COMPETITION BETWEEN AGE-0 LARGEMOUTH BASS AND JUVENILE BLUEGILLS IN A VIRGINIA POND

by

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Committee Chair: Brian R. Murphy

(ABSTRACT)

I assessed the potential for trophic competition between age-0 largemouth bass and juvenile bluegills by quantifying food resource use similarity in a Virginia recreational small impoundment and by experimentally stocking the species sympatrically and allopatrically in 1.0 m^3 cages and monitoring mortality, growth, and resource use.

Niche breadth of bluegills in the small impoundment was greater than that of largemouth bass for eight out of nine sampling dates during the summer and fall of 1997. Virtually every type of item consumed by largemouth bass also was consumed by bluegills. In spite of this, diet overlap between the species was low. Largemouth bass fed primarily on Calanoida, Ephemeroptera, and fish, while bluegills consumed Diptera and Cyclopoida. The fishery of the impoundment consisted of relatively high and moderate densities of slow- and average-growing largemouth bass and panfish, respectively. If the fishery was managed to provide a high density of small bluegill, largemouth bass and bluegill might compete considering the number of prey items shared.

Manipulative cage experimentation, which consisted of stocking 5 largemouth bass alone, 10 bluegill alone, 5 largemouth bass and 10 bluegill, 5 largemouth bass and 30 bluegill, and 15 largemouth bass and 10 bluegill in cages, indicated that largemouth bass and bluegills can compete and that there exists a strong asymmetry in their competitive relationship. Bluegills had a much stronger impact on largemouth bass than the reverse. When stocked alone, largemouth bass grew significantly larger than when stocked with either 10 or 30 bluegills. There were no significant differences in bluegill growth rates except between bluegills stocked alone and bluegills stocked with 15 largemouth bass. The analysis of food resource use indicates that

Copepoda and Diptera larvae may be the limiting resources catalyzing the competitive interaction.

This research suggests that a competitive juvenile bottleneck could occur, depending largely on whether overwinter survival of largemouth bass is size related. Competition between largemouth bass and bluegills may explain why enhancement stocking of fingerling largemouth bass typically is not successful. Further research is needed on the appropriate timing and length at stocking of introductory largemouth bass stockings. Additionally, I recommend that resource partitioning and competition between largemouth bass and bluegills be explored in connection with studies concerning overwinter survival and angling opportunities in small impoundments. Competition between the species may impose an ecological constraint that restricts achievable options in certain systems.

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Introduction

The coupled stocking of largemouth bass *Micropterus salmoides* and bluegills *Lepomis macrochirus* has been one of the major management practices for North American small impoundments since the 1930s (Smitherman 1975; Novinger and Legler 1978). Their interaction typically is viewed as a predator-prey relationship. However, fishery managers must be aware that there exists a potential for competition between the species and that ignoring its role in structuring communities could handicap management actions (Larkin 1956; Roell and Orth 1998).

Even though largemouth bass is considered the principal warmwater piscivore species in small impoundments (Heidinger 1975; Hackney 1979), age-0 fish feed on zooplankton and aquatic insects before becoming piscivorous (Gilliam 1982; Keast and Eadie 1985; Hirst and DeVries 1994; Olson 1996). Both juvenile and adult largemouth bass are associated with the littoral zone, although larger fish also will occupy open water (Heidinger 1975). Conversely, bluegills forage on invertebrates throughout their life but undergo a series of limnodromous movements that are attributed to their varying susceptibility to predation (Keast 1978; Kelso 1983; Mittelbach 1981; Werner et al. 1983; Werner and Hall 1988). Bluegills vulnerable to predation (hereafter referred to as juvenile bluegills) reside in the littoral zone due to its structural complexity, which impedes predators' ability to forage (Cooper and Crowder 1979; Savino and Stein 1982). It is reasonable to assume that age-0 largemouth bass also may be restricted to the littoral zone partially due to the threat of predation, as cannibalism does occur in largemouth bass populations (Applegate and Mullan 1967; Pasch 1975; Hackney 1979).

The ontogenetic niche shifts that largemouth bass and bluegills experience are characteristic of size-structured populations, and function to reduce intraspecific competition (Werner and Gilliam 1984; Ebenman 1988). For example, if the predatory threat is removed, juvenile bluegills will shift to the pelagic zone, a potentially more profitable foraging habitat (Werner et al. 1983; Werner and Hall 1988). Ultimately, this habitat shift reduces growth of adult bluegills already occupying the pelagic zone (Werner et al. 1983). This potentially explains why bluegill populations invariably become overcrowded with stunted individuals when bluegills are stocked without largemouth bass or when largemouth bass are overharvested (Swingle and Smith 1940; Novinger and Legler 1978). The ontogenetic niche shift of bluegills may concurrently increase interspecific competition due to the high density of juvenile fish residing in the littoral zone (Kelso 1983; Gilliam and Fraser 1988; Mittelbach 1988).

Even though both age-0 largemouth bass and juvenile bluegills generally reside in the littoral zone and feed on invertebrates, trophic competition may not necessarily occur. The structural complexity of the littoral zone allows extensive specialization in diet and microhabitat (Menge and Sutherland 1976), although research has found that largemouth bass and bluegills do overlap spatially (Werner 1977; Gilliam 1982) and feed at similar time periods (Zweiacker and Summerfelt 1974; Kelso 1983). Competition additionally requires either that resources are limited or that one organism excludes another from utilizing those resources (Keddy 1989). However, bluegills independently may have the ability to limit food resources. Sunfish, in general, are size-selective feeders and research has found them capable of negatively affecting food resources (Hall et al. 1970; Crowder and Cooper 1982; Mittelbach 1988). Therefore, any system that contains high densities of bluegills could be limited in its quantity of large invertebrate food resources, which both juvenile bluegills and age-0 largemouth bass prefer (Olson et al. 1995).

Empirical evidence indicates that bluegill populations can depress largemouth bass populations. Bennett et al. (1969) found that survival of largemouth bass fry was low when high densities of small bluegills were present, and survival was highest when no bluegills were present. Stone and Modde (1982) also determined that first-year survival and growth of largemouth bass was higher when stocked alone than when stocked with bluegills or other forage fish. An extensive review of small impoundment stocking strategies by Dillard and Novinger (1975) found that when some managers stocked largemouth bass in the summer followed by bluegills in the fall, largemouth bass typically reproduced the first year after stocking. Alternatively when bluegills were stocked in the fall followed by largemouth bass in the early summer, largemouth bass failed to spawn the first year after stocking, which was attributed to slow growth of largemouth bass. Additionally, some managers achieved the highest biomass yield of largemouth bass when they were stocked in ponds alone (Dillard and Novinger 1975). Olson et al. (1995) found a negative correlation between the density of small bluegills and age-0 largemouth bass growth. While the question of how small bluegills depress largemouth bass populations has never been resolved, competitive superiority seems a viable explanation.

The importance of determining whether age-0 largemouth bass and juvenile bluegills compete stems from the possible management implications for small impoundments (Kelso 1983). One possible consequence is a competitive juvenile bottleneck (Neill 1975), where competition between juveniles limits recruitment to adult stages and affects population dynamics or size structures (Persson 1987; Persson and Greenberg 1990). For example, when redside shiners *Richardsonius balteatus* were introduced to a North American lake containing rainbow trout *Oncorhynchus mykiss*, early growth of rainbow trout slowed and fishing success declined due to young rainbow trout competing with redside shiners. This occurred even though adult rainbow trout growth improved as a result of them feeding on redside shiners (Larkin and Smith 1954; Johannes and Larkin 1961). It generally is recommended that a prey species should not compete with its eventual predator (Li et al. 1976; Li and Moyle 1981; Kohler and Ney 1982) as even brief periods can detrimentally affect predator populations (Larkin and Smith 1954; von Geldern and Mitchell 1975; Persson and Greenberg 1990).

To test whether age-0 largemouth bass and juvenile bluegills compete for food resources in a Virginia pond, I first quantified similarity in food resource use. This allowed the opportunity to initially determine the likelihood of the two species competing for food resources. Additionally, I used the results to design an experiment where I monitored growth, mortality, and resource use of age-0 largemouth bass and juvenile bluegills when stocked inside cages both separately and together. This research will further the understanding of largemouth bass and bluegill population dynamics in small impoundments as they relate to stocking and management strategies.

Study Site

This study occurred at the Kennedy Tree Farm, which is located in the Piedmont physiographic province in Virginia (Figure 1), approximately 2.0 km north of the town of Dillwyn. This is a 525-ha privately owned tree farm that contains four small impoundments: Big Pond, Greenhouse Pond, Hidden Pond, and No-Name Pond (Figure 2). I selected Big Pond as the primary study site. It was formed by damming Gold Mine Branch creek in the 1940s and has a surface area of 2.4 ha. Fish species in Big Pond include largemouth bass, bluegill, redear sunfish *L. microlophus,* warmouth *L. gulosus,* black crappie *Pomoxis nigromaculatus,* and chain pickerel *Esox niger*. Access to the impoundment is restricted and fishing pressure is light. Largemouth bass and bluegills were collected from this impoundment for the diet similarity aspect (**Chapter 1**) of my research. However, only largemouth bass were collected from this impoundment for the cage experiment (**Chapter 2**). I collected bluegills for the cage experiment from Greenhouse Pond, which prior sampling indicated contained only largemouth bass, bluegill, and American eel *Anguilla rostrata*. Collecting fish from this impoundment ensured that bluegills, rather than other sunfish species, were used in the experiment.

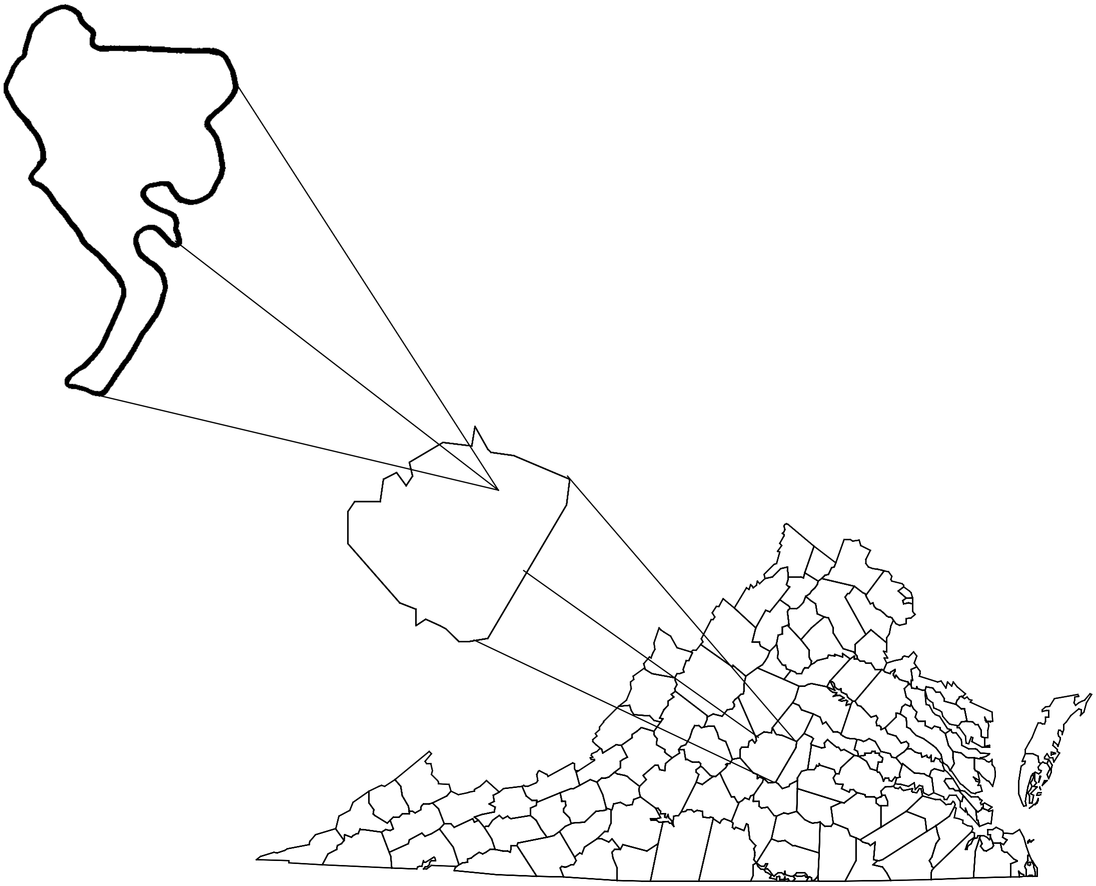

Figure 1. Location of the Kennedy Tree Farm in Virginia and outline of Big Pond.

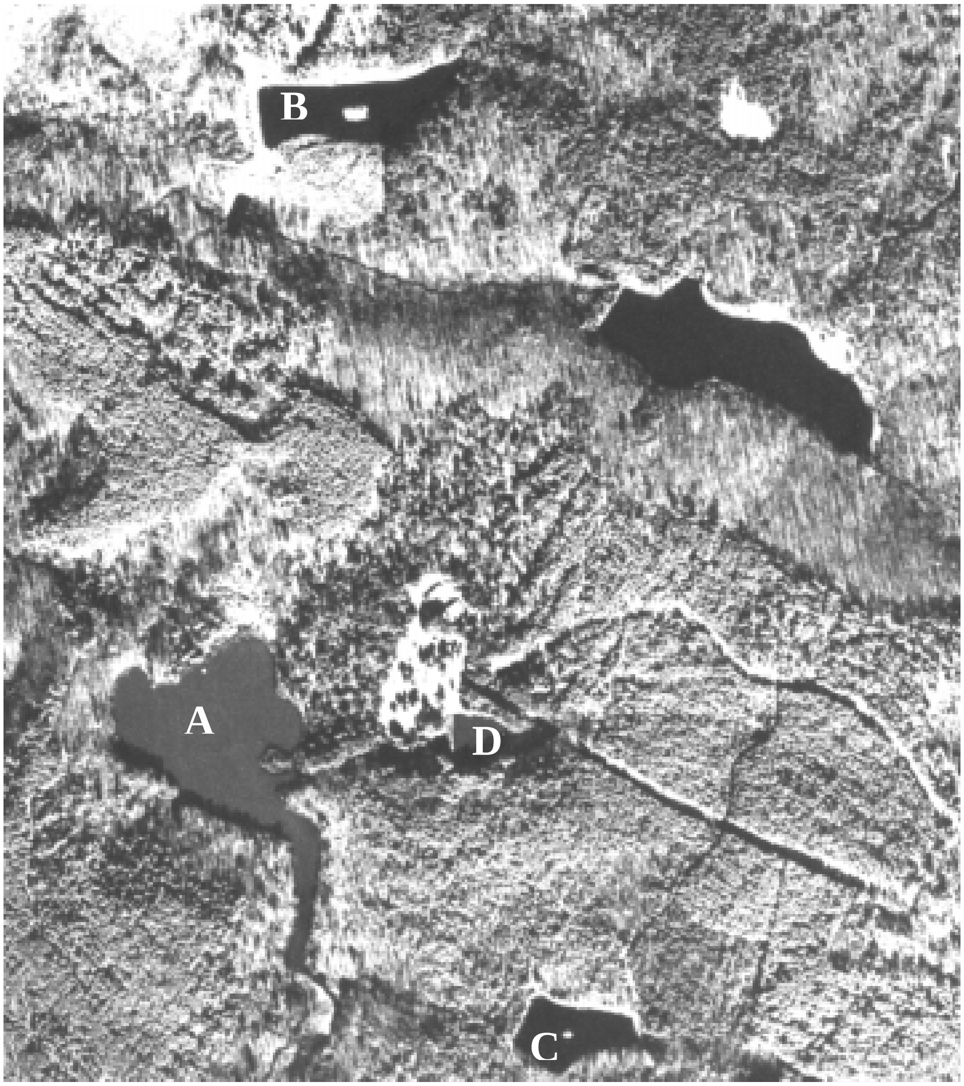

Figure 2. Aerial photograph of the Kennedy Tree Farm and its impoundments: Big Pond (A), Green House Pond (B), Hidden Pond (C), and No Name Pond (D). The impoundment not labeled is not part of the Kennedy Tree Farm.

Chapter 1

Diet Overlap of Age-0 Largemouth Bass and Juvenile Bluegills Under a Panfish Management Option

Abstract

Previous research on diet overlap between age-0 largemouth bass and juvenile bluegills has given little consideration to community structure. As a result, information concerning early trophic interactions of largemouth bass and bluegills under various management options is relatively unavailable. To expand information available to support management decisions, I compared food resource use of age-0 largemouth bass and juvenile bluegills in a recreational small impoundment in Virginia in conjunction with my assessment of the fishery. Fish were collected during the summer and fall 1997 by shoreline seining and boat electrofishing. Similarities in diet were quantified with niche-breadth and overlap indices. The fishery was assessed with stock density and condition indices, and by aging fish. Juvenile bluegills had a significantly greater diet breadth than did age-0 largemouth bass for eight out of nine sampling date. Nearly every item consumed by largemouth bass also was consumed by bluegills. In spite of this, measures of diet overlap were consistently low. The fishery of the impoundment consisted of relatively high and moderate densities of slow- and average-growing largemouth bass and panfish, respectively. Given that certain management options require high densities of bluegills, competition with largemouth bass seems a potential occurrence, which may complicate management efforts.

