

Transactions of the American Fisheries Society, volume 120, issue 3 (May 1991) pp. 368-381.
ISSN 0002-8487

DOI: 10.1577/1548-8659(1991)120<0368:STSCFY>2.3.CO;2

<http://afs.allenpress.com/perlserv/?request=get-archive>

<http://afs.allenpress.com/archive/1548-8659/120/3/pdf/i1548-8659-120-3-368.pdf>

© American Fisheries Society

Stocking Threadfin Shad: Consequences for Young-of-Year Fishes

DENNIS R. DeVRIES,¹ ROY A. STEIN, AND JEFFREY G. MINER²

Ohio Cooperative Fish and Wildlife Research Unit³ and Department of Zoology
The Ohio State University, Columbus, Ohio 43210, USA

GARY G. MITTELBACH

Kellogg Biological Station, Michigan State University
Hickory Corners, Michigan 49060, USA

Abstract.—Threadfin shad *Dorosoma petenense* are commonly introduced into reservoirs to supplement prey available to piscivorous fishes. To determine how early life stages of threadfin shad and their potential competitors and predators interact, we introduced this species into two Ohio lakes—Clark and Stonelick—and evaluated how its young of year influenced young-of-year bluegills *Lepomis macrochirus* and largemouth bass *Micropterus salmoides*. After adults were stocked in April, peak abundance of young-of-year threadfin shad occurred in August in both lakes. Bluegills generally spawned earlier than threadfin shad, which apparently reduced competition between young of these species. In Clark Lake, young-of-year threadfin shad did not reduce zooplankton populations, but in Stonelick Lake, peak abundance of young-of-year threadfin shad was followed by a precipitous decline in zooplankton. Data on cladoceran birth rates indicated this decline was due to increased predation by threadfin shad. Survival of bluegills to a size at which they move into the littoral zone also declined in Stonelick Lake, perhaps because of the virtual elimination of zooplankton. Limited survival of bluegills in turn contributed to reduced growth of young-of-year largemouth bass dependent on them as prey. Given that zooplankton declined in one but not the other lake, interactions among young-of-year fishes due to annually introduced threadfin shad will likely vary among systems and years. Nonetheless, introduced threadfin shad could, in some systems in some years, negatively affect growth and recruitment of the very species they were meant to enhance.

Manipulation of prey has become a popular technique for increasing production of sport fishes (Ney 1981; Noble 1981, 1986; Wydoski and Bennett 1981; DeVries and Stein 1990). Manipulations may involve the introduction of prey to increase the food base or the removal of planktivores to reduce competition between them and sport fishes. Numerous taxa have been used in these manipulations, including members of the Atherinidae, Catostomidae, Clupeidae, Coregonidae, Cyprinidae, and Percidae (see references in DeVries and Stein 1990). These manipulations, based primarily on predator-prey interactions between introduced prey and adults of the target species, sought to enhance the target sport species. However, enhancement has not always been the result. In a recent review, DeVries and Stein (1990)

described manipulations involving two clupeid species (gizzard shad *Dorosoma cepedianum* and threadfin shad *D. petenense*) and four target species (white crappie *Pomoxis annularis*, black crappie *P. nigromaculatus*, largemouth bass *Micropterus salmoides*, and bluegill *Lepomis macrochirus*) that resulted in positive, neutral, and negative effects on the target species. Thus, introducing prey for predators or removing presumably undesirable competitors may not increase adult growth of target species and may result in other, unexpected consequences.

Because anglers are interested in large fish, the adult stage of sport fish has been most studied in relation to prey manipulations. Other life stages (larvae, juveniles) of prey and predators have been largely ignored (but see Kirk 1984; Kirk and Davies 1987). Because fish often change their diets and habitats as they grow (Werner and Gilliam 1984), species that interact as predator and prey as adults may compete at earlier life stages. Examples include largemouth bass and bluegills (Gilliam 1982) and European perch *Perca fluviatilis* and roach *Rutilus rutilus* (Persson 1988). Many fishes have limnetic, zooplanktivorous larvae (Werner 1967; Barger and Kilambi 1980; Keast 1980; Beard 1982; Mills et al. 1987); where such

¹ Present address: Department of Fisheries and Allied Aquacultures, Auburn University, Auburn, Alabama 36849, USA.

² Present address: Department of Zoology, Miami University, Oxford, Ohio 45056, USA.

³ The Unit is sponsored jointly by the U.S. Fish and Wildlife Service, Ohio Department of Natural Resources, The Ohio State University, and the Wildlife Management Institute.

fishes are introduced as prey, they may compete during this life stage with larvae of their subsequent predators. Because year-class strength is typically set early in life (Cushing 1975; Lasker 1975; Ware 1980; Mills and Forney 1988), interactions during this critical period may have major effects on sport-fish survival and subsequent harvest. Thus, interactions at all life stages may determine the success of any prey manipulation, the overall outcome depending on some combination of potential positive and negative effects.

We quantified how young bluegills responded to the introduction of threadfin shad in two Ohio lakes and we demonstrated the potential for negative effects due to interactions among larvae. Because young-of-year bluegills are also important prey for young-of-year largemouth bass after moving into the littoral zone at a size between 10 and 25 mm standard length (Werner 1967; Storck 1978; Werner and Hall 1988), we also determined how the offshore interaction of bluegills with threadfin shad might indirectly affect growth and survival of largemouth bass.

Methods

Study lakes.—Clark and Stonelick lakes are shallow, turbid reservoirs in southwestern Ohio. Clark Lake, in Clark County, has an area of 40 hectares, 4.5 km of shoreline, a maximum depth of 2 m, and Secchi depths varying from 25 to 75 cm. Stonelick Lake, in Clermont County, has an area of 69 hectares, 16 km of shoreline, a maximum depth of 4 m, and Secchi depths from 22 to 119 cm. During our study, submersed vegetation was never abundant in either lake and emergent vegetation occupied about 25% of the shoreline of Clark Lake (cattails *Typha* spp.) and 70% of the shoreline of Stonelick Lake (*Typha* spp. and water willow *Justicia americana*). Neither lake stratified thermally, and dissolved oxygen concentrations fell below 3 mg/L only within 0.5 m of the bottom in Clark Lake and below 2 m in Stonelick Lake. Fish communities in both lakes consisted primarily of largemouth bass, white crappies, bluegills, longear sunfish *Lepomis megalotis*, brown bullhead *Ictalurus nebulosus*, and common carp *Cyprinus carpio*.

In collaboration with personnel from the Ohio and Kentucky Departments of Natural Resources, we stocked adult threadfin shad from Herrington Lake (Mercer County, Kentucky) at densities of 48 fish/hectare in Clark Lake and 59 fish/hectare in Stonelick Lake on 14–18 April 1988. Transport mortality was visually estimated at less than 1%

during both stockings. Poststocking predatory mortality was monitored for 3 d; one largemouth bass of 22 collected in Clark Lake and one of 103 collected in Stonelick Lake had eaten one threadfin shad each. For additional details concerning collection, transport, and stocking procedures, see Buynak et al. (1989) and Austin and Hurley (1989).

