DC</b>	56	0.11	0.74	56	1.91	0.17	56	0.02	0.88

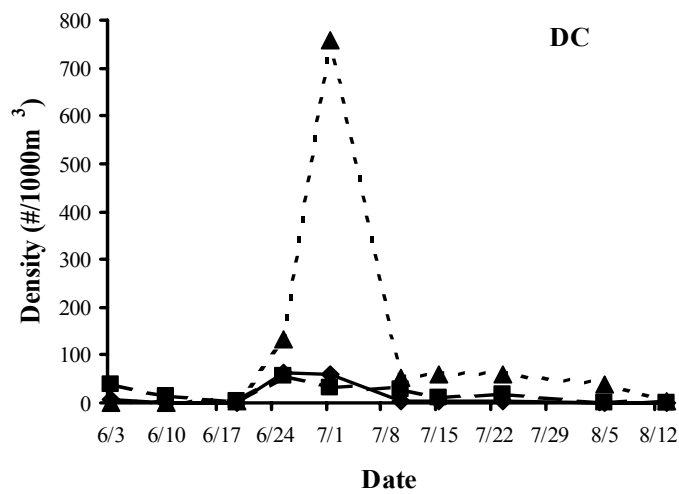
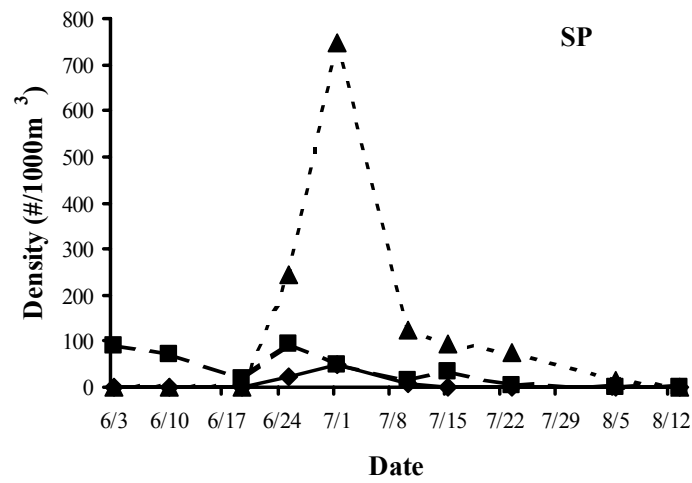
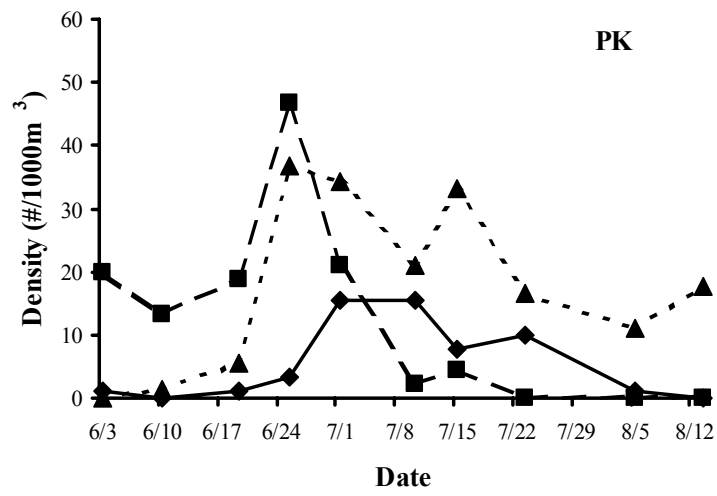
**Table 3.** Mean total lengths (with standard deviation) of limnetic larval fish collected during 1997.

Date	Gizzard Shad		Alewife		<i>Lepomis</i> spp.	
	Length (mm)	S.D.	Length (mm)	S.D.	Length (mm)	S.D.
6/3	9.7	0.9	11.3	1.7	-	-
6/10	-	-	13.0	2.2	-	-
6/19	7.3	1.9	12.4	3.1	-	-
6/25	9.7	1.7	11.1	3.6	6.7	1.0
7/1	11.3	2.3	12.5	2.6	7.0	1.1
7/10	12.6	1.9	16.7	4.4	8.4	3.3
7/15	10.7	2.2	14.3	2.8	7.3	2.2
7/23	13.4	2.2	15.3	2.4	8.1	4.0
8/5	-	-	-	-	14.1	5.5
8/13	-	-	-	-	9.9	3.6



**Figure 2.** Patterns of larval density from June 3 to August 5, 1997. Density estimates calculated as the mean of 18 tows per date (solid line, diamonds = gizzard shad; dashed line, squares = alewife; dotted line, triangles = *Lepomis* spp.).





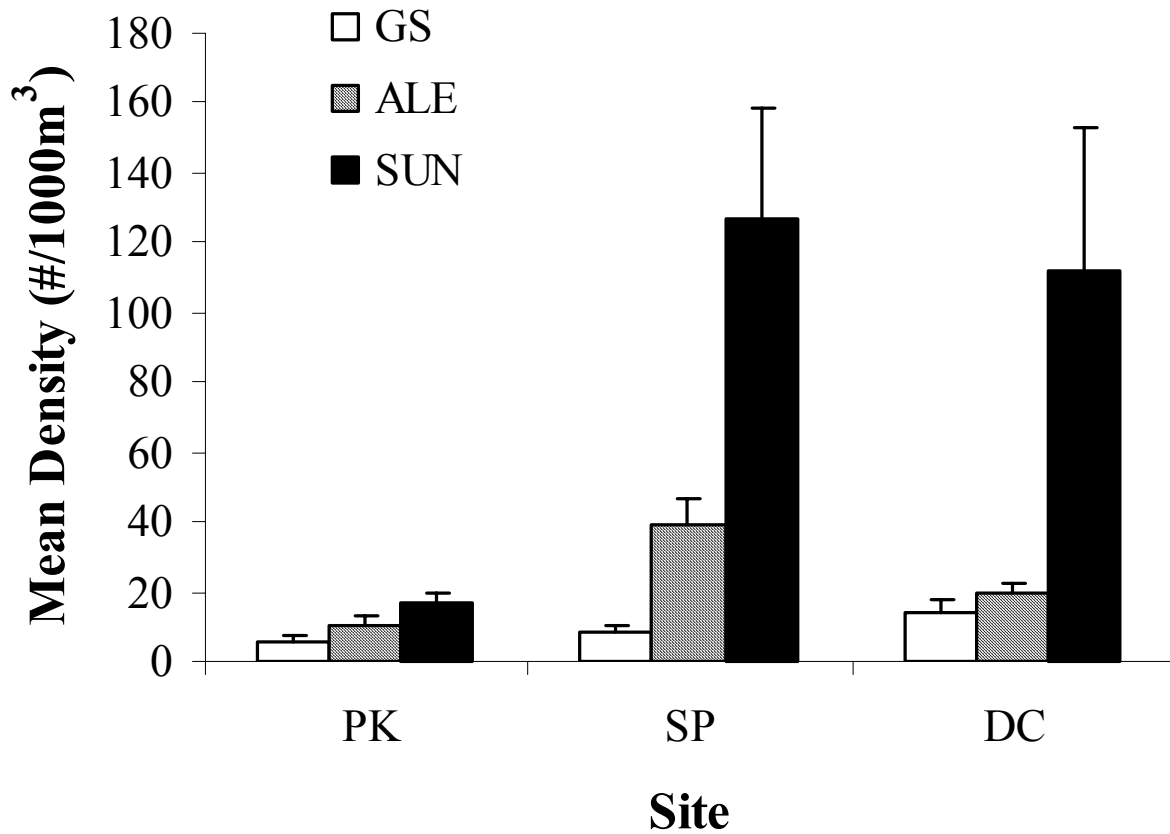
**Figure 3.** Patterns of larval density by site from June 3 to August 5, 1997. Density estimates calculated as the mean of 6 tows per site per date (solid line, diamonds = gizzard shad; dashed line, squares = alewife; dotted line, triangles = *Lepomis* spp.). Note the different y-axis scales.

Average seasonal densities of larval fishes at each individual site were calculated as the mean of approximately 66 total replicate larval tows during 1997 (6 tows at each site on each of 11 dates). Mean densities ( $\#/1000\text{m}^3$ ) of gizzard shad during the summer of 1997 were 5.7, 8.3, and 13.6 at site PK, SP, and DC, respectively. Densities did not differ significantly between any of the three sites (PK vs. SP,  $P=0.52$ ; PK vs. DC,  $P=0.25$ ; SP vs. DC,  $P=0.073$ ). However, there did appear to be a slight trend towards higher densities downlake (Figure 4).

Alewives were generally more abundant than gizzard shad in 1997, with mean densities ( $\#/1000\text{m}^3$ ) of 10.6, 39.4, and 19.3 at site PK, SP, and DC, respectively. Mean densities were significantly lower at site PK than at site DC ( $P=0.011$ ), and were also significantly lower at site PK than at site SP ( $P<0.01$ ). Densities were not significantly different between sites DC and SP ( $P=0.25$ ) (Figure 4).

Larval *Lepomis* spp. were more abundant than larval clupeids on most dates during 1997. Mean densities ( $\#/1000\text{m}^3$ ) were 16.7, 126.4, and 112.3 at site PK, SP, and DC, respectively. Mean densities were significantly lower at site PK than at site SP ( $P=0.020$ ). Although not quite significantly different ( $P=0.054$ ), mean densities at sites PK and DC differed by almost an order of magnitude due to substantial peaks during two dates at site DC (Figure 4). Densities were not significantly different between sites SP and DC ( $P=0.69$ ).

Across all sites and dates in 1997, mean density of alewife ( $23.1/1000\text{m}^3$ ) was significantly higher ( $P<0.01$ ) than mean gizzard shad densities ( $9.3/1000\text{m}^3$ ). Similarly, mean *Lepomis* spp. density ( $86.1/1000\text{m}^3$ ) was also significantly higher ( $P<0.01$ ) than mean gizzard shad densities. Although more abundant on most dates, mean *Lepomis* spp. densities were not significantly different from alewife during 1997 ( $P=0.071$ ).



**Figure 4.** Mean larval fish densities (#/1000m<sup>3</sup>) for each site during 1997. Density estimates for each site calculated as the mean of 66 tows (6 tows taken on 11 separate dates). Error bars represent plus one standard error.

## Distribution in 1998

Sampling for larval fishes in 1998 also began on May 20 as water temperatures reached 23° C, with alewife being the only fish species collected on this date. However, all larval fish species were present in samples by the next sampling date on May 28. Lengths of limnetic fish collected in 1998 ranged in size from 5.2-36.0 mm for gizzard shad, 4.9-32.0 mm for alewife, and 4.1-26.0 mm for *Lepomis* spp. Total lengths of all three species increased in my collections throughout the summer ( $P < 0.01$ ) (Table 4). As in 1997, all three species followed similar trends in abundance throughout the season (Figure 5). Gizzard shad, alewife, and *Lepomis* spp. exhibited peaks in abundance during the week of June 24. Subsurface water temperature on this date was 27° C. *Lepomis* spp. also peaked again during the two weeks of July 15 and 22. Subsurface water temperature on these dates had reached nearly 30° C. Clupeid densities generally declined after June 24 and reached zero by August 4. Similar to 1997, the first substantial peak in larval abundance corresponded to an increase in water temperatures during the weeks of June 10 to June 24 (Figure 5). Surface water temperatures increased from approximately 23° C to 27° C during this time period. This temporal pattern of larval abundance generally held true for all three sampling sites, with the exception being a lack of a noticeable peak at site PK during early June witnessed at the other two sites (Figure 6). As in 1997, the high degree of temporal and spatial overlap shown by all three species during 1998 increases the potential for interspecific competition.

During 1998, larval gizzard shad were collected in neuston net samples beginning in late May (Figure 5) at a water temperature of 25.1° C. Total catch of larval shad from May 28 to August 4 was 309 fish. After larval shad appeared on May 28 (19.4/1000m<sup>3</sup>), catch and mean density remained relatively steady during the next three sampling dates (12-14/1000m<sup>3</sup>). On

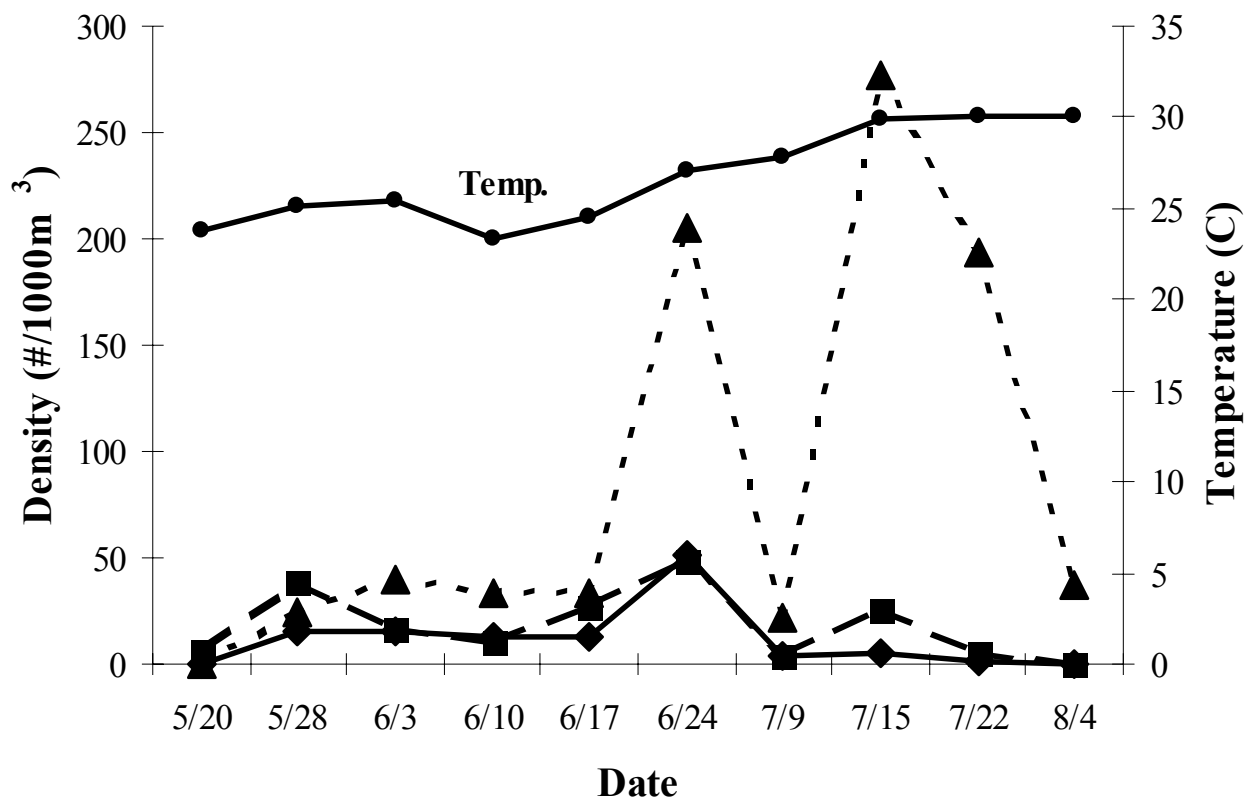
June 24, as water temperature reached 27° C, density of larval shad peaked at 50.7/1000m<sup>3</sup> (N=137). Catch declined thereafter, and they were no longer collected after July 22.

Larval alewives were the first ichthyoplankton collected in neuston net samples in late May of 1998, appearing on the first sampling date of May 20 (Figure 5). Total catch of larval alewife from May 20 to August 4 was 468 fish. Abundance of larval alewife immediately increased to 44.8/1000m<sup>3</sup> (N=91) on May 28. Although not a statistically significant peak, abundance on this date was high. Density then declined, but increased again to peak on June 24 (48.2/1000m<sup>3</sup>, N=130). Abundance dropped after this date, then increased slightly on July 15 (25.9/1000m<sup>3</sup>, N=69). Alewives were not collected after July 22.

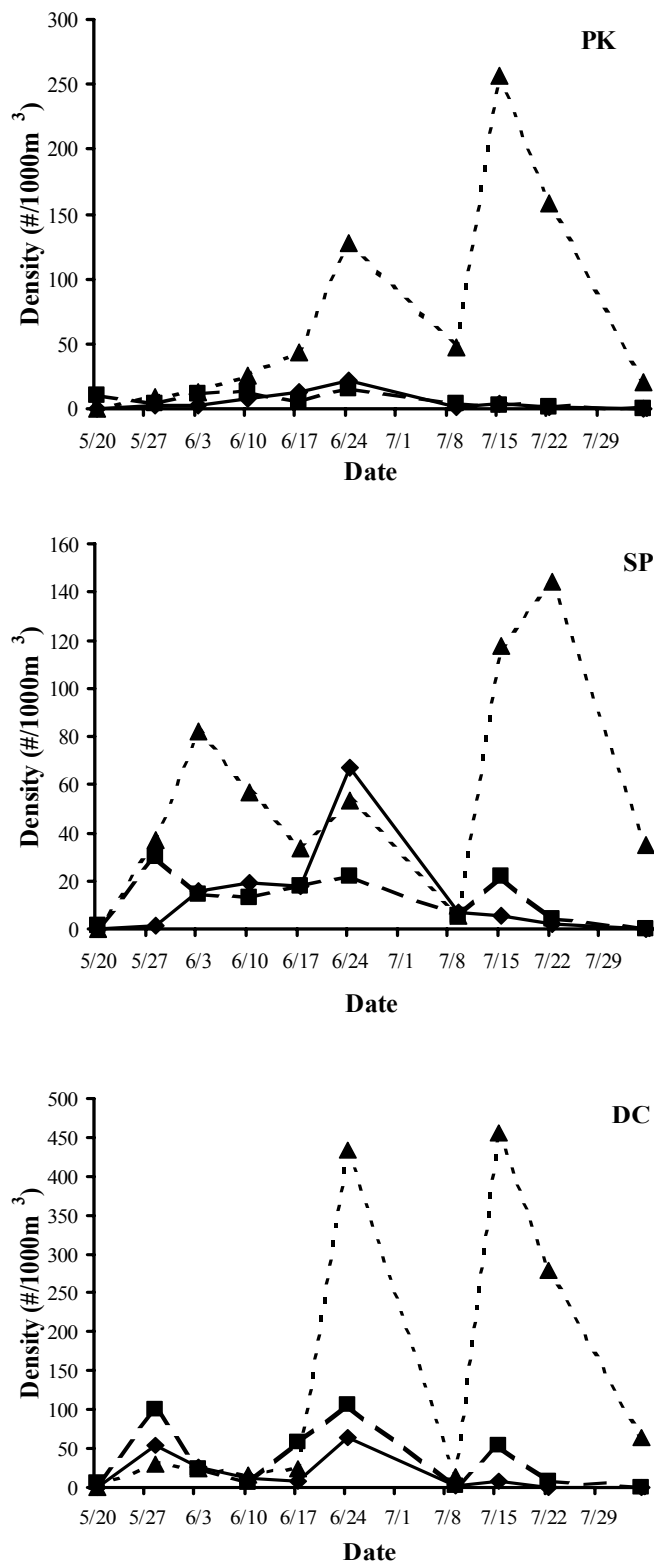
Larval *Lepomis* spp. were also collected in neuston net samples in late May of 1998 (Figure 5) as water temperature reached just above 25° C. Total catch of larval *Lepomis* spp. from May 20 to August 4 was 2305 fish. Abundance first increased on June 3 (39.2/1000m<sup>3</sup>, N=106), declined the next two sampling dates to less than 33.3/1000m<sup>3</sup>, and first peaked on June 24 at 204.8/1000m<sup>3</sup> (N=553). Surface water temperature on this date was 27° C. Abundance dropped dramatically on the next sampling date (21.9/1000m<sup>3</sup>, N=59), yet peaked a third time on July 15 at 277.1/1000m<sup>3</sup> (N=748) when water temperature was at almost 30° C. After this greatest peak, larval *Lepomis* spp. density declined to less than 40/1000m<sup>3</sup> (N=77) on the last sampling date of August 4.

**Table 4.** Mean total lengths (with standard deviation) of limnetic larval fish collected during 1998.

<b>Date</b>	<b>Gizzard Shad</b>		<b>Alewife</b>		<b><i>Lepomis</i> spp.</b>	
	<b>Length (mm)</b>	<b>S.D.</b>	<b>Length (mm)</b>	<b>S.D.</b>	<b>Length (mm)</b>	<b>S.D.</b>
<b>5/20</b>	-	-	10.1	2.1	-	-
<b>5/28</b>	9.9	1.7	12.1	2.8	6.9	0.6
<b>6/3</b>	10.9	2.6	10.1	2.6	6.0	0.6
<b>6/10</b>	9.9	2.3	10.6	2.9	6.6	0.7
<b>6/17</b>	10.1	2.2	8.4	2.2	6.8	0.8
<b>6/24</b>	11.0	2.5	10.5	2.9	7.2	1.0
<b>7/9</b>	13.7	6.5	16.0	4.5	8.1	3.0
<b>7/15</b>	24.5	6.2	19.1	5.2	8.6	3.0
<b>7/22</b>	18.3	7.9	19.2	5.8	8.6	3.2
<b>8/4</b>	-	-	-	-	13.7	4.2



**Figure 5.** Patterns of larval density from May 20 to August 4, 1998. Density estimates calculated as the mean of 18 tows per date (solid lines, diamonds = gizzard shad; dashed lines, squares = alewife; dotted lines, triangles = *Lepomis* spp.).