Introduction

When selecting fish to stock as forage, ecologists recommend that candidate species should not overlap the niche of their intended predators (Li et al. 1976; Li and Moyle 1981; Kohler and Ney 1982). Even brief periods of competition can detrimentally affect predator populations by reducing growth, reproduction, or survival (Larkin and Smith 1954; von Geldern and Mitchell 1975; Persson and Greenberg 1989). As such, Noble (1981) recommended thorough exploration of the ecology of forage and predator fish prior to stocking. However, this recommendation was subsequent to the establishment of largemouth bass and bluegills as one of the most commonly stocked fish combinations in North American small impoundments (Novinger and Legler 1978).

Bluegills are considered the ideal forage fish for largemouth bass in small impoundments because of high fecundity, sufficient growth for vulnerability to predation, and provision of an additional angling opportunity (Dillard and Novinger 1975; Novinger and Legler 1978; Flickinger and Bulow 1993). From an ecological perspective, however, bluegill may not be ideal as a forage species due to potential competition with early life stages of largemouth bass (Gilliam 1982; Wallace 1982; Olson et al. 1995). Both age-0 largemouth bass and bluegills feed on zooplankton and aquatic insects (Keast 1978; Gilliam 1982; Kelso 1983; Keast and Eadie 1985; Hirst and DeVries 1994; Olson 1996). In addition, bluegills that are vulnerable to predation (hereafter referred to as juvenile bluegills) occupy essentially the same habitat and feed at similar times of the day as age-0 largemouth bass (Zweiacker and Summerfelt 1974; Werner 1977; Gilliam 1982; Kelso 1983), which precludes spatial or temporal segregation. Similarity in food resource use is further complicated by the ability of bluegills to reduce abundance of invertebrates in some systems (Hall et al. 1970; Crowder and Cooper 1982; Mittelbach 1988).

Diet similarity between age-0 largemouth bass and juvenile bluegills previously has been quantified by Gilliam (1982), Wallace (1982), Keast and Eadie (1985), and Olson et al. (1995). Overlaps typically have been low with the species segregating consumption of Cladocera, Copepoda, Diptera, fish, and various insect nymphs. However, the usefulness of these previous studies is questionable from a fisheries management perspective. Wallace (1982) and Olson et al. (1995) based most of their research in experimental ponds stocked solely with age-0 largemouth bass and juvenile bluegills, which limits the scope of their findings to new or renovated impoundments. Although Wallace (1982) and Olson et al. (1995) did quantify diet overlap in other systems, only Gilliam (1982) and Keast and Eadie (1985) exclusively studied resource similarity under uncontrolled conditions. However, none of these researchers provided information concerning the community structure (e.g. species assemblage, density, growth rates) of these other systems. Such information could improve management efforts by allowing fishery managers to identify the potential relationship between competition and certain small impoundment community aspects.

Gabelhouse et al. (1982) and Gabelhouse (1984) identified three management options (balance, big bass, and panfish) for small impoundments based primarily on the predatory role largemouth bass were to play in the community. The balance option provides anglers the opportunity to harvest various sizes or largemouth bass and panfish. The big bass and panfish options emphasize the consistent production of trophy largemouth bass and panfish, respectively (Flickinger and Bulow 1993). Target stock-density-index ranges subsequently have been established to facilitate achievement of these management options (Willis et al. 1993). However, no information is readily available concerning early interactions between largemouth bass and bluegills under these various management options, even though it previously has been hypothesized that competition between largemouth bass and bluegills may hamper management efforts and prevent certain options from being achieved (Gabelhouse 1987). By studying species interactions in conjunction with fisheries assessments, fishery managers can begin to correlate ecological interactions with management options, which will improve their predictive capabilities and allow more informed benefit/risk analyses regarding fish community manipulations (Kelso 1983).

The purpose of my research was to determine whether age-0 largemouth bass and juvenile bluegills compete for food resources in a small recreational impoundment in Virginia. In this study, I assess the potential for competition by quantifying diet similarities. I simultaneously describe the fishery of the pond in an attempt to increase understanding of the biotic interactions of largemouth bass and bluegill in small impoundments.

Methods

Field Collection and Laboratory Protocol

Sampling began on June 28, 1997 and continued every 15 ± 1 ($\bar{x}$ ± 2 SE) days until October 9, 1997, with an additional collection period on November 9, 1997. A total of 9 collections were made. Fish were collected by a combination of shoreline seining and boat electrofishing. When seining, I used a 7.62- × 1.22-m bag seine with 0.318-cm (bar measure) mesh. Seine hauls were conducted by wading parallel to shore at depths of less than 1.5 m. Electrofishing was done from a 4.27-m jon boat using a 2.5 GPP Smith-Root electrofisher powered by a GX-150 Honda generator with pulsed-DC output. The anode consisted of a Smith-Root one-piece telescoping prod pole ending in a 27.94-cm diameter ring electrode. Sampling continued until at least 25 age-0 largemouth bass and 50 juvenile bluegills were captured. Fish were collected from a variety of locations in the littoral zone of the impoundment.

Time-of-day that sampling was conducted was contingent on when largemouth bass stomachs were the fullest. Sampling on June 28 consisted of a 24-h series of collections at 4-h intervals (0000, 0400, 0800, 1200, 1600, and 2000 hours). After completing this series, qualitative examination determined that largemouth bass stomachs were the fullest at 0800 hours. All subsequent sampling periods began at 0800 hours and generally were completed by 1100 hours. I later used the percent fullness index of Knight and Margaraf (1982) and Herbold (1986) to quantitatively determine when stomachs were the fullest. The percent fullness index is calculated as:

$$\%\,\mathrm{S.F.} = 100 \times \frac{\text{observed gut content volume}}{\text{expected maximum gut content volume}}.$$

Expected maximum gut content volume was estimated by regressing the volume of the fullest stomachs per 1-mm length group of largemouth bass with least squares simple linear regression after $\log_{10}$ transformation of the variables. Expected maximum gut content volume for largemouth bass was

$$\log_{10}\ \text{volume}\,(\text{mm}^3) = 1.61 \times \log_{10}\ \text{total length(mm)} + 1.84\,.$$

(least-squares simple linear regression: $r^2 = 0.71$, F = 24.97, d.f. = 10; P = 0.0001). An overall difference in stomach fullness by time of collection was tested with the Kruskal-Wallis (1952) test at $\alpha = 0.10$ after residuals failed a Shapiro-Wilk (1965) test of normality (Shapiro-Wilk test: $W = 0.666$, $N = 73$; $P < 0.0001$). Bonferroni's multiple-comparison procedure (Dunn 1964) was used as a follow-up test to the Kruskal Wallis test at an experimentwise-error rate of 0.20 (testwise error rate = 0.0067). When calculating niche breadth and overlap for the June 28 sampling date, fish from the various collection times were combined.

Upon capture, each fish was measured in total length (TL) to the nearest mm and assigned an identification number. Fish were sacrificed by severing the spinal column and placed in 10% formalin. The coelom was slit to allow formalin entry into the pleuroperitoneal cavity to prevent postcapture digestion. Within two weeks, fish were transferred to 90% ethanol after soaking in water for several hours.

The visceral mass was extracted by severing the esophagus, the last few millimeters of the intestine, and the dorsal mesentery. Stomachs then were separated from the viscera. Contents were removed by slitting the stomachs lengthwise and rinsing with water from a wash bottle. Each stomach was visually inspected to ensure complete removal. After inspection, stomachs and their contents were again stored in 90% ethanol.

The stomachs of all largemouth bass sampled were examined, while I initially selected 25 bluegill stomachs to examine. When empty stomachs were encountered, I selected additional stomach samples until I had examined 25 bluegill stomachs with contents. Each species and sampling date was then evaluated for diet characterization (described below). If bluegill diets were not adequately characterized, additional stomach samples were selected until the criterion was met. I tested sampling dates for differences in lengths of bluegills examined with the Kruskal-Wallis (1952) test at $\alpha = 0.10$ after residuals failed a test of normality (Shapiro-Wilk test: $W = 0.927$, $N = 252$; $P < 0.0001$). Bonferroni's multiple comparison procedure (Dunn 1964) was used as the follow-up test as previously described.

Stomach contents were identified with the aid of a stereozoom microscope and the taxonomic keys of Merrit and Cummins (1984) and Thorp and Covich (1991). Each diet item was identified to the lowest taxonomic level practical. Some categories were combined to ensure accurate classification and for data reduction when reporting results (Table 1.1). Items were measured in length, width, and depth with an ocular micrometer and enumerated. If items were abundant, I measured the first 25 items encountered and counted the remaining. If measurements were consistently similar, I stopped measuring at 10 items and counted the remaining. Volumes of diet items were estimated by geometric approximation based on the shape of items and the formulas for either a cylinder or a sphere (Bowen 1996; Pert 1997). For common diet items and items that were well digested (but all or most parts were present), I developed prediction equations by regressing maximum head width to total volume with the Theil-Sen regression method (Hollander and Wolfe 1973) after $\log_{10}$ transformation linearized the data (Table 1.2). This nonparametric method was used for all taxa regressions even though I failed to reject normality at $\alpha = 0.20$ for several of the relationships (Table 1.2). This was done for consistency and the relative efficiency of the nonparametric procedure (Hollander and Wolfe 1973). Additionally, I tested the association between maximum head width and total volume with the Spearman (1904) rank-order correlation coefficient at $\alpha = 0.10$ (Table 1.2). When enumerating and estimating the volume of stomach contents, I followed the assumptions of Pert (1997). An additional assumption was that I classified detritus as incidental material.

Intraspecific Diet Overlap

To confirm adequate characterization of largemouth bass and bluegill diets for each sampling date, I calculated intraspecific overlaps as recommended by Wallace and Ramsey (1983). For each species and sampling date, I randomly divided fish into two equal-size subsets. I then compared the two subsets with a diet overlap index as if they were separate species. I used Schoener's (1970) niche overlap index, which for intraspecific overlap is calculated as:

$$C_{x_1x_2} = 1 - \frac{1}{2}\left(\sum_{i=1}^{n} \left| p_{x_1i} - p_{x_2i} \right| \right),$$

Table 1.1. Taxonomic levels that stomach contents were identified to for overlap calculations and for graphical display. In addition, items eaten by largemouth bass only, by bluegills only, and by both largemouth bass and bluegills are shown. For reporting purposes, items that did not comprise at least 5% of the volume of either species on any sampling date were grouped as other.

Food items used in diet overlap calculations			Items used for reporting purposes
Largemouth bass only	Bluegills only	Largemouth bass & bluegills	Amphipoda Cladocera
Decapoda	Bivalvia	Amphipoda	Copepoda
Gerridae	Gastropoda	Anisoptera	Diptera
	Megaloptera	Calanoida	Ephemeroptera
	Seed	Cladocera	Fish
	Trichoptera	Corixidae	Hemiptera
	Veliidae	Cyclopoida	Hydracarina
		Diptera – larvae	Odonata
		Diptera – pupae	Trichoptera
		Ephemeroptera	Other
		Fish	
		Hydracarina	
		Ostracoda	
		PDUI	
		Plecoptera	
		Zygoptera	

Table 1.2. Parameters for invertebrate taxa describing a $\log_{10}$-$\log_{10}$ relationship between volume (mm^3) and maximum head width (mm). The linear relationship has an intercept (a) and slope (b). In addition, sample size (N), Shapiro-Wilk test statistic (W), Shapiro-Wilk P-value (P_{sw}) for H_0: normal distribution, Spearman correlation coefficient (r_s), Spearman test statistic (Z), and Spearman P-value (P_{sc}) for the test H_0: $\rho = 0$ are shown.

Taxa	N	W	P_{sw}	a	b	R_s	Z	P_{sc}
Diptera								
Ceratopogonidae	46	0.94	0.022	1.47	2.64	0.81	5.42	0.000
Chironomidae (l.)	99	0.98	0.549	0.73	2.45	0.91	8.97	0.000
Chironomidae (p.)	40	0.98	0.686	0.67	2.51	0.70	4.39	0.000
Ephemeroptera								
Baetidae	100	0.99	0.973	0.52	2.96	0.91	9.04	0.000
Hemiptera								
Corixidae	48	0.94	0.034	0.28	3.37	0.90	6.17	0.000
Gerridae	13	0.92	0.284	0.24	2.06	0.70	2.42	0.016
Veliidae	9	0.90	0.255	0.55	2.87	0.94	2.65	0.008
Odonata								
Anisoptera	17	0.97	0.825	0.17	3.08	0.96	3.85	0.000
Zygoptera	19	0.81	0.001	0.02	2.38	0.95	4.03	0.000
Trichoptera	66	0.96	0.103	1.67	0.24	0.63	5.06	0.000

where $C_{x_1x_2}$ is the intraspecific overlap measure for species x, p_{x_1i} is the proportion of resource state i used by one half of species x, and p_{x_2i} is the proportion of resource state i used by the other half of species x. As with all other indices used in my research, proportions were based on the mean of the volume percentages (Wallace 1981). This random assignment of fish to subsets was repeated 50 times, which permitted the calculation of a mean intraspecific overlap and its variance. I assumed that the distribution of intraspecific overlap values was approximately normal and used a one-sample t-test (Gosset 1908) to determine whether intraspecific diet overlap was significant (i.e. H_0: $C_{x_1x_2} \leq 0.6$) at $\alpha = 0.10$ (Wallace and Ramsey 1983). The use of 0.6 as indicative of a high overlap, an assumption originally used by Zaret and Rand (1971) and widely utilized today, was selected due to the lack of a more appropriate measure. For any particular sampling period and species, I considered the diet adequately characterized if I rejected my null hypothesis of an intraspecific diet overlap ≤ 0.60.

Diet Breadth

I calculated diet breadth for each species and sampling date with the index proposed by Levins (1968) for niche breadth:

$$B = \frac{1}{\sum_{i=1}^{n} p_i^2}$$

where B is diet breadth, and p_i is the proportion of resource state i consumed by individuals. Additionally, the data from each sampling date were combined to estimate an overall diet breadth for each species. The variance of each measure was estimated by bootstrapping (Efron 1979) the data 1,000 times (Manly 1997; Krebs 1999). Diet breadth was adjusted for bias [see Manly (1997) or Krebs (1999) for reasoning behind bias adjustment] and the distribution assumed approximately normal (Bickel and Freedman 1981). Differences between the diet breadth of largemouth bass and bluegills were tested (i.e. H_0: $B_x = B_y$) using a two-sample t-test for unequal variances (Welch 1937) at $\alpha = 0.10$.

Interspecific Diet Overlap

To quantify diet similarities between largemouth bass and bluegills, I used Schoener's (1970) niche overlap index, which for interspecific overlap is calculated as:

$$C_{xy} = 1 - \frac{1}{2}\left(\sum_{i=1}^{n} \left|p_{xi} - p_{yi}\right|\right),$$

where C_{xy} is the interspecific overlap measure, p_{xi} is the proportion of resource state i consumed by individuals of species x, and p_{yi} is the proportion of resource state i consumed by individuals of species y. As with diet breadth, an overall interspecific diet overlap was calculated, in addition to the interspecific overlap for each sampling date. The variance also was estimated by bootstrapping (Efron 1979) each data set 1,000 times (Smith 1985; Manly 1997; Krebs 1999). Overlaps were bias-adjusted [see Manly (1997) or Krebs (1999) for reasoning behind bias adjustment] and the distributions assumed approximately normal (Bickel and Freedman 1981; Smith 1985). I used a one-sided t-test (Gosset 1908) to determine whether diet similarity was significant (i.e. H_0: $C_{xy} \leq 0.60$) at $\alpha = 0.10$ (Smith 1985).

Fishery Assessment

The Big Pond fishery was sampled with nighttime boat electrofishing in the fall of 1997. The equipment used was similar to that previously described, although sampling was conducted from a slightly larger boat with boom-suspended anodes. Sampling consisted of five 5-10 minute passes (37 minutes total shocking time). All collected fish were weighed, measured, and a sample had scales removed for age and growth analysis.