Sampling methods.—We sampled during April through October in preshad (1987) and shad (1988) years. Because threadfin shad cannot overwinter in Ohio lakes, any effects they have on resident fish must occur during the growing season after stocking. Larval fish (limnetic young-of-year fish susceptible to the sampling gear) were collected offshore once per week in two replicate surface tows with a 0.75-m-diameter, 500- μ m-mesh ichthyoplankton net towed in the limnetic zone at 1.5 m/s or faster. A flowmeter mounted in the mouth of the net allowed calculation of the total volume of water filtered. Juveniles were collected biweekly at four (Clark Lake) or five (Stonelick Lake) sites in the littoral zone with a 9-m bag seine (4-mm mesh). All fish were preserved and returned to the laboratory where they were identified and measured (total length to the nearest mm, up to 50 individuals per species), and their diets (up to 10 individuals per species per date) were quantified. Diets were quantified from weekly collections of limnetic fish samples and from monthly collections of littoral samples (i.e., from every other sample date). We identified prey to the lowest taxonomic category possible (>80% were identified to genus) and measured them to the nearest 0.1 mm. Lengths were converted to biomass by use of taxon-specific length–dry-weight regressions (G. G. Mittelbach, unpublished data).

Integrated zooplankton samples (two tube hauls per sample, three replicate samples per date) were collected with a 2-m tube sampler (7.30-cm inside diameter, 54- μ m mesh size; DeVries and Stein 1991) at the same time larval fish were collected. Samples were preserved in 5% sucrose formalin (Haney and Hall 1973) to prevent cladoceran egg loss. Zooplankton taxa with less than 200 individuals per sample were counted in their entirety; subsamples were taken for more abundant taxa until at least 200 individuals were counted. At least 20 individuals of each taxon in a sample were measured (total body length excluding spines, helmets, and caudal rami) with an ocular micrometer.

To evaluate the degree of resource overlap between young-of-year bluegills and young-of-year threadfin shad when both were present in the lim-

netic zone, we used Schoener's (1970) index α , based on the average proportion that each prey taxon contributes to total biomass in fish diets. The proportion was calculated for individual fish and averaged across fish for particular dates (Wallace 1981). The formula for this index is

$$\alpha = 1 - 0.5 \left(\sum_{i=1}^n |r_{xi} - r_{yi}| \right);$$

r_{xi} is the proportion of prey taxon i in the diet of species x , r_{yi} is the proportion of prey taxon i in the diet of species y , and n is the number of prey categories. This index ranges from 0 to 1; values near zero indicate little overlap, and overlap increases as values approach 1. Because young-of-year fish and zooplankton communities changed through time, we treated overlap measures calculated for each sample date as replicates.

To evaluate prey selection, we compared diets of young-of-year fish with zooplankton samples by means of Chesson's alpha (Chesson 1978, 1983), treating individual fish within a size range as replicates. The formula for this index is

$$\text{alpha} = \frac{r_i/p_i}{\sum_i (r_i/p_i)};$$

p_i is the proportion of prey item i in the environment (i.e., the lake), and r_i is the proportion of prey item i in the fish's diet. Calculation of this index was based on representation of prey in individual fish guts and in the zooplankton community. Preference for various zooplankton taxa was determined by comparing alpha values ($\pm 95\%$ confidence interval, CI) for a taxon with the alpha value expected if prey had been eaten in proportion to their availability (i.e., the reciprocal of the number of prey types in the environment; Chesson 1978, 1983). Alpha values exceeding the reciprocal indicate positive selection for a prey taxon. Because soft-bodied rotifers were digested quickly and rarely identified in young-of-year fish diets, we only included hard-bodied rotifer genera (*Brachionus* spp. and *Keratella* spp.) in these analyses. Four taxa (*Chydorus sphaericus*, *Moina* spp., *Simocephalus* spp., and ostracods) were sampled but were never eaten; they are not considered in our results.

To analyze young-of-year fish and zooplankton abundance data, we used repeated-measures analysis of variance (ANOVA; SAS Institute 1985). With 1 year of pretreatment data and 1 year of posttreatment data, years with and without threadfin shad represented treatments. Because we

were interested in changes within a lake across years, sample sites within a lake were treated as replicates. All data were log-transformed.

Results

Young-of-Year Fish Abundance

Although young-of-year threadfin shad were first collected offshore in Clark and Stonelick lakes in mid-May, their densities remained low (< 0.2 fish/ m^3) until peaks of 8.8 fish/ m^3 in Clark Lake and 2.3 fish/ m^3 in Stonelick Lake were reached in August 1988 (Figure 1). Young of year were collected through September 1988 in both lakes (Figure 1).

In Clark Lake, young-of-year bluegills collected offshore peaked at 3.6 fish/ m^3 in 1987, whereas several peaks occurred in 1988; however, 1988 densities were always less than 0.2 fish/ m^3 (Figure 2). Abundance differed between years ($F = 130.24$; $df = 1, 2$; $P = 0.008$), although the year \times time interaction term was significant ($F = 80.23$; $df = 18, 36$; $P = 0.007$) because of protracted spawning during 1988. As would be expected from differences in limnetic young-of-year bluegill abundance between years, more juvenile bluegills were caught in littoral seine hauls during 1987 than in 1988 (Figure 2; $F = 50.42$; $df = 1, 6$; $P = 0.0004$). As with offshore larvae, the protracted spawning during 1988 led to a significant year \times time interaction term for inshore bluegill abundance ($F = 16.69$; $df = 10, 60$; $P = 0.0001$). In spite of the overall between-year differences in abundance, no difference in littoral bluegill densities was detectable after August (univariate ANOVA, $F = 0.06$; $df = 1, 40$; $P = 0.81$).

In Stonelick Lake, young-of-year bluegills continuously recruited to the open water during May through August in both years (Figure 2). Because bluegills spawned at different times in the two years, the year \times time interaction term was significant ($F = 29.02$; $df = 20, 40$; $P = 0.006$); however, overall abundance of offshore young-of-year bluegills did not vary between years ($F = 0.01$; $df = 1, 2$; $P = 0.92$). This continued presence of young-of-year bluegills in the limnetic zone, and their subsequent littoral migration, led to increasing littoral catches through summer and fall of the pre-threadfin shad year. In contrast, after threadfin shad were introduced, littoral bluegill abundance peaked in mid-July (Figure 2; year effect: $F = 7.00$; $df = 1, 8$; $P = 0.03$; year \times time interaction term: $F = 4.76$; $df = 10, 80$; $P = 0.006$). Apparently, there was low survival from the peak production of limnetic larvae in late July.