**Figure 6.** Patterns of larval density by site from May 20 to August 4, 1998. Density estimates calculated as the mean of 6 tows per site per date (solid lines, diamonds=gizzard shad; dashed lines, squares=alewife; dotted lines, triangles=*Lepomis* spp.). Note different y-axis scales.

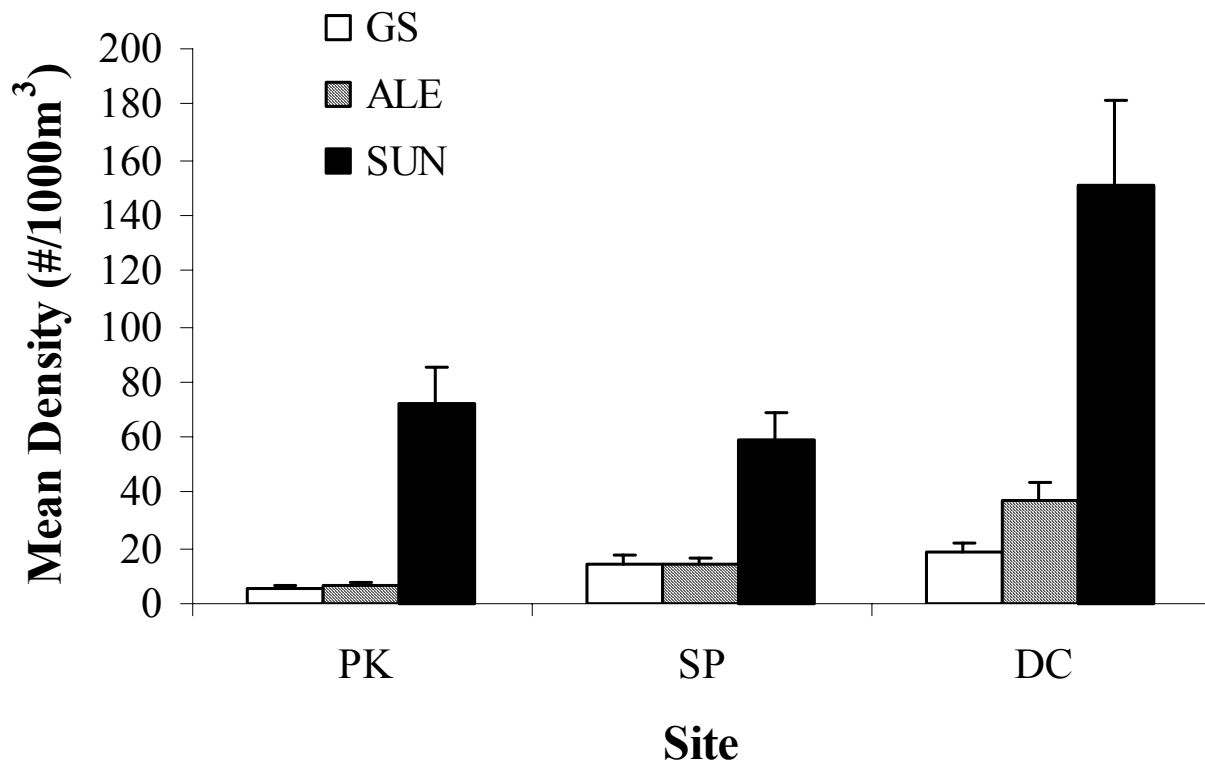


Average seasonal densities of larval fishes at each individual site during 1998 were calculated as the mean of approximately 66 total replicate larval tows (6 tows at each site on each of 11 dates). Mean densities ( $\#/1000\text{m}^3$ ) of gizzard shad during the summer of 1998 were 5.4, 14.4, and 18.1 at site PK, SP, and DC, respectively. Mean densities were significantly lower at site PK than at both site SP ( $P<0.01$ ) and site DC ( $P<0.01$ ). Densities at sites SP and DC were not significantly different ( $P=0.59$ ) (Figure 7).

Mean densities ( $\#/1000\text{m}^3$ ) of alewife were 6.4, 14.1, and 37.7 at site PK, SP, and DC, respectively. Again, mean densities were significantly lower at site PK than at DC ( $P<0.01$ ). In addition, abundance at site SP was significantly lower than at site DC ( $P=0.011$ ). Densities at sites PK and SP were not statistically different at the  $\alpha=0.05$  level ( $P=0.054$ ), although mean density at site SP was more than twice the abundance at site PK.

Larval *Lepomis* spp. again appeared to be generally more abundant than larval clupeids in the limnetic zone during 1998. Mean densities ( $\#/1000\text{m}^3$ ) of *Lepomis* spp. were 72.3, 59.3, and 151.0 at site PK, SP, and DC, respectively (Figure 7). Mean *Lepomis* spp. densities in 1998 did not differ significantly between any of the three sites. Although average density at site DC was almost three times that at site SP, these two sites were not statistically different at the  $\alpha=0.05$  level ( $P=0.057$ ).

Overall mean density of alewife in 1998 averaged more than 60% greater than gizzard shad ( $18.8/1000\text{m}^3$  vs.  $12.4/1000\text{m}^3$ ), but this difference was only marginally significant ( $P=0.054$ ). As in 1997, mean *Lepomis* spp. density ( $92.6/1000\text{m}^3$ ) was significantly higher ( $P<0.01$ ) than mean gizzard shad densities. Mean *Lepomis* spp. densities were also significantly higher than mean alewife density in 1998 ( $P<0.01$ ).



**Figure 7.** Mean larval fish densities ( $\#/1000\text{m}^3$ ) for each site during 1998. Density estimates for each site calculated as the mean of 66 tows (6 tows taken on 11 separate dates). Error bars represent plus one standard error.

## Interannual Variability

Mean lake-wide total densities of larval fishes in ichthyoplankton tows were significantly greater in 1998 than in 1997 ( $P < 0.01$ ) because gizzard shad and *Lepomis* spp. were generally more abundant. At individual sites, larval fish at PK and DC were significantly more abundant during 1998 than in 1997 ( $P < 0.01$  and  $0.015$ , respectively), while mean density at site SP was not significantly different between years ( $P = 0.32$ ).

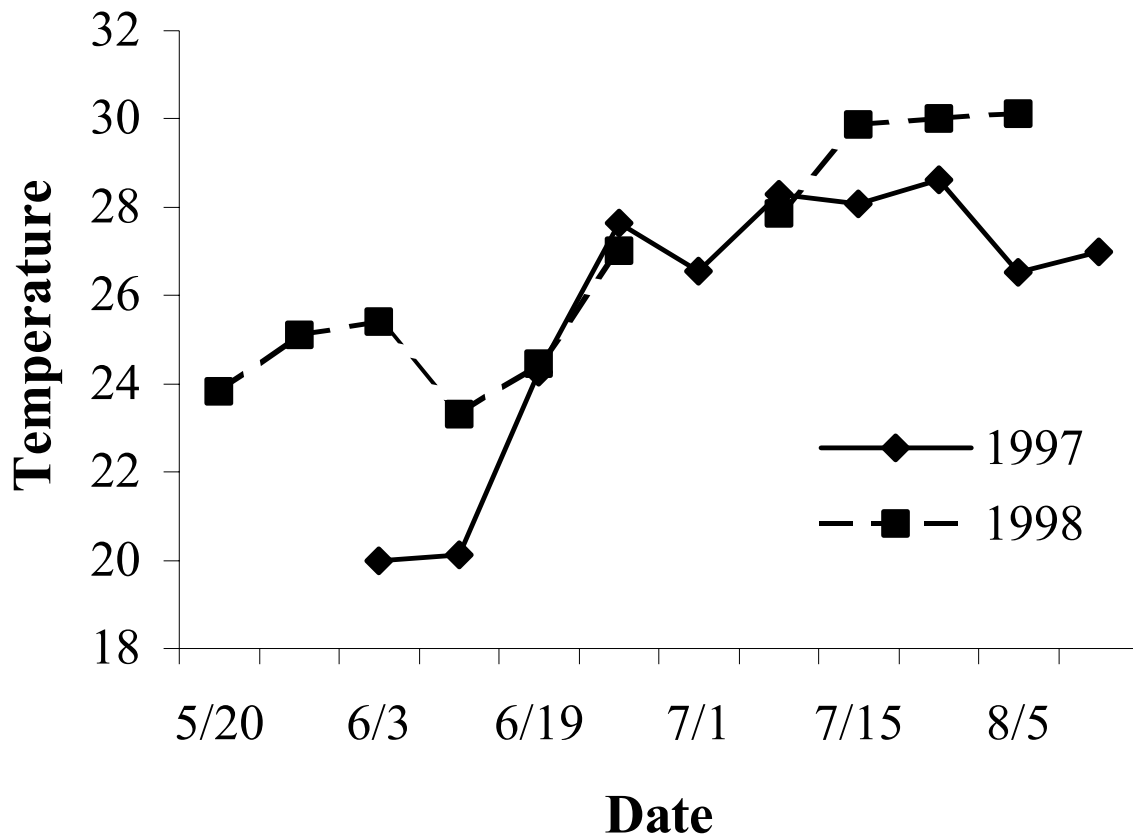
Mean density of gizzard shad for all sites combined was 25% greater in 1998 than in 1997 ( $P < 0.01$ ). Although gizzard shad densities at site PK were very similar between years ( $P = 0.95$ ), densities at site SP and at site DC were both more than 25% greater during 1998 ( $P < 0.01$ ).

Unlike gizzard shad, overall alewife densities were significantly greater during 1997 than in 1998 ( $P < 0.01$ ), with mean densities of 23.1 and 18.8/1000m<sup>3</sup>, respectively. Alewives were 40% more abundant at site PK in 1997 than in 1998, while abundance at site SP was more than double in 1997 ( $P = 0.047$  and  $P < 0.01$ , respectively). Although densities at site DC were not significantly different ( $P = 0.83$ ), they were almost 50% greater during 1998.

*Lepomis* spp. densities for all sites combined were 7% greater in 1998 than in 1997 ( $P < 0.01$ ). *Lepomis* spp. at sites PK and DC were significantly more abundant during 1998 than in 1997 ( $P < 0.01$ ); the mean density at site PK was more than four times greater during 1998. Abundance of *Lepomis* spp. between years at site SP was not significantly different ( $P = 0.19$ ).

Temporal patterns in larval abundance during 1997 and 1998 appeared to differ somewhat. In general, greatest larval abundance during 1997 was concentrated during a one to three week period during late June and early July. At this time, the three species studied all peaked in abundance and then declined throughout the remainder of the summer. Prior to these

peaks in abundances, my collection of larval fishes was limited mostly to alewives, which were also abundant at the beginning of the sampling season. Changes in water temperature were abrupt during the two week period between June 10 and June 25, increasing more than 7° C during this time (Figure 8). Data from 1998 suggest that peaks in spawning activity and subsequent larval abundances of all three species were less concentrated than in 1997, as larvae showed higher densities on three noticeable occasions during the 2.5 months studied. Although only one of these peaks was statistically significant, it included an apparent peak in mid to late July not witnessed in 1997. Water temperatures were generally higher early in the sampling season than in 1997 and then increased more gradually the remainder of the summer (Figure 8).



**Figure 8.** Surface water temperatures (0.25 m depth) at Claytor Lake during 1997 and 1998 measured in degrees Celsius. Mean temperature for each date calculated from six readings (two readings at each of three sites).

## Diet Composition

### Larval Diet

Larval fish utilized for diet analyses were taken from 1998 nighttime neuston net collections and additional early-evening (before sunset) neuston tows made once per week throughout the sampling season. These additional collections were made because larvae collected solely at night during 1997 rarely contained food items. Approximately 150 gizzard shad, 200 alewife, and 300 *Lepomis* spp. were examined for diet composition from both evening and nighttime collections. Of those collected at night, more than 66% of gizzard shad, 72% of alewife, and 65% of *Lepomis* spp. had empty guts. Though few larvae were collected prior to dark, of those, only 33% of alewife and 22% of *Lepomis* spp. had empty guts. However, like those collected at night, a large percentage (75%) of gizzard shad collected during the evening were also empty. Larval fish stomachs rarely contained more than one to six prey items (Table 5). In general, larval alewife and *Lepomis* spp. both appeared to be more active feeders than gizzard shad.

The diet of gizzard shad larvae (% composition by weight) was dominated by the cladoceran *Diaphanosoma* (Table 6). Copepod nauplii were also important in their diet, while cyclopoid copepods, *Bosmina*, and Daphnidae were less important. Larval gizzard shad showed overall electivity for three food items (Table 7). *Diaphanosoma* were the most selected food item among the zooplankton taxa that comprised >1% of the community by weight, while copepod nauplii and *Daphnia* were also either preferred or accessible prey. Copepod nauplii were greatly preferred among smaller gizzard shad larvae (7.1-9.0 mm TL), and electivity values for *Diaphanosoma* were higher among larger larvae (Table 8). Although not further evaluated,

approximately five individual rotifers were identified in the guts of three larval gizzard shad ranging in size from 7.5 to 17.5 mm TL.

The diet of larval alewife was also dominated by the cladoceran *Diaphanosoma* (Table 6). Cyclopoid copepods and *Bosmina* were also important in their diet, while copepod nauplii were less important. Larval alewife showed overall electivity for two food items (Table 7). As with gizzard shad, *Diaphanosoma* were the most selected food item among those zooplankton comprising >1% of the community by weight, while copepod nauplii were also either preferred or accessible prey. Small copepod nauplii were generally preferred among alewife larvae less than 15.0 mm TL, while electivity values for *Diaphanosoma* were consistently greater than zero for larvae of all sizes (Table 9).

Similar to both larval gizzard shad and alewife, the diet of *Lepomis* spp. larvae was dominated by *Diaphanosoma* (Table 6). Cyclopoid copepods, copepod nauplii, and *Bosmina* were also important in their diet, while chydorids were also occasionally observed in *Lepomis* spp. diets. Diet analysis results for larval *Lepomis* spp. came primarily from small *Lepomis* spp. larvae 5.1-7.0 mm TL. This size class accounted for more than 57% of the larval *Lepomis* spp. examined due to their abundance in the collections. Larvae >10 mm TL were rarely collected in limnetic larval samples. Larval *Lepomis* spp. showed overall electivity for three food items (Table 7). Again, *Diaphanosoma* were the most selected food item among zooplankton comprising >1% of the community by weight, while copepod nauplii and cyclopoid copepods were also either preferred or accessible prey. Small copepod nauplii were only preferred among smaller *Lepomis* spp. larvae (5.1-7.0 mm TL), while electivity values for *Diaphanosoma* were high among all size ranges of larvae (Table 10).

**Table 5.** Mean number of zooplankton prey items contained in larval fish stomachs. N represents the number of fish examined, excluding those larvae with empty guts.

<b>Prey Items</b>	<b>Gizzard shad N = 68</b>	<b>Alewife N = 62</b>	<b><i>Lepomis</i> spp. N = 59</b>
Cyclopoids	0.09	1.11	0.41
Nauplii	0.29	0.15	0.12
<i>Bosmina</i>	0.09	0.32	0.08
<i>Diaphanosoma</i>	0.94	3.47	2.59
Total Zooplankton	1.41	5.05	3.20



**Table 6.** Percent of diet by weight of food items in stomachs of larval gizzard shad, alewife, and *Lepomis* spp. from May through August 1998.

<b>Prey Taxa</b>	<b>Gizzard Shad % by weight</b>	<b>Alewife % by weight</b>	<b><i>Lepomis</i> spp. % by weight</b>
<b><u>Copepoda</u></b>			
Cyclopoid	6.9	19.2	6.2
Nauplii	15.4	4.8	2.5
<b><u>Cladocera</u></b>			
<i>Diaphanosoma</i>	63.7	61.2	82.8
<i>Bosmina</i>	6.2	14.9	5.1
Daphnidae	4.9	—	—
Chydoridae	—	—	3.4

**Table 7.** Strauss' linear food selection index of larval gizzard shad, alewife, and *Lepomis* spp. for major zooplankton taxa (> 1% of composition by weight). Percent composition by weight (%) of the reservoir zooplankton community is shown. N represents the number of fish examined, excluding those with empty guts.

<b>Prey Taxa</b>	<b>%</b>	<b>Shad N=68</b>	<b>Alewife N=62</b>	<b><i>Lepomis</i> spp. N=59</b>
<b><u>Copepoda</u></b>				
Cyclopoid	34	-0.27	-0.15	-0.28
Calanoid	3	-0.03	-0.03	-0.03
Nauplii	2	0.14	0.03	0.01
<b><u>Cladocera</u></b>				
<i>Diaphanosoma</i>	38	0.28	0.24	0.46
<i>Bosmina</i>	20	-0.13	-0.05	-0.15
Daphnidae	2	0.03	-0.02	-0.02
Leptodoridae	2	-0.02	-0.02	-0.02

**Table 8.** Food habits of larval gizzard shad showing size range of larvae, mean length of larvae in each size category, number of larvae examined in each size category (N), mean number of food items eaten per larvae, and Strauss' linear food selection index values by prey taxa and larval size.

<b>Size (mm)</b>	7.1-9.0	9.1-11.0	11.1-13.0	13.1-25.0
<b>Mean Length (mm)</b>	7.6	10.2	11.9	17.6
<b>N</b>	10	20	24	8
<b>Mean # Food Items</b>	1.6	2.2	1.2	2.5
<b><u>Copepoda</u></b>				
Cyclopoid	-0.34	-0.34	-0.17	-0.26
Calanoid	-0.03	-0.03	-0.03	-0.03
Nauplii	0.73	0.06	0.09	-0.02
<b><u>Cladocera</u></b>				
<i>Diaphanosoma</i>	-0.13	0.47	0.13	0.54
<i>Bosmina</i>	-0.20	-0.12	-0.11	-0.20
Daphnidae	-0.02	-0.02	0.12	-0.02
Leptodoridae	-0.02	-0.02	-0.02	-0.02

**Table 9.** Food habits of larval alewife showing size range of larvae, mean length of larvae in each size category, number of larvae examined in each size category (N), mean number of food items eaten per larvae, and Strauss' linear food selection index values by prey taxa and larval size.

<b>Size (mm)</b>	7.1-9.0	9.1-11.0	11.1-13.0	13.1-15.0	15.1-17.0	17.1-19.0	19.1-27.0
<b>Mean Length (mm)</b>	8.1	10.3	11.9	14.2	16.3	18.0	21.5
<b>N</b>	11	5	6	10	11	11	7
<b>Mean # Food Items</b>	1.9	2.6	3.0	2.7	6.2	8.5	10.4
<b><u>Copepoda</u></b>							
Cyclopoid	-0.24	0.06	0.06	-0.17	-0.30	-0.21	0.07
Calanoid	-0.03	-0.03	-0.03	-0.03	-0.03	-0.03	-0.03
Nauplii	0.15	-0.02	0.10	0.01	-0.02	-0.02	-0.02
<b><u>Cladocera</u></b>							
<i>Diaphanosoma</i>	0.36	0.03	0.11	0.23	0.40	0.13	0.20
<i>Bosmina</i>	-0.20	0.00	-0.20	0.00	-0.02	0.17	-0.16
Daphnidae	-0.02	-0.02	-0.02	-0.02	-0.02	-0.02	-0.02
Leptodoridae	-0.02	-0.02	-0.02	-0.02	-0.02	-0.02	-0.02

**Table 10.** Food habits of larval *Lepomis* spp. showing size range of larvae, mean length of larvae in each size category, number of larvae examined in each size category (N), mean number of food items eaten per larvae, and Strauss' linear food selection index values by prey taxa and larval size.