Fish population structures were assessed with indices of Proportional Stock Density (PSD) (Anderson 1976) and Relative Stock Density (RSD) (Wege and Anderson 1978) using the 5-cell length categorization system proposed by Gabelhouse (1984). Confidence intervals for PSD and RSD were estimated using the normal approximation method from Gustafson (1988). Relative weight (W_r) (Wege and Anderson 1978) was evaluated by comparing individual weights to standard weights (W_s). Standard weights for each species were calculated from the equations given in Anderson and Neuman (1996). I tested for differences in W_r among the length categories for largemouth bass and bluegills with ANOVA at $\alpha = 0.10$ after residuals satisfied tests of normality (largemouth bass Shapiro-Wilk test: W = 0.947, N = 24; P = 0.2410) (bluegills Shapiro-Wilk test: W = 0.977, N = 33; P = 0.7499). Differences in W_r of redear sunfish among stock and quality lengths were tested with the Wilcoxon (1945) rank sum test after W_r's of quality length fish failed a test of normality (Shapiro-Wilk test: W = 0.782, N = 69; P < 0.0001).

Either whole scales or scale impressions were viewed with a microfiche projector and annuli counted to estimate age. Scales were read by two people. When estimates of age differed, the readers made a second reading. If estimates again differed, that fish was disqualified from age and growth analysis. Growth was estimated using the Fraser-Lee method of back-calculation (DeVries and Frie 1996) with the intercept parameters from Carlander (1982). Fish growth was compared to Virginia statewide means as reported in Banach (1989).

Results and Discussion

Diet of Age-0 Largemouth Bass and Juvenile Bluegills

A significant difference was observed in fullness of largemouth bass stomachs among times of collection during the June 28 sampling period (Kruskal-Wallis test: H = 42.69, d.f. = 5; P = 0.000) (Table 1.3). Few items were found in the stomachs of largemouth bass at 0000 or 0400 hours, indicating that age-0 largemouth bass do not feed nocturnally. My results are similar to that of Zweiacker and Summerfelt (1974) who also observed a lack of feeding at night, but contradict Heidinger (1975). Although stomach fullness, based on ranking, was higher at 1600 hours, it was not significantly different than stomach fullness at 0800 hours, indicating that my morning sampling optimized the information collected per fish (Bowen 1996).

Items eaten by largemouth bass and bluegills throughout the study are shown in Table 1.1. Measured at this scale, the trophic niche of largemouth bass is contained almost entirely within the trophic niche of bluegills. The only items consumed by largemouth bass but not by bluegills were Gerridae (Hemiptera) and Decapoda, which overall comprised < 1.0% of the diet of largemouth bass by volume.

My findings are in general agreement with previous research on the individual diets of largemouth bass (Keast and Eadie 1985; Hirst and DeVries 1994; Olson 1996) and bluegills (Keast 1978; Kelso 1983). Largemouth bass progressed through a series of ontogenetic niche shifts in diet (Figure 1.1). Initial use of zooplankton (i.e. Amphipoda, Copepoda, and Cladocera) was high, but declined with length. Conversely, largemouth bass initial use of Ephemeroptera was low, but increased with length. Largemouth bass did forage on Diptera larvae and pupae, but overall use was low. Some discrepancy exists in the literature as to the length at which largemouth bass become piscivorous. However, there is no universal method by which this is assessed (Bettoli et al. 1992; Traxler and Murphy 1995) and size of piscivory will probably vary among systems and years. Based on the definition of Bettoli et al. (1992), largemouth bass in Big Pond became piscivorous at approximately 90 mm TL, although fish was a major diet item of largemouth bass when 70 mm TL. This is midrange of previously reported lengths (Applegate and Mullan 1967; Pasch 1975; Bettoli et al. 1992; Traxler and Murphy 1995; Olson 1996). I did find largemouth bass as small as 21 mm TL feeding on fish, while larger fish collected on the same sampling date consumed zooplankton. This indicates that differences in individual capability may influence the niche shift to piscivory (Pasch 1975).

Diet of largemouth bass by sample date was highly variable (Figure 1.1). Without concurrent data on the availability of food items in the environment, any explanation of this variability would be entirely speculative. However, the variability may be influenced by the wide range of largemouth bass lengths that were collected with each sampling date (Table 1.4). Variability in length is common with age-0 largemouth bass and it has been attributed to insufficient food resources (Shelton et al. 1979; Timmons et al 1980; DeAngelis and Coutant 1982).

Diet of bluegills by length and sampling date are shown in Figure 1.2. There was no difference in the lengths of bluegills with stomach contents that were examined among the sampling dates (Kruskal-Wallis test: $H = 7.30$, d.f. = 8; $P = 0.504$). Bluegills fed primarily on Cladocera, Copepoda, and Diptera throughout the summer and fall and at all sizes (as noted by Keast 1978; Kelso 1983), although consumption of Cladocera declined with size (as noted by Keast 1978). Bluegills did not feed heavily on Ostracoda, which was found to be a major diet item of bluegills by Keast (1978) and Kelso (1983).

Table 1.3. Number collected (N) and mean ($\bar{x}$) ± 2 SE, median ($\dot{x}$), and mean rank ($\bar{R}$) stomach fullness of age-0 largemouth bass at time of collection. A significant difference in stomach fullness was observed (Kruskal-Wallis: H = 42.69, d.f. = 5; P = 0.000). Collection times with different letters are significantly different (Bonferroni multiple comparison procedure) at a family error rate = 0.20 (individual error rate = 0.0067).

	Time of Collection					
	0000	0400	0800	1200	1600	2000
N	28	7	12	3	14	9
$\bar{x}$ ± 2 SE	8.34 ± 7.78	0.00 ± N.A.	54.15 ± 21.33	28.86 ± 42.94	84.58 ± 39.44	114.29 ± 120.11
$\dot{x}$	0.00	0.00	47.85	15.75	83.01	58.74
$\bar{R}$	22.7	15.5	51.1	36.8	55.5	50.8
Multiple Comparison	A	A	B	AB	B	B

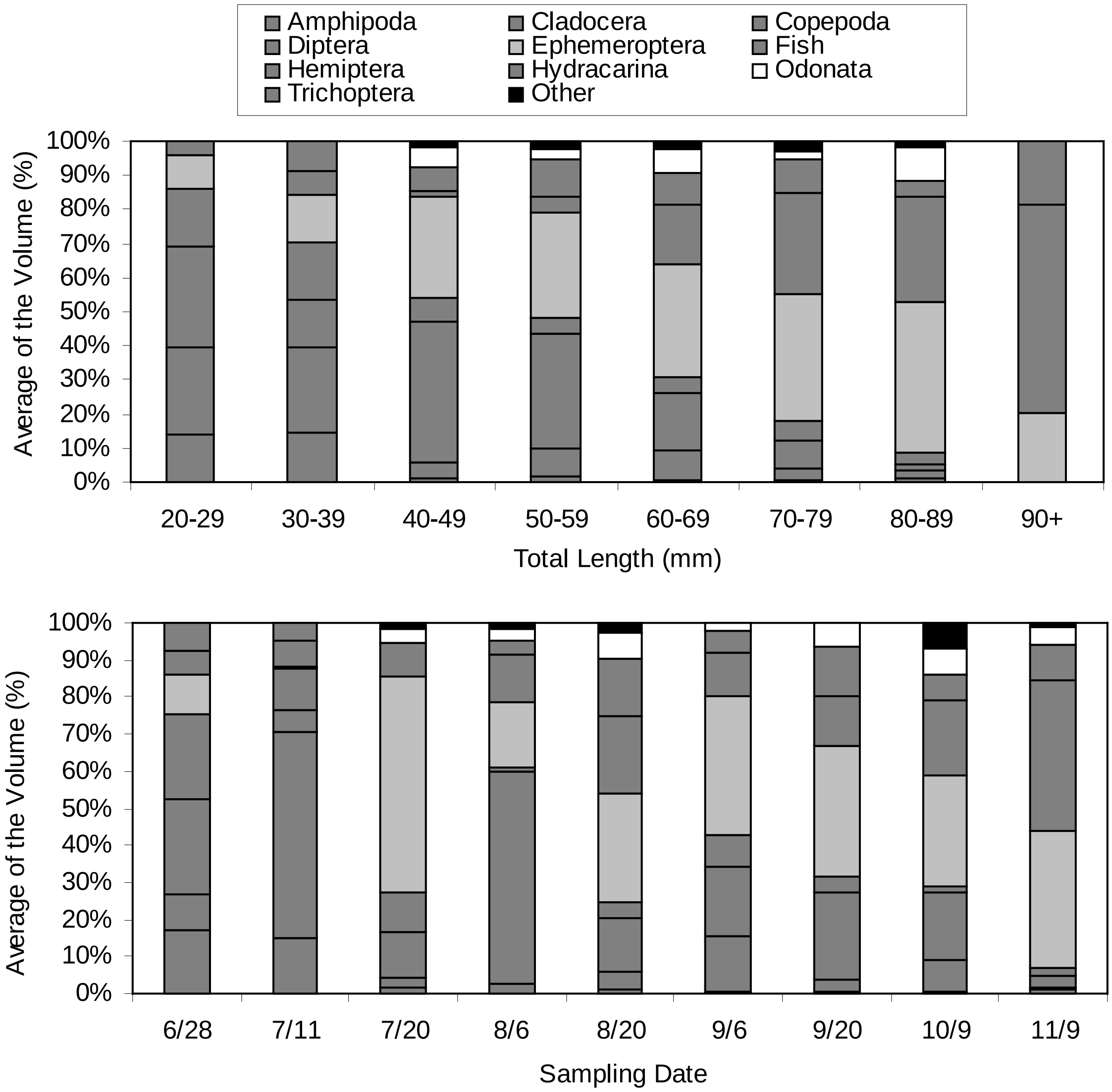

Figure 1.1. Diet of age-0 largemouth bass by TL and sampling date.

Table 1.4. Number of stomachs with contents examined (N), length ranges of fish, mean intraspecific overlap ($\overline{C}_{x_1x_2}$) ± 2 SE, t-test statistic (t) for H_0: $C_{x_1x_2} \leq 0.6$, and P-value (P) for largemouth bass and bluegills on each sampling date.

	Largemouth Bass					Bluegill				
Date	N	Lengths	$\overline{C}_{x_1x_2}$ ± 2 SE	t	P	N	Lengths	$\overline{C}_{x_1x_2}$ ± 2 SE	t	P
06/28	43	21 – 39	0.74 ± 0.02	15.06	$P < 0.0005$	36	25 – 72	0.74 ± 0.02	16.22	$P < 0.0005$
07/11	25	27 – 42	0.71 ± 0.05	4.88	$P < 0.0005$	26	16 – 58	0.68 ± 0.03	5.68	$P < 0.0005$
07/20	24	30 – 56	0.71 ± 0.03	8.28	$P < 0.0005$	28	18 – 62	0.80 ± 0.02	18.79	$P < 0.0005$
08/06	27	39 – 73	0.73 ± 0.03	8.99	$P < 0.0005$	25	25 – 70	0.76 ± 0.02	15.97	$P < 0.0005$
08/20	27	45 – 76	0.67 ± 0.04	3.82	$P < 0.0005$	27	19 – 70	0.72 ± 0.02	11.14	$P < 0.0005$
09/07	35	52 – 89	0.72 ± 0.03	10.10	$P < 0.0005$	29	26 – 72	0.73 ± 0.02	12.04	$P < 0.0005$
09/20	29	54 – 87	0.66 ± 0.02	5.24	$P < 0.0005$	25	29 – 69	0.72 ± 0.02	9.91	$P < 0.0005$
10/09	30	52 – 136	0.69 ± 0.03	5.47	$P < 0.0005$	31	19 – 79	0.74 ± 0.02	14.46	$P < 0.0005$
11/09	24	63 – 112	0.72 ± 0.04	6.25	$P < 0.0005$	25	26 – 70	0.71 ± 0.03	6.83	$P < 0.0005$

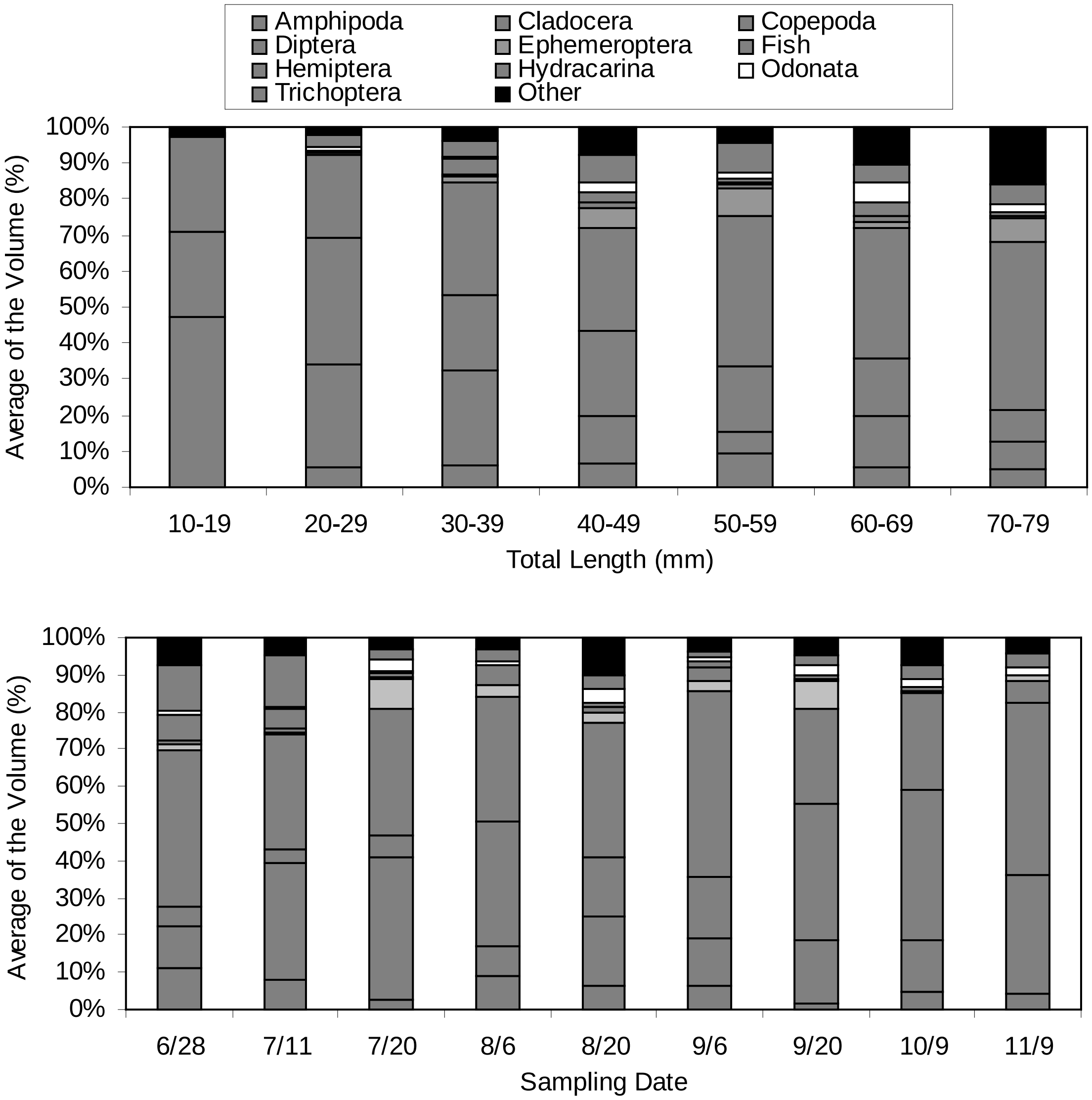

Figure 1.2. Diet of juvenile bluegills by TL and sampling date.

Bluegills have been observed to shift to foraging primarily on zooplankton when 50-80 mm standard length (SL), in response to the limnodromous movement of bluegills from the littoral zone to the pelagic zone (Werner and Hall 1988). I did not observe such a shift. On the contrary, Diptera was the predominant diet item in the largest size classes of bluegills examined. However, my sampling may have been biased against fish that had switched to primarily a zooplankton diet since I restricted collections to the littoral zone.

Intraspecific Diet Overlap

For each species and sampling period, I rejected my null hypothesis of a low intraspecific diet overlap (H_0: $C_{x_1 x_2} \leq 0.6$; $P < 0.0005$) (Table 1.4). Based on this test, I adequately characterized the diet of both largemouth bass and bluegills on each sampling date. Since overlap measures assume the diet of each species has been adequately characterized, greater reliance can be placed on the accuracy of my diet overlap measures (Wallace and Ramsey 1983).

Diet Breadth

The diet breadth of largemouth bass and bluegills was significantly different ($P < 0.10$) overall and for each sampling date (Table 1.5). Only on June 28 was the diet breadth of largemouth bass higher than that of bluegills. On all other sampling dates, bluegills had a higher diet breadth than largemouth bass, indicating that bluegills fed on more items or fed on items at more equal proportions. Wallace (1982) also found that diet breadth of bluegills typically was higher than that of largemouth bass. Based on diet breadth measurements, Keast (1979) characterized bluegills as generalist feeders, while largemouth bass were characterized as specialists. My results support that assessment. Direct comparison of diet breadths that I observed with other studies is inappropriate due to the measure depending on the level of food category taxonomic identification.