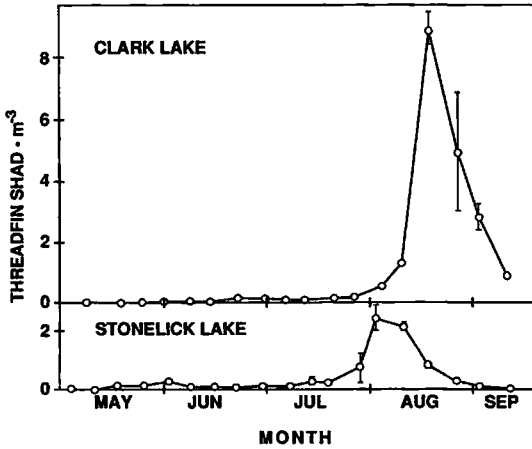


FIGURE 1.—Densities (mean \pm SE) of larval threadfin shad in Clark and Stonelick lakes, Ohio, after adults were stocked in April 1988.

Diets of Young-of-Year Fish

In both lakes, young-of-year bluegills collected offshore consumed only zooplankton during 1987 and 1988. In Clark Lake during 1987, young-of-year bluegills began feeding at 4–7 mm by selecting copepod nauplii and *Diaphanosoma leuchtenbergianum* (Table 1). As bluegills grew, selection decreased for copepod nauplii while increasing for

D. leuchtenbergianum (Table 1). Among other taxa, calanoid copepods and *Ceriodaphnia* spp. were negatively selected by all size-classes; *Bosmina longirostris*, *Daphnia parvula*, cyclopoid copepods, and rotifers either were eaten in proportion to their availability or were selected against. In 1988, all sizes of young-of-year bluegills selected *D. leuchtenbergianum* (Table 1). Other prey taxa either were eaten in proportion to their availability or negatively selected (Table 1).

In Stonelick Lake during 1987, first-feeding bluegills selected copepod nauplii; as they grew, they shifted to cyclopoid copepods and *D. leuchtenbergianum* (Table 1). Prey selection patterns were similar in 1988: copepod nauplii were selected by first-feeding fish, and *D. leuchtenbergianum* and calanoid copepods were selected by larger young of year (Table 1). Other prey taxa were either eaten in proportion to their availability or negatively selected (Table 1).

Young-of-year threadfin shad in both lakes fed entirely on limnetic zooplankton, as did limnetic young-of-year bluegills. In Clark Lake, threadfin shad selected *D. leuchtenbergianum* and calanoid and cyclopoid copepods, whereas in Stonelick Lake, first-feeding threadfin shad selected copepod nauplii, then *D. leuchtenbergianum* and calanoid copepods (Table 2).

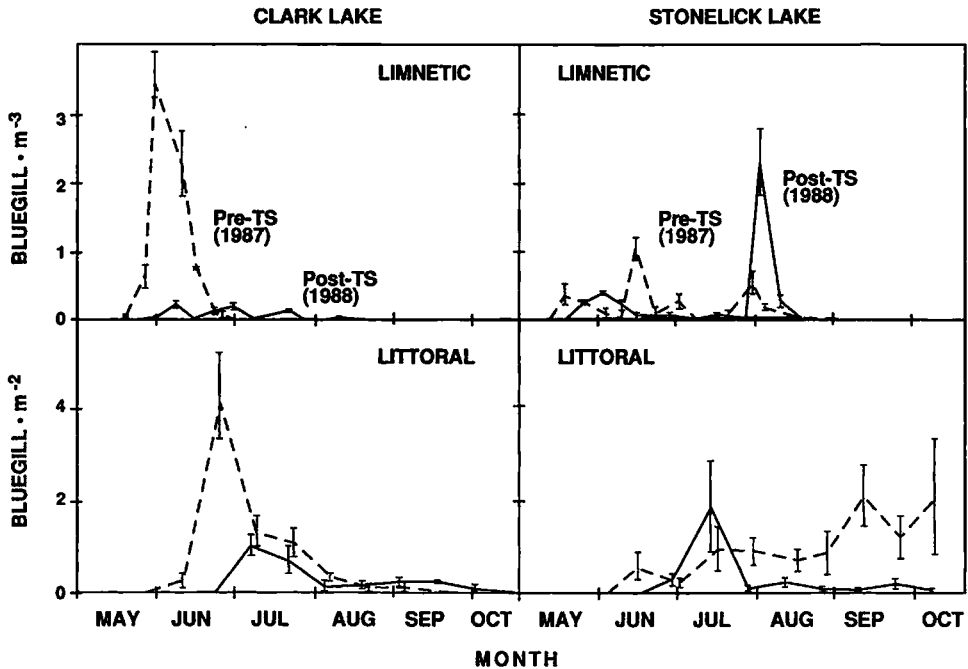


FIGURE 2.—Densities (mean \pm SE) of larval bluegills in limnetic larval tows and littoral seine samples in Clark and Stonelick lakes, Ohio, before (1987, dashed line) and after (1988, solid line) threadfin shad (TS) were introduced.

TABLE 1.—Food selection (estimated by Chesson's alpha; Chesson 1978, 1983) by larval bluegills collected offshore in Clark and Stonelick lakes before (1987) and after (1988) threadfin shad introduction. Data are presented as means \pm 95% confidence interval (N indicates sample size). Values greater than neutral selection (i.e., between 0.09 and 0.13, the reciprocal of the number of prey taxa in the lake) indicate positive selection; values less than this indicate avoidance. Bluegills 13.0 mm or larger were not collected during 1988 in Clark Lake.