<b>Size (mm)</b>	5.1-7.0	7.1-9.0	9.1-11.0	11.1-13.0	13.1-20.0
<b>Mean Length (mm)</b>	6.4	8.0	10.7	12.1	16.2
<b>N</b>	35	13	4	4	5
<b>Mean # Food Items</b>	2.2	3.8	2.0	5.0	7.2
<b><u>Copepoda</u></b>					
Cyclopoid	-0.30	-0.31	-0.34	0.01	-0.12
Calanoid	-0.03	-0.03	-0.03	-0.03	-0.03
Nauplii	0.03	-0.02	-0.02	-0.02	-0.02
<b><u>Cladocera</u></b>					
<i>Diaphanosoma</i>	0.49	0.44	0.63	0.27	0.16
<i>Bosmina</i>	-0.17	-0.04	-0.20	-0.20	-0.20
Daphnidae	-0.02	-0.02	-0.02	-0.02	-0.02
Leptodoridae	-0.02	-0.02	-0.02	-0.02	-0.02

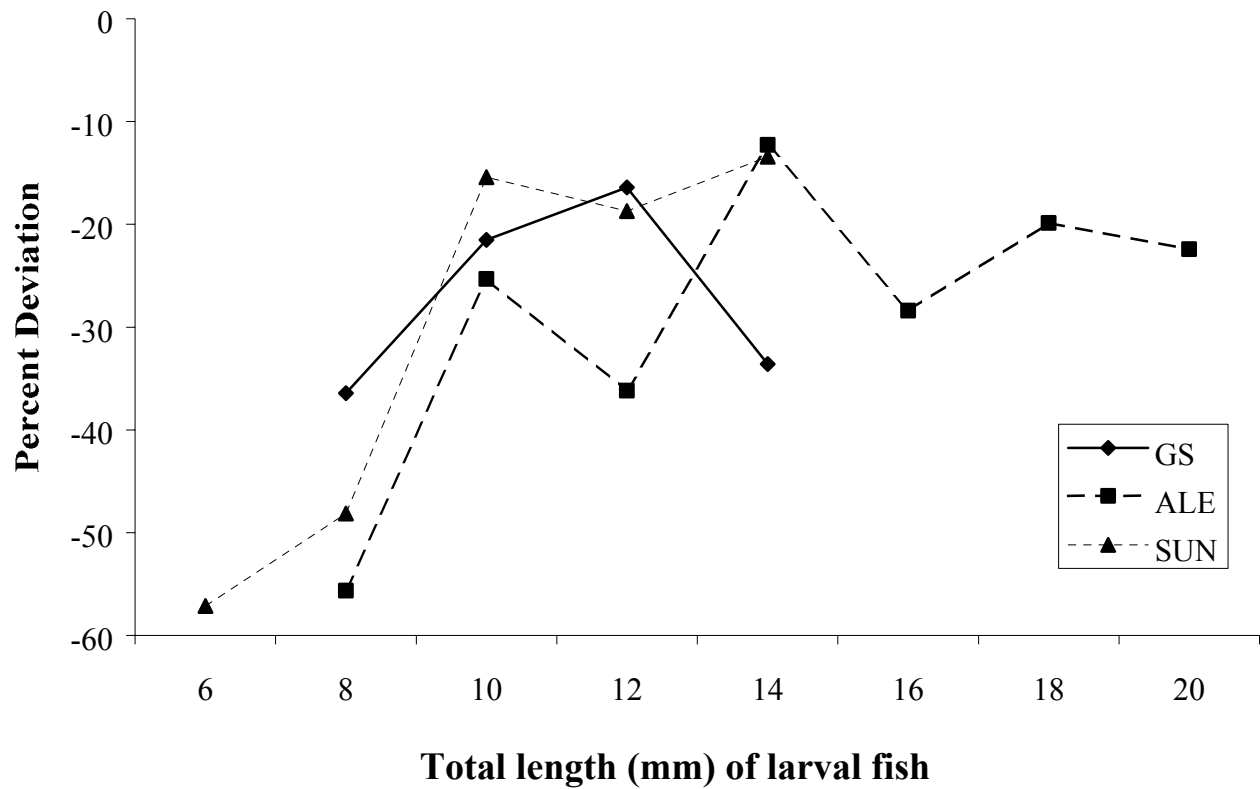
## Size-Selectivity

*Diaphanosoma* were chosen as an index of size-selectivity because of their broad length distribution (~ 0.24-1.34 mm TL), occurrence in the diets of all sizes and species of larvae examined, and their high abundance in the water column. Size-selective zooplanktivory by larval gizzard shad, alewife, and *Lepomis* spp. was apparent based on comparisons made between the size of *Diaphanosoma* in their guts and the mean size of *Diaphanosoma* available in the reservoir. The percent deviation in mean total length of *Diaphanosoma* in the gut contents of larvae from the mean total length of *Diaphanosoma* in the water column was used as a measure of size-selectivity (Figure 9). Without exception, larval gizzard shad, alewife, and *Lepomis* spp. less than 25 mm TL consumed *Diaphanosoma* significantly smaller than the mean size collected in limnetic zooplankton samples ( $P < 0.01$ ).

Comparisons made between the size of larvae and the size of *Diaphanosoma* in the diet showed that gizzard shad 7.5 to 25 mm TL did not consistently consume larger *Diaphanosoma* as larvae increased in size (Figure 10). In contrast, larval alewife and *Lepomis* spp. did show a positive relationship between size of larvae and size of *Diaphanosoma* consumed (Figure 10).

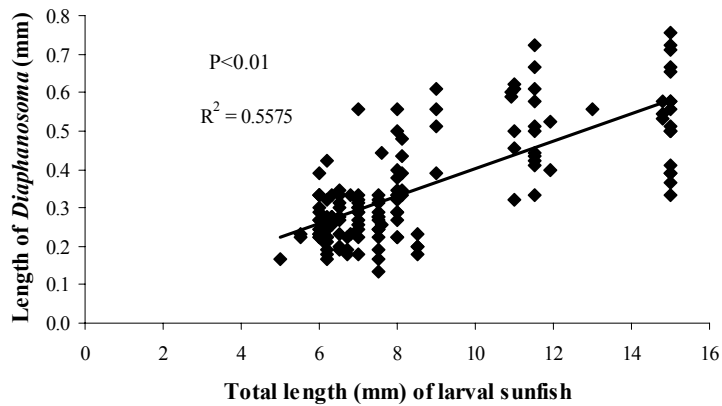
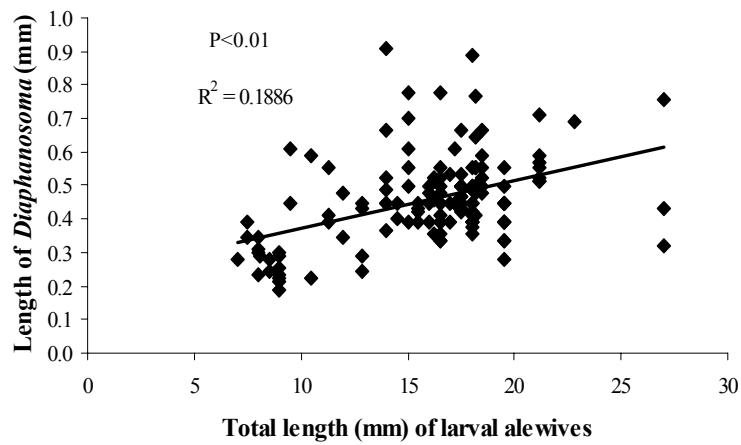
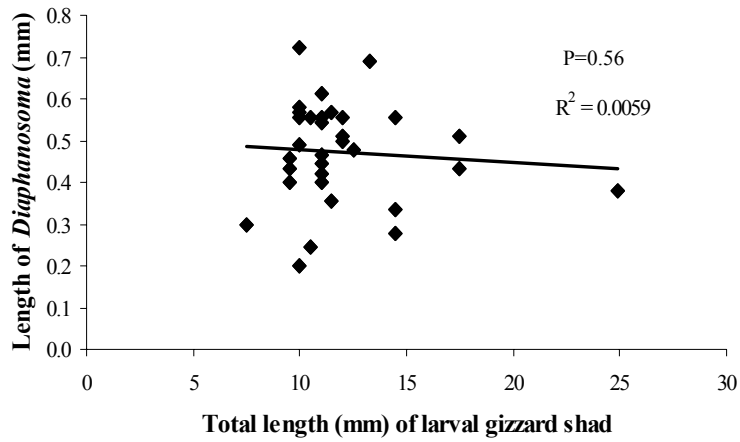
Size-selectivity by larval gizzard shad for smaller *Diaphanosoma* than were available in the water column led me to examine whether larval shad depleted small *Diaphanosoma* after peaks in shad abundance, thereby altering the size distribution of *Diaphanosoma* toward larger, morphologically unavailable sizes. I predicted that mean length of *Diaphanosoma* would increase in the week(s) following peaks in larval shad abundance due to a depletion of smaller individuals. Mean length of *Diaphanosoma* for each sampling date in both 1997 and 1998 was therefore compared to larval shad abundance (Figure 11). During 1997, larval shad peaked on consecutive weeks of June 25 and July 2. Mean length of *Diaphanosoma* collected in limnetic

samples did increase on July 2, but only to 0.725 mm, the maximum size eaten by larval shad (0.725 mm, versus 0.911 and 0.756 for larval alewife and *Lepomis* spp., respectively). Mean length of *Diaphanosoma* declined on the following sampling date of July 10 (Figure 11). During 1998, larval shad peaked on June 24, which was followed by a slight decrease in mean length of *Diaphanosoma* during the following sampling date of July 9 (Figure 11).

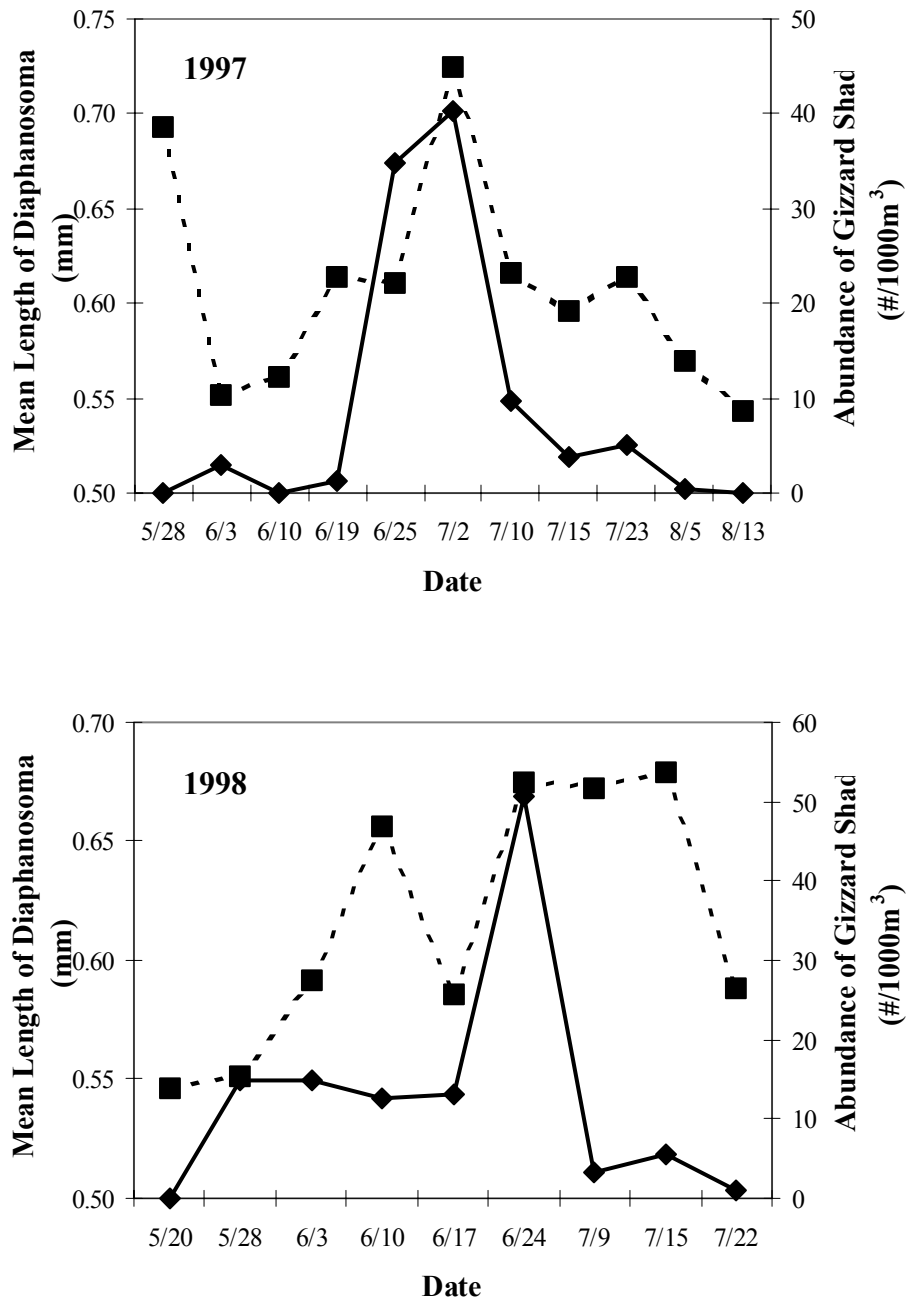


**Figure 9.** Percent deviation in mean total lengths of *Diaphanosoma* in the gut contents of larval gizzard shad, alewife, and *Lepomis* spp. from those in the water column. Note negative scale on y-axis (solid lines, diamonds=gizzard shad; dashed lines, squares=alewife; dotted lines, triangles=*Lepomis* spp.).





**Figure 10.** Comparisons between total length of larval gizzard shad, alewife, and *Lepomis* spp. and the length of *Diaphanosoma* consumed in their diets.



**Figure 11.** Comparison of mean length of *Diaphanosoma* collected in the water column and abundance of larval gizzard shad during 1997 and 1998 (solid lines, diamonds=gizzard shad; dashed lines, squares=*Diaphanosoma*).

## Diet Overlap

Larval fish examined in this study shared various components of the zooplankton community. Analyses of trophic overlap based on Schoener's index show high overlap in the diets of larval gizzard shad, alewife, and *Lepomis* spp. (Table 11). Index values greater than 0.6, indicating likely interactions between organisms (Zaret and Rand 1971), occurred in comparisons among all three taxa. Similar preferences for *Diaphanosoma* and daphnids resulted in the majority of the index value between gizzard shad and alewife, as well as alewife and *Lepomis* spp., while cyclopoid copepods and *Bosmina* heavily influenced diet overlap between gizzard shad and alewife. Although *Diaphanosoma* was the most important component in the diets of all three larval species, it also constituted one of the most abundant zooplankton prey categories found in the reservoir.

**Table 11.** Schoener's index of food resource overlap between larval gizzard shad and alewife, larval gizzard shad and *Lepomis* spp., and larval alewife and *Lepomis* spp. Values of  $|p_{xi} - p_{yi}|$  are inversely related to degree of overlap.

<b>Prey Taxa</b>	<b>Shad x Alewife <math> p_{xi} - p_{yi} </math></b>	<b>Shad x <i>Lepomis</i> spp. <math> p_{xi} - p_{yi} </math></b>	<b>Alewife x <i>Lepomis</i> spp. <math> p_{xi} - p_{yi} </math></b>
Cyclopoid	0.12	0.01	0.13
Nauplii	0.11	0.13	0.02
<i>Diaphanosoma</i>	0.05	0.17	0.22
<i>Bosmina</i>	0.09	0.01	0.10
Daphnidae	0.05	0.02	0.03
$\Sigma p_{xi} - p_{yi} $	0.41	0.34	0.50
<b>Index Value</b>	<b>0.79</b>	<b>0.83</b>	<b>0.75</b>

### ***Micropterus* spp. Diets**

A total of 88 larval and juvenile *Micropterus* spp. collected between May 20 and July 15, 1998 were examined for diet composition. Diet overlap with larval gizzard shad, as well as their utilization of larval gizzard shad as prey, was evaluated. Fish were collected from daytime seine samples taken in the littoral zone at the same sampling sites previously described, and ranged in size from 19 to 63 mm TL. All *Micropterus* spp. examined had food in their stomachs. The diets of *Micropterus* spp. examined included a diversity of zooplankton, terrestrial and aquatic insects, as well as larval fish (Table 12). Cyclopoid copepods, *Diaphanosoma* and daphnid cladocerans, and aquatic macroinvertebrates such as chironomids, were commonly found in more than 50% of the stomachs examined. In contrast to the diets of other larval fish species examined in this study, copepod nauplii were either undetected or absent from the diets of *Micropterus* spp. In addition, the large cladoceran *Leptodora* was present in almost 20% of *Micropterus* spp. stomachs, but was absent from the diets of gizzard shad, alewife, and *Lepomis* spp.

Based on results from Schoener's index analysis, it appears that age-0 *Micropterus* spp. do not compete with larval gizzard shad for food resources (Table 13). Out of a combined total of 11 different food categories consumed by *Micropterus* spp. and larval gizzard shad, these fish shared only four of those in their diets: *Bosmina*, cyclopoid copepods, *Diaphanosoma*, and daphnids. *Micropterus* spp. diets were dominated by aquatic insects (32%), while gizzard shad diets were dominated by *Diaphanosoma* (66%). This distinction led to a low overlap value of only 0.30.

Due to the gape limitations of larval shad used in this comparison, I separately examined the diets of small *Micropterus* spp. 19-30 mm TL (N=19) to utilize as a potentially better

indicator of trophic overlap. Unexpectedly, Schoener's index analysis indicated even weaker overlap between these groups, resulting in a value of 0.21. The diet of these smaller *Micropterus* spp. was dominated by daphnids (35%) and *Bosmina* (24%), which were nearly absent from the diet of larval shad (11% combined). Larval gizzard shad diets were dominated by *Diaphanosoma* (66%), which were similarly almost nonexistent in the diet of small *Micropterus* spp. (3%).

Zooplankton were important in the diets of all sizes of bass examined, but appeared to decline in importance as size of fish increased (Figure 12). Conversely, aquatic insects became increasingly important as bass size increased, accounting for approximately 70% by frequency and 50% by weight of the diets of larger juvenile bass. Larval fish became evident in bass diets after approximately 45 mm TL (Figure 12). However, only six of the *Micropterus* spp. examined contained any evidence of larval fish in their stomachs. In all cases, larval fish found in the stomachs of these bass were unidentifiable and consisted mostly of pieces of tissue and fin rays. No whole fish were found, and we were therefore unable to determine if these *Micropterus* spp. utilized larval shad in their diets.

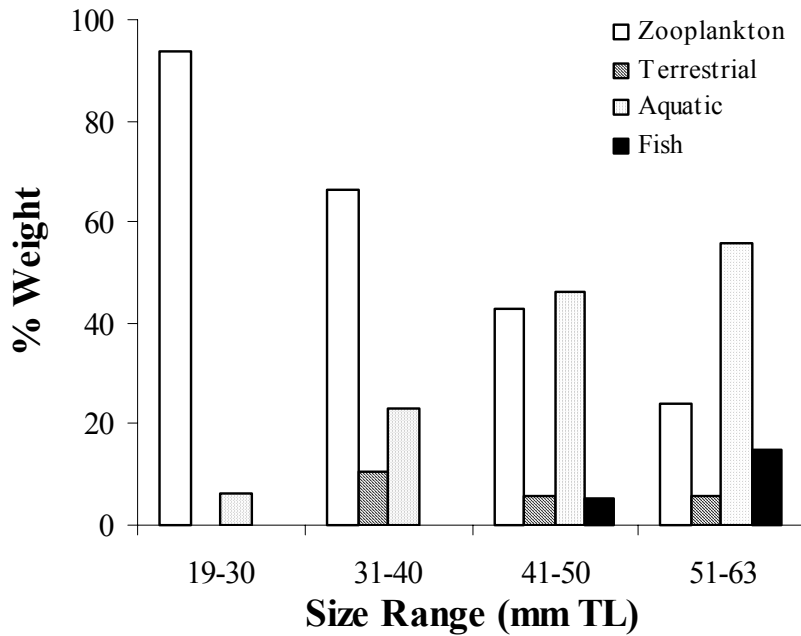
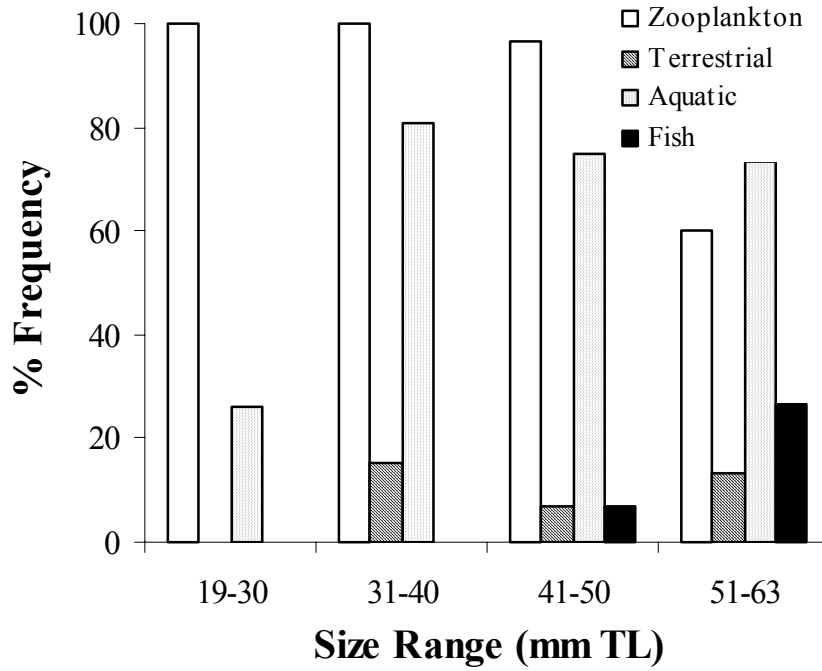
**Table 12.** Diet composition of age-0 *Micropterus* spp. (percent composition by frequency and weight). N represents the number of fish examined.

<b>Prey Taxa</b>	<b><i>Micropterus</i> spp. (N=88)</b>	
	<b>% frequency</b>	<b>% weight</b>
<b><u>Copepoda</u></b>		
Cyclopoid	59.1	6.0
Calanoid	11.4	6.8
Nauplii	0.0	0.0
<b><u>Cladocera</u></b>		
<i>Diaphanosoma</i>	52.3	13.5
<i>Bosmina</i>	27.3	5.4
Daphnidae	50.0	10.4
Chydoridae	29.5	4.8
Leptodoridae	18.2	10.5
<b><u>Insect</u></b>		
Terrestrial	9.1	6.0
Aquatic	65.9	32.4
<b><u>Fish</u></b>		
Unidentified	6.8	4.2

**Table 13.** Schoener's index of food resource overlap between larval gizzard shad and age-0 *Micropterus* spp. Values of  $|p_{xi} - p_{yi}|$  are inversely related to degree of overlap.