Interspecific Diet Overlap

I failed to reject my null hypothesis of a low interspecific overlap (H_0: $C_{xy} \leq 0.60$; $P > 0.10$) overall and for each sampling period (Table 1.5). A comparison of diets is shown in Figure 1.3. Of the studies that have specifically investigated diet similarities between age-0 largemouth bass and juvenile bluegill diets, only Wallace (1982) and Keast and Eadie (1985) have observed high diet overlaps. Keast and Eadie (1985) determined that small age-0 largemouth bass overlapped significantly with age-0 and age-1 bluegills, although they did not indicate which resources caused the overlap. Wallace (1982) found that largemouth bass and bluegill diets overlapped significantly in experimental ponds, due to their simultaneous use of Cyclopoida, Chironomidae larvae, Cladocera, and Ostracoda. However, Wallace (1982) also observed a low diet overlap between age-0 largemouth bass and juvenile bluegills in False River, LA. The low overlap was attributed to largemouth bass consuming Amphipoda, Ephemeroptera, fish, and Mysidae, while bluegills utilized Cladocera, Chironomidae larvae, Copepoda, fish eggs, and Ostracoda. Gilliam (1982) and Olson et al. (1995) also observed low diet overlaps due to largemouth bass feeding on Calanoida, Ephemeroptera, Odonata, and Diptera pupae, and bluegills consuming predominantly Diptera larvae. Low diet overlaps in this study were due primarily to largemouth bass feeding on Calanoida, Ephemeroptera, and fish, while bluegills consumed Diptera and Cyclopoida. Both species fed primarily on zooplankton and Diptera when overlap was moderate, although the proportions of use were different.

Community Structure

Catch-per-unit effort ($\overline{x} \pm 2$ SE) for largemouth bass, bluegills, and redear sunfish was 58 ± 16, 40 ± 7, and 136 ± 68 fish/electrofishing hour, respectively. Overall catch of warmouth, black crappies, and chain pickerel was low and I excluded these species from further analysis. Proportional stock density and RSD-P (± 90% CI) was 30 ± 20 and 9 ± N.A.[1] for largemouth bass, 67 ± 20 and 13 ± N.A. for bluegills, and 82 ± 8 and 1 ± N.A. for redear sunfish. Predator and weighted-mean prey PSD is shown in Figure 1.4. Ney (1993) described this area of the

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[1] Normal approximation confidence intervals can not be calculated for small sample sizes or when stock density indices approach 0 or 100 (Gustafson 1988).

graph as a situation where a high population of small predators is excessively cropping young prey.

Relative weights for each species and length category are shown in Table 1.6. Largemouth bass W_r did not differ among length categories (ANOVA: F = 1.37, d.f. = 29; P = 0.273). However, bluegill W_r did differ among length categories (ANOVA: F = 5.39, d.f. = 23; P = 0.013). Tukey's (1953) multiple comparison procedure indicated that W_r of stock-length bluegills was significantly greater than that of quality- or preferred- length fish at a family error rate = 0.10. Stock- and quality-length redear sunfish did not differ in W_r (Wilcoxon rank sum test: T_x = 2909.5; P = 0.7927). Overall, W_r for all species was low, indicating a problem may exist in food or feeding conditions (Anderson and Neuman 1996). Growth of largemouth bass (Figure 1.5), which was among the slowest in Virginia, reflects this hypothesis. However, despite their low W_r, bluegills and redear sunfish were able to sustain average growth in length for Virginia (Figure 1.5).

The Big Pond fishery would be best described as a panfish-option impoundment (Gabelhouse et al. 1982; Gabelhouse 1984; Flickinger and Bulow 1993). A relatively high density of largemouth bass appears to be extensively foraging on panfish populations. This high predator density is resulting in intraspecific competition for forage fish, which explains the low W_r and slow growth of largemouth bass. The W_r of largemouth bass is not problematic as Gabelhouse (1987) recommend a target range of 85 to 95 when managing a small impoundment for this option. Under this management option, higher W_r's for bluegills and redear sunfish are desirable. However, overall fishing pressure on the impoundment was light, which may cause overcrowding of quality-length panfish and which could explain the low W_r for both prey species (Anderson 1980). The panfish option typically is managed with minimum-length limits on largemouth bass (Flickinger and Bulow 1993). Although no such regulation existed on Big Pond, most anglers refused to harvest small largemouth bass.

Table 1.5. Diet breadth ± 2 SE for largemouth bass (B_x) and bluegills (B_y), degrees of freedom (d.f.), two sample t-test statistic (*t*) for H_0: $B_x = B_y$, and P-value (P) overall and for each sampling date is shown. In addition, the interspecific diet overlap (C_{xy}) ± 2 SE, degrees of freedom (d.f.), t-test statistic (*t*) for H_0: $C_{xy} \geq 0.6$, and P-value (P) is shown.

	Diet Breadth					Interspecific Diet Overlap			
Date	B_x ± 2 SE	B_y ± 2 SE	d.f.	*t*	P	C_{xy} ± 2 SE	d.f.	*t*	P
06/28	7.81 ± 0.18	7.40 ± 0.19	75	3.19	$0.005 < P < 0.001$	0.54 ± 0.01	77	-9.06	$P > 0.10$
07/11	3.04 ± 0.22	6.24 ± 0.29	46	-17.63	$P < 0.001$	0.60 ± 0.01	49	0.08	$P > 0.10$
07/20	2.92 ± 0.21	4.08 ± 0.14	41	-8.93	$P < 0.001$	0.33 ± 0.01	50	-40.61	$P > 0.10$
08/06	2.90 ± 0.17	5.23 ± 0.19	48	-18.36	$P < 0.001$	0.14 ± 0.01	50	-101.84	$P > 0.10$
08/20	6.33 ± 0.23	7.12 ± 0.23	51	-4.83	$P < 0.001$	0.27 ± 0.01	52	-53.28	$P > 0.10$
09/07	5.13 ± 0.21	6.27 ± 0.26	56	-6.77	$P < 0.001$	0.36 ± 0.01	62	-37.27	$P > 0.10$
09/20	5.97 ± 0.25	7.31 ± 0.19	50	-8.51	$P < 0.001$	0.48 ± 0.01	52	-13.24	$P > 0.10$
10/09	6.50 ± 0.24	6.85 ± 0.23	58	-2.15	$0.025 < P < 0.05$	0.34 ± 0.01	59	-39.27	$P > 0.10$
11/09	3.54 ± 0.15	5.05 ± 0.24	39	-10.48	$P < 0.001$	0.15 ± 0.00	47	-87.98	$P > 0.10$
Overall	7.07 ± 0.05	7.40 ± 0.04	480	-10.55	$P < 0.001$	0.46 ± 0.00	514	-472.49	$P > 0.10$

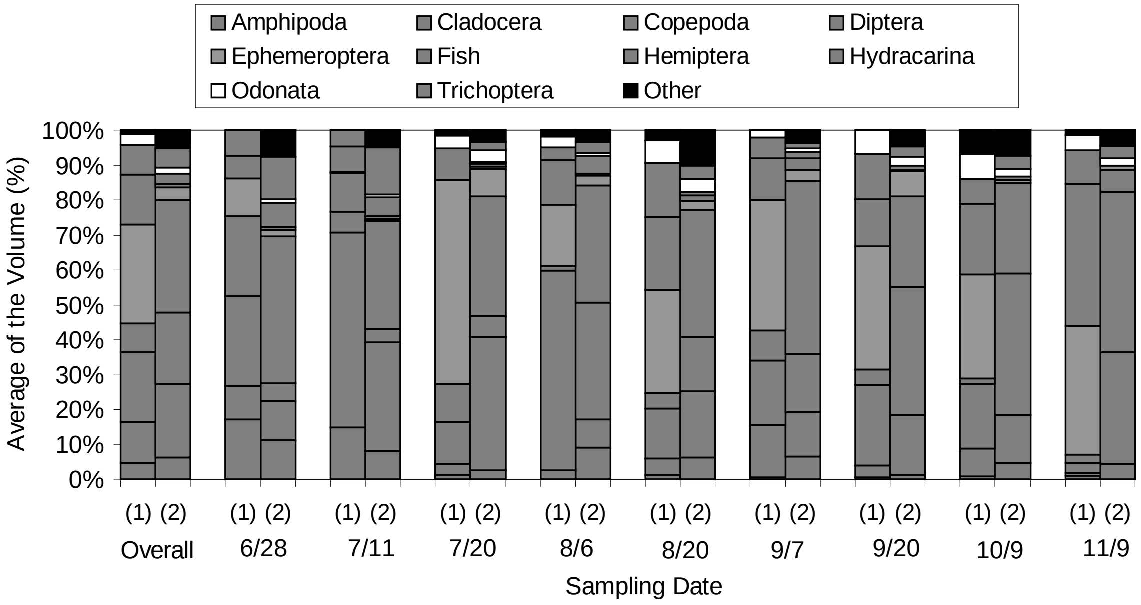

Figure 1.3. Comparison of age-0 largemouth bass (1) and juvenile bluegill (2) diets overall and by sampling date.

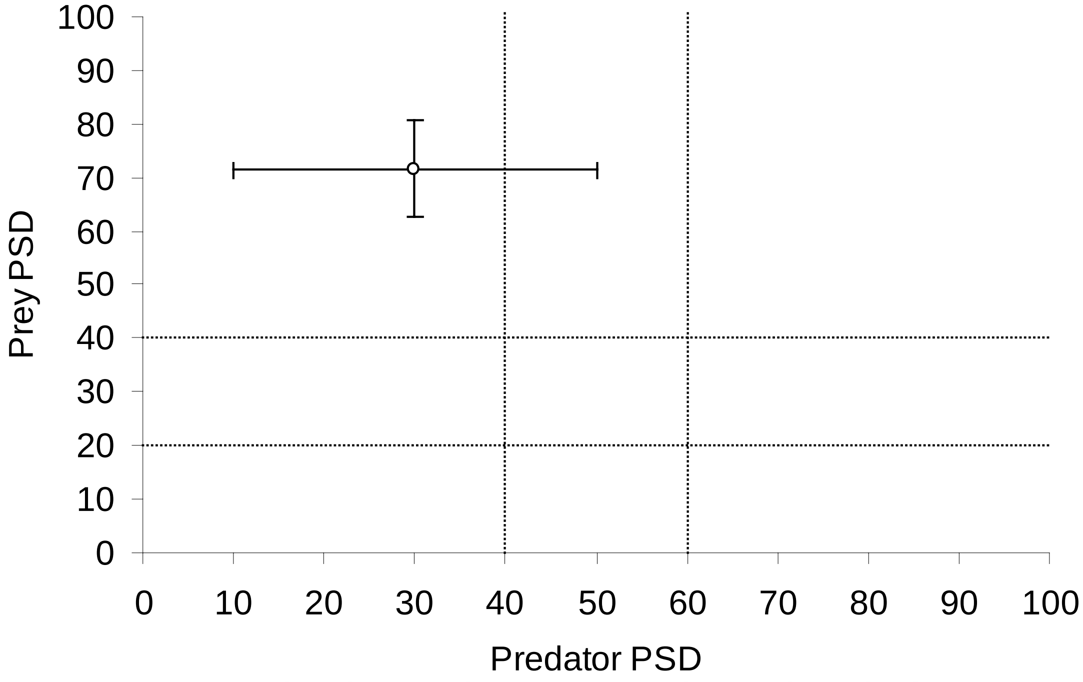

Figure 1.4. Tic-tac-toe (total quality) graph comparing predator and weighted – mean prey PSD. Confidence intervals (90%) as calculated from Gustafson (1988), also are shown.

Table 1.6. Relative weight (W_r) ($\bar{x}$ ± 2 SE) at various length categories of largemouth bass, bluegills, and redear sunfish.

Length Category	Largemouth Bass	Bluegill	Redear Sunfish
Pre-stock	86 ± 4	–	–
Stock	83 ± 2	97 ± 11	83 ± 3
Quality	80 ± 6	83 ± 4	82 ± 1
Preferred	83 ± 3	75 ± 16	82 ± N.A.

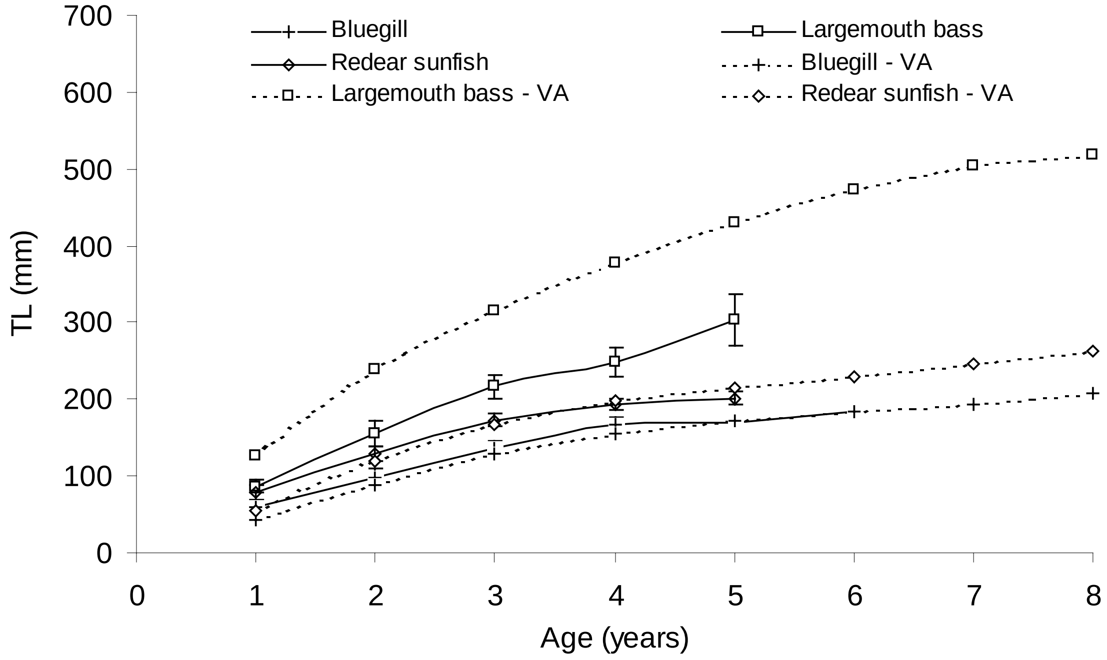

Figure 1.5. Back-calculated length ($\bar{x} \pm 2$ SE) at age of largemouth bass, bluegill, and redear sunfish in Big Pond. For comparison, average growth rates in Virginia (Banach 1989) also are shown.

Management Implications

I found diet overlap between age-0 largemouth bass and juvenile bluegills to be low in a panfish-option small impoundment. Based on CPUE, redear sunfish were the most abundant species in the impoundment. Any direct or indirect effect redear sunfish have on the diet of largemouth bass and bluegills is unknown and should be further explored. Adult redear sunfish are well adapted for feeding on snails and mussels, but as juveniles may feed on items similar to those eaten by age-0 largemouth bass and bluegills (Jenkins and Burkhead 1993). I focused my research on the trophic interactions of largemouth bass and bluegills as they are the most common stocking combination. It is not recommended that largemouth bass and redear sunfish be stocked together without other forage fish (Gabelhouse 1978). Nevertheless, redear sunfish are frequently stocked in conjunction with largemouth bass and bluegills (Gabelhouse 1978; Flickinger and Bulow 1993) so their presence in Big Pond does not diminish the utility this study.

I believe that largemouth bass and bluegill could be competing due to the number of shared resources and the slowed growth of largemouth bass in the study impoundment. Although estimated diet overlap was low, one species may have shifted resource use in response to competition (MacArthur 1968). Even if competition was not occurring, it should be considered a potential occurrence and incorporated into management planning for the fishery. The panfish option may not be desirable to anglers due to the small sizes of largemouth bass caught (Flickinger and Bulow 1993). If this impoundment was managed for an alternative option, it might be necessary to increase densities of small bluegills. For example, when managing for the big bass option, a high density of small bluegills is preferred in order to provide plenty of forage for trophy-length largemouth bass. At higher densities, it is likely that the trophic niche breadth of bluegills would expand due to intraspecific competition. Given the number of resources shared by largemouth bass and bluegill in Big Pond, high densities of bluegills could depress food resource availability for age-0 largemouth bass, further slowing growth of largemouth bass (Gilliam 1982; Wallace 1982; Olson et al. 1995). Reduced age-0 growth can affect adult largemouth bass differently depending on whether overwinter survival is size related, on which there is no consensus (Aggus and Elliot 1975; Toneys and Coble 1979; Kohler et al. 1993;

Miranda and Hubbard 1994). Therefore, different management strategies may be necessary in order to effectively achieve the big bass option. Managers may need to implement a fairly conservative minimum-length limit if a largemouth bass year class is greatly weakened due to slow growth. Otherwise, managers may need anglers to harvest small largemouth bass in order to prevent intraspecific competition and to ensure sufficient growth to trophy lengths.