Bluegill total length (mm)	N	Prey selected							
		<i>Bosmina longirostris</i>	<i>Ceriodaphnia</i> spp.	<i>Daphnia parvula</i>	<i>Diaphanosoma leuchtenbergianum</i>	Calanoid copepods	Cyclopoid copepods	Copepod nauplii	Rotifers
Clark Lake before threadfin shad introduction (1987)									
4.0–6.9	19	0.00 \pm 0.01	0	0.06 \pm 0.04	0.36 \pm 0.23	0	0.06 \pm 0.09	0.49 \pm 0.22	0.03 \pm 0.05
7.0–9.9	20	0.00 \pm 0.01	0.00 \pm 0.01	0.01 \pm 0.01	0.80 \pm 0.15	0	0.04 \pm 0.03	0.06 \pm 0.10	0.08 \pm 0.10
10.0–12.9	14	0.02 \pm 0.04	0.02 \pm 0.02	0.02 \pm 0.02	0.58 \pm 0.14	0.01 \pm 0.01	0.24 \pm 0.13	0.01 \pm 0.01	0.09 \pm 0.06
\geq 13.0	4	0.06 \pm 0.11	0.03 \pm 0.01	0	0.78 \pm 0.20	0.00 \pm 0.01	0.06 \pm 0.08	0	0.07 \pm 0.08
Clark Lake after threadfin shad introduction (1988)									
4.0–6.9	14	0.09 \pm 0.21	0.19 \pm 0.24	0.14 \pm 0.22	0.43 \pm 0.31	0	0	0.14 \pm 0.22	0.02 \pm 0.03
7.0–9.9	28	0.00 \pm 0.01	0	0.01 \pm 0.01	0.93 \pm 0.08	0.02 \pm 0.03	0	0	0.04 \pm 0.07
10.0–12.9	19	0.01 \pm 0.01	0.00 \pm 0.01	0.01 \pm 0.01	0.94 \pm 0.04	0.04 \pm 0.04	0	0	0
Stonelick Lake before threadfin shad introduction (1987)									
4.0–6.9	27	0.01 \pm 0.03	0	0	0.12 \pm 0.19	0	0.02 \pm 0.02	0.84 \pm 0.12	0.07 \pm 0.08
7.0–9.9	29	0	0	0.02 \pm 0.02	0.71 \pm 0.15	0.02 \pm 0.02	0.18 \pm 0.09	0.18 \pm 0.11	0.04 \pm 0.05
10.0–12.9	30	0.01 \pm 0.01	0	0.03 \pm 0.02	0.52 \pm 0.16	0.02 \pm 0.02	0.36 \pm 0.14	0.05 \pm 0.03	0.01 \pm 0.01
\geq 13.0	16	0	0.03 \pm 0.03	0.10 \pm 0.05	0.44 \pm 0.20	0.04 \pm 0.04	0.35 \pm 0.19	0.03 \pm 0.03	0
Stonelick Lake after threadfin shad introduction (1988)									
4.0–6.9	25	0.08 \pm 0.11	0.04 \pm 0.08	0	0.23 \pm 0.22	0.12 \pm 0.13	0.07 \pm 0.10	0.50 \pm 0.20	0.04 \pm 0.08
7.0–9.9	38	0.08 \pm 0.08	0.02 \pm 0.04	0.02 \pm 0.04	0.40 \pm 0.17	0.39 \pm 0.15	0.10 \pm 0.08	0.03 \pm 0.05	0.05 \pm 0.05
10.0–12.9	20	0.24 \pm 0.14	0.04 \pm 0.06	0.05 \pm 0.09	0.36 \pm 0.29	0.38 \pm 0.18	0.01 \pm 0.01	0.03 \pm 0.04	0.01 \pm 0.01
\geq 13.0	11	0.13 \pm 0.20	0.00 \pm 0.01	0.03 \pm 0.05	0.76 \pm 0.24	0.07 \pm 0.05	0.02 \pm 0.05	0.01 \pm 0.03	0.03 \pm 0.07

Schoener's overlap index (Schoener 1970), which varies from 0 (no overlap) to 1 (complete overlap), indicated diet overlaps between young-of-year threadfin shad and bluegills collected offshore of 0.37 \pm 0.20 (mean \pm 95% CI, n = 8 comparisons involving 65 bluegill and 63 threadfin shad stomachs) in Clark Lake and 0.43 \pm 0.08 (n = 13 com-

parisons involving 88 bluegill and 76 threadfin shad stomachs) in Stonelick Lake. Diet overlap values exceeded 0.50 on 2 of 8 dates in Clark Lake and on 5 of 13 dates in Stonelick Lake.

Bluegills collected by seining were feeding predominantly on littoral prey such as chironomid larvae and pupae, although some limnetic prey

TABLE 2.—Food selection (estimated by Chesson's alpha; Chesson 1978, 1983) by larval threadfin shad in Clark and Stonelick lakes during 1988. Data are presented as means \pm 95% confidence interval (N indicates sample size). Values greater than neutral selection (i.e., the reciprocal of the number of prey taxa in the lake, here between 0.09 and 0.13) indicate positive selection; values less than this indicate avoidance. Threadfin shad smaller than 7.0 mm were not present in Clark Lake.

Threadfin shad total length (mm)	N	Prey selected							
		<i>Bosmina longirostris</i>	<i>Ceriodaphnia</i> spp.	<i>Daphnia parvula</i>	<i>Diaphanosoma leuchtenbergianum</i>	Calanoid copepods	Cyclopoid copepods	Copepod nauplii	Rotifers
Clark Lake									
7.0–9.9	8	0.14 \pm 0.35	0	0.06 \pm 0.15	0.50 \pm 0.57	0	0.13 \pm 0.30	0.13 \pm 0.29	0.18 \pm 0.30
10.0–12.9	22	0	0	0.05 \pm 0.09	0.31 \pm 0.21	0.11 \pm 0.13	0.40 \pm 0.22	0.05 \pm 0.09	0.09 \pm 0.13
\geq 13.0	91	0.01 \pm 0.01	0	0.02 \pm 0.02	0.42 \pm 0.08	0.35 \pm 0.08	0.19 \pm 0.07	0.01 \pm 0.01	0.02 \pm 0.02
Stonelick Lake									
4.0–6.9	3	0	0	0	0	0	0	1.00 \pm 0.00	0
7.0–9.9	26	0	0	0	0.18 \pm 0.20	0.08 \pm 0.11	0.14 \pm 0.12	0.56 \pm 0.19	0.11 \pm 0.11
10.0–12.9	38	0.03 \pm 0.05	0	0	0.33 \pm 0.16	0.35 \pm 0.15	0.11 \pm 0.09	0.12 \pm 0.09	0.11 \pm 0.10
\geq 13.0	72	0.02 \pm 0.02	0.02 \pm 0.03	0.02 \pm 0.03	0.24 \pm 0.11	0.54 \pm 0.10	0.09 \pm 0.05	0.09 \pm 0.06	0.06 \pm 0.05