<b>Prey Taxa</b>	<b>Shad vs. <i>Micropterus</i> spp. <math> p_{xi} - p_{yi} </math></b>
<b><u>Copepoda</u></b>	
Cyclopoid	0.01
Calanoid	0.07
Nauplii	0.16
<b><u>Cladocera</u></b>	
<i>Diaphanosoma</i>	0.52
<i>Bosmina</i>	0.01
Daphnidae	0.05
Chydoridae	0.05
Leptodoridae	0.11
<b><u>Insect</u></b>	
Terrestrial	0.06
Aquatic	0.32
<b><u>Fish</u></b>	
Unidentified	0.04
$\Sigma p_{xi} - p_{yi} $	1.40
<b>Index Value</b>	<b>0.30</b>





**Figure 12.** Diet composition of age-0 *Micropterus* spp. by size range. Percent frequency and percent weight of general prey categories are shown (crustacean zooplankton, terrestrial insects, aquatic insects, and fish).

## Adult Alewife Diet

Seventy-two alewife ranging in size from 101 to 134 mm TL were examined for diet composition to determine if there were similarities between their diet and the diet of larval gizzard shad. All alewife examined had food in their stomachs. Alewife diet consisted primarily of cyclopoid copepods, *Diaphanosoma*, and aquatic and terrestrial insects (Table 14). *Bosmina* and leptodorids were less common, while calanoid copepods, copepod nauplii, daphnids, and chydorids were absent from the diets of these fish. Larval fish, which appeared to be *Lepomis* spp., were found in four of the fish examined.

Alewife utilize some of the same zooplankton taxa as larval gizzard shad (Table 15). These clupeids shared three zooplankton taxa in their diets: cyclopoid copepods, *Diaphanosoma*, and *Bosmina*. Adult alewife diet was dominated by cyclopoid copepods, while larval gizzard shad appeared to either avoid or not be able to capture this prey item. Although both fed heavily on *Diaphanosoma*, the resulting overlap value based on Schoener's index was only 0.38, suggesting low resource overlap and potential for competition. Despite similarities in the utilization of *Diaphanosoma*, it is likely that larval shad fed on smaller *Diaphanosoma* than did adult alewife. I did not measure sizes of food items in the stomachs of adult alewife I examined, however the median length of *Diaphanosoma* consumed by larval shad in this study (0.48 mm) was smaller than the median length of *Diaphanosoma* consumed by adult alewife in Claytor Lake (0.77 mm) as reported in Kohler (1980).

**Table 14.** Diet composition of alewife 101-134 mm TL (percent composition by frequency and weight). N represents the number of fish examined.

<b>Prey Taxa</b>	<b>Alewife (N=72)</b>	
	<b>% frequency</b>	<b>% weight</b>
<b><u>Copepoda</u></b>		
Cyclopoid	100.0	40.4
Calanoid	0.0	0.0
Nauplii	0.0	0.0
<b><u>Cladocera</u></b>		
<i>Diaphanosoma</i>	94.4	30.6
<i>Bosmina</i>	11.1	0.1
Daphnidae	0.0	0.0
Chydoridae	0.0	0.0
Leptodoridae	16.7	2.5
<b><u>Insect</u></b>		
Terrestrial	22.2	8.1
Aquatic	44.4	13.9
<b><u>Fish</u></b>		
Unidentified	5.6	3.9

**Table 15.** Schoener's index of food resource overlap between larval gizzard shad and adult alewife. Values of  $|p_{xi} - p_{yi}|$  are inversely related to degree of overlap.

Prey Taxa	Shad vs. Alewife $ p_{xi} - p_{yi} $
<b><u>Copepoda</u></b>	
Cyclopoid	0.33
Nauplii	0.16
<b><u>Cladocera</u></b>	
<i>Diaphanosoma</i>	0.35
<i>Bosmina</i>	0.06
Daphnidae	0.05
Leptodoridae	0.03
<b><u>Insect</u></b>	
Terrestrial	0.08
Aquatic	0.14
<b><u>Fish</u></b>	
Unidentified	0.04
$\Sigma p_{xi} - p_{yi} $	1.24
<b>Index Value</b>	<b>0.38</b>

## Zooplankton Distribution

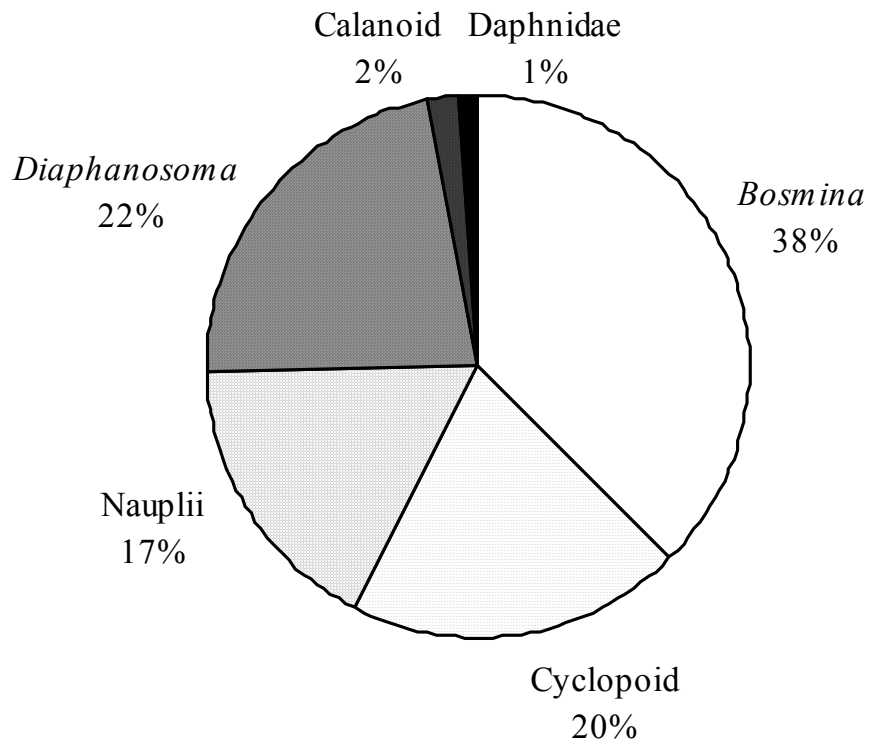
Spatial and temporal distributions of crustacean zooplankton were described to evaluate the availability of food resources for larval fishes in Claytor Lake. All taxa co-occurred at each of the three sampling sites on the reservoir. A total of eight taxa in both years were identified from zooplankton samples collected using vertical plankton net tows. Cladocerans were identified to family and copepods were identified as nauplii, calanoids, or cyclopoids. As with larval fish, nearshore versus offshore distributions of zooplankton did not differ significantly by location in 1997 ( $P=0.85$ ), and were therefore combined for all subsequent analyses. Zooplankton abundance was described in each year as percent by number for analyses of taxa composition.

### 1997 - General Description and Composition

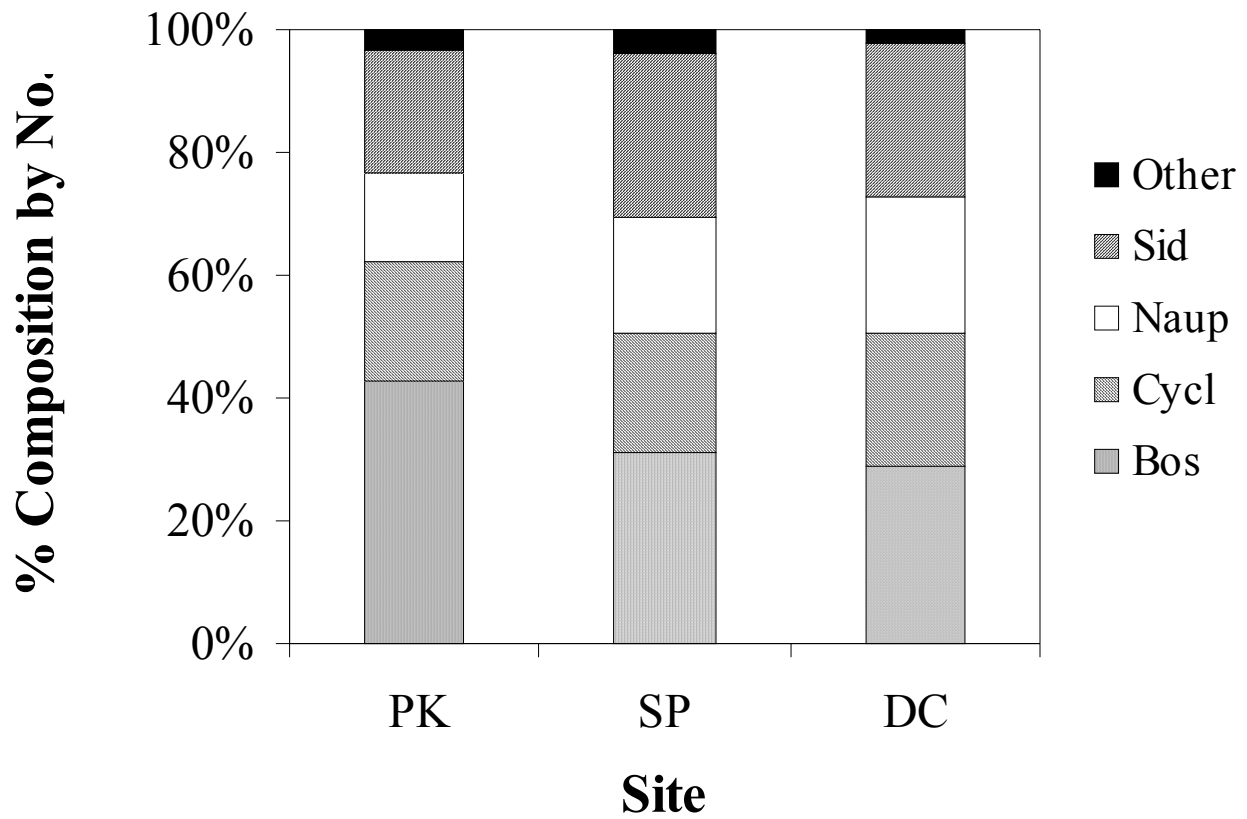
Pelagic crustacean zooplankton samples in 1997 were dominated by cladocerans, especially *Bosmina* and *Diaphanosoma* (38% and 22% by number, respectively). Additional cladoceran families examined included Daphnidae, which only accounted for 1% of the zooplankton composition. Cladocerans in the families Chydoridae and Leptodoridae were also collected in low percentages (<1% each), as were calanoid copepods (2%). Leptodorids, primarily *Leptodora kindtii*, and calanoid copepods were probably underrepresented in plankton tows. Although they likely occurred in greater numbers than I found, these zooplankters are very mobile, and their relatively large size limits their availability and importance as food for larval fishes (O'Brien 1979; Drenner and McComas 1980). In addition to abundant cladocerans, cyclopoid copepods and copepod nauplii accounted for over 37% of the zooplankton community by number (Figure 13). In general, three taxa combined, the cladocerans *Diaphanosoma* and

*Bosmina*, and cyclopoid copepods, represented the majority (79.6%) of zooplankton collected in 1997.

Crustacean zooplankton composition throughout the entire sampling area appeared to be very similar in 1997 based on results from the three individual sampling sites. As in the prior description of composition for all sites combined, the cladocerans *Diaphanosoma* and *Bosmina*, and cyclopoid copepods, accounted for a total of 81.9%, 76.6%, and 75.1% of the zooplankton composition at site PK, SP, and DC, respectively (Figure 14). *Bosmina* made up the greatest percentage by number at all three sites, while copepod nauplii were also an important part of the assemblage at all three sites.



**Figure 13.** Percent composition (by number) of major pelagic crustacean zooplankton during the 1997 sampling season. Values calculated as the mean percent composition from 167 lake-wide zooplankton tows.



**Figure 14.** Percent composition (by number) of major pelagic crustacean zooplankton at each site during the 1997 sampling season. Values represent the mean percent composition from approximately 55 samples taken at each site throughout the sampling season (Sid = *Diaphanosoma*).



### Community Composition and Abundance Patterns

Percent composition and related abundance of crustacean zooplankton were variable at different periods during the summer of 1997, resulting in fluctuations in the availability of various taxa as food resources for larval fish (Figure 15). *Bosmina* accounted for the majority of pelagic prey organisms in June (80-90% by number), but declined in importance by July; *Bosmina* declined to less than 1% of the total composition by mid July. As *Bosmina* declined in percent composition and abundance by mid July, *Diaphanosoma*, cyclopoid copepods, and copepod nauplii increased in total abundance during this same period. *Diaphanosoma* were most abundant from mid to late July (30-55% of the total composition), while cyclopoids and copepod nauplii increased in abundance towards the end of the summer, generally accounting for 30-40% each of the total community composition.

Although patterns of total zooplankton abundance were generally similar across sites (Figure 16), overall mean density appeared to decline progressively from uplake to downlake. Mean densities were significantly different across all sites. Densities were significantly higher at site PK than at both site SP ( $P < 0.01$ ) and site DC ( $P < 0.01$ ), while density at site SP was significantly higher than at site DC ( $P < 0.01$ ). Density estimates included the four major taxa previously described as well as less common taxa such as the cladocerans Daphnidae, Chydoridae, and Leptodoridae, in addition to calanoid copepods. Total crustacean zooplankton abundance early in the sampling season was heavily influenced by the dominance of *Bosmina*, and peaked at a density of 1,051/L on June 19. Overall zooplankton densities (mean of 625/L across all dates) declined somewhat during early July as *Bosmina* virtually disappeared from the system. From July 1 to August 12, total zooplankton composition was composed almost entirely of *Diaphanosoma*, cyclopoid copepods, and copepod nauplii. *Diaphanosoma* were most

abundant on July 15, but were found in relatively similar proportions to cyclopoid copepods and copepod nauplii the remainder of the summer. Although the zooplankton composition was dominated by only three major taxa during late summer, mean density never declined to less than 400/L throughout the reservoir.

Abundance of *Bosmina* at all sites was primarily limited to the period between early June and mid July, after which densities declined to less than 1/L (Figure 15). Mean densities reported for all dates combined are therefore somewhat misleading, as mean densities were much higher during the period when *Bosmina* were abundant in the system. Mean densities were significantly greater at site PK than at either of the other two sampling sites, and averaged approximately 825/L during the early part of the summer (Table 16). Mean densities for all dates combined were more than twice as abundant at site PK than at site SP ( $P < 0.01$ ), and more than three times as abundant at site PK than at site DC ( $P < 0.01$ ). Densities at sites SP and DC were not significantly different ( $P = 0.13$ ).

*Diaphanosoma* were most abundant at all three sites from late June to the end of the sampling season (Figure 15). Although mean densities at sites PK and SP were not significantly different in this year ( $P = 0.15$ ), it does appear that density of *Diaphanosoma* declined progressively downlake (Table 16). Density of *Diaphanosoma* was greatest at site PK on every date during the summer except one. Mean densities for all dates combined were almost twice as high at site PK than at site DC ( $P < 0.01$ ), and were significantly higher at site SP than at site DC ( $P = 0.014$ ).

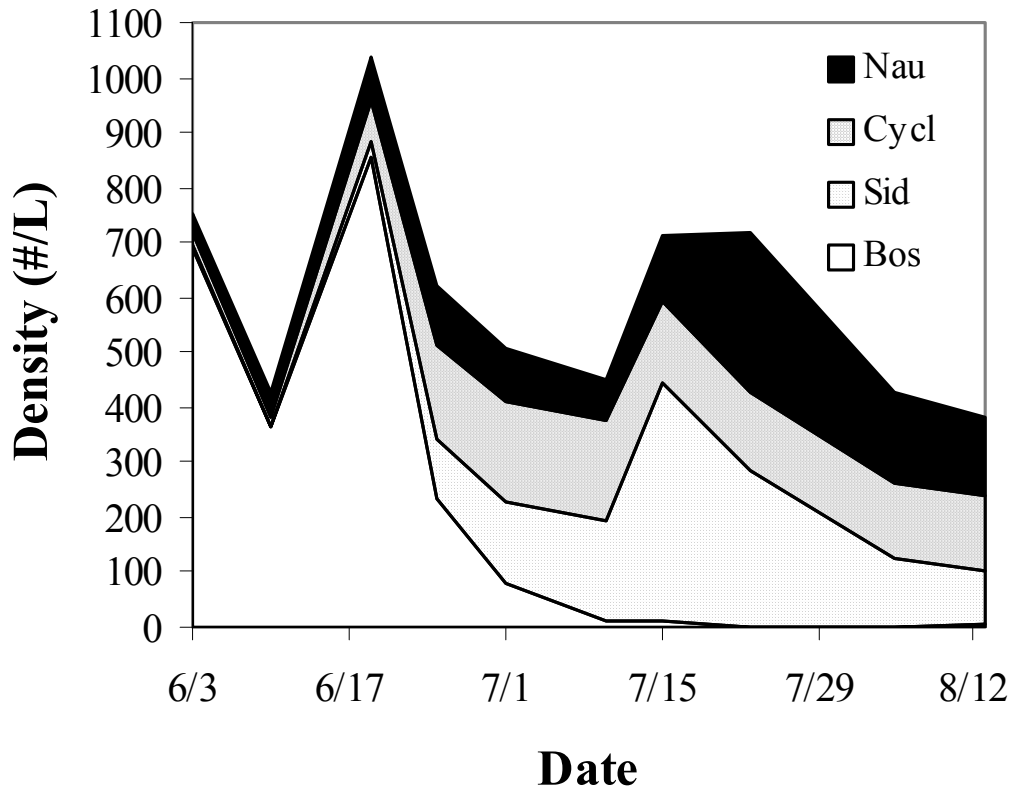
Similar to *Diaphanosoma*, abundance of cyclopoids increased concurrently with the decline in abundance of *Bosmina* during mid to late June (Figure 15). After late June, cyclopoid densities remained generally consistent, and ranged from approximately 100-300/L. Density of

cyclopoid copepods was greatest at site PK (Table 16), as mean densities for all dates combined were significantly higher at site PK than at both site SP ( $P<0.01$ ) and site DC ( $P<0.01$ ). Densities at sites SP and DC were not significantly different ( $P=0.83$ ).

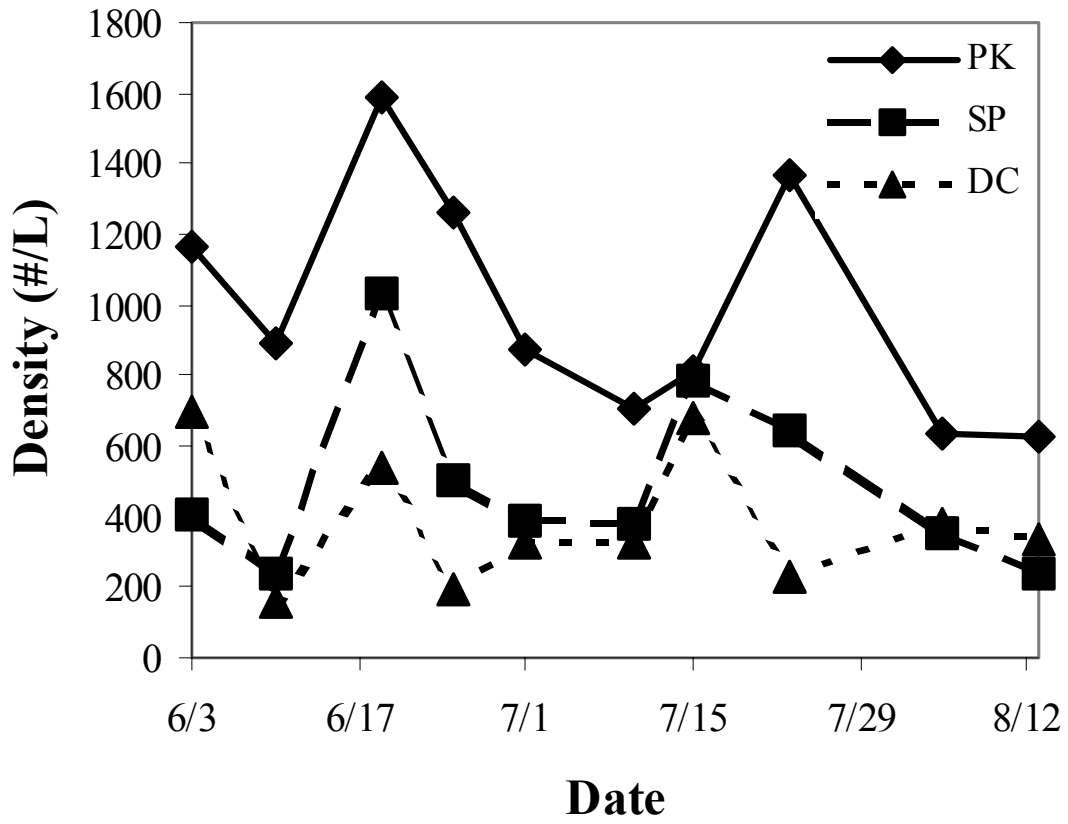
Copepod nauplii increased gradually in abundance from the start of the sampling season until mid July (Figure 15). They peaked in late July (approx. 500/L at site PK) and remained abundant the remainder of the summer. Again, site PK produced significantly greater densities of these zooplankters (Table 16). As with *Bosmina* and cyclopoid copepods, mean densities for all dates combined were significantly higher at site PK than at sites SP ( $P<0.01$ ) and DC ( $P<0.01$ ). Densities at sites SP and DC were not significantly different ( $P=0.79$ ).