In an effort to improve the population structure of largemouth bass in a Kansas pond consisting primarily of small largemouth bass and large bluegills, Gabelhouse (1987) imposed a 30-38 cm slot limit and simulated angler harvest via removal with electrofishing. It was determined that the regulation was ineffective in producing a balance-option impoundment, potentially due to competition between largemouth bass < 30 cm and bluegills > 15 cm. Although evidence favors the potential for competition between age-0 largemouth bass and juvenile bluegills (Gilliam 1982; Wallace 1982; Olson et al. 1995), Gabelhouse (1987) realized that competition could have a major influence on the outcome of management efforts and that ignoring its influence runs counterproductive to fisheries management (Larkin 1956). Likewise, DeVries and Stein (1990) believed that competition between early life stages of predator and prey could influence the success of a forage fish manipulation. A better understanding of early interactions of fish communities will allow fishery managers to better place their management decisions in the overall context of fish ecology, which should lead to more sound management. I suggest that further study be conducted concerning resource partitioning between largemouth bass and bluegill when sympatric and at different densities. Guidelines could be established that, in combination with other stock assessment statistics such as size structure indices, CPUE, and fish condition, could be used to help determine the feasibility of managing small impoundments for specific options. Specifically, I recommend that similarity in resource use be measured in combination with efforts to manage small impoundments for specific options. Responses to management actions at different similarities of resource use should be tracked with tic-tac-toe (total quality) graphs (Figure 1.4) to determine whether patterns may emerge. For example, it may be determined that efforts to manage an impoundment for the big bass option fail when resource use similarity between largemouth bass and panfish is high. This could be interpreted as an ecological constraint on the effectiveness of management actions. If particular patterns do emerge, fishery managers will be able to add to their “arsenal” another assessment tool that could make fisheries management more reliable (Willis et al. 1993).

Chapter 2

Trophic Competition Between Age-0 Largemouth Bass and Juvenile Bluegills with Implications for Pond Fisheries

Abstract

I tested whether age-0 largemouth bass and juvenile bluegills compete for food resources in a recreational small impoundment in central Virginia. The species were stocked allopatrically and sympatrically in 1.0-m^3 cages and their mortality, growth, and food resource use monitored over a three-month period. Assignment of cage stocking densities was based on rotenone sampling data for the region. I found that the species did compete and that there was a strong asymmetry in their competitive relationship. Bluegills had a much stronger impact on largemouth bass than the reverse. When stocked alone, largemouth bass grew significantly larger than when stocked with either 10 or 30 bluegills. Additionally, largemouth bass stocked with 10 bluegills grew significantly larger than those stocked with 30 bluegills during the second half of the experiment. Largemouth bass stocked alone consumed significantly more Amphipoda, Diptera larvae, and Odonata, and less Copepoda and Hemiptera than largemouth bass stocked with bluegills. There were no significant differences in bluegill growth except between bluegills stocked alone and bluegills stocked with 15 largemouth bass. Bluegills stocked alone consumed significantly more Amphipoda than did bluegill stocked with largemouth bass, although overall Amphipoda comprised a small proportion of bluegill diet. Largemouth bass and bluegill mortalities were not affected by the other species, thus suggesting that the mechanism of competition may be exploitation rather than interference. My findings suggest that a competitive juvenile bottleneck could occur, depending largely on whether overwinter survival of largemouth bass is size-related. Competition between largemouth bass and bluegills may explain why maintenance stocking of fingerling largemouth bass typically is not successful. Further research is needed on the appropriate timing and length at stocking of introductory largemouth bass stockings. I recommend that competition between largemouth bass and bluegills be explored in connection with regional studies concerning overwinter survival and angling opportunities in small impoundments. Competition between the species may impose an ecological constraint that restricts achievable management options in small impoundments.

Introduction

The coupled stocking of largemouth bass and bluegills has been one of the major management practices for North American small impoundments since the 1930s (Smitherman 1975; Novinger and Legler 1978). Their interaction typically is viewed as a predator-prey relationship. However, age-0 largemouth bass feed on zooplankton and aquatic insects before becoming piscivorous (Gilliam 1982; Keast and Eadie 1985; Hirst and DeVries 1994; Olson 1996), which is similar to the diet of bluegills (Keast 1978; Kelso 1983). Furthermore, age-0 largemouth and juvenile bluegills occupy essentially the same habitat (Werner 1977; Gilliam 1982) and feed at similar time periods (Zweiacker and Summefelt 1974; Kelso 1983; Chapter 1). This creates a potential for competition between the species, and ignoring its role in structuring communities could handicap management efforts (Larkin 1956).

Empirical evidence indicates that bluegill populations can depress largemouth bass populations; the mechanism has never been established, although competitive superiority seems a viable explanation. Bennett et al. (1969) in Ridge Lake, Illinois found that survival of largemouth bass fry was low when high densities of small bluegills were present, and survival was highest when no bluegills were present. Stone and Modde (1982) in several South Dakota ponds also determined that first-year survival and growth of largemouth bass was higher, although not significantly, when stocked alone than when stocked with bluegills or other forage fish. An extensive review of small impoundment stocking strategies by Dillard and Novinger (1975) found that when some managers stocked largemouth bass in the summer followed by bluegills in the fall, largemouth bass typically reproduced the first year after stocking. Conversely when bluegills were stocked in the fall followed by largemouth bass in the early summer, largemouth bass failed to spawn the first year after stocking, which was attributed to slow growth of largemouth bass. Additionally, some managers consistently achieved the highest biomass yield of largemouth bass when they were stocked in ponds alone (Dillard and Novinger 1975). Olson et al. (1995) found a negative correlation between the density of small bluegills and age-0 largemouth bass growth in Michigan lakes.

Several studies have looked at similarity in diet between age-0 largemouth bass and juvenile bluegills. Diet overlap indices, a relative measure of the extent to which species use the same food resources (Bowen 1996), generally indicate that diet similarity is low (Wallace 1982; Olson et al. 1995; **Chapter 1**). Species typically segregate consumption of Copepoda, Diptera, Ephemeroptera, and fish (Gilliam 1982; Wallace 1982; Olson et al. 1995; **Chapter 1**). While it may be argued that this is evidence against competition, the relationship between diet overlap and competition is complex and not well understood (Holt 1987). In fact, it is not known whether a high or low diet overlap would be indicative of competition (Keast 1978; Schoener 1982). Competition does seem a potential occurrence given that age-0 largemouth bass and juvenile bluegills do feed on many of the same items and that bluegills can reach high densities in small impoundments (**Chapter 1**).

Although descriptive evidence provides only a weak inference to the existence of competition (Crowder 1990), ecological research is best approached synthetically from observational, experimental, and theoretical viewpoints (Tilman 1987). Manipulative experimentation, where the species are studied separately and together in replicated treatments, provides the strongest single line of evidence when demonstrating competition (Sale 1979; Hurlbert 1984; Franklin 1987; Crowder 1990). The most convincing evidence of this type comes from Gilliam (1982) and Olson et al. (1995) who stocked age-0 largemouth bass and juvenile bluegills in partitioned experimental ponds in Michigan and found that largemouth bass growth was suppressed by the presence of juvenile bluegills. The largemouth bass and bluegill combination is relatively unpopular with fisheries managers in the northern United States due to the tendency of bluegills to overpopulate (Flickinger and Bulow 1993). In the southern United States where the stocking combination is still favored, the only experimental study on competition between largemouth bass and bluegills was undertaken by Wallace (1982), who stocked largemouth bass and bluegills in plastic pools at different densities and supplied a standardized amount of zooplankton. Largemouth bass growth was indeed suppressed by the presence of bluegills (Wallace 1982). However, the artificiality of this design complicates its applicability, and further research on the competitive potential between largemouth bass and bluegills in the southern United States is warranted.

The purpose of my research was to determine whether age-0 largemouth bass and juvenile bluegills compete for food resources in a recreational small impoundment in Virginia. In this study, I assessed the effect largemouth bass and bluegills have on one another's mortality, growth, and resource use when stocked allopatrically and sympatrically inside cages at different densities.

Methods

Cage Construction and Placement

I constructed 30 1-m^3 cages out of galvanized steel and polyethylene mesh (Brenden et al. 1999). The maximum bar measure of the mesh was 3.17 mm. Cages were transported by boat to an isolated cove of Big Pond, a privately owned 2.4-ha impoundment in Buckingham County, Virginia, and aligned in approximately 1-m deep water. Distance ($\bar{x} \pm 2$ SE) between cages was 58.7 ± 12.3 cm. I placed six tree branches (≈ 2 cm in diameter; three 50 cm and three 90 cm in length) upright in plastic planting pots in each cage to provide structural complexity for fish and substrate for invertebrates.

Field Collection

Fish were collected by electrofishing from a 4.27-m jon boat using a 2.5 GPP Smith-Root electrofisher powered by a GX-150 Honda generator with pulsed-DC output. The anode consisted of a Smith-Root one-piece telescoping prod pole ending in a 27.94-cm diameter ring electrode. Electrofishing was conducted with 0.5 – 1.0 A electricity pulsed at 30 pulses/s to alleviate stress.

Largemouth bass were sampled on the morning of 3 June 1998 from Big Pond. Upon capture, fish were monitored for several hours to assess initial mortality. Fish assigned to cages were sampled with a 500-mL glass beaker. I attempted to measure fish for total length (TL), however handling proved too stressful. The first 20 fish measured died. Because excessive mortality could have prevented successful completion of the experiment, I then chose not to measure fish, but instead immediately released fish into the cages upon capture. Subsampling (N = 30) indicated initial TL ($\overline{x}$ ± 2 SE) of largemouth bass was 19 ± 1 mm.

Bluegills were collected on the following day, also by electrofishing, from another nearby pond that contained only largemouth bass, bluegill, and American eel *Anguilla rostrata*. Previous sampling of Big Pond determined that it contained several *Lepomis* spp., which can be difficult to differentiate when younger. Collecting fish from this other pond ensured that bluegills, rather than other *Lepomis* spp., were stocked inside the cages. I targeted bluegills ranging in size from 20 - 70 mm TL (< age 2) as I did not want fish to grow beyond the size at which they are restricted to the littoral zone during this experiment (Werner and Hall 1988). Bluegills assigned to cages were measured for TL and marked by partially clipping one fin (right pectoral, left pectoral, right pelvic, left pelvic, anal, dorsal, lower caudal, or upper caudal), as outlined in Guy et al. (1996). I divided fish into 10-mm length groups (i.e. 21-30, 31-40, 41-50, 51-60, and 61-70 mm) and assigned an equal proportion of fish from each group to each cage. Since early growth of bluegills is linearly related to age and growth rates do not begin to decline until age 4 when fish are approximately 150 mm TL (Banach 1989), I assumed that all experimental fish had similar growth potential. This made slight differences in initial lengths of bluegills (Table 1.1) inconsequential. Some identically marked fish were placed in each cage because the number of bluegills assigned to each cage was greater than the number of individual marks. I ensured that such fish were approximately the same length or sufficiently different that individual distinction was still possible. After marking, bluegills were monitored for one hour to assess handling mortality. Mortality resulted in replacement of that fish with another. Bluegills were then released into the cages.

Stocking Density

Cage stocking densities were based on Virginia Department of Game and Inland Fisheries (VDGIF) rotenone sampling data from four Virginia impoundments: Lake Brunswick, Lake Conner, Lake Gordon, and Smith Mountain Lake (VDGIF unpublished data; Table 2.2). I used data from collections that utilized standardized sampling protocol (e.g. use of block nets) and where the number of age-0 largemouth bass and juvenile bluegills was recorded. I adjusted for nonrecovery using the constants given by Davies and Shelton (1983). Number/m^2 was obtained by dividing adjusted counts by cove surface area. To determine number/m^2 of littoral zone, I used the inverse of the open-water adjustment factors given by Aggus et al. (1980). Estimated density of fish/m^2 of littoral zone ($\bar{x}$ ± 2 SE) was 1.0 ± 1.0 and 7.0 ± 2.0 for age-0 largemouth bass and juvenile bluegills, respectively. Based on these data and because mortality of fish can be high in this type of research (Olson et al. 1995; Traxler and Murphy 1995), the stocking density of largemouth bass and bluegills chosen to mimic "normal" conditions was five largemouth bass and ten bluegills/cage.

To study the competitive interactions of largemouth bass and bluegills, I used a target-neighbor approach (Goldberg and Werner 1983; Mittelbach 1988; Olson et al. 1995). In this approach, a constant density of the "target" species is stocked with various densities of the "neighbor" species. Because I was interested in determining the effect of bluegills on largemouth bass as well as the effect of largemouth bass on bluegills, both largemouth bass and bluegills were treated as "target" species. To study the effect of bluegills on largemouth bass, five largemouth bass (target species) were stocked with 0 (bass alone), 10 (bass + norm blg), and 30 (bass + hi blg) bluegills. When studying the effect of largemouth bass on bluegills, ten bluegills (target species) were stocked with 0 (blg alone), 5 (blg + norm bass), and 15 (blg + hi bass) largemouth bass. The high-density treatments (i.e. bass + hi blg; blg + hi bass) were intended to mimic overcrowded, yet realistic, conditions. The five stocking densities (Note: bass + norm blg = blg + norm bass) resulted in six replicates being assigned to each treatment (Figure 2.2).

Table 2.1. Initial TL ($\bar{x}$ ± 2 SE) of bluegills among the stocking densities for Phases 1 and 2.

Time Period	Density	Initial TL (mm)
Phase 1	Blg alone	40 ± 3
	Blg + norm bass	44 ± 4
	Blg + hi bass	45 ± 3
	Bass + hi blg	44 ± 3
Phase 2	Blg alone	41 ± 4
	Blg + norm bass	43 ± 4
	Blg + hi bass	43 ± 4
	Bass + hi blg	44 ± 2

Table 2.2. VDGIF (unpublished data) rotenone sampling data from four Virginia impoundments. Number of fish/m^2 was estimated by multiplying the number of fish collected by nonrecovery correction constants of 1.67 and 1.89 (Davies and Shelton 1983) for largemouth bass and bluegills, respectively, and dividing by the cove surface area. Number of fish/m^2 of littoral zone was estimated using the inverse of the open-water adjustment factor from Aggus et al. 1980.