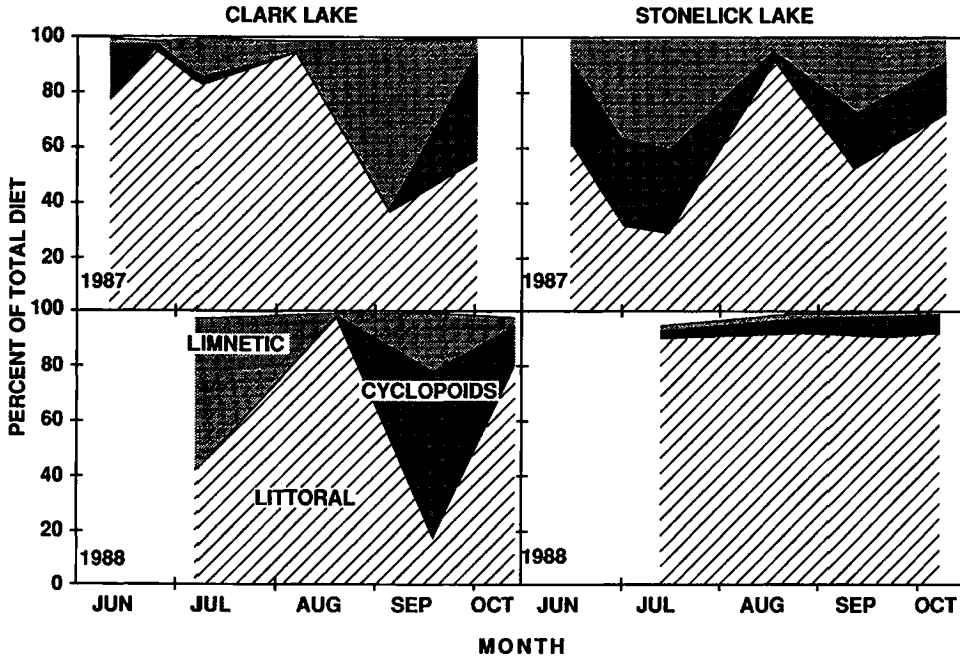


FIGURE 3.—Diets of young-of-year bluegills collected in the littoral zone of Clark and Stonelick lakes, Ohio, during 1987 and 1988. Prey were divided into limnetic zooplankton, littoral prey, and cyclopid copepods (which occur in either habitat; Mittelbach 1981). Results were combined across sample sites and are presented as percentages of the total biomass of prey found in all fish guts on that date. Sample sizes were 5–15 fish for each date.

also were consumed. In Clark Lake, bluegills collected in the littoral zone fed on prey from both littoral and limnetic habitats during both preshad and shad years (Figure 3). On five of six dates in 1987 and two of four dates in 1988, most bluegill food came from the littoral zone (e.g., chironomid larvae and pupae), and the remainder was primarily cyclopid copepods. However, limnetic zooplankton remained an important diet component (>20% by dry weight) on two of six dates in 1987 and one of four dates in 1988 (Figure 3).

In Stonelick Lake, inshore bluegill diets differed dramatically between 1987 and 1988 (Figure 3). In 1987, bluegills fed as in Clark Lake, consuming primarily littoral prey on four of six dates and limnetic prey on the other two dates (Figure 3). In 1988, limnetic prey never made up more than 2% of bluegill diets (never more than 10% if cyclopid copepods were considered to be exclusively in open water; Figure 3). Across all dates during 1988, more than 90% of the bluegill diet originated in the littoral zone.

Largemouth Bass Abundance, Growth, and Diet

During both years in both lakes, young-of-year largemouth bass were collected only in the littoral

zone. In Clark Lake, the difference in abundance of young-of-year largemouth bass was not quite significant between years (year effect $F = 5.42$; $df = 1, 6$; $P = 0.06$), although the year \times time interaction term was significant ($F = 9.34$; $df = 11, 66$; $P = 0.006$) as a result of peak abundance being a month later in 1988 (Figure 4). As a consequence of later spawning in 1988, young-of-year largemouth bass were smaller in June–July 1988 than in 1987, but the difference was made up by the beginning of August (Figure 4), and fall sizes did not differ between years (two-way ANOVA, $F = 0.84$; $df = 1, 466$; $P = 0.36$). In contrast to 1987, when young-of-year largemouth bass in Clark Lake fed on fish in the littoral zone when available, young-of-year largemouth bass did not feed on fish during 1988 (see Figures 2, 5). However, biomass in young-of-year largemouth bass stomachs, measured as dry weight of prey per gram of fish, did not differ between preshad and shad years (two-way ANOVA, $F = 2.06$; $df = 1, 35$; $P = 0.16$), and growth was similar between years (Figure 4).

In Stonelick Lake, young-of-year largemouth bass were about 20 times more abundant at their peak in 1988 than in 1987 (overall year effect, $F = 9.67$; $df = 1, 8$; $P = 0.01$); however, abundance

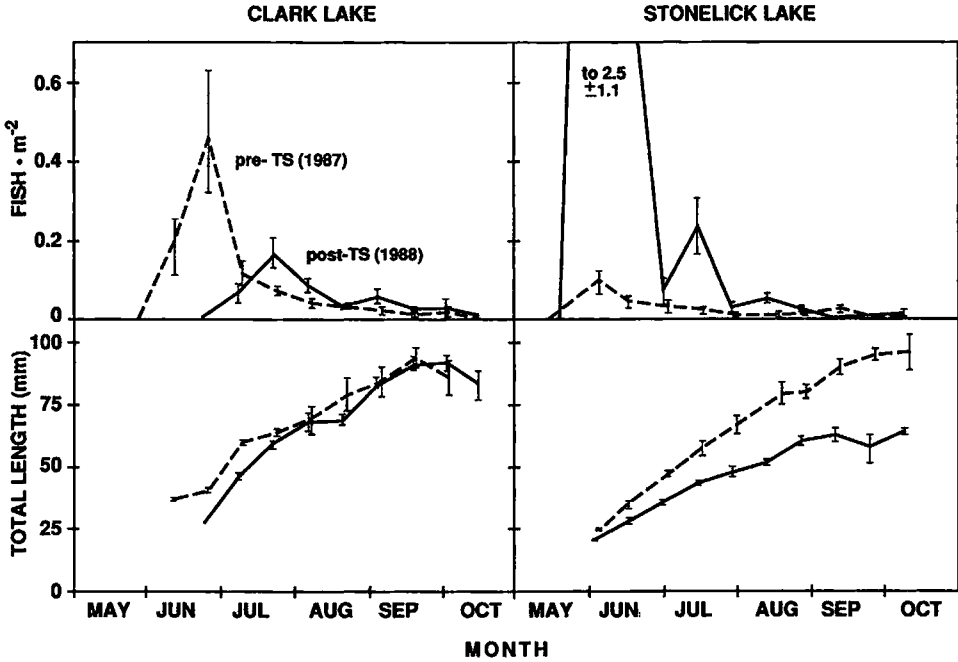


FIGURE 4.—Densities (mean \pm SE) and lengths of young-of-year largemouth bass in Clark and Stonelick lakes, Ohio. Dashed and solid lines represent estimates from before (1987) and after (1988) threadfin shad (TS) introductions, respectively.

was similar between years by late summer (Figure 4). In addition, young-of-year largemouth bass in Stonelick Lake grew more slowly in 1988 than in 1987 (Figure 4; two-way ANOVA, year \times time interaction: $F = 9.29$; $df = 4, 380$; $P = 0.0001$; year effect: $F = 74.07$; $df = 1, 380$; $P = 0.0001$). Young-of-year largemouth bass primarily ate fish during 1987, but they ate fish only on one date during 1988 (Figure 5). Although young-of-year threadfin shad were present during much of the summer in 1988 (see Figure 1), young-of-year largemouth bass never consumed them. In addition, biomass of prey in largemouth bass stomachs (quantified as dry weight of prey per gram of fish) was lower in 1988 than in 1987 (two-way ANOVA, $F = 14.01$; $df = 1, 35$; $P = 0.0007$).