**Table 16.** Mean densities by site of major crustacean zooplankton during 1997 (number of organisms/L). Values represent the mean of 53-57 samples collected at each site throughout the sampling season. Standard deviation is located in parentheses.

Site	<i>Bosmina</i>	<i>Diaphanosoma</i>	Daphnidae	Cyclopoid	Calanoid	Nauplii	Total
<b>PK</b>	419.5 (529.5)	192.4 (154.4)	18.0 (19.2)	193.0 (108.5)	16.1 (15.3)	141.2 (135.7)	982.4 (388.6)
<b>SP</b>	151.7 (300.0)	129.7 (174.6)	8.0 (6.9)	94.8 (72.8)	12.3 (9.9)	92.6 (62.1)	490.9 (311.5)
<b>DC</b>	112.2 (219.0)	96.7 (133.2)	1.4 (1.9)	84.9 (57.2)	8.9 (11.5)	85.9 (47.1)	391.0 (212.2)



**Figure 15.** Temporal density (#/L) and composition of major pelagic crustacean zooplankton during the 1997 sampling season (Sid = *Diaphanosoma*). Values on each date represent the mean of approximately 18 samples collected from all sites.

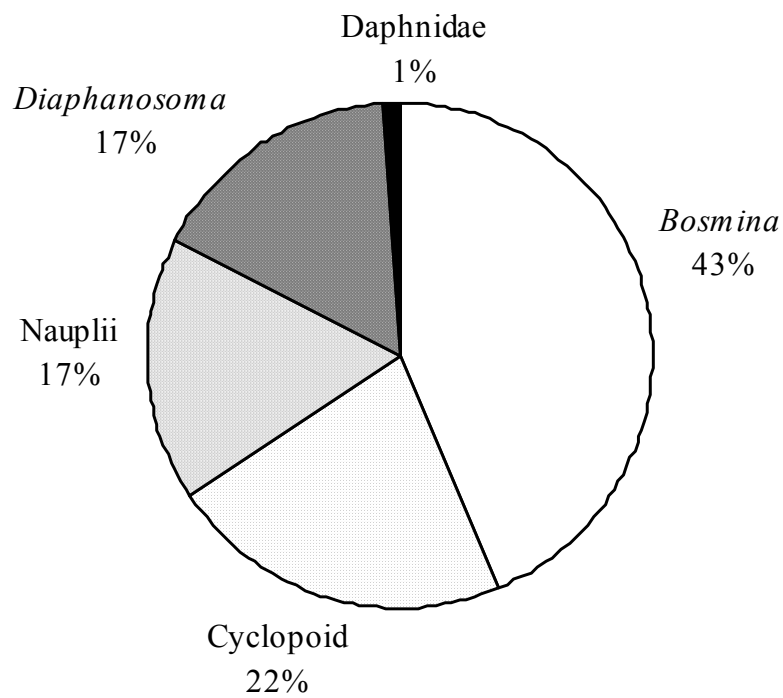


**Figure 16.** Temporal density (#/L) of total pelagic crustacean zooplankton by site during the 1997 sampling season.

## 1998 - General Description and Composition

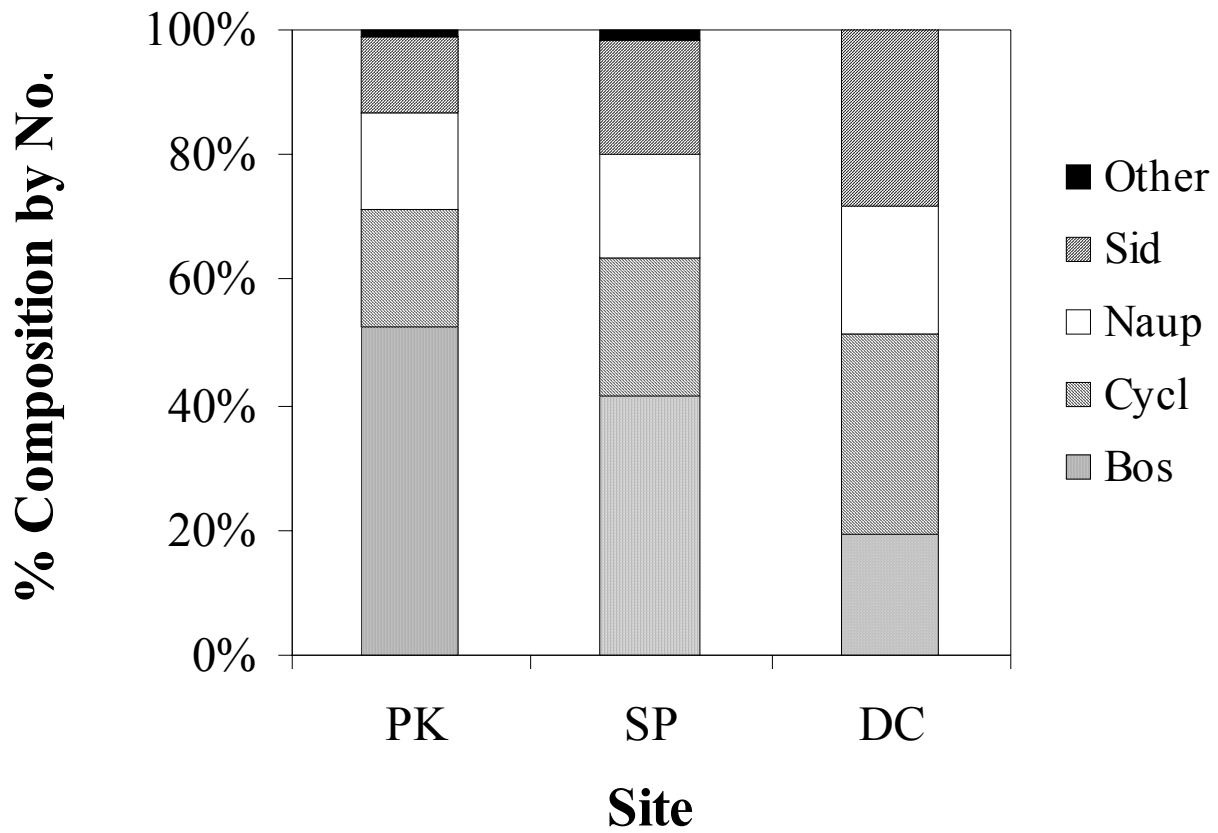
Pelagic crustacean zooplankton samples in 1998 were also dominated by cladocerans, including *Bosmina* and *Diaphanosoma* (Figure 17). Again, *Bosmina* was the most abundant taxon of zooplankton by number based on the total number of zooplankters collected throughout the sampling period (43.4% of the total community composition). However, in this year, *Diaphanosoma* were not as dominant and made up a smaller percentage by number than both cyclopoids and copepod nauplii. Additional cladoceran families examined in 1998 included Daphnidae, which only accounted for 1% of the zooplankton composition, and Chydoridae and Leptodoridae, which were also collected in low percentages (<1% each). In addition to abundant cladocerans, cyclopoid copepods and copepod nauplii combined accounted for over 38.3% of the zooplankton community by number.

Crustacean zooplankton percent composition in 1998 appeared to be similar throughout most of the reservoir based on results from the three individual sampling sites. *Diaphanosoma*, *Bosmina*, and cyclopoid copepods accounted for 82.8% at PK (Figure 18). *Bosmina* at this site were extremely important by number, accounting for more than half the total composition (52.2%). Results were similar at site SP, with *Bosmina*, *Diaphanosoma*, and cyclopoids accounting for 81.3% of the composition (Figure 18). Again, *Bosmina* were most abundant by number (41.25%) at this site. Zooplankton composition at site DC varied, with cyclopoids accounting for the greatest percentage (31.0%). *Bosmina* were less important at this site in 1998, accounting for only 19.1% by number (Figure 18). Copepod nauplii were also an important part of the assemblage by number at all three sites. Calanoid copepods were rarely observed at any site in 1998, and made up less than 1% of the total composition.



**Figure 17.** Percent composition by number of major pelagic crustacean zooplankton during the 1998 sampling season. Values calculated as the mean percent composition from 88 lake-wide zooplankton tows.





**Figure 18.** Percent composition (by number) of major pelagic crustacean zooplankton at each site during the 1998 sampling season (Sid = *Diaphanosoma*). Values represent the mean percent composition from approximately 30 samples taken at each site throughout the sampling season.

### Community Composition and Abundance Patterns

Percent composition and related abundance of crustacean zooplankton were also variable at different periods during the summer of 1998, resulting in fluctuations in the availability of various taxa as food resources for larval fish (Figure 19). *Bosmina* accounted for the majority of pelagic prey organisms in late May and early June (85% of the total community composition by number), but declined in importance to less than 1% by the end of June. As *Bosmina* declined in abundance by late June, *Diaphanosoma*, cyclopoid copepods, and copepod nauplii increased in percent composition and total abundance during this same period. *Diaphanosoma* were more important by number through late June (45%), while cyclopoids and copepod nauplii increased in both absolute and relative abundance towards the end of the summer, generally accounting for 60-70% of the zooplankton community combined.

Total crustacean zooplankton abundance peaked at 754/L early in the sampling season due to the predominance of *Bosmina* (Figure 19). Overall zooplankton densities declined by more than half during mid and late June as *Bosmina* virtually disappeared from the system. Recovery of the overall crustacean zooplankton population began by early July, with *Diaphanosoma*, cyclopoid copepods, and copepod nauplii increasing in abundance. Mean density of all zooplankters never declined to less than 265/L throughout the reservoir, and averaged 454/L across all dates. Although patterns of total zooplankton abundance were generally similar across sites (Figure 20), overall mean density appeared to decline progressively downlake (Table 17). Mean densities for all dates combined were significantly higher at site PK than at both sites SP and DC ( $P < 0.01$ ). However, densities at sites SP and DC were not significantly different ( $P = 0.40$ ).

As in 1997, mean densities reported for all dates combined are somewhat misleading, as mean densities were much higher during the period when *Bosmina* were abundant in the system. Although not significantly higher than site SP ( $P=0.12$ ), mean densities of *Bosmina* at site PK were more than eight times higher than at site DC ( $P<0.01$ ), and averaged approximately 970/L during the first three weeks of sampling (Table 17). Mean densities for all dates combined were also significantly higher at site SP than at site DC ( $P<0.01$ ).

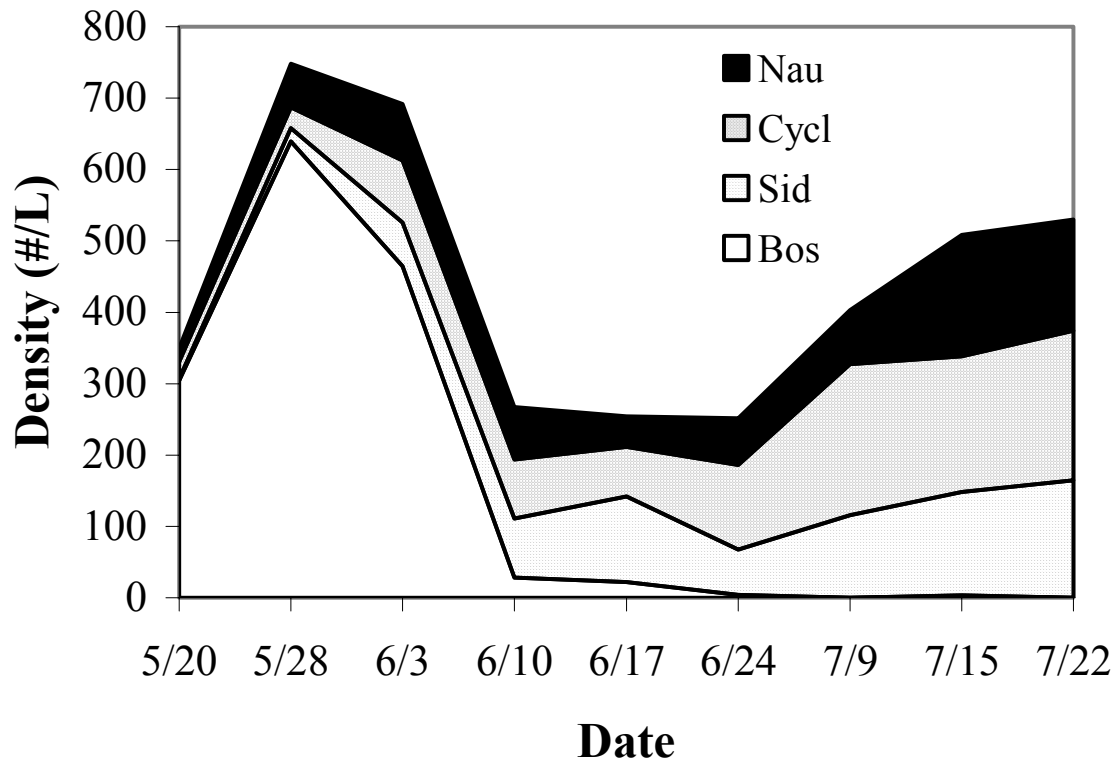
Density of *Diaphanosoma* increased gradually throughout the summer and peaked during the last weeks of the sampling season (Figure 19). Mean density at all three sites showed similar patterns in abundance, and were not significantly different between any of the three sites (Table 17).

Cyclopoids at all three sites showed similar patterns in abundance and peaked towards the end of the sampling season (Figure 19). Although similar in temporal pattern, mean density of cyclopoids at site PK was significantly higher than at the other downlake sample sites (Table 17). Mean densities for all dates combined were significantly different between sites PK and SP ( $P<0.01$ ), and sites PK and DC ( $P<0.01$ ). Densities at sites SP and DC were not significantly different ( $P=0.068$ ).

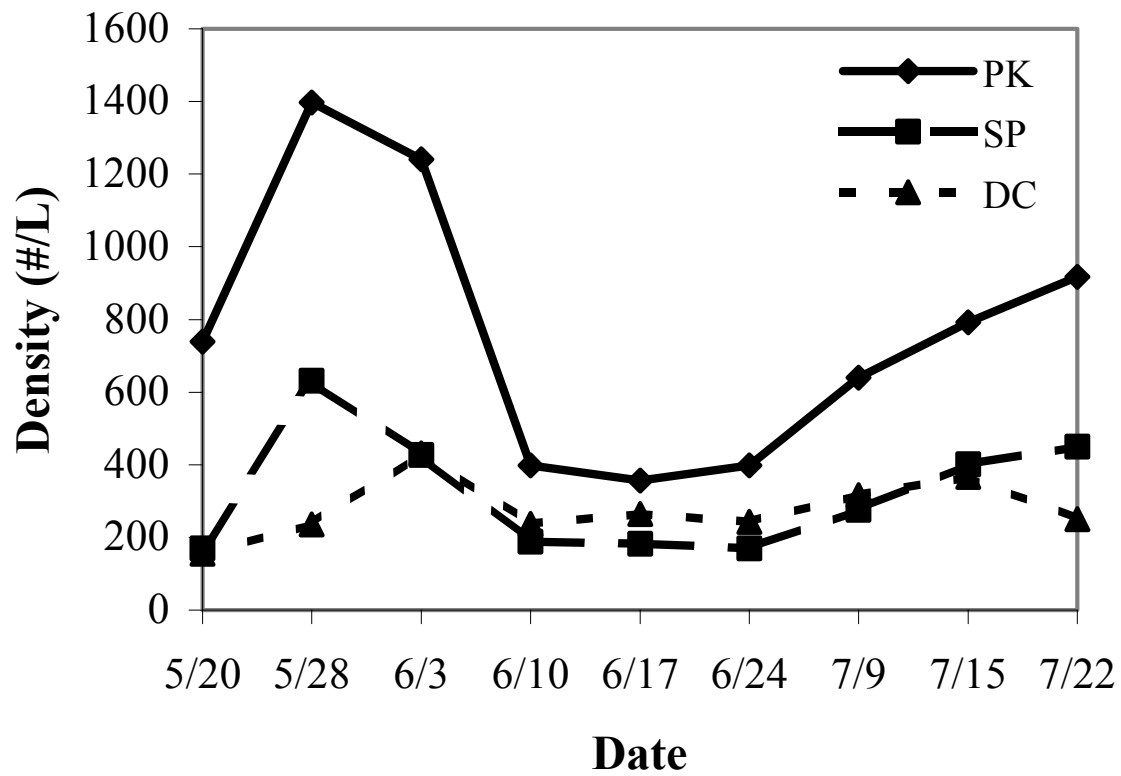
Patterns in abundance of copepod nauplii were generally similar and consistent throughout the summer between all sites (Figure 19). However, nauplii abundance peaked during the last two weeks of the sampling season at site PK (approx. 300/L), and mean densities were greatest at this site (Table 17). As with cyclopoid copepods, mean densities for all dates combined were significantly higher at site PK than at both sites SP and DC ( $P<0.01$ ). Densities at sites SP and DC were not significantly different ( $P=0.20$ ).

**Table 17.** Mean densities by site for major crustacean zooplankton during 1998 (number of organisms/L). Values represent the mean of 29-30 samples collected at each site throughout the sampling season. Standard deviation in parentheses.

Site	<i>Bosmina</i>	<i>Diaphanosoma</i>	Daphnidae	Cyclopid	Calanoid	Nauplii	Total
<b>PK</b>	439.8 (562.3)	100.8 (88.2)	8.0 (8.3)	156.6 (128.8)	2.9 (5.1)	131.7 (98.8)	842.3 (447.5)
<b>SP</b>	139.0 (225.5)	61.5 (56.1)	5.6 (7.0)	73.9 (62.2)	1.3 (2.7)	54.7 (38.2)	337.3 (213.8)
<b>DC</b>	53.0 (82.3)	77.1 (58.9)	1.7 (3.0)	86.1 (60.5)	0.8 (2.4)	56.2 (38.3)	277.7 (101.2)



**Figure 19.** Temporal density (#/L) and composition of major pelagic crustacean zooplankton during the 1998 sampling season (Sid = *Diaphanosoma*). Values on each date represent the mean of 9 to 18 samples collected from all sites.



**Figure 20.** Temporal density (#/L) of total major pelagic crustacean zooplankton by site during the 1998 sampling season.

## Response of Zooplankton to Peak Larval Fish Densities

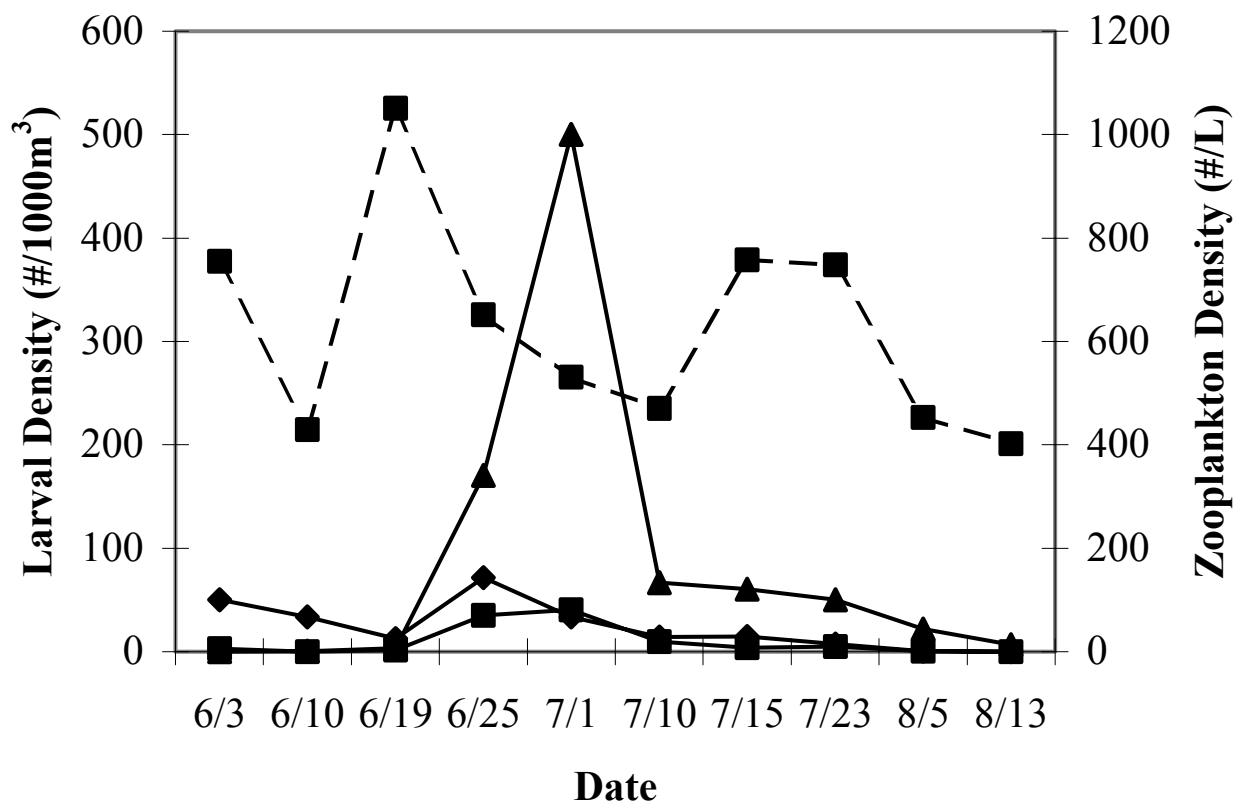
I examined the temporal pattern of crustacean zooplankton abundance versus peak larval fish densities in 1997 and 1998 to determine if zooplankton populations appeared to respond negatively to peaks in larval fish abundance. This was based on reports that zooplanktivory by larval gizzard shad during periods of peak abundance can have significant negative impacts on the abundance of zooplankton, thereby limiting the availability of this food resource for other larval fishes and adult zooplanktivores (Drenner et al. 1982; DeVries et al. 1991; DeVries and Stein 1992). I determined periods of peak gizzard shad and total larval fish abundance for both years using Tukey's multiple comparison analyses. Once peak larval fish densities were identified during both years, I also used Tukey's multiple comparisons to examine the response of zooplankton abundance during those time periods. I examined three successive sampling events, where  $x$  refers to the date of peak larval abundance:  $x - 1$  week,  $x$ , and  $x + 1$  week.