Sample Year	System	Cove Surface Area (ha)	Number of age-0 largemouth bass collected	Number of juvenile bluegill collected	Largemouth bass / m^2 littoral zone	bluegill/ m^2 littoral zone
1981	Brunswick	2.12	460	52,112	1.12	53.49
1984	″	2.12	139	12,749	0.34	13.09
1987	″	2.12	12	20,643	0.03	21.19
1990	″	2.12	30	11,922	0.07	12.24
1983	Conner	0.83	428	690	2.66	1.81
1984	″	0.83	604	9,002	3.75	23.60
1987	″	0.83	326	458	2.03	1.20
1990	″	0.83	292	1,353	1.81	3.55
1980	Gordon	1.95	247	13,393	0.65	14.94
1981	″	0.81	27	6,442	0.17	17.31
1983	″	1.95	151	2,047	0.4	2.28
1986	″	1.95	127	1,858	0.34	2.07
1989	″	1.95	74	3,494	0.20	3.90
1989	Smith Mtn.	1.40	161	4,279	0.59	4.33
1989	″	1.60	320	656	1.03	1.02
1989	″	1.75	170	5,652	0.50	7.03
1989	″	2.15	922	2,759	2.21	3.75
1990	″	1.40	144	5,602	0.53	5.67
1990	″	1.60	210	455	0.68	0.62
1990	″	1.75	244	4,306	0.72	6.69
1990	″	2.15	189	3,850	0.45	4.79
1991	″	1.40	106	855	0.39	0.87
1991	″	1.60	152	2,263	0.49	3.52
1991	″	1.75	42	2,166	0.12	2.69
1991	″	2.15	88	4,046	0.21	5.50
1992	″	1.40	496	1,824	1.83	2.48
1992	″	1.60	461	722	1.49	1.12
1992	″	1.75	145	2,778	0.43	3.45
1992	″	2.15	594	4,126	1.43	4.18
1993	″	1.40	824	2,925	3.04	4.55
1993	″	1.60	185	2,516	0.60	2.74
1993	″	2.00	515	1,429	1.33	1.94
1993	″	2.15	541	3,178	1.30	3.22
1994	″	1.40	61	4,948	0.22	5.01
1994	″	1.60	118	7,084	0.38	9.63
1994	″	2.00	63	10,565	0.16	11.49
1994	″	2.15	117	2,032	0.28	3.16
1995	″	1.40	93	3,715	0.34	3.76
1995	″	1.60	95	8,701	0.31	9.47
1995	″	2.00	237	4,322	0.61	5.88
1995	″	2.15	243	1,493	0.58	2.32
1996	″	1.12	250	4,971	1.15	6.76
1996	″	1.40	142	6,394	0.52	6.47
1996	″	1.60	160	7,845	0.52	15.24
1996	″	2.15	321	5,711	0.77	8.88
1997	″	1.12	558	6,665	2.57	10.36
1997	″	1.40	343	2,451	1.26	3.33
1997	″	1.60	316	6,705	1.02	6.79
1997	″	2.15	470	4,988	1.13	9.69
			Number ($\overline{X}$ ± 2 SE) / m^2 littoral zone		1 ± 1	7 ± 2

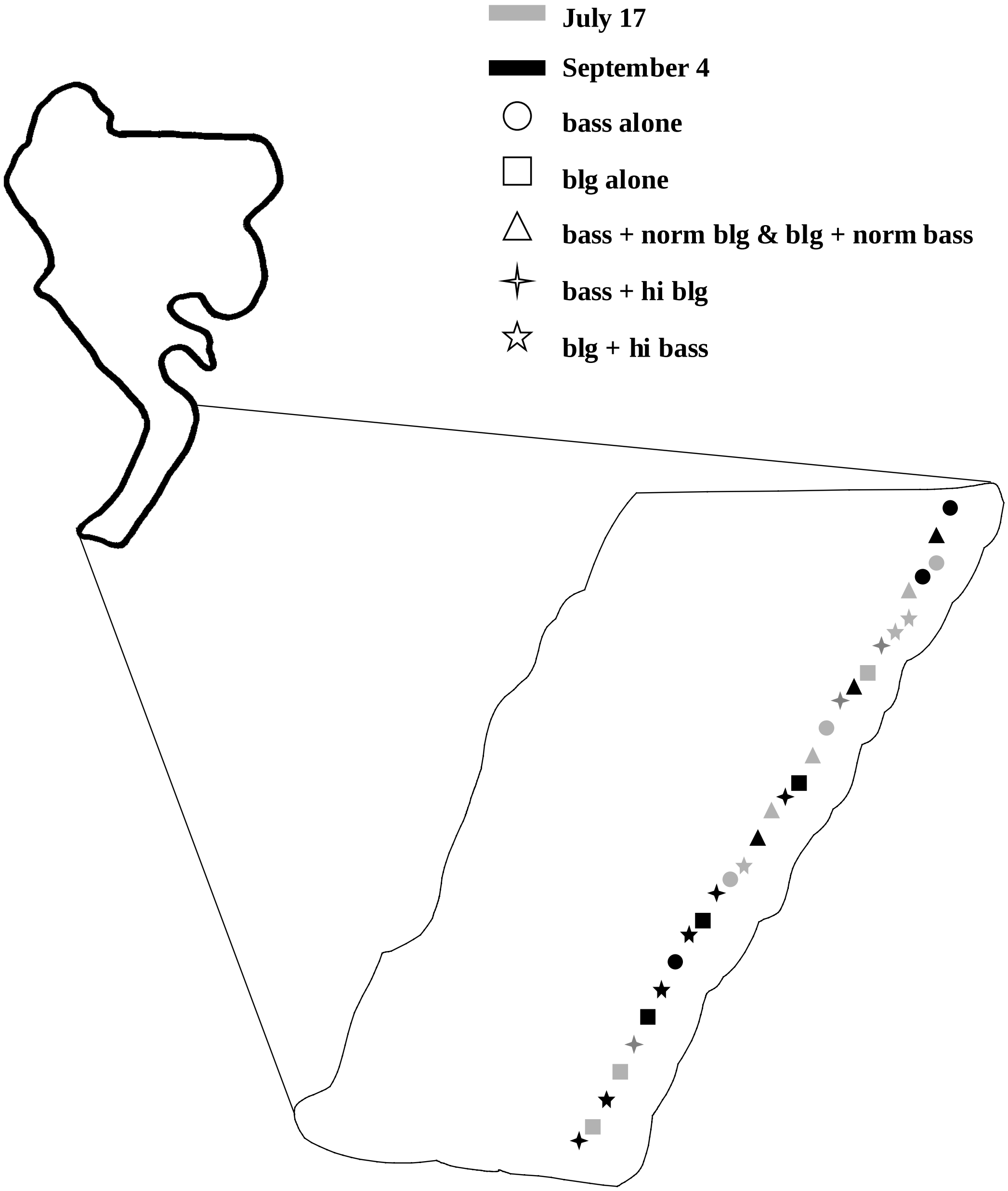

Figure 2.1. Cage placement in the study pond and the stocking density and time of removal assigned to each cage.

Cage and Fish Removal

To evaluate temporal differences in competitive effects (Franklin 1987), three replicates from each treatment were removed on July 17 (Phase 1; 43 days post-stocking) and September 4 (Phase 2; 91 days post-stocking). Research the previous year indicated that largemouth bass in the study pond began switching to primarily a piscivorous diet at approximately 70-mm TL, which was the mean length of largemouth bass in early September (**Chapter 1**). Fish were removed from the cages, assigned an identification number, measured for TL, sacrificed by severing the spinal column, and stored in 10% formalin. To prevent postcapture digestion of stomach contents, the coelom was slit to ensure formalin entry into the pleuroperitoneal cavity. Fish were removed from the formalin after one week, allowed to soak in water for two days, and transferred to 90% ethanol. Stomach contents of fish later were removed for identification and volumetric measurement. Contents were identified to the lowest taxonomic level practical with the aid of a stereozoom microscope and the taxonomic keys of Merrit and Cummins (1984) and Thorp and Covich (1991). Items were measured for length, width, and depth with an ocular micrometer and enumerated. If items were abundant, I measured the first 25 items encountered and counted the remaining. Volumes of the diet items were estimated by geometric approximation based on their shape using the formulas for either a cylinder or a sphere (Bowen 1996; Pert 1997). For common diet items and items that were well digested (but all or most parts were present), I used previously established regression equations for head capsule width to volume relations (**Chapter 1**). My assumptions when enumerating and determining volume were the same as those used in **Chapter 1**. I examined the stomachs of only the target species of each stocking density and 50% of the target bluegill stomachs because of the time involved in analyzing stomach contents.

Experimental Design

The experimental design for this study was a modified split plot (Hinkelman and Kempthorne 1994). The whole plot was a two-factor random assignment of time of removal and density of stocking to a cage. The whole plot experimental unit was an individual cage. The split plot experimental unit was the species in each cage. The observational unit was each individual fish. The linear model for this design is:

$$Y_{ijklm} = \mu + T_i + D_j + (T \times D)_{ij} + e^A_{ijk} + S_l + (T \times S)_{il} + (D \times S)_{jl} + (T \times D \times S)_{ijl} + e^B_{ijkl} + \eta_{ijklm}$$

where μ is the overall mean, T_i is the time effect, D_j is the stocking density effect, S_l is the species effect, e^A_{ijk} is the whole plot error component, e^B_{ijkl} is the split plot error component, and η_{ijklm} is the observational error component. Components in parentheses are interaction effects.

Data Analyses

I tested for differences in mortality and growth with ANOVA (PROC MIXED; SAS Institute 1996) using linear contrasts of means. My contrasts of interest were bass alone versus bass + norm blg, bass alone versus bass + hi blg, and bass + norm blg versus bass + hi blg for the effect of bluegills on largemouth bass. For the effect of largemouth bass on bluegills, the contrasts of interest were blg alone versus blg + norm bass, blg alone versus blg + hi bass, and blg + norm bass versus blg + hi bass. Additionally, I contrasted growth and mortality of the neighbor species at each phase to assess intraspecific competition. Contrasts were analyzed independently for each time period. Because contrasts were designated *a priori*, a significant overall effect was not a prerequisite to the multiple comparison procedure (Lentner and Bishop 1993).

To test for differences in mortality, I used a binary response factor (i.e. 1 = survival; 0 = mortality) for each fish. Differences in growth were tested using the same model, but the response factor was incremental increase in length. This was known for bluegills, but required estimation for largemouth bass. I estimated largemouth bass growth rates by randomly assigning initial lengths to largemouth bass based on the parameters (i.e. mean and variance) of the subsampled largemouth bass. To determine how variability in initial lengths could influence my results, I repeated this random assignment of individual starting lengths 50 times, recording the contrast results with each iteration. In essence, I considered the p-values from each contrast as independent and identically distributed variables from an unknown distribution (C. W. Coakley, VPI&SU Department of Statistics, personal communication). Because it is unknown how a distribution of p-values behaves statistically, I used the interquartile range of the distribution of p-values from each contrast to determine whether differences in largemouth bass and bluegill growth were significant (C. W. Coakley, VPI&SU Department of Statistics, personal communication). In order to conclude differences in growth were significant, the 25th and 75th percentile p-values both had to be less than α.

Differences in proportions of diet items by volume among stocking densities were tested using a Kruskal-Wallis (1952) test. I pooled the data from the two time periods to increase sample size. Bonferroni's multiple-comparison procedure (Dunn 1964) was used as a follow-up test at a family error rate = 0.20 (individual error rate = 0.033). Otherwise, $\alpha = 0.10$ was the level of significance used throughout this study.

Results

One cage from the bass + hi blg density for Phase 1 was found to have a hole in it from which fish were able to escape. The few fish that were recovered from this cage were excluded from further analysis. The overall finite mortality rates ($\overline{x} \pm 2$ SE) for largemouth bass and bluegills were 0.60 ± 0.08 and 0.24 ± 0.05, respectively. The difference in mortality rates among the species was significant ($F_{1,488} = 60.10$; $P < 0.0001$).

Bluegills Effect on Largemouth Bass

For Phase 1, mortality rates of largemouth bass (Table 2.3) among the stocking densities were not significantly different (bass alone versus bass + norm blg: $F_{1,488} = 1.47$; $P = 0.226$) (bass alone versus bass + hi blg: $F_{1,488} = 0.29$; $P = 0.588$) (bass + norm blg versus bass + hi blg: $F_{1,488} = 0.29$; $P = 0.588$). Although the final density of bluegills (Table 2.3) in the bass + hi blg cages was three times that of the bass + norm blg cages, bluegill mortality rates did not vary with bluegill density (bass + norm blg versus bass + hi blg: $F_{1,488} = 0.44$; $P = 0.509$).

Final lengths of largemouth bass among the stocking densities did differ (Figure 2.2). Largemouth bass growth rates for the bass alone density was significantly greater than the growth rates for the bass + norm blg and bass + hi blg densities for Phase 1 (Table 2.4).

However, the growth rates of largemouth bass for the bass + norm blg and the bass + hi blg were not significantly different (Table 2.3). Growth rates of bluegills (Figure 2.2) in the bass + norm blg density was greater than those of bluegills in the bass + hi blg densities (Table 2.4), indicating that intraspecific competition occurred.

For Phase 2, mortality rates (Table 2.3) of largemouth bass among the densities again did not differ (bass alone versus bass + norm blg: $F_{1,488} = 2.56$; $P = 0.110$) (bass alone versus bass + hi blg: $F_{1,488} = 2.48$; $P = 0.116$) (bass + norm blg versus bass + hi blg: $F_{1,488} = 0.00$; $P = 0.979$). Similar to Phase 1, bluegill mortality rates (Table 2.3) in the bass + norm blg and the bass + hi blg densities did not differ (bass + norm blg versus bass + hi blg: $F_{1,488} = 0.79$; $P = 0.376$).

Final length differences of largemouth bass as a “target” species in Phase 2 are shown in Figures 2.2 and 2.3. Largemouth bass when alone reached much high final lengths than when stocked with 10 or 30 bluegills (Table 2.4). Whereas a significant difference was not observed in Phase 1, largemouth bass final lengths when with 10 bluegills were significantly greater than largemouth bass final lengths when with 30 bluegills during Phase 2 (Table 2.3). As with Phase 1, bluegill growth rates (Figure 2.3) in the bass + norm blg and the bass + hi blg densities were significantly greater (Table 2.4).

Largemouth bass food resource use among the stocking densities did vary (Table 2.5). When alone, largemouth bass consumed significantly greater amounts of Amphipoda, Diptera larvae, and Odonata than when stocked with normal densities of bluegills. However, largemouth bass when alone also consumed significantly less Copepoda than largemouth bass stocked with normal densities of bluegills. When contrasted with largemouth bass with a high density of bluegills, largemouth bass alone consumed significantly greater amounts of Odonata and significantly lesser amounts of Copepoda and Hemiptera. Largemouth bass with normal densities of bluegills and largemouth bass with high densities of bluegills differed significantly only in their consumption of Hemiptera, which the latter consumed more heavily.

Table 2.3. Final densities ($\bar{x}$ ±2 SE) of largemouth bass (target species) and bluegills (neighbor species) for Phases 1 and 2.

Time Period	Stocking Density	Density (fish/cage)	
		Largemouth Bass	Bluegill
Phase 1	Bass alone	3 ± 2	-
	Bass + norm blg	2 ± 0	7 ± 1
	Bass + hi blg	2 ± 1	22 ± 2
Phase 2	Bass alone	3 ± 1	-
	Bass + norm blg	1 ± 1	9 ± 1
	Bass + hi blg	1 ± 1	23 ± 3

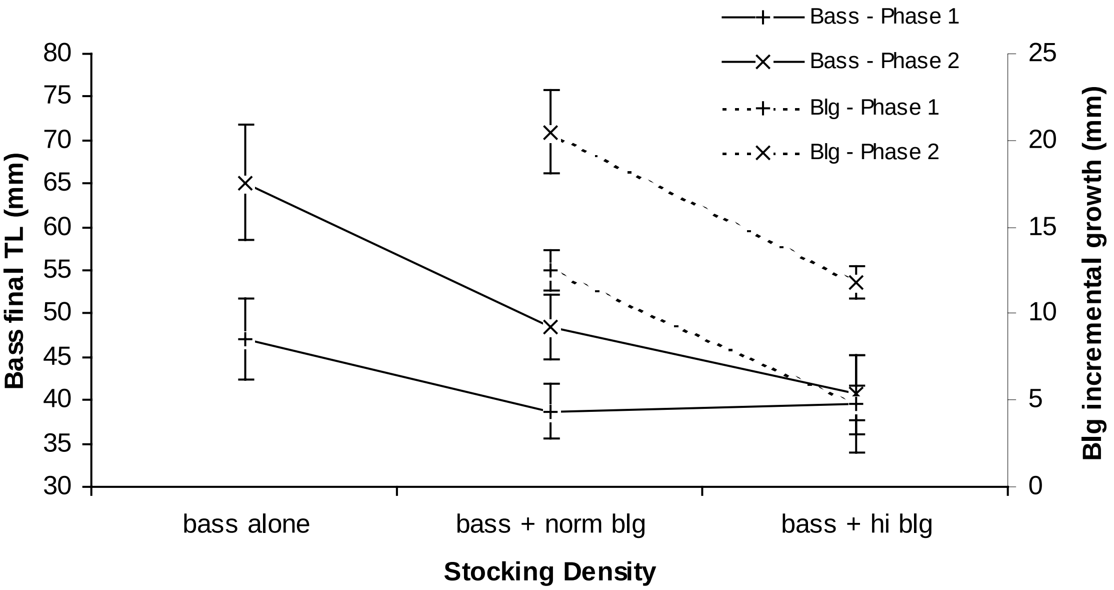

Figure 2.2. Final TL ($\bar{x}$ ± 2 SE) of largemouth bass (target species) for Phases 1 and 2 among the stocking densities. Additionally, incremental growth rates ($\bar{x}$ ± 2 SE) of bluegills (neighbor species) for the bass + norm blg and the bass + hi blg densities are shown.

Table 2.4. Contrast results for the effect of bluegills on largemouth bass for Phases 1 and 2. Estimated incremental growth rates of largemouth bass (target species) when stocked alone and with "normal" and "high" densities of bluegills (neighbor species) were tested. In addition, growth rates of bluegills were contrasted to evaluate intraspecific competition effects. For differences to be considered significant, both the 25th and 75th % must be < 0.10.