Zooplankton Abundance

Total zooplankton abundance in Clark Lake fluctuated during 1987 and 1988 (Figure 6) but did not differ across years (year effect: $F = 2.00$; $df = 1, 4$; $P = 0.23$; year \times time interaction: $F = 8.22$; $df = 16, 64$; $P = 0.004$). Further, species composition did not appear to differ between years (Figure 7). Density did not decline during late August and early September 1988 after limnetic young-of-year threadfin shad abundance peaked

(Figure 6). If young-of-year threadfin shad had reduced zooplankton abundance, the reduction should have been apparent after mid-August (see Figure 1).

In Stonelick Lake, as in Clark Lake, zooplankton density fluctuated during 1987 and 1988 (Figure 6) but was lower during May through July 1987 than during this period in 1988 (year \times time interaction: $F = 29.49$; $df = 19, 76$; $P = 0.0001$; year effect: $F = 61.00$; $df = 1, 4$; $P = 0.002$). As in Clark Lake, zooplankton species composition did not appear to differ between years until after mid-August, when small forms (copepod nauplii) predominated (Figure 7). During August 1988, zooplankton density declined, and all taxa except copepod nauplii were essentially eliminated (Figure 7). To determine whether this decline could be explained in part by decreased zooplankton birth rates (i.e., by reduced egg production), as opposed to increased predation, we regressed mean fecundity (the product of the proportion of individuals carrying eggs and the mean number of eggs per individual carrying eggs) of *Daphnia parvula*, *Bosmina longirostris*, and *Ceriodaphnia* spp. (the only abundant cladoceran taxa present in August) on time during the zooplankton decline. Mean cladoceran fecundity did not change during the zoo-

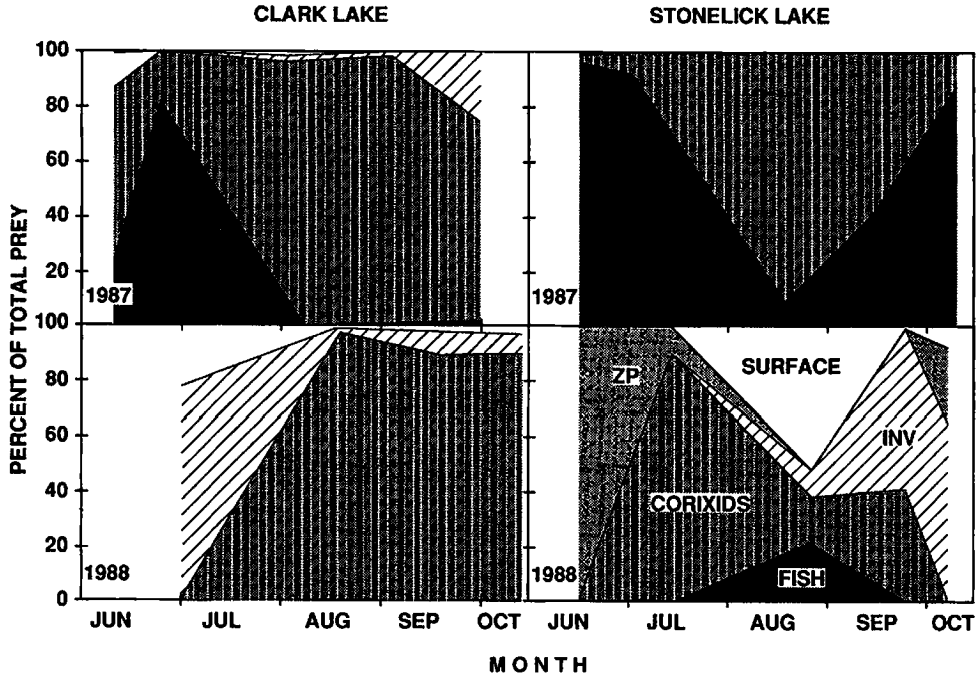


FIGURE 5.—Diets of young-of-year largemouth bass collected in the littoral zone of Clark and Stonelick lakes, Ohio, during 1987 and 1988. Prey categories consisted of fish, zooplankton (ZP), corixids, surface-dwelling invertebrate such as gerrids (SURFACE), and other littoral invertebrates (INV). Results were combined across sample sites and are presented as percentages of the total biomass of prey present in all fish guts on that date. Sample sizes were 2–7 (usually 5) fish for each date.

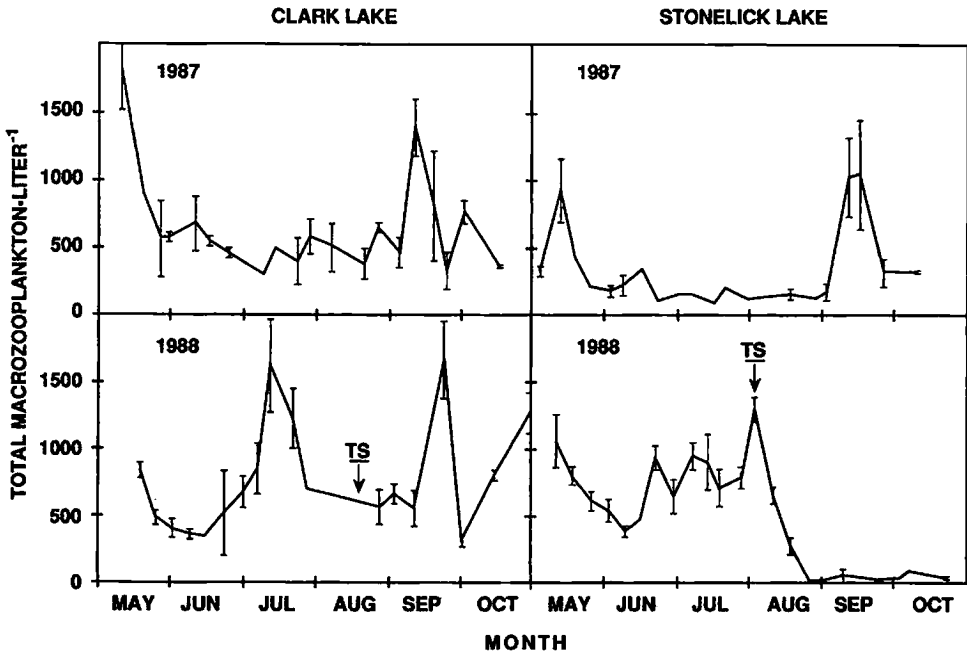


FIGURE 6.—Densities (mean \pm SE) of macrozooplankton in Clark and Stonelick lakes, Ohio, before (1987) and after (1988) threadfin shad introductions. Arrows indicate the date of peak abundance of limnetic young-of-year threadfin shad (TS).