For 1997, I identified significant peaks in larval shad abundance during the weeks of June 25 and July 1 (Figure 21). Also, I identified a significant peak in total larval fish abundance on July 1. I therefore analyzed significant changes in the density of major crustacean zooplankton taxa (*Bosmina*, *Diaphanosoma*, cyclopoid copepods, copepod nauplii, and total zooplankton) from June 19 to July 1, and also from June 25 to July 10. *Bosmina* and total zooplankton both showed significant declines in abundance ( $P < 0.01$ ) between June 19 and July 1, while only *Bosmina* declined from June 25 to July 10. Other zooplankton taxa either significantly increased or showed no response during these time periods.

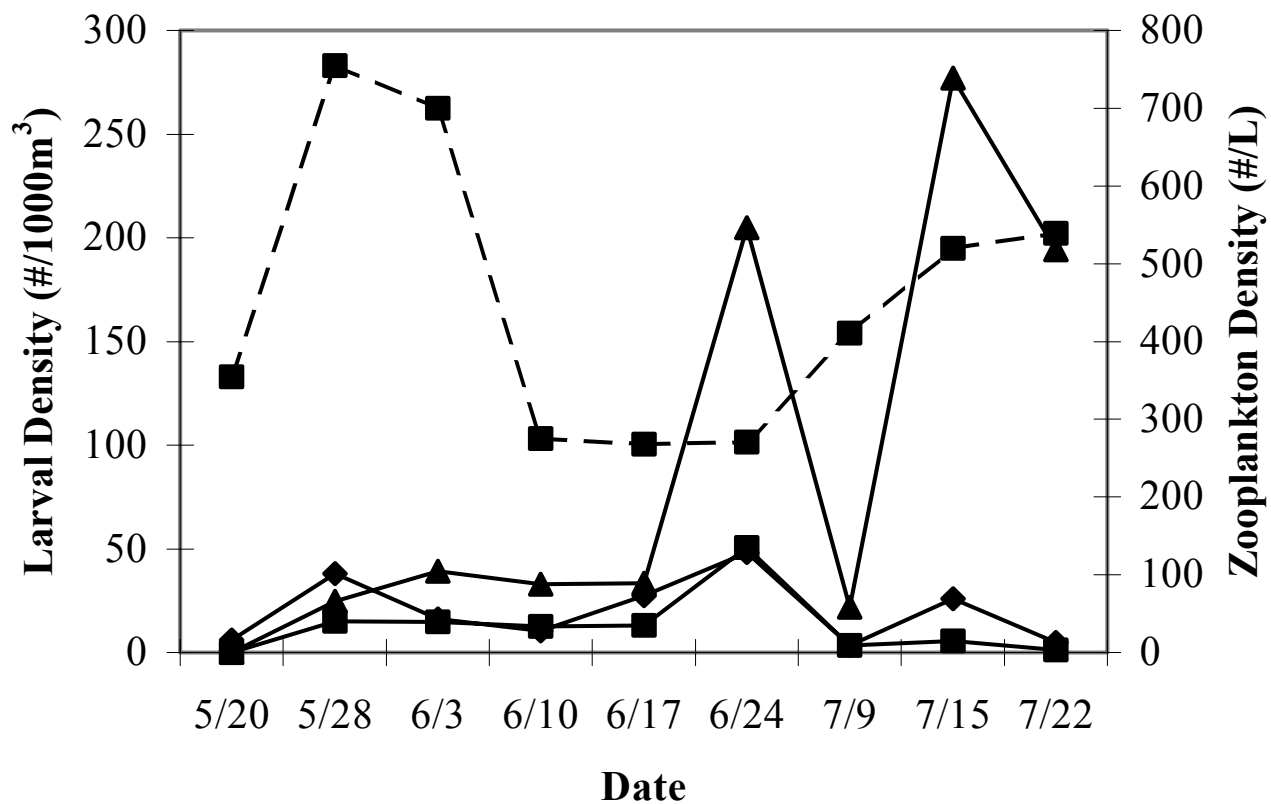
For 1998, I identified a significant peak in larval shad abundance during the week of June 24 (Figure 22). Additionally, I identified significant peaks in total larval fish abundance on both June 24 and July 15. I then analyzed changes in the density of major crustacean zooplankton

taxa (*Bosmina*, *Diaphanosoma*, cyclopoid copepods, copepod nauplii, and total zooplankton) from June 17 to July 9, and again from July 9 to July 22. As in 1997, *Bosmina* showed a significant decline in abundance ( $P < 0.01$ ) between June 17 to July 9. Other zooplankton taxa, including total zooplankton, either significantly increased or showed no response during this time. In response to the second peak in total larval fish density during the week of July 15, no zooplankton taxa significantly declined in abundance. By this date, approximately 90% of the larval fish collected were *Lepomis* spp.





**Figure 21.** Larval fish and total zooplankton densities during the 1997 sampling season (solid line and squares = gizzard shad, solid line and diamonds = alewife, solid line and triangles = *Lepomis* spp., dashed line and squares = zooplankton).



**Figure 22.** Larval fish and total zooplankton densities during the 1998 sampling season (solid line and squares = gizzard shad, solid line and diamonds = alewife, solid line and triangles = *Lepomis* spp., dashed line and squares = zooplankton).

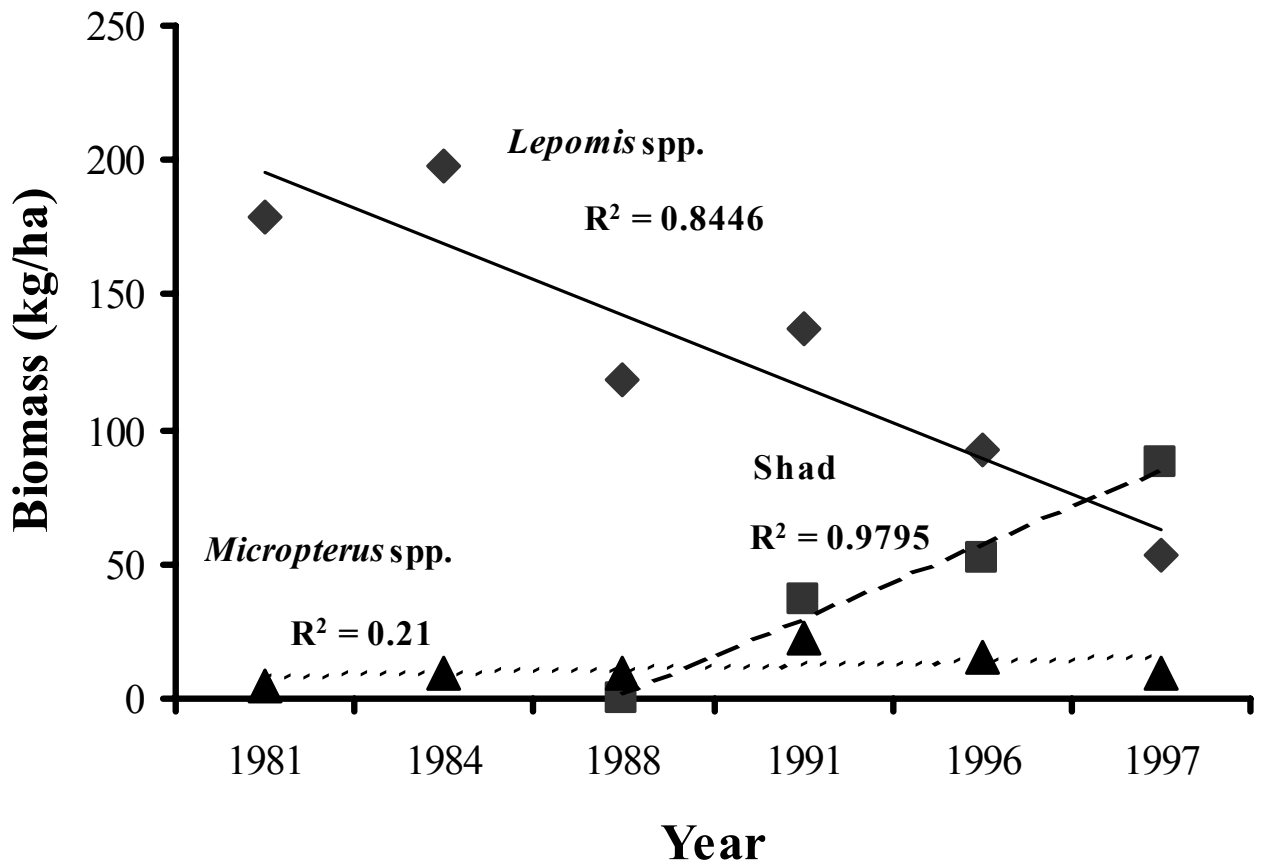
## **Response of Resident Fish Populations to Gizzard Shad Introduction**

Potential negative impacts by larval gizzard shad due to competition with resident fish species in Claytor Lake would likely be evidenced through declines in growth and/or abundance of competitors. As other researchers have suggested (Davies et al. 1982; Hill 1983; Mosher 1983; Neuswanger 1983), I predicted that biomass and early growth of *Micropterus* spp. and *Lepomis* spp. would have declined since gizzard shad became established in Claytor Lake. Available data collected on Claytor Lake by the VDGIF and other researchers have been summarized for the following analyses. Unfortunately, standing stock and growth data for alewife were unavailable, and limited any analysis of changes in biomass or growth rates for this resident fish species before and after gizzard shad establishment.

### **Trends in Biomass of Gizzard Shad, *Lepomis* spp., and *Micropterus* spp.**

Cove rotenone data collected between 1981 and 1997 by the VDGIF showed that gizzard shad biomass in Claytor Lake has steadily increased since their first appearance in 1988 ( $P=0.06$ ) (Figure 23). By 1997, they constituted more than 35% (88 kg/ha) of littoral fish biomass (V. DiCenzo, VDGIF unpublished data). Coincidentally, since 1984, biomass of *Lepomis* spp. has steadily declined from a high of 198 kg/ha, prior to gizzard shad introduction, to less than 53 kg/ha in 1997 ( $P=0.01$ ) (Figure 23). Although these data do not differentiate between young-of-year and adult *Lepomis* spp. (except data collected in 1997), overall *Lepomis* spp. biomass has decreased steadily since the early 1980's. By comparison, there have been no significant changes in the biomass of *Micropterus* spp. since 1981 ( $P=0.33$ ) (Figure 23). Total standing stock of the littoral fish community has remained remarkably consistent over this same time

period, averaging about 265 kg/ha (Bonds 2000). The only two littoral fish species to show declines in biomass were carp (-77%) and *Lepomis* spp. (Figure 23) (Bonds 2000).



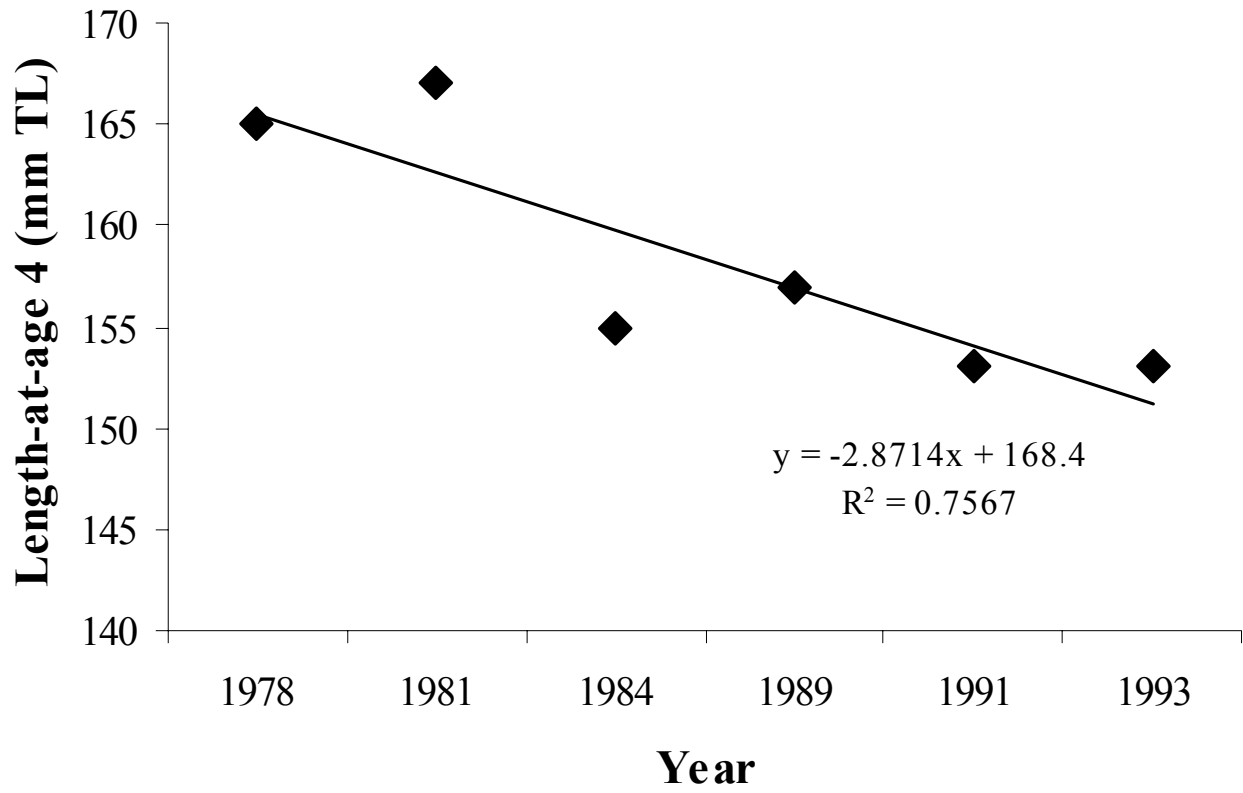
**Figure 23.** Total biomass (kg/ha) estimates from cove rotenone surveys for gizzard shad, *Lepomis spp.*, and *Micropterus spp.* Squares represent gizzard shad, diamonds represent *Lepomis spp.*, and triangles represent *Micropterus spp.*

### **Trends in Growth Rates of *Lepomis* spp. and *Micropterus* spp.**

Unfortunately, age and growth data for *Lepomis* spp. in Claytor Lake was somewhat incomplete for young fish, but complete length-at-age data was available for six years between 1978 and 1993 for age-4 fish. Length-at-age for 4-year-old *Lepomis* spp. significantly declined based on a regression analysis of the time period examined ( $P=0.025$ ; Figure 24). Based on very sparse data for growth of young *Lepomis* spp., lengths at age 1 were 53 and 59 mm TL for fish examined in 1984 (prior to gizzard shad introduction) and 1993 (post gizzard shad introduction), respectively. From these limited data, I was unable to determine whether early growth rates for young *Lepomis* spp. have been adversely impacted by competitive interactions with gizzard shad.

Prior to gizzard shad establishment in Claytor Lake, Kohler (1980) determined growth rates of all three species of *Micropterus* spp. collected during his research in 1976-1978. Because no individual fish, back-calculated lengths-at-age data were available from previous studies, percent change in mean back-calculated lengths-at-age was determined for fish collected by Bonds (2000), and for those collected by Kohler (1980). This information was used to compare growth rates of *Micropterus* spp. before and after gizzard shad establishment. Growth rates for all three species of *Micropterus* spp. and all age classes studied (1-4) have declined since gizzard shad establishment. Percent change in mean back-calculated lengths-at-age before and after gizzard shad introduction ranged from -5% for age-1 largemouth bass to -31% for age-4 smallmouth bass. In addition, percent change in mean annual growth increment in back-calculated lengths-at-age before and after gizzard shad introduction ranged from -5% for age-1 largemouth bass to -50% for age-4. Largemouth bass showed an average decrease of nearly 7% in growth for the first four age classes. Growth of smallmouth bass for ages one and two have

both declined nearly 18%, growth of age-3 smallmouth bass has declined by 25%, and growth rates of smallmouth bass ages 4-7 have decreased an average of 33%. Spotted bass growth has also declined an average of almost 24% for ages 1-6 (Bonds 2000). For a more detailed discussion of changes in adult piscivore growth rates before and after gizzard shad establishment in Claytor Lake, please refer to Bonds (2000).



**Figure 24.** Length-at-age for 4 year old *Lepomis* spp. in Claytor Lake from 1978 to 1993.



## DISCUSSION

### Larval Distribution

The opportunity for feeding competition among larval gizzard shad, alewife, and *Lepomis* spp. does exist in Claytor Lake, as all three zooplanktivorous fishes co-occurred both temporally and spatially in the reservoir during both years of this study. The presence of these fish in the limnetic zone of the lake extensively overlapped and extended throughout much of the summer. Larval clupeids and *Lepomis* spp. were generally present from late May to early August. However, larval clupeids generally appeared before *Lepomis* spp. in early samples, while larval *Lepomis* spp. were still present in August after clupeids disappeared from these later samples. Peak densities of all three fish species also coincided during both years. Significant peaks occurred during the same late June to early July time period during 1997 and 1998, while *Lepomis* spp. showed another later peak in July 1998. The high degree of temporal overlap shown by all three species increases the potential for interspecific competition.

It is probable that the main peak in larval abundance witnessed in 1997 was directly related to an increase in water temperatures during the weeks of June 10 to June 25 (Figure 2). Surface water temperatures increased from approximately 20° C to greater than 27° C during this time period, likely stimulating increased spawning activity among the fish studied. Miller (1960) and Bodola (1966) observed gizzard shad spawning during rising temperatures, with most activity occurring above 18° C. Tisa (1988) reported that gizzard shad spawned at 17-29° C in Smith Mountain Lake, Virginia, while alewife similarly spawned at 18-29° C. Nigro and Ney (1982) observed that the temperature at which alewife spawning began in Claytor Lake was 16-18° C and continued until waters reached 27° C. Although *Lepomis* spp. may spawn at multiple

times throughout the summer, Lemly and Dimmick (1982) observed the first of two major spawning peaks in three North Carolina lakes when water temperatures were between 20-22° C. Earlier studies suggest bluegill begin spawning at temperatures of 17-27° C in Ohio (Morgan 1951) and 18-21° C in California (Moyle 1976).

Gizzard shad and bluegill are hatched in the littoral zone and move offshore soon after hatching (Miller 1960; Bodola 1966; Werner 1969). While alewife larvae have been reported to remain in nursery habitat until approximately 19 mm TL, when they then move offshore to deeper water (Wagner 1972; Scott and Crossman 1973; O’Gorman 1983), results from this study as well as those from Tisa and Ney (1991) suggest alewife larvae as small as 5-10 mm TL may inhabit the offshore, limnetic zone. Gizzard shad will remain in the limnetic zone as sight-feeding zooplanktivores until reaching a total length of approximately 20 mm (Kutkuhn 1957; Cramer and Marzolf 1970), at which time they begin to switch to filter-feeding omnivores (Yako et al. 1996). Bluegills (and other *Lepomis* spp.) also remain in the limnetic zone to feed on zooplankton after leaving their littoral nests at approximately 6 mm TL (Werner 1969; Werner and Hall 1988). However, at total lengths of between 10 and 25 mm, they return to the littoral zone to begin feeding on macroinvertebrates (Werner 1969; Werner and Hall 1988). Bluegills usually begin spawning several weeks after gizzard shad, and their entry into the limnetic zone also usually follows that of gizzard shad (Storck et al. 1978; Beard 1982; DeVries and Stein 1992). Welker et al. (1994) concluded that co-occurrence of larval gizzard shad and larval bluegills in the limnetic zone of Lake Shelbyville, Illinois was limited to a 3-week period during the summer. DeVries and Stein (1992) also found that larval gizzard shad and larval bluegill typically overlapped in the limnetic zone of Kokosing Lake, Ohio for only a 2 to 4-week period during the summer. During both years of their study, bluegill spawned later than gizzard shad,

and larval bluegill arrived in the limnetic zone as crustacean zooplankton densities were dramatically declining. The exploitative feeding competition witnessed by both Welker et al. (1994) and DeVries and Stein (1992) was a result of gizzard shad entering the limnetic zone in high densities and depressing zooplankton populations before the arrival of *Lepomis* spp. In both of these studies, larval gizzard shad peaked approximately two weeks before larval *Lepomis* spp. In Smith Mountain Lake, Virginia, larval gizzard shad peaked two weeks before larval alewife, though spatial segregation of these clupeids in this reservoir limited competitive interactions (Tisa and Ney 1991).