Time Period	Target or Neighbor	Contrast	$F_{d.f.}$	75th % P-value 25th % P-value
Phase 1	Target	Bass alone vs.	$F_{1,33.4} = 8.33$	0.007
		Bass + norm blg	$F_{1,31.7} = 10.63$	0.003
	Target	Bass alone vs.	$F_{1,30.2} = 5.10$	0.031
		Bass + hi blg	$F_{1,33.5} = 6.66$	0.014
	Target	Bass + norm blg vs.	$F_{1,34.6} = 0.01$	0.906
		Bass + hi blg	$F_{1,33.7} = 0.30$	0.586
	Neighbor	Bass + norm blg vs.	$F_{1,13.0} = 7.75$	0.015
		Bass + hi blg	$F_{1,14.1} = 8.79$	0.010
Phase 2	Target	Bass alone vs.	$F_{1,57.1} = 24.02$	0.000
		Bass + norm blg	$F_{1,47.3} = 28.99$	0.000
	Target	Bass alone vs.	$F_{1,53.2} = 51.26$	0.000
		Bass + hi blg	$F_{1,54.5} = 56.86$	0.000
	Target	Bass + norm blg vs.	$F_{1,81.1} = 3.40$	0.069
		Bass + hi blg	$F_{1,77.0} = 4.67$	0.034
	Neighbor	Bass + norm blg vs.	$F_{1,13.5} = 12.67$	0.003
		Bass + hi blg	$F_{1,13.7} = 14.96$	0.002

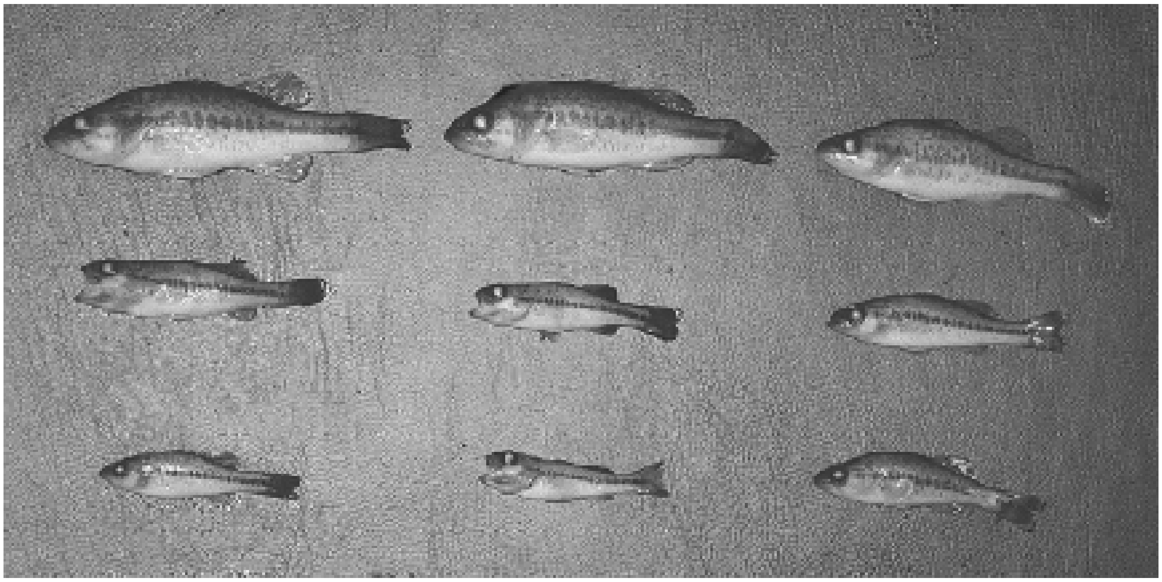

Figure 2.3. Largemouth bass from Phase 2 illustrating the competitive effect of bluegills on largemouth bass. Growth of largemouth bass when alone (top 3 fish) was significantly greater ($P < 0.0001$) than that of largemouth bass stocked with normal (middle 3 fish) and high (bottom 3 fish) densities of bluegills. Growth of largemouth bass when with a normal density of bluegills was greater ($P < 0.10$) than when with a high density of bluegill.

Table 2.5. Mean of the volume percentages of diet items consumed by largemouth bass among the different stocking densities. The Kruskal-Wallis test static (H) and P-value (P) for the null hypothesis (H_0: no difference in consumption of taxa among the stocking densities) are shown. Taxa marked with an * were consumed in significantly different amounts ($P < 0.10$). Densities marked with different letters were significantly different at a family error rate of 0.20 as indicated by Bonferroni's multiple comparison procedure. Items that did not comprise at least 5% of the volume for either species in any density were grouped as Other (Arachnidia, Bivalvia, Coleoptera, Decapoda, Gastropoda, Hymenoptera, Plecoptera, unidentifiable).

	H	P		Bass Alone		Bass + norm blg		Bass + hi blg	
Amphipoda	7.57	0.023	*	0.05	A	0.00	B	0.01	AB
Cladocera	3.46	0.177		0.13		0.23		0.11	
Copepoda	7.17	0.028	*	0.20	A	0.50	B	0.50	B
Diptera – larvae	4.60	0.100	*	0.25	A	0.10	B	0.14	AB
Diptera – pupae	2.28	0.320		0.06		0.10		0.02	
Ephemeroptera	2.65	0.266		0.07		0.03		0.10	
Fish	2.99	0.224		0.03		0.00		0.02	
Hemiptera	7.99	0.018	*	0.01	A	0.00	A	0.07	B
Hydracarina	0.03	0.986		0.00		0.00		0.00	
Odonata	14.53	0.001	*	0.17	A	0.00	B	0.00	B
Ostracoda	2.01	0.366		0.00		0.01		0.00	
Other	0.28	0.870		0.01		0.02		0.01	
Trichoptera	0.93	0.629		0.00		0.00		0.00	

Largemouth Bass Effect on Bluegills

Bluegill mortality rates (Table 2.6) among the stocking densities were not significantly different for Phase 1 (blg alone versus blg + norm bass: $F_{1,488} = 0.08$; $P = 0.7751$) (blg alone versus blg + hi bass: $F_{1,488} = 1.31$ $P = 0.2533$) (blg + norm bass versus blg + hi bass: $F_{1,488} = 2.04$; $P = 0.1535$). Likewise, mortality rates of largemouth bass (Table 2.6) in the blg + norm bass and blg + hi bass contrast were not significantly different (blg + norm bass versus blg + hi bass: $F_{1,488} = 0.03$; $P = 0.8690$).

For Phase 1, the only significant difference in incremental growth rates (Figure 2.4) of bluegills occurred when the blg alone and blg + hi bass densities were contrasted (Table 2.7). Growth rates of bluegill when alone were higher than those of bluegill in the blg + hi bass density. The other density contrasts for bluegills were not significant (Table 2.7). Likewise, estimated growth rates of largemouth bass as a neighbor species in the blg + norm bass and blg + hi bass densities did not differ significantly (Table 2.7).

During Phase 2, mortality rates of bluegills (Table 2.6) among the various stocking densities did not differ significantly (blg alone versus blg + norm bass: $F_{1,488} = 1.57$; $P = 0.2110$) (blg alone versus blg + hi bass: $F_{1,488} = 1.90$; $P = 0.1687$) (blg + norm bass versus blg + hi bass: $F_{1,488} = 0.01$; $P = 0.9339$). Mortality rates of largemouth bass (Table 2.6) in the blg + norm bass and blg + hi bass densities also were not significantly different (blg + norm bass versus blg + hi bass: $F_{1,488} = 1.62$; $P = 0.2031$).

As with Phase 1, the only difference in incremental growth rates of bluegills (Figure 2.4) among the stocking densities was between the blg alone and blg + hi bass densities (Table 2.7), with bluegill in the blg alone density having higher growth rates. Bluegill growth when alone did not differ from that of bluegills when stocked with normal densities of largemouth bass, nor did it differ between blg + norm bass and blg + hi bass densities (Table 2.6). Unlike Phase 1, largemouth bass growth rates during Phase 2 did vary with largemouth bass density. Largemouth in the blg + norm bass density reached higher final lengths than did largemouth bass in the blg + hi bass density (Figure 2.4; Table 2.7), indicating that fish were competing intraspecifically.

Food item utilization by bluegills only differed among the stocking densities in their consumption of Amphipoda (Table 2.8). Bluegills when stocked alone consumed significantly more Amphipoda than did bluegills when stocked with a high density of largemouth bass. However, overall consumption of Amphipoda at all stocking densities was low.

Discussion

Competition can be defined as multiple organism's simultaneous demand, or one organism's controlling of access to, a resource of limited availability and which negatively affects at least one of the organisms. In this study, I focused on food resources and quantified negative effects through changes in mortality, growth, and resource use. I assessed changes in mortality and growth due to their relevancy to fishery managers. I also investigated changes in resource use (i.e. niche shifts; Diamond 1978), as they too can be consequences of competition (Schoener 1975; Werner and Hall 1977) even though such shifts may not necessarily affect growth or mortality (Keddy 1989).

I found that incremental growth rates of age-0 largemouth bass and juvenile bluegills were reduced when stocked sympatrically. Furthermore, largemouth bass growth rates were reduced when stocked with both “normal” and “high” densities of bluegills, whereas bluegill growth rates were reduced only when stocked with a “high” density of largemouth bass. This type of interaction, where one species is more affected than the other, is classified as asymmetric competition (Keddy 1989). In the context of trophic competition and its effect on growth, bluegills appear to be the dominant competitor while largemouth bass is the subordinant. Additionally, I found that growth of the “neighbor” species in the “normal” and “high” densities typically was different, indicating that intraspecific competition was occurring and that resources were indeed limiting.

Table 2.6. Final densities ($\bar{x}$ ± 2 SE) of bluegills (target species) and largemouth bass (neighbor species) for Phases 1 and 2.

Time Period	Stocking Density	Density (fish/cage)	
		Bluegill	Largemouth Bass
Phase 1	Blg alone	7 ± 2	-
	Blg + norm bass	7 ± 1	2 ± 0
	Blg + hi bass	8 ± 1	6 ± 2
Phase 2	Blg alone	7 ± 2	-
	Blg + norm bass	9 ± 1	1 ± 1
	Blg + hi bass	8 ± 1	6 ± 1

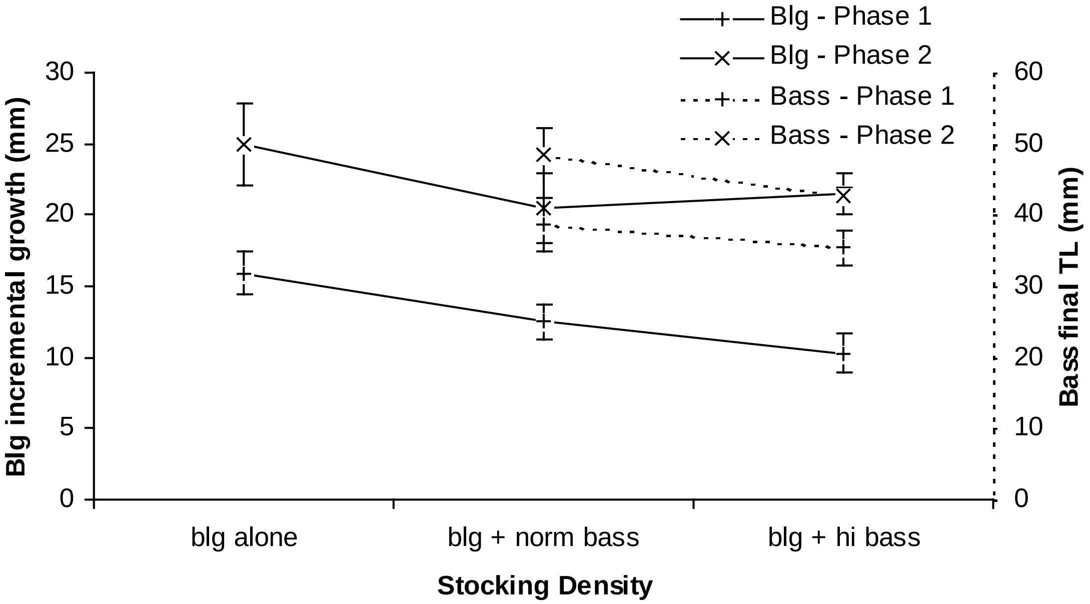

Figure 2.4. Bluegill (target species) incremental growth rates ($\bar{x}$ ± 2 SE) for Phases 1 and 2 among the stocking densities. Additionally, final TL ($\bar{x}$ ± 2 SE) of largemouth bass (neighbor species) for the blg + norm bass and blg + hi bass densities are shown.

Table 2.7. Contrast results for the effect of largemouth bass on bluegills for Phases 1 and 2. Incremental growth rates of bluegills (target species) when stocked alone and with “normal” and “high” densities of largemouth bass (neighbor species) were tested. In addition, estimated incremental growth rates of largemouth bass were contrasted to evaluate intraspecific competition effects. For differences to be considered significant, both the 25th and 75th % must be < 0.10.

Time Period	Target or Neighbor	Contrast	$F_{d.f.}$	75th % P-value 25th % P-value
Phase 1	Target	Blg alone vs.	$F_{1,17.0} = 1.99$	0.176
		blg + norm bass	$F_{1,17.2} = 2.26$	0.151
	Target	Blg alone vs.	$F_{1,15.4} = 5.15$	0.038
		blg + hi bass	$F_{1,17.0} = 5.84$	0.027
	Target	Blg + norm bass vs.	$F_{1,15.1} = 0.69$	0.421
		blg + hi bass	$F_{1,15.0} = 0.80$	0.384
	Neighbor	Blg + norm bass vs.	$F_{1,25.4} = 0.76$	0.393
		blg + hi bass	$F_{1,23.6} = 1.56$	0.224
Phase 2	Target	Blg alone vs.	$F_{1,14.5} = 1.84$	0.196
		blg + norm bass	$F_{1,16.3} = 2.08$	0.168
	Target	Blg alone vs.	$F_{1,15.6} = 3.36$	0.086
		blg + hi bass	$F_{1,16.0} = 3.96$	0.064
	Target	Blg + norm bass vs.	$F_{1,14.2} = 0.15$	0.700
		blg + hi bass	$F_{1,15.1} = 0.22$	0.643
	Neighbor	Blg + norm bass vs.	$F_{1,28.3} = 3.77$	0.062
		blg + hi bass	$F_{1,32.8} = 5.30$	0.028

Table 2.8. Mean of the volume percentages of diet items consumed by largemouth bass among the different stocking densities. The Kruskal-Wallis test static (H) and P-value (P) for the null hypothesis (H_0: no difference in consumption of taxa among the stocking densities) also are shown. Taxa marked with an * were consumed in significantly different amounts ($P < 0.10$). Densities marked with different letters were significantly different at a family error rate of 0.20 as indicated by Bonferroni's multiple comparison procedure. Items that did not comprise at least 5% of the volume for either species in any density were grouped as Other (Arachnidia, Bivalvia, Coleoptera, Decapoda, Gastropoda, Hymenoptera, Plecoptera, unidentifiable).

	H	P_H		Blg Alone		Blg + norm bass		Blg + hi bass	
Amphipoda	6.61	0.037	*	0.03	A	0.01	AB	0.01	B
Cladocera	0.57	0.753		0.10		0.16		0.11	
Copepoda	3.73	0.155		0.10		0.06		0.03	
Diptera – larvae	1.79	0.410		0.37		0.47		0.44	
Diptera – pupae	1.38	0.502		0.06		0.02		0.05	
Ephemeroptera	1.33	0.515		0.05		0.00		0.02	
Fish	-	-		-		-		-	
Hemiptera	0.66	0.720		0.01		0.00		0.02	
Hydracarina	2.85	0.240		0.09		0.05		0.04	
Odonata	3.70	0.157		0.01		0.02		0.00	
Ostracoda	1.23	0.540		0.02		0.06		0.10	
Other	1.88	0.584		0.10		0.07		0.14	
Trichoptera	1.07	0.391		0.06		0.04		0.04	

This experiment was designed to be able to evaluate temporal differences in the interaction between largemouth bass and bluegill. This is important to consider because complex dynamic responses (i.e. significant shifts in consequences over time) can occur when ecological systems are manipulated (Franklin 1987; Tilman 1987). The competitive effects between largemouth bass and bluegill remained relatively constant through the time, although the competition intensity for the effect of bluegill on largemouth bass may have slightly increased. This static competition intensity can have important consequences for both species, but in particular for that of largemouth bass. Largemouth bass need to attain a distinct size advantage to be able to begin feeding upon bluegill (Timmons et al. 1980; Olson 1996). It is questionable how many largemouth bass would have been able to convert to piscivory since competition remained relatively constant through the summer. Even if largemouth bass had a sufficient size advantage over bluegill early in life due to a difference in spawning times, it is possible that largemouth bass may have lost the size advantage and needed to revert to insectivory (Pasch 1975).

Because age-0 largemouth bass and juvenile mortality rates did not differ among the stocking densities, any intraspecific competition effects also should have remained constant. Additionally, because mortality was not affected, I hypothesize that the mechanism of their competition is exploitation rather than interference. Diana (1995) defined exploitation competition as a situation where one organism’s use of a resource in limited supply reduces resource abundance and removes it from use by another organism, and interference competition as a situation where one organism directly or indirectly limits another organism’s access to a resource. Exploitation competition for food resources between fish species typically results in slowed growth rather than increased mortality (Weatherly 1963), although it is not known if this would be the case with competition between juveniles. If largemouth bass and bluegills interacted through interference competition, we might expect increased mortality when the species were sympatric, although interference competition can be more subtle than outright physical attack (Keddy 1989) and individuals may establish dominance within a few encounters (Pusey and Packer 1997). Since I did not attempt to measure agonistic interactions between the species, I can not conclude with certainty what the mechanism for their competition is.