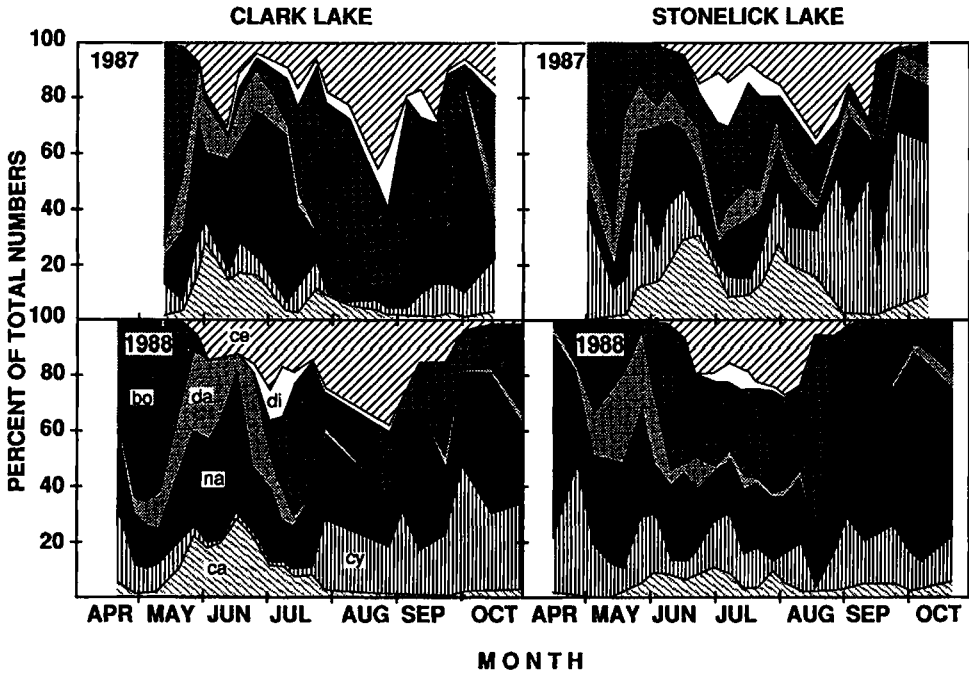


FIGURE 7.—Representation of macrozooplankton taxa in Clark and Stonelick lakes, Ohio, before (1987) and after (1988) threadfin shad introductions. Taxa abbreviations: ca, calanoid copepods; cy, cyclopoid copepods; na, copepod nauplii; da, *Daphnia parvula*; bo, *Bosmina longirostris*; ce, *Ceriodaphnia* spp.; di, *Diaphanosoma leuchtenbergianum*.

plankton decline ($P > 0.16$ for all three taxa). Similarly, during the threadfin shad peak in Clark Lake (mid-August through mid-September), mean fecundity of *Bosmina longirostris* and *Ceriodaphnia* spp. did not change ($P > 0.31$), and mean fecundity of *Daphnia parvula* increased ($P = 0.03$).

Discussion

Zooplankton Responses

We quantified differential responses of zooplankton to threadfin shad introductions into Clark and Stonelick lakes. In Clark Lake, threadfin shad densities peaked in August without a commensurate decline in zooplankton. Conversely, as young-of-year threadfin shad abundance peaked in August in Stonelick Lake, zooplankton declined precipitously, and only cyclopoid copepods and copepod nauplii remained at densities greater than 1.5 organisms/L by late August. Because birth rates did not decline across cladoceran taxa in Stonelick Lake, declining abundance was not due to reduced zooplankton reproduction (i.e., resources did not limit the zooplankton); instead, it was due to increased death rates.

This differential response across systems cannot

be easily explained. Zooplankton densities and species compositions were similar for the two lakes, yet peak larval threadfin shad density was almost four times higher in Clark Lake than in Stonelick Lake. This differential response most likely derived from other differences between the two systems. First, young-of-year bluegill abundance peaked simultaneously with young-of-year threadfin shad in Stonelick Lake but not in Clark Lake. However, limnetic young-of-year bluegills were absent after 9 August, yet zooplankton continued to decline through August. Though limnetic young-of-year bluegills may have contributed to the zooplankton decline in Stonelick Lake, it is more likely that young-of-year threadfin shad, present through 7 September, were responsible. Second, turbidity was higher in Clark Lake than in Stonelick Lake; Secchi depths during August ranged from 27 to 41 cm in Clark Lake and from 80 to 81 cm in Stonelick Lake. This difference may have had an effect on community-wide zooplanktivory. Foraging efficiency of juvenile and adult planktivores declines with increasing turbidity (Vinyard and O'Brien 1976; Gardner 1981), suggesting that the potential for planktivory could be greater in Stonelick Lake (with relatively low tur-

bidity) than in Clark Lake. Although both lakes support large populations of small white crappies (Austin and Hurley 1989), which are zooplanktivorous (Ellison 1984; O'Brien et al. 1984), catch of adult white crappies per unit effort, estimated with trap nets during October 1988, was about three times higher in Stonelick Lake than in Clark Lake (Austin and Hurley 1989). Thus, planktivory by young-of-year threadfin shad and young-of-year bluegills, coupled with planktivory by resident adult white crappies, was sufficient to cause the zooplankton decline in Stonelick Lake.

The hypothesis that young-of-year threadfin shad contributed to reduced zooplankton abundance in Stonelick Lake is supported by analogous studies with gizzard shad. In Kokosing Lake, Ohio, zooplankton density during the past 4 years typically decreased to near zero within 2 weeks of peak young-of-year gizzard shad density (DeVries 1989). To determine whether young-of-year gizzard shad were responsible for the decline, one of us (DeVries 1989) manipulated fish in 2-m³ enclosures (~19 fish/m³) and found that gizzard shad reduced macrozooplankton density from 700 to less than 10 animals/L within 2 weeks, a decline similar in magnitude to that observed in Stonelick Lake. In field studies at other lakes, zooplankton declines have also been documented after threadfin or gizzard shad introductions (VonGeldern and Mitchell 1975; Prophet 1982, 1985, 1988; Ziebell et al. 1986); however, none of those studies monitored densities of young-of-year fish. Thus, the extent to which zooplanktivory by young-of-year fish was related to zooplankton declines cannot be determined. In previous work, the co-occurrence of young-of-year gizzard or threadfin shad and the midsummer decline of zooplankton has been noted (Cramer and Marzolf 1970; Johnson 1970; Mayhew 1977; Kashuba and Matthews 1984; Kiszick 1988). These suggestive field data, in combination with our enclosure experiment, support the hypothesis that predation by young-of-year threadfin shad contributed to reduced zooplankton densities in Stonelick Lake.