It is unlikely that zooplanktivory by larval gizzard shad alone, or larval gizzard shad and alewife combined, prior to the arrival of larval *Lepomis* spp. in the limnetic zone, resulted in exploitative feeding competition. At this time (late May and early June), densities of larval gizzard shad and alewife were low while crustacean zooplankton abundance was at its seasonal high in both 1997 and 1998.

Even peak larval gizzard shad densities were extremely low throughout the season compared to those documented in other reservoir systems. Larval gizzard shad in high densities appear to compete with, or outcompete, the larvae of other species for food resources during critical larval stages. Much of this research has been performed in small, shallow, turbid, and eutrophic lakes in Ohio where gizzard shad dominate the fish biomass. Peak densities of larval gizzard shad in these systems have been reported as high as 84/m<sup>3</sup> in both Kokosing Lake (DeVries and Stein 1992) and Clark Lake, Ohio (Dettmers and Stein 1992). In general, density estimates from other midwestern and southeastern reservoirs have been reported as two to three orders of magnitude higher than the peak of 40-60 fish/1000m<sup>3</sup> (0.04-0.06 fish/m<sup>3</sup>) found in

Claytor Lake during 1997 and 1998 (20-25 fish/m<sup>3</sup>, Mayhew 1977; 10 fish/m<sup>3</sup>, Downey and Toetz 1983; ~4 fish/m<sup>3</sup>, Matthews 1984; 0.5 fish/m<sup>3</sup>, Tisa et al. 1985).

Not only were larval gizzard shad densities in Claytor Lake low compared to studies on other reservoir populations, but they were also significantly lower than both larval alewife and larval *Lepomis* spp. densities within the same reservoir. Mean abundance of larval gizzard shad ranged from 1.5 to 2.5 times lower than the mean abundance of larval alewife, and was approximately 7.5 to 9 times lower than that of larval *Lepomis* spp. during the two years of my study. In contrast, larval gizzard shad density was usually higher than alewife density in Smith Mountain Lake, Virginia (Tisa 1988). Welker et al. (1994) found gizzard shad densities in Lake Shelbyville, Illinois to be two orders of magnitude higher than bluegill density on all dates. Density of larval gizzard shad in Claytor Lake during the period of peak abundance in 1997 was also less than larval alewife (41 and 65 fish/1000m<sup>3</sup>, respectively), while peak abundance in 1998 was very similar (51 and 48 fish/1000m<sup>3</sup>, respectively). In contrast to other studies of larval gizzard shad and bluegill, peak abundance of larval gizzard shad was significantly less than larval *Lepomis* spp. during both years in Claytor Lake. In fact, peak abundance was approximately one eighth that of the peak larval *Lepomis* spp. density in 1997, and one fourth that of the peak larval *Lepomis* spp. density in 1998.

It is possible, yet unlikely, that my sampling regime underestimated actual density of larval gizzard shad, and potentially other larval fishes. As previously stated, although I sampled larval fishes spatially throughout much of Claytor Lake, I did not extend my efforts to the extreme uplake regions of the reservoir (uplake of the confluence of Peak Creek). There did appear to be a general spatial trend in larval fish densities in Claytor Lake, but the trend was actually towards higher larval density downlake. In his study of larval alewife in Claytor Lake,

Nigro (1980) similarly found the greatest densities of these larvae at sampling sites located within 4.0 km of the dam. In fact, the highest measured median density during his study was at the site closest to the dam. Densities of larval gizzard shad and *Lepomis* spp., as well as alewife, followed this same pattern during my study, and were almost always consistently higher at the midlake and downlake sites compared to the Peak Creek site. It is doubtful, therefore, that higher larval gizzard shad densities would have existed in the far uplake regions of Claytor Lake not examined in this study.

It is also possible, however, that my use of the 0.5-m x 1.0-m neuston net might have resulted in underestimates of larval fish abundance. The one disadvantage of using this particular net was that it only sampled the upper 0.5 m of the water column. Obviously, this limited my collections to only those larvae that were truly surface-oriented at night. I did not employ any other method to collect limnetic larval fish at greater depths, but as previously stated, significant numbers of shad and alewife had previously been sampled at a depth of 1 m in nearby Smith Mountain Lake, Virginia (Tisa 1988), while larval gizzard shad were almost exclusively distributed in the top 1 m of the water column in Kansas reservoirs (Willis 1987). Tisa (1988) also collected larval clupeid samples at 3 m and 5m depth in Smith Mountain Lake. Few larvae were found at 5 m during the first year of that study, and sampling at that depth was therefore discontinued the second year; densities of larvae did not differ significantly between 1 m and 3 m depth during that year. During the second year of his study, significantly more larval alewife were collected at 3 m depth at only one of the eight locations sampled. Although it is possible that higher densities of larval fish existed below 0.5-m depth in Claytor Lake during my study, I am unable to present any evidence which supports or disputes this.

The similarity between offshore (main channel) and nearshore (cove) larval densities in Claytor Lake was surprising. Because cove and shallow water habitat is limited in this riverine impoundment, the sharp distinction between the selected main channel and cove locations led me to believe that concentrated spawning activity and nursery habitat would have occurred in the coves that I sampled. I anticipated that density of larval fish, particularly larval *Lepomis* spp., would have been much greater in nearshore locations. This did occur for larval *Lepomis* spp. at the Peak Creek site only, but I did not witness a difference between offshore and nearshore larval density for the other species or at the other sites. Netsch et al. (1971) found shad equally abundant in offshore and nearshore locations in Beaver Reservoir, Arkansas. Distributional patterns of larval gizzard shad in other reservoir systems have been varied. Edwards et al. (1977) and Shelton (1972) observed shad spawning activity and larval fish in open water, while Storck et al. (1982) reported higher larval shad densities in main channel areas than in embayments in Lake Shelbyville, Illinois. In contrast, Tisa (1988) found higher densities of larval gizzard shad in coves versus main channel locations in Smith Mountain Lake, Virginia, as did Mayhew (1974) in Lake Rathbun, Iowa.

### **Diet Composition**

The digestive tract of larval fish less than approximately 20 mm TL in Claytor Lake rarely contained more than a few food items. The proportion of empty guts from larvae collected at night ranged from 65-72% for all three species. Empty guts were less common in alewife and *Lepomis* spp. collected just before dark, yet the great majority of larval gizzard shad during this time still did not contain any food items. As Dettmers and Stein (1992) witnessed among larval gizzard shad in Knox and Kokosing Lakes, Ohio, larval fish in Claytor Lake did not appear to

actively feed after dark. An early study on larval bluegill in Crane Lake, Indiana also reported that larval bluegill in the limnetic zone appeared to be daylight feeders, depending on sight to capture food organisms (Werner 1969). Mallin et al. (1985) also found that, in general, daytime feeding by larval gizzard shad and *Lepomis* spp. in Hyco Lake, North Carolina was much more extensive than nighttime feeding. However, even in daytime samples, many researchers have found that few larval gizzard shad may contain food items. In Alabama, Pope and DeVries (1994) found that 76% of larval gizzard shad collected during the day in experimental ponds had empty stomachs. In Weiss Reservoir, Alabama, Hirst and DeVries (1994) found that 91% of small gizzard shad ( $\leq 10$  mm TL) collected during the day did not contain food. Based on this information, the apparent lack of nighttime feeding activity by larval gizzard shad, *Lepomis* spp., and alewife in Claytor Lake might, in fact, be indicative of the usual pattern of diel feeding activity for these fish in many reservoir systems.

Dettmers and Stein (1992) were able to conclude that the biomass of prey consumed by larval gizzard shad did not change during daylight hours. Stomach fullness of these larvae declined sharply by 2300 hours, and stomachs were usually empty for the remainder of the night. Experiments performed by Werner (1969) indicated that larval bluegill were not capable of feeding in the dark at zooplankton concentrations lower than 510 organisms/L. However, chance tactile encounters were thought to allow them to feed in the presence of much higher zooplankton concentrations (4,160 organisms/L). My sampling of larvae just prior to dark (1800 to 2100 hours) during 1998 resulted in the capture of larval fish with guts that were more full than those collected at night, but sample sizes were too low to make a comparison between daytime and nighttime feeding by larvae in Claytor Lake. Mallin et al. (1985) concluded that because few food items were ingested at night by larval gizzard shad and *Lepomis* spp. in Hyco

Reservoir, North Carolina, diet analyses of larvae collected at night are impractical. However, larvae are much more difficult to collect during the day (Dettmers and Stein 1992). Dettmers and Stein (1992) suggested that nighttime larval densities were always at least twice the daytime estimates taken from Ohio reservoirs. Based on the consistently low densities of larval fish found during my study, collection of these fish during daylight in Claytor Lake, for the purpose of diet analyses, would itself be extremely difficult and impractical.

Based on the diet data I obtained for 1998, it appears that larval alewife and larval *Lepomis* spp. in Claytor Lake fed more heavily than larval gizzard shad. These larvae generally contained three to four times the number of individual zooplankters found in most larval gizzard shad stomachs. This was also the case in Hyco Reservoir, North Carolina, as Mallin et al. (1985) found larval *Lepomis* spp. to be more voracious zooplankton feeders than larval gizzard shad. Potentially less successful feeding by larval gizzard shad, combined with their occurrence at lower densities than either larval alewife or *Lepomis* spp., would appear to limit their impact on the zooplankton food resource in Claytor Lake, and negate any competitive advantage over larval alewife or *Lepomis* spp.

Larval fish in Claytor Lake showed feeding preference for *Diaphanosoma* and copepod nauplii, two of the most numerous zooplankton taxa sampled during both years. Smaller larvae of all three species generally preferred copepod nauplii, while all sizes of larval fish appeared to feed preferentially on *Diaphanosoma*. Cyclopoid copepods and *Bosmina* spp. were also common in the diets of larval fishes. Larval gizzard shad collected from Hyco Reservoir, North Carolina, exhibited general preferences for copepod nauplii and the rotifer *Polyarthra* spp. (Mallin et al. 1985). Larval gizzard shad < 10 mm TL in Kokosing Lake, Ohio generally preferred copepod nauplii and cyclopoid copepods during both years of the study, while larvae



10.0-12.9 mm TL also selected copepod nauplii and cyclopoid copepods during one year (DeVries and Stein 1992). Pope and DeVries (1994) found that larval gizzard shad in Alabama positively selected for *Bosmina*, *Diaphanosoma*, and copepod nauplii, and exhibited negative selection for larger zooplankton such as *Ceriodaphnia*, *Chydorus*, *Daphnia*, and cyclopoid copepods. DeVries and Stein (1992) found that larval bluegill < 7.0 mm TL also preferred small prey such as copepod nauplii, while fish 7.0-9.9 mm showed positive selection for *Bosmina* during one year of the study. Also, during one year of that study, bluegill > 10.0 mm TL selected *Diaphanosoma*. Larval *Lepomis* spp. in Alabama selected *Diaphanosoma*, in addition to *Bosmina*, copepod nauplii, and the rotifers *Polyarthra* spp. and *Filinia longiseta* (Pope and DeVries 1994). Although prey selectivity was not specifically evaluated by Nigro (1980), he did report that cyclopoid copepods were the principal food item in the diets of young alewife 6-35 mm TL collected in Claytor Lake, while copepod nauplii and *Diaphanosoma* were also important in the diet of larval alewife 6-15 mm TL. Nigro (1980) found a significant positive relationship between the relative abundance of major zooplankters in the reservoir and in the diet of larval alewife. For example, cyclopoid copepods dominated the diet of young alewife, while also dominating the zooplankton community. During my study, larval diets in Claytor Lake appear to be relatively similar to those in many other reservoir systems, with copepod nauplii preferred by smaller larvae, and *Diaphanosoma* dominating the diets of all sizes and species of larval fish. Although larval fishes showed strong preference for these two particular zooplankton taxa, both remained abundant throughout the period when larval fish were present.

The analysis of diet overlap between larval zooplanktivores in Claytor Lake revealed that the potential for competitive interactions between the larval zooplanktivores examined in this study does exist. While diet overlap values greater than 0.5 to 0.6, based on Schoener's Index,

are indicative of potential resource overlap, interactions between all three taxa examined resulted in index values greater than 0.7. Index value greater than 0.7 would seem to indicate considerable overlap for food resources by the three larval taxa studied. The highest overlap value reported was between gizzard shad and *Lepomis* spp. (0.83). The utilization of *Bosmina*, cyclopoid copepods, and daphnids (based on percent composition by weight) were almost identical in their diets.

Unlike filter-feeding, adult planktivores, larval gizzard shad, alewife, and *Lepomis* spp. are gape-limited predators. As this limits the ability of larvae to consume zooplankters larger than their gapes allow, this may restrict the availability of preferred prey items. Researchers have found that larval planktivores initially remove small zooplankton and only include larger prey items in their diet as they grow and their gape increases (Rosenthal and Hempel 1970; Wang and Ward 1972; Zaret 1980; Hansen and Wahl 1981). This selection (or requirement) for small prey items during the early stages of larval grow could potentially lead to a depletion of these organisms during peaks in larval abundance and feeding. In order to characterize size-selectivity of zooplankton by larval planktivores, I chose *Diaphanosoma* as an index of size-selectivity for larval gizzard shad, alewife, and *Lepomis* spp. in Claytor Lake, and found that these planktivores consumed significantly smaller individuals than the mean size collected in reservoir samples. Nigro and Ney (1982) chose cyclopoid copepods as their index of size-selectivity for larval alewife diet in Claytor Lake, and also documented that larval alewife less than 30 mm TL consumed these zooplankters significantly smaller than the median size found in the reservoir. As expected, the size of *Diaphanosoma* consumed by larval alewife and *Lepomis* spp. in my study did increase as size of larvae increased, however, this was not true for larval gizzard shad. The sample size of larval gizzard shad was smaller than both alewife and *Lepomis*

spp. (N=64 versus 143 and 148, respectively), but showed no relationship between total length of larvae and length of *Diaphanosoma*. It is likely that the small sample size and lack of larger larval gizzard shad (> 15 mm TL) in my samples hindered my ability to detect a positive relationship between total length of larvae and size of prey.

Because larval gizzard shad examined during this study continued to prey upon small zooplankters throughout the sampling season, I predicted that peaks in larval gizzard shad abundance would have a negative influence on the size distribution of zooplankton, depleting smaller individuals and shifting the size distribution towards larger, morphologically unavailable sizes. This influence on the size distribution of zooplankton could have led to a lack of preferred prey sizes for other larval zooplanktivores and increased trophic competition between them and larval gizzard shad for remaining food resources. Again, *Diaphanosoma* was chosen as the zooplankter of interest in determining whether mean length of the individuals in this population increased following peaks in larval gizzard shad abundance. Results from this analysis were not very convincing, and actually showed that mean length of *Diaphanosoma* appeared to decrease following larval gizzard shad peaks in both years of this study. In fact, the response observed in mean length of *Diaphanosoma* was contrary to the predicted response; the size distribution of *Diaphanosoma* did not shift towards larger, morphologically unavailable sizes. Mean length of *Diaphanosoma* was never observed to be greater than the maximum size eaten by larval shad, alewife, or *Lepomis* spp. during this study (0.725, 0.911, and 0.756 mm, respectively). Considering the relatively low density of larval gizzard shad in Claytor Lake, even during peaks in abundance, it appears that their feeding activity had little influence on the size distribution of *Diaphanosoma*.

I was unable in this study to evaluate the utilization of larval gizzard shad in the diets of juvenile *Micropterus* spp. Limited data on 88 age-0 *Micropterus* spp. 19-63 mm TL showed that larval fish were present in bass stomachs after they reached approximately 45 mm, but I was unable to determine the identity of these prey items. Age-0 bass greater than 63 mm TL were not collected in this study, which certainly limited the number of piscivorous *Micropterus* spp. examined. Piscivory by young largemouth bass has been observed in fish as small as 38 mm TL in Lake Jordan, North Carolina (Jackson et al. 1990), but fish did not become the principal food item for these bass until 55 mm TL. Sutton (1997) found that *Micropterus* spp. in Smith Mountain Lake, Virginia did not become primarily piscivorous until 70 mm TL. Juvenile *Micropterus* spp. collected in Smith Mountain Lake fed heavily on age-0 *Lepomis* spp., but did not appear to utilize young gizzard shad in their diets (Sutton 1997).

Small *Micropterus* spp. to approximately 30 mm TL were present during the time of the summer when larval gizzard shad were at their greatest abundance in 1998 (until early July). These bass fed on a variety of food items, including an increasing percentage of aquatic insects. Like larval shad and other larval zooplanktivores, young bass utilized abundant *Diaphanosoma* in their diet. However, their diet mainly consisted of daphnids and *Bosmina*, which were not important in the diets of limnetic zooplanktivores, and was void of copepod nauplii that were important to larval shad, alewife, and *Lepomis* spp. Hirst and DeVries (1994) found low trophic overlap and no direct negative feeding interactions between larval shad and larval *Micropterus* spp. in Alabama reservoirs, and Jackson et al. (1990) also found no evidence that zooplanktivory by larval shad directly impacted growth or feeding dynamics of juvenile bass. Although I did not specifically target larval gizzard shad in littoral fish sampling, only one larvae of this species was noted in any of the seine hauls. Likewise, limnetic neuston net collections captured a total

of only ten young-of-year *Micropterus* spp. in both years combined. Of these, the majority were collected from the Dam Cove site when the neuston net occasionally came close to the littoral zone. As noted by Jackson et al. (1990), it is likely that spatial segregation of zooplanktivorous larval gizzard shad and young-of-year *Micropterus* spp. in Claytor Lake is an important factor in limiting the potential for predatory or competitive feeding interactions. Young *Micropterus* spp. probably do not directly compete with larval gizzard shad for food, while the opportunity for piscivorous *Micropterus* spp. to utilize them as an additional prey resource is similarly restricted by habitat segregation.

Adult alewife diet was consistent with those reported by Nigro (1980), Kohler (1980), and Kelso (1983) in their earlier studies of alewife in Claytor Lake. All evaluated diets of these fish and found that cyclopoid copepods generally dominated the diets of juvenile and adult alewife. *Bosmina* were also important when they were most numerous in the reservoir, while Kelso (1983) also found *Diaphanosoma* to be positively selected for by adult alewife feeding at night. In my study, adult alewife and larval gizzard shad shared three zooplankton taxa in their diets, but the majority of the alewife diet consisted of cyclopoid copepods. *Diaphanosoma* were common in both diets, but were similarly plentiful in the reservoir. The current diet of adult alewife does not appear to have changed appreciably since after gizzard shad introduction into Claytor Lake. These fish still feed heavily on cyclopoid copepods, and also appear to utilize *Bosmina* as well as *Diaphanosoma*. Although adult alewife and larval shad in this study were found to share *Diaphanosoma* in their diets, increasing the opportunity for resource overlap, Kohler's (1980) study of alewife diet in Claytor Lake suggests that they prey upon larger individuals than did larval shad in my study (median size equals 0.77 and 0.48 mm, respectively). Although I did not obtain size information for prey items found in adult alewife

stomachs during my study, differences in size of *Diaphanosoma* consumed by adult alewife versus larval shad inferred from previous studies, as well as the abundance of these zooplankters in the reservoir, limits the potential for direct competition.

### **Zooplankton Density**

Crustacean zooplankton abundance did not appear to be a limiting resource for larval fishes in Claytor Lake. Mean crustacean zooplankton densities in Claytor Lake never dropped below approximately 250-400 organisms/L during either year of my study. The lowest densities of crustacean zooplankton measured in Claytor Lake were similar to peak density of 311-366 organisms/L in West Point Reservoir, and were almost 20 times the peak density of 13 organisms/L found in Weiss Reservoir (Hirst and DeVries 1994). Zooplankton in Lake Jordan, North Carolina peaked in late May at approximately 170 organisms/L and progressively declined the remainder of the summer (Jackson et al. 1990). Corresponding larval gizzard shad densities in Claytor Lake during the periods of zooplankton decline were no greater than 0.06 fish/m<sup>3</sup>. In experimental enclosures/exclosures on Kokosing Lake, Ohio, DeVries and Stein (1992) concluded that larval gizzard shad densities < 6 fish/m<sup>3</sup> did not cause crustacean zooplankton to crash. Zooplankton densities at the end of their experiments ranged from 493 organisms/L (with 1.5 fish/m<sup>3</sup>) to 96 organisms/L (with 5.5 fish/m<sup>3</sup>). Therefore, they were able to conclude that at least in Kokosing Lake, larval gizzard shad densities must exceed 6 fish/m<sup>3</sup> to drive zooplankton to crash. Jackson et al. (1990) did find significant reductions in the density of *Bosmina* and copepod nauplii after peak shad densities in Jordan Lake, North Carolina, while Welker et al. (1994) found biomass of macrozooplankton declined in mesocosm treatments with high bluegill density (70 fish/m<sup>3</sup>), and in treatments with low bluegill (35 fish/m<sup>3</sup>) and low gizzard shad

densities (35 fish/m<sup>3</sup>). The range of larval fish densities was chosen to span the range of natural densities observed in Lake Shelbyville, central Illinois, and in other midwestern reservoirs (Dettmers and Stein 1992; DeVries and Stein 1992). In Lake Shelbyville itself, zooplankton abundance declined greatly after larval gizzard shad peaked and remained low while bluegills were present in limnetic zone (Welker et al. 1994).