Largemouth bass and bluegills did shift resource use when stocked together, which may clarify the catalyst behind their competition. The most notable shift was that largemouth bass when stocked alone consumed primarily Diptera larvae and Copepoda, but when stocked with bluegills consumed primarily Copepoda. Consumption of Diptera larvae was significantly less when with "normal' densities of bluegills, and also was less, albeit not significantly, when with "high" densities of bluegills. It is possible that these differences in consumption are morphologically related (i.e. bass alone grew larger and thus were better able to consume certain items), which complicates the issue. However, previous research indicates that largemouth bass generally are not morphologically adapted for consuming Diptera larvae, while bluegills are (Werner 1977; Gilliam 1982).

If largemouth bass are not well adapted to consuming Diptera larvae, why would largemouth bass rely heavily upon that resource when stocked alone? One might predict that largemouth bass would avoid Diptera larvae unless forced to consume it. However, the pattern of use I observed could be explained by the energy-maximizing strategy of optimal foraging theory (Schoener 1971) and the findings of Werner and Hall (1974). When bluegills are absent, Diptera larvae may be plentiful such that largemouth bass can be selective for these items due to search and handling times being reduced. But when bluegill are present, largemouth bass may need to shift to other items (e.g. Copepoda) due to Diptera larvae being exploited and reduced in abundance by bluegills. Applegate and Mullan (1967) previously linked fast growth rates of largemouth bass to consumption of Diptera larvae, which implies such items have sufficient energy content.

The only significant change in resource use by bluegills was consumption of Amphipoda, which overall comprised a small proportion of bluegill's diet. It is of interest to note, however, that bluegills consumed less Diptera larvae and more Copepoda when alone than when stocked with largemouth bass, although these differences were not significant. This correlates well with the diet shift of largemouth bass. Largemouth bass and bluegills stocked separately consume Copepoda and Diptera larvae; but when stocked together, largemouth feed primarily on Copepoda while bluegills consume Diptera larvae. Since largemouth bass and bluegill growth rates were reduced when stocked together, Copepoda and Diptera larvae may be complementary resources in that consumption of both enhances growth more than equivalent amounts of either resource individually (Keddy 1989).

This study supports previous findings regarding competition between largemouth bass and bluegills. Gilliam (1982), Wallace (1982), and Olson et al. (1995) found that growth of largemouth bass indeed was reduced when in the presence of bluegills. Furthermore, Olson et al. (1995) determined that the competitive relationship was asymmetric with largemouth bass being the competitive subordinant. My results differ somewhat from those of Olson et al. (1995), who found that largemouth bass had no significant effect on bluegills. However, the bass treatment of Olson et al. (1995) corresponded to an initial stocking density of 2.5 largemouth bass/m^2, which may not have been high enough to influence bluegill growth. Neither Gilliam (1982) nor Wallace (1982) attempted to quantify the effect of largemouth bass on bluegills. My findings also support the empirical evidence of Bennett et al. (1969), Dillard and Novinger (1975), Stone and Modde (1982), and Olson et al. (1995) that bluegill populations can have a depressing effect on largemouth bass populations.

In size-structured populations, the effects of competition at one stage can be inverse to the effects of competition at other stages (Osenberg et al. 1992). Therefore, it is important to consider the effects of competition on the adult stages of largemouth bass and bluegills, as well as the juvenile stages. Because of an inherent stochastic factor, one would expect a disparity (i.e. a heavier-tailed distribution) of age-0 largemouth bass lengths resulting from competition. Such length disparity is commonly observed with largemouth bass populations (Pasch 1975; Keast and Eadie 1985; Olson 1996). Additionally, competition could explain the occurrence of bimodal length distributions in age-0 largemouth bass cohorts, which have been attributed to limitations in food resources (Shelton et al. 1979; Timmons et al. 1980; DeAngelis and Coutant 1982). The effect that differential growth rates will have on adult largemouth bass depends largely on whether overwinter survival of age-0 largemouth bass is size related (Aggus and Elliot 1975; Shelton et al. 1979; Wicker and Johnson 1987; Miranda and Hubbard 1994). If so, the influence of competition on largemouth bass recruitment could vary depending on its severity and the size that largemouth bass need to attain to ensure survival. If competition is severe and only a few fish are able to attain a size sufficient for survival, recruitment would be significantly reduced.

The ability of a prey species to reduce recruitment of its eventual predator through competition has been termed a competitive juvenile bottleneck (Neill 1975). Those few remaining fish, which DeAngelis and Coutant (1982) referred to as “jumpers”, would experience fast growth rates and would recruit to the fishery quickly. However, the probability of overharvesting these few fish would be high. Conversely, if competition is not severe and a majority of the age-0 cohort attains a size sufficient for survival or if overwinter mortality is not size related (Toneys and Coble 1979; Kohler et al. 1993), the year class would be much stronger. The higher density of largemouth bass could result in slow growth rates due to intraspecific competition. If anglers refused to harvest these smaller fish, the condition could endure without management intervention.

Much of what has been mentioned also is applicable when considering the effect of competition on adult bluegill. This consequence has received much less attention, possibly due to the asymmetric relationship. One would predict that if competition resulted in the displacement of one species that largemouth bass would be the species displaced due it being the competitive subordinant (Hardin 1960). Alternatively, focus may be placed on the effect of bluegill on largemouth bass due to the popularity of largemouth bass as a sportfish. Nevertheless, the effect on adult bluegill will depend largely on the severity of competition and whether mortality of bluegills is size related (Toneys and Coble 1979). If competition reduces recruitment, the likelihood for overharvest of bluegill populations will be increased (Coble 1988; Reed and Parsons 1999). Additionally, competition could simply result in an overcrowding of slow-growing individuals. Given that small impoundment owners frequently describe angling opportunities as poor and typically attribute it to stunting (Lopinot 1978), it is important to determine whether competition between largemouth bass and bluegill could be a driving force behind this condition.

Management Implications

Although the importance of competition was once an issue of debate (Schoener 1982), most generally recognize it as one of the major biotic interactions structuring communities (Keddy 1989). Yet, its incorporation into management paradigms has been delayed due in part to its subtlety (Ricklefs 1990). An event such as predation is fairly simple to document, while competition is much more difficult to evaluate. Perhaps that is why studies that relate largemouth bass population dynamics with that of its prey typically focus on the predation aspect of the relationship and seemingly ignore even the potential for competition (Swingle 1950; Garvey and Stein 1998; Allen et al. 1999). Occasionally studies will mention the potential for competition (Swingle and Smith 1940; Pasch 1975), but typically only in passing when explaining why expected results did not occur (Gabelhouse 1987; DeVries and Stein 1990). Ignoring the role competition plays in structuring fish communities is a serious handicap to fishery managers (Larkin 1956; Roell and Orth 1998); and given our poor understanding of predator-prey interactions (Noble 1981), considering these early interactions may improve management efforts (Noble 1986; Hirst and DeVries 1994).

Previous research has determined that largemouth bass and bluegills may compete for spawning sites (Smith 1976). Smith (1976) proposed supplemental stocking of fingerling largemouth bass in order to offset this potential management problem. However, the effectiveness of enhancement stocking of fingerling largemouth bass is questionable (Loska 1982), possibly due to trophic competition between largemouth bass and bluegills. Boxrucker (1985, 1986) determined that many small impoundment fisheries do not benefit from supplemental stocking of fingerling (35-64 mm TL) largemouth bass due to low survival and potentially slow growth. This may be due to the fact that fingerling largemouth bass are likely to compete with their future prey. If largemouth bass are failing to recruit due to a trophic bottleneck resulting from a high density of small forage fish, stocking more-advanced sizes of largemouth bass (e.g. 150-200 mm TL) may be more effective than stocking fingerlings (Lawson and Davies 1979; Smith and Reeves 1986; Buynak and Mitchell 1999). The ability of largemouth bass to become piscivorous while age-0 is largely dependent on being physically capable of feeding on forage fish (Pasch 1975; Shelton et. al 1979; Olson 1996). It therefore seems prudent that, before initiation of an enhancement-stocking program, managers first should determine the cause of low recruitment. If trophic competition between age-0 largemouth bass and forage fish is a potential cause, I suggest that fishery managers stock largemouth bass of a size already capable of feeding on the smallest available size class of bluegills. Additionally, it may be necessary to repeat stocking as largemouth bass grow beyond the size at which they effectively prey on the forage fish, as natural reproduction can not be relied upon in a system with stunted bluegills (Smith 1976).

Introductory stocking of new or renovated impoundments also may benefit from the knowledge that largemouth bass and bluegills compete trophically. One strategy for stocking impoundments is to introduce fingerling bluegills in the fall and fingerling largemouth bass the following spring. The purpose is to allow bluegills time to spawn, which will produce prey for largemouth bass (Flickinger and Bulow 1993). But again, this ignores the fact that largemouth bass may compete with the offspring of the originally stocked bluegills, limiting largemouth bass recruitment to the fishery. Recruitment could be improved by stocking largemouth bass fingerlings in the spring, followed by bluegills in the fall or the following spring (Dillard and Novinger 1975; Stone and Modde 1982). Alternatively, if it is necessary to stock bluegills first, managers could reduce costs by stocking advanced fingerling largemouth bass. The cost of culturing largemouth bass in certain regions of the United States appears linearly related to length (Figure 2.5; AFS 1992). If fingerling largemouth bass compete with bluegills and suffer reduced growth and survivability, it may be more cost-effective to delay stocking until larger sizes when largemouth bass have a higher probability of surviving the winter. Such questions concerning appropriate stocking time and cost effectiveness have been explored relatively recently for other highly sought after sportfish, such as walleye *Stizostedion vitreum* (Madenjian et al. 1991) and striped bass *Morone saxatilis* (Sutton 1997). Yet for largemouth bass, fishery managers continue to rely upon information collected almost half a century ago. Given advancements in culturing techniques (e.g. Snow 1975), expansion of management options (Gabelhouse et al. 1982; Gabelhouse 1984), and increased sophistication in stocking and management practices (Funk 1974; Dillard and Novinger 1975; Anderson 1976; Novinger and Dillard 1978; Copeland and Noble 1994), perhaps it is time to revisit the issue.

Competition between largemouth bass and bluegills also may limit achievable management options in small impoundments. For example, Gabelhouse (1987) hypothesized that competition between largemouth bass and bluegill prevented the achievement of a balanced option management goal in a Kansas pond overcrowded with small largemouth bass. Similarly, it

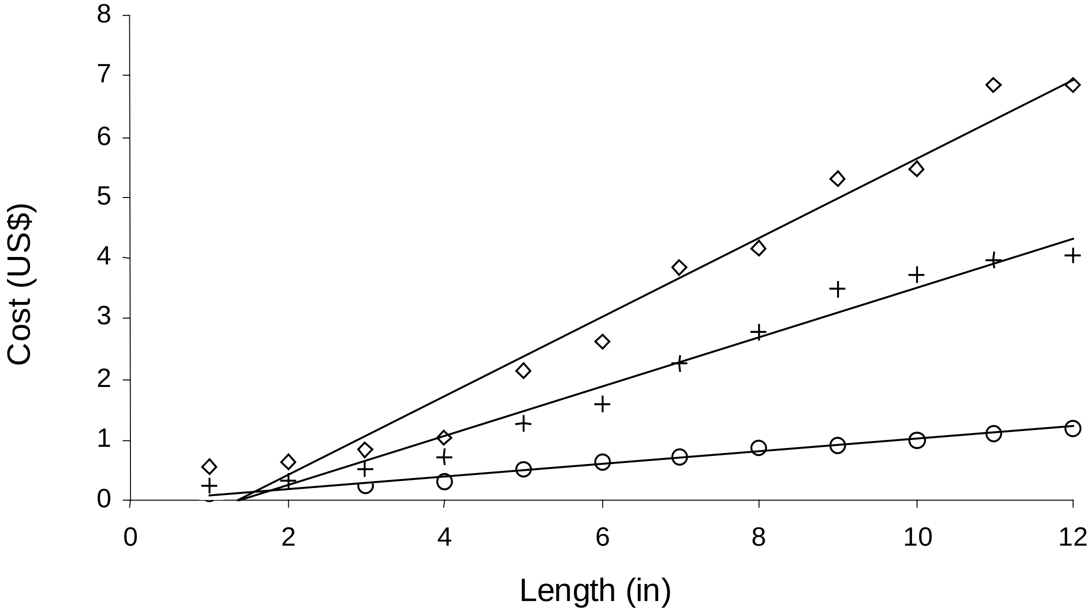

Figure 2.5. Mean cost of culturing largemouth bass in northeastern U.S. (◊), southeastern U.S. (O), and the entire U.S. (+) in relation to length of stocking. Data taken from AFS (1992).

might be difficult to manage for the panfish option if competition between largemouth bass and bluegills is resulting in low recruitment of largemouth bass. These scenarios emphasize the importance of considering the potential for competition when formulating management decisions (Larkin 1956).

As fisheries managers, our underlying motivation for understanding competition is to be able to better predict how a fishery will respond to particular management actions or other perturbations (Keddy 1989). To this end, models, such as the Lotka–Voltera model (Lotka 1932) and community matrices (Levins 1968), are extremely helpful. However, the use of such models depends on knowing how each population is affected by the presence of the other (Keddy 1989). Unfortunately, it may be premature for us to claim we know precisely how largemouth bass and bluegill populations competitively affect one another. While both largemouth bass and bluegill growth rates were reduced during this study, Olson et al. (1995) found that only largemouth bass growth was affected when the species were stocked sympatrically. Olson et al. (1995) documented a textbook definition for asymmetric competition, but which may be more appropriately considered amensalism. This dichotomy illustrates the need for further study concerning the biotic interactions between largemouth bass and bluegill before findings are applied to particular situations. I recommend that largemouth bass and bluegill competition be explored on a regional basis and that these studies consider the relationship between competition, overwinter survival, and resulting angling opportunity in small impoundments. It may be determined that competition between the species imposes an ecological constraint on the extent to which the stocking of largemouth bass and bluegill can be considered an appropriate management action. Until such information becomes available, fishery managers will need to determine for themselves whether the possibility of largemouth bass and bluegill competing is of importance for the particular systems they manage.

Summary

1) Juvenile bluegills consistently had a greater diet breadth than did age-0 largemouth bass in the study impoundment. The trophic niche (measured to the taxonomic levels of Order and Family) of largemouth bass was contained almost entirely within the trophic niche of bluegills. The only items consumed by largemouth bass and not bluegills were Decapoda and Gerridae (Hemiptera), which overall comprised < 1.0% of the diet of largemouth bass by volume.

2) In spite of the number of shared resources, diet overlap between largemouth bass and bluegills was low. Largemouth bass consumed primarily Calanoida, Ephemeroptera, and fish, while bluegills consumed Diptera and Cyclopoida. When overlap was moderately high, both species fed primarily on zooplankton and Diptera, although the proportions of use were different.

3) The fish community structure of the study impoundment would be best described as a panfish management option, consisting of a relatively high density of slow-growing largemouth bass and a moderate density of average-growing bluegills. Largemouth bass and bluegill potentially may compete due to the number of shared resources. If this impoundment was to be managed differently (e.g. big bass option), competition between the species may limit the effectiveness of management actions.

4) Manipulative cage experimentation involving the stocking of largemouth bass and bluegills allopatrically and sympatrically in 1.0-m^3 cages indicated that mortality rates of the fish were not affected by the presence of the other species. However, incremental growth rates of the fish were affected. Largemouth bass growth rates were reduced when stocked with both "normal" and "high" densities of bluegills. Growth rates of bluegills were reduced when stocked with "high" densities of largemouth bass. Analysis of food resource use by largemouth bass and bluegills indicated that Copepoda and Diptera larvae might be the limiting resources driving their competition.

5) In the context of trophic competition, the interaction between largemouth bass and bluegills can be classified as asymmetric, with bluegill as the competitive dominant and largemouth bass the competitive subordinant. Furthermore, the mechanism of competition is hypothesized to be exploitation rather than interference.

6) Trophic competition between largemouth bass and bluegills may partially explain the ineffectiveness of supplemental stocking of fingerling largemouth bass. If a trophic bottleneck at the invertebrate feeding stage is limiting recruitment of largemouth bass, stocking advanced fingerlings may be warranted.

7) Introductory stocking strategies of largemouth bass and bluegills in small impoundments continue to rely on information collected nearly half a century ago concerning appropriate time and length of fish at stocking. The management of small impoundments may be improved by revisiting this issue.

8) Fishery managers need to consider the role of competition in structuring small impoundment fish communities due to its management implications. Recruitment of both largemouth bass and bluegill may be affected, which could prevent goal achievement. Competition between the species may impose an ecological constraint on the effectiveness of management actions. Competition between age-0 largemouth bass and juvenile bluegills should be researched on a regional scale, and in conjunction with studies concerning overwinter survival and angling opportunities in small impoundments.

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