Crustacean zooplankton densities in Claytor Lake did not generally decline or respond negatively as a result of peak larval fish abundance. Out of the four major zooplankton taxa examined, as well as total crustacean zooplankton abundance, *Bosmina* was the only group that appeared to respond negatively to peaks in larval fish densities during either year. During 1997, *Bosmina* densities significantly declined during the period from June 19 to July 10, corresponding with the time surrounding peak gizzard shad density from June 25 to July 1 and peak total larval fish density on July 1. Total zooplankton density also significantly declined then, but the percent composition of the zooplankton community was heavily influenced by *Bosmina* during this time. *Bosmina* accounted for over 80% of the zooplankton community composition by number on June 19. No other individual zooplankton taxa significantly declined during this period, and *Diaphanosoma* and cyclopoid copepods actually increased during the time of peak larval fish abundance. Results were similar for 1998, with *Bosmina* being the only zooplankton taxa to experience an overall decline in abundance during the weeks surrounding peak larval fish densities. Gizzard shad and total larval fish first peaked on June 24, and *Bosmina* significantly declined from June 17 to July 9. Total larval fish densities peaked a second time during the week of July 15 as a result of high *Lepomis* spp. abundances, but no zooplankton taxa responded negatively during this period. Because *Bosmina* in reservoir systems are typically most abundant early in late spring and experience a gradual decline

throughout the summer (Smith 2001; Thorp and Covich 2001), it is unlikely that the decline in *Bosmina* density witnessed in Claytor Lake was in response to heavy zooplanktivory by larval gizzard shad and other larval fishes, but was instead a result of natural population declines due to decreased reproduction (Smith 2001; Thorp and Covich 2001). DeVries and Stein (1992) did document dramatic mid-summer declines in crustacean zooplankton abundance, including *Bosmina*, in Kokosing Lake, Ohio during 1987 and 1988 following peaks in larval gizzard shad density (14 and 84 fish/m<sup>3</sup>, respectively). In both years of their study, the period of most rapid decline occurred within two weeks of peak larval gizzard shad density. Results from diet analyses during my study suggest that *Bosmina* were minimally important in the diets of larval zooplanktivores, even during late spring and early summer when they were most abundant. Therefore, it is unlikely that larval zooplanktivory during times of peak density negatively influenced abundance of *Bosmina*, or any other major crustacean zooplankton taxa.

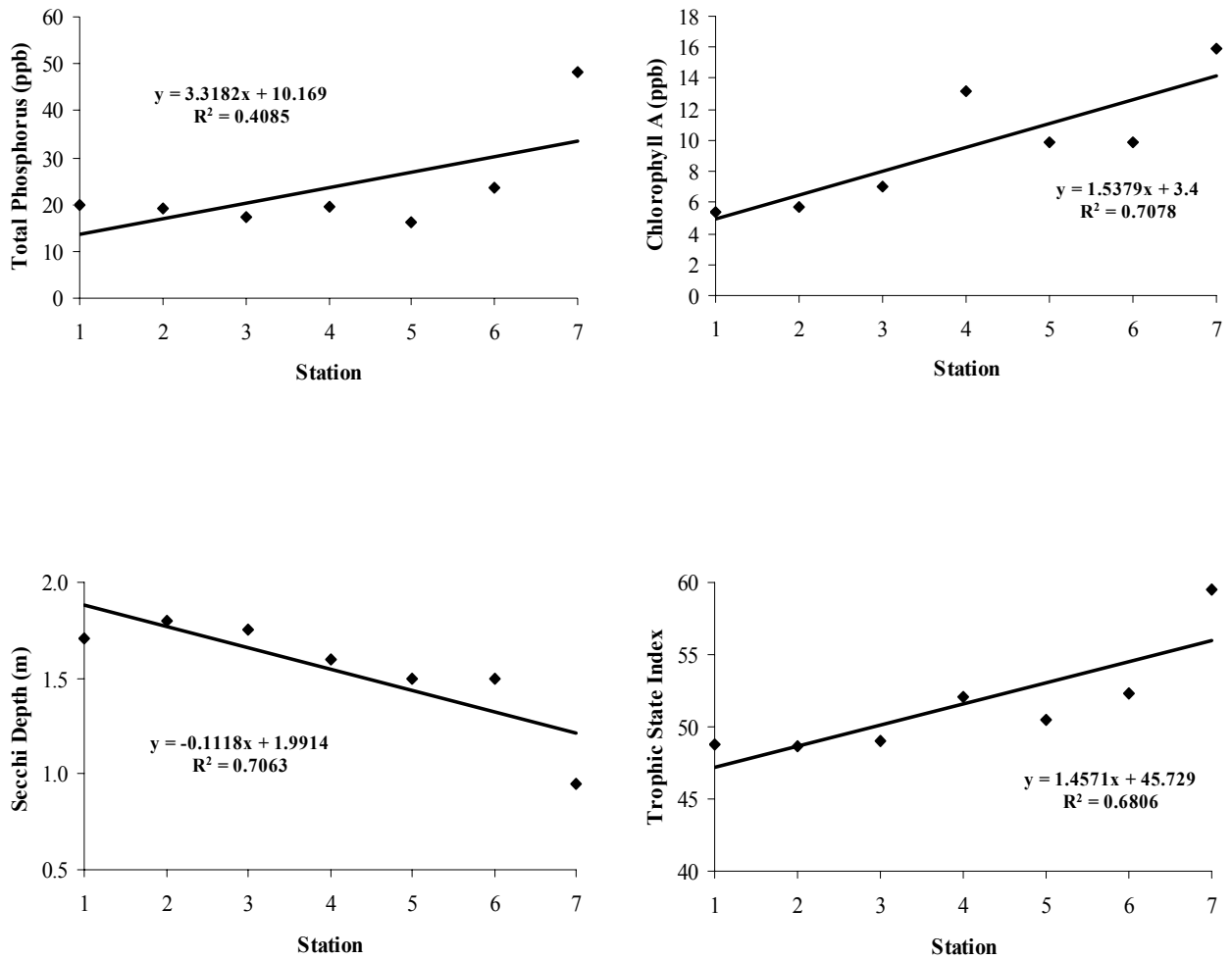
Although it is unlikely that larval zooplanktivory during times of peak larval density negatively influenced abundance of major crustacean zooplankton, I did observe an inverse relationship between the spatial abundance of larval fishes and crustacean zooplankton during both years of the study. While larval fishes showed an overall inverse relationship between abundance and distance from the dam (Figures 4 and 7), crustacean zooplankton collected during my study showed an opposite, positive relationship between abundance and distance from the dam (Tables 16 and 17). Based on water quality data collected on Claytor Lake during the summer of 1998 as part of a monitoring effort developed through Ferrum College and Friends of Claytor Lake (Thomas and Johnson 1998), spatial distributions of zooplankton collected during my study corresponded to a fertility gradient in the reservoir (measured as total phosphorus, chlorophyll a, Secchi depth, and the overall Trophic State Index). As expected, all four of these



measures of productivity, or trophic status, followed patterns of increasing productivity as the samples progressed uplake from the dam into Peak Creek (Table 18; Figure 25). Higher productivity in upstream locations such as Peak Creek, which suggests higher levels of algal production in those areas, would likely result in higher abundances of zooplankton. It is therefore possible that this inverse relationship between the spatial abundance of larval fishes and crustacean zooplankton could be explained by gradients in reservoir water quality rather than predation by zooplanktivorous larval fishes.

**Table 18.** Claytor Lake water quality sampling station locations presented in Thomas and Johnson (1998). Stations 1-3 represent areas near DC, station 4 and 5 represent areas near SP, while station 6 and 7 represent locations near PK.

<b>Station</b>	<b><u>Distance from Dam</u></b>	
	<b>Miles</b>	<b>Kilometers</b>
1	0.3	0.5
2	2.0	3.2
3	2.0	3.2
4	4.0	6.4
5	6.3	10.1
6	7.8	12.6
7	12.0	19.3



**Figure 25.** Spatial trends in water quality parameters (Total Phosphorus, Chlorophyll A, Secchi Depth, and Trophic State Index) collected from Claytor Lake in 1998 and presented in Thomas and Johnson (1998).

*Diaphanosoma*, as well as copepod nauplii, were both preferred prey items for larval fishes in Claytor Lake. A great decline in their numbers or a reduction in their importance to the zooplankton community as a result of heavy zooplanktivory by larvae could affect the feeding success, growth, and subsequent survival of larval zooplanktivores. However, these zooplankters typically accounted for approximately half of the zooplankton community by number throughout the summer. Although they were less numerous in May and early June when *Bosmina* dominated the zooplankton community, they generally dominated later in the sampling season. Both *Diaphanosoma* and copepod nauplii increased in abundance as larval fishes appeared and peaked in the limnetic zone. It is apparent that the preferred *Diaphanosoma* and copepod nauplii were not limiting to larval fishes, but in fact were abundant and constituted the greatest percentage of the zooplankton community during the period when larvae were most abundant.

Although density of rotifers was not evaluated in this study, their abundance did appear to be significant based on zooplankton samples. The contribution of rotifers to the diet of larval fish in this study was not evaluated based on concerns that small, soft-bodied rotifers are more quickly digested than crustacean zooplankters, and may be difficult to properly identify or characterize in the gut (Mallin et al. 1985). Although several studies (Mallin et al 1985; Dettmers and Stein 1992; DeVries and Stein 1992) have found rotifers to be an important component in the diets of small gizzard shad and bluegill, rotifers only became important in the diets of these fish after crustacean zooplankton declined or crashed in these reservoirs. Although rotifers appeared to be abundant in Claytor Lake, the abundance of preferred crustacean zooplankton throughout my study probably limited the need for larvae to feed on smaller, possibly less-preferred rotifers.

## **Response of Resident Fish Populations to Gizzard Shad Introduction**

As Welker et al. (1994) suggested, data support that gizzard shad can affect zooplankton populations, and could potentially compete with bluegills and other species with pelagic larvae, but the strength of competitive interactions may vary considerably among systems. Gizzard shad may have their greatest impact on food resources and resident fish populations in small, relatively closed systems without rapid throughflow or renewal of nutrients (Dettmers and Stein 1992). In larger systems like Claytor Lake, with rapid flushing time, high year-to-year and seasonal variability of limnological conditions, and complex morphometry, these effects may be less pronounced (McQueen et al. 1986).

It is certainly evident, based on cove rotenone data collected by the VDGIF, that biomass of gizzard shad in Claytor Lake has increased rapidly since their initial introduction and subsequent establishment in the mid to late 1980s. Of concern for resource managers should be future patterns of growth in the gizzard shad population, and whether they continue to increase in biomass to a point that results in evident impacts to resident fish populations.

My prediction was that high peak densities of larval gizzard shad would lead to reduced crustacean zooplankton density, which, in turn, would reduce food availability, growth, and ultimately recruitment of larval *Lepomis* spp. DeVries and Stein (1992) related total larval bluegill catch-per-effort (total number of larval bluegill captured per minute of larval fish tow) to peak larval gizzard shad densities during four years in Kokosing Lake, Ohio, which resulted in a negative relationship that was marginally significant ( $r^2=0.87$ ,  $P=0.066$ ). Although I do not have enough years of data to show a similar relationship, it is unlikely that the densities of larval gizzard shad currently witnessed during my study, compared to either larval *Lepomis* spp. densities in Claytor Lake or larval gizzard shad densities in other reservoirs, are great enough to

ultimately impact recruitment of *Lepomis* spp. It does appear, however, that biomass of *Lepomis* spp. in Claytor Lake is declining. Although this study does not present any direct evidence that larval gizzard shad have negatively impacted *Lepomis* spp. populations, the apparent decline in *Lepomis* spp. biomass should be further investigated to determine whether gizzard shad introduction has exacerbated the impacts from other factors (e.g. changes in fishing pressure and harvest, predation by resident piscivores such as flathead catfish, etc.).

Through either direct (competition for zooplankton food resources) or indirect (competition with young *Lepomis* spp.) trophic interactions, I also predicted that high densities of larval gizzard shad would ultimately lead to negative impacts to the *Micropterus* spp. community. Similar to potential changes to the *Lepomis* spp. community, these impacts would most likely be witnessed in reduced biomass and growth of *Micropterus* spp. Unlike steady declines in biomass of *Lepomis* spp. observed since at least 1981 (prior to gizzard shad introduction), biomass of *Micropterus* spp. has not significantly changed in that same time period based on cove rotenone data collected on Claytor Lake. However, all three *Micropterus* spp. species displayed decreased growth rates from those reported by Kohler (1980), with lower incremental growth in length-at-age, except for age-4 spotted bass. Decreased *Micropterus* spp. growth is not necessarily a consequence of gizzard shad establishment because it should be manifested most at age-1 instead of (incrementally) in successive years if a result of interactions with larval gizzard shad (see Garvey and Stein 1998). Although a clear understanding of the declining biomass of *Lepomis* spp. and declining growth rates of resident *Micropterus* spp. in Claytor Lake is not evident, the addition of gizzard shad to the fish community structure of Claytor Lake is likely to directly or indirectly impact these populations in the future, as biomass of adult gizzard shad continues to increase.

## SUMMARY AND CONCLUSIONS

1. The opportunity for trophic competition among larval gizzard shad, alewife, and *Lepomis* spp. does exist in Claytor Lake, as all three zooplanktivorous fishes co-occurred both temporally and spatially in the reservoir during both years of this study. Peak densities of all three fish species also coincided during both years.
2. Mean and peak abundances of larval gizzard shad were much lower than expected (0.01 fish/m<sup>3</sup> and 0.04-0.06 fish/m<sup>3</sup>, respectively), compared to the mean densities of other larval fishes collected in this study (mean density of alewife, 0.02 fish/m<sup>3</sup>; mean density of *Lepomis* spp., 0.09 fish/m<sup>3</sup>), and reports of peak larval gizzard shad density from other studies (20-25 fish/m<sup>3</sup>, Mayhew 1977; 10 fish/m<sup>3</sup>, Downey and Toetz 1983; ~4 fish/m<sup>3</sup>, Matthews 1984; 0.5 fish/m<sup>3</sup>, Tisa et al. 1985; 84 fish/m<sup>3</sup>, DeVries and Stein 1992, Dettmers and Stein 1992). The relatively low densities of larval gizzard shad in Claytor Lake during the years of this study would seemingly limit their trophic impact on resident zooplanktivores.
3. The digestive tracts of larval fish less than approximately 20 mm TL collected at night in Claytor Lake rarely contained more than a few food items. The proportion of empty guts from larvae ranged from 65-72% for all three species. It may be more appropriate, though more difficult, to target collections of limnetic larval fish during the day for future diet studies of larval fish in Claytor Lake.

4. Based on the diet data I obtained during 1998, it appears that larval alewife and *Lepomis* spp. in Claytor Lake fed more heavily than larval gizzard shad. These larvae generally contained three to four times the number of individual zooplankters found in most larval gizzard shad stomachs. Potentially less successful feeding by larval gizzard shad, combined with their occurrence at lower densities than either larval alewife or *Lepomis* spp., would appear to limit their impact on the zooplankton food resource in Claytor Lake, and negate any competitive advantage over larval alewife or *Lepomis* spp.
5. Limnetic larval fish in Claytor Lake showed feeding preferences for *Diaphanosoma* and copepod nauplii, two of the most numerous zooplankton taxa sampled during both years. Although larval fishes showed strong preferences for these two particular zooplankton taxa, both remained abundant and constituted the greatest percentage of the zooplankton community throughout the period when larval fish were present and most abundant.
6. The analysis of diet overlap between larval zooplanktivores in Claytor Lake revealed that the potential for competitive interactions between larvae examined in this study does exist. Diet overlap values greater than 0.5 to 0.6, based on Schoener's Index, are indicative of potential resource overlap, and interactions between all three taxa examined during this study resulted in index values greater than 0.7.
7. In order to characterize size-selectivity of zooplankton by larval planktivores, I chose *Diaphanosoma* as an index of size-selectivity for larval gizzard shad, alewife, and *Lepomis* spp. in Claytor Lake, and found that these planktivores consumed significantly



smaller individuals than the mean size collected in reservoir samples. As expected, the size of *Diaphanosoma* consumed by larval alewife and *Lepomis* spp. in my study did increase as size of larvae increased, however, this was not true for larval gizzard shad.

8. *Diaphanosoma* was chosen as the zooplankter of interest in determining whether feeding by larval gizzard shad had an effect on the size distribution of preferred prey. I predicted that mean length of individuals in this population would increase following peaks in larval gizzard shad abundance, but results from this analysis actually showed that mean length of *Diaphanosoma* decreased following larval gizzard shad peaks during both years of this study. The response observed in mean length of *Diaphanosoma* was contrary to the predicted response; the size distribution of *Diaphanosoma* did not shift towards larger, morphologically unavailable sizes.
9. It is likely that spatial segregation of zooplanktivorous larval gizzard shad and young-of-year *Micropterus* spp. in Claytor Lake limits the potential for predatory or competitive feeding interactions. Young *Micropterus* spp. (19-30 mm TL) fed on a variety of food items, including an increasing percentage of aquatic insects. Young bass utilized abundant *Diaphanosoma* in their diet, but their diet was dominated by daphnids and *Bosmina*, which were not important in the diets of limnetic zooplanktivores, and was void of copepod nauplii that were important to larval shad, alewife, and *Lepomis* spp.
10. Adult alewife and larval gizzard shad shared three zooplankton taxa in their diets, but only resulted in a diet overlap index value of 0.38. The majority of the alewife diet

consisted of cyclopoid copepods. *Diaphanosoma* were common in both diets, but were similarly plentiful in the reservoir. The abundance of these zooplankters in the reservoir, as well as likely differences in the sizes of prey eaten by adult alewife and larval shad, limited the potential for direct competition.

11. Crustacean zooplankton abundance did not appear to be a limiting resource for larval fishes in Claytor Lake, as mean crustacean zooplankton densities in Claytor Lake never dropped below approximately 250-400 organisms/L during either year of my study.
12. Crustacean zooplankton densities in Claytor Lake did not generally decline or respond negatively as a result of peak larval fish abundance. Out of the four major zooplankton taxa examined, as well as total crustacean zooplankton abundance, *Bosmina* was the only group that appeared to respond negatively to peaks in larval fish densities during either year. However, *Bosmina* were not preferred prey, and they typically show a gradual decline in abundance throughout the summer.
13. Biomass of gizzard shad in Claytor Lake has increased steadily since their initial introduction and subsequent establishment in the mid to late 1980s, while biomass of *Lepomis* spp. has continued to decline during this same time period. Although this study provides no direct evidence that larval gizzard shad have negatively affected the early growth and/or subsequent survival of age-0 *Lepomis* spp., the introduction of gizzard shad may have exacerbated the recent decline in biomass of *Lepomis* spp. through other interactions.

14. Unlike biomass of *Lepomis* spp., biomass of *Micropterus* spp. has remained steady since at least 1981. However, all three species of *Micropterus* displayed decreased growth rates from those reported by Kohler (1980), with lower incremental growth in length-at-age, except for age-4 spotted bass. Again, although this study provides no direct evidence that larval gizzard shad have directly or indirectly affected the early growth and/or subsequent survival of age-0 *Micropterus* spp., the introduction of gizzard shad may have exacerbated the recent decline in growth of adult *Micropterus* spp.

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## VITA

Ron Small was born on July 26, 1973 in Greensboro, North Carolina. Ron graduated from Grimsley High School in June 1991, and entered the honor's program at Clemson University that same fall. There he pursued and received a Bachelor of Science degree in Fisheries and Wildlife Biology in May 1995. Eager to travel following graduation, Ron worked as a biological science technician for the Colorado River Fish Project in Vernal, Utah. He then accepted a position as a fisheries technician with the Virginia Department of Game and Inland Fisheries in Verona, Virginia, and later as a research technician at the Savannah River Ecology Laboratory in Aiken, South Carolina. Ron was fortunate to be accepted into the Department of Fisheries and Wildlife Sciences at Virginia Polytechnic Institute and State University in August 1996 in order to pursue a Master of Science degree in Fisheries Science. During his tenure at Virginia Tech, he served as both a Teaching and Research Assistant in the Department while studying the trophic interactions between larval gizzard shad and resident zooplanktivores in Claytor Lake, Virginia. Prior to completing his Master's thesis, Ron accepted a position as an assistant fisheries biologist with the North Carolina Wildlife Resources Commission in his hometown of Greensboro. He then went on to work for the City of Greensboro's Stormwater Management Division as an environmental specialist. Ron finally completed his Master's thesis in September 2002, and will soon own, manage, and operate his own environmental consulting firm, Piedmont Environmental Solutions, LLC, located in Greensboro.

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