Threadfin Shad-Bluegill Interactions

Abundance of young-of-year fishes.—Spawning by threadfin shad peaked during August in Clark and Stonelick lakes. This contrasts with the spring spawning documented for threadfin and gizzard shad in other systems (Baglin and Kilambi 1968; Mayhew 1977; Barger and Kilambi 1980; Van Den Avyle and Wilson 1980; Downey and Toetz 1983; Tisa et al. 1987; Willis 1987; but see Santucci

1985 for an example of late-summer spawning by threadfin shad). In Clark Lake, young-of-year bluegills occurred in the limnetic zone before—but not during or after—peak abundance of young-of-year threadfin shad, thereby reducing the potential for competition between these species. In Stonelick Lake, however, bluegills spawned during May through August, and the peak abundance of young-of-year bluegills occurred before and during the peak abundance of young-of-year threadfin shad. Thus, competition between young-of-year threadfin shad and bluegills was likely.

The late-summer peak abundance of young-of-year threadfin shad in Clark and Stonelick lakes could have been due to several factors; for example, spawning could have been delayed by stocking stress, drought (which reduced water levels during 1988), or late-summer maturation of young-of-year threadfin shad (as documented by Heidinger and Imboden 1974). The ability to predict the time of spawning by threadfin shad after they are introduced is critical to determining the species' value as prey; if spawning is delayed, interspecific competition among young-of-year fishes can be minimized. Whether this late spawning by threadfin shad will be consistent requires additional research.

Because zooplankton remained abundant and densities were similar across years in Clark Lake, competition with threadfin shad (either larvae or adults) probably was not responsible for the reduced abundance of offshore young-of-year bluegill during 1988. Further, abundance of young-of-year threadfin shad did not peak in Clark Lake until after bluegills had moved to the littoral zone. It is possible that predation by adult threadfin shad reduced young-of-year bluegill densities between 1987 and 1988. However, even though threadfin shad may be capable of piscivory (Kimsey 1958; see also Dendy 1946 for an example of piscivory by gizzard shad; but see Heidinger 1983 for a review of difficulties associated with detecting such piscivory), fish were not found in stomachs of threadfin shad from either lake during 1988 ($N = 41$ adult threadfin shad stomachs examined). Alternatively, the 1988 drought that lowered Clark Lake by about 1 m during the nesting season may have disrupted bluegill reproduction (see review in Ploskey 1986).

Young-of-year threadfin shad, though their abundance peaked in late summer, co-occurred at low densities with limnetic young-of-year bluegills during May through September in Clark Lake. When both species co-occurred in the limnetic

zone, they ate only limnetic zooplankton; however, diet overlap values were typically ≤ 0.50 . Once blue gills moved inshore, the potential for competition with threadfin shad declined greatly. Diets of bluegills collected from the littoral zone did not change between 1987 and 1988 in Clark Lake; all prey types (littoral, limnetic, and cyclopoid copepods) were eaten. Though collected inshore, bluegills apparently moved far enough offshore to consume some limnetic prey, but they ate enough littoral prey to reduce overlap with threadfin shad, which continued to feed entirely on limnetic prey.

In Stonelick Lake, abundance of limnetic young-of-year bluegills before and after the introduction of threadfin shad did not differ. Several peaks occurred during both years. Fish from the protracted spawning season of 1987 continued to migrate to the littoral zone, as evidenced by their increasing inshore abundance through summer. In 1988, fish from the early-June peak migrated to the littoral zone during July; however, fish from the August peak never appeared inshore. These August fish were lost to our offshore gear 2 weeks after their peak abundance and were never collected in the littoral zone, which suggests poor survival of the limnetic life stage. As suggested earlier, predation by adult threadfin shad probably was not responsible. Reduced densities of all zooplankton in August, coupled with moderately high diet overlap between young-of-year bluegills and threadfin shad (range, 0.45–0.64), may have reduced bluegill survival and recruitment through exploitative competition with threadfin shad. Similar results were obtained in a pond experiment where young-of-year shad (both gizzard and threadfin shad) reduced the abundance of young-of-year white crappies (Guest et al. 1990).

Diet overlap.—Diets of bluegills collected inshore in both lakes included littoral prey; thus overlap with threadfin shad was reduced once bluegills became littoral. In Clark Lake, the proportion of littoral and limnetic prey consumed by bluegills collected in the littoral zone did not differ across years. In Stonelick Lake during 1987, bluegills collected in the littoral zone fed on littoral and limnetic prey, apparently moving far enough offshore to consume limnetic prey. However, in 1988 limnetic prey formed an extremely small component of the bluegill diet; reduced zooplankton abundance after August 1 may have contributed to this.

Few published data indicate whether or not young-of-year threadfin shad and bluegills com-

pete for limnetic zooplankton. Diets of young bluegills and gizzard shad or threadfin shad rarely have been quantified, and interpretation of published results remains tenuous. Most investigators agree that first-feeding gizzard shad and bluegills select copepod nauplii (Mayhew 1977; Mallin et al. 1987; Kissick 1988); consequently, these species could compete if they co-occurred as larvae. As young-of-year threadfin shad grew in our lakes, they preferred larger prey such as *Diaphanosoma leuchtenbergianum*. This observation conflicts with published results that, as gizzard and threadfin shad grow, they feed on progressively smaller prey such as rotifers and *Bosmina* spp. (Barger and Kilambi 1980; Van Den Avyle and Wilson 1980). However, without data on zooplankton availability, we cannot evaluate the prey preferences of shad of either species in these studies. For example, if zooplankton abundance declined, as in Stonelick Lake in August and as documented in other lakes containing gizzard or threadfin shad, both species of shad would be forced to feed on smaller prey items as they grew. Under these conditions, shad might simply be consuming available zooplankton rather than actively selecting smaller prey. Several studies, including ours, have documented selection of *Diaphanosoma* spp. by larval fish (Van Den Avyle and Wilson 1980; Mallin et al. 1987), but this is certainly not a universal finding (Cramer and Marzolf 1970). Consequently, although competition between young-of-year bluegills and young-of-year threadfin shad may occur (particularly during August in Stonelick Lake), the outcome of such interactions in a lake ultimately depends on abundance and species composition of the zooplankton community and on the relative spawning times of the predator fishes. As demonstrated by our results, these factors vary among lakes and years, making generalization difficult.

Complex Effects on Young-of-Year Largemouth Bass

Because young-of-year largemouth bass remained in the littoral zone and fed primarily on littoral prey in both lakes, their diets did not overlap with those of threadfin shad. Furthermore, owing to this spatial segregation, young-of-year largemouth bass did not consume young-of-year threadfin shad. Thus, the apparent effect of young-of-year threadfin shad on young-of-year largemouth bass in Stonelick Lake was complex and unexpected. In Clark Lake, largemouth bass spawned several weeks later in 1988 than in 1987;

consequently, when juvenile bluegills moved inshore, they were too large for largemouth bass to consume. In 1988, however, largemouth bass compensated by eating other foods (primarily coxids), so prey biomass in their stomachs did not differ across years. In Stonelick Lake during 1987, small fish (primarily centrarchids) were a major component of largemouth bass diets, in part because of the continual recruitment of young-of-year bluegills inshore. In 1988, juvenile bluegills did not recruit to the littoral zone after mid-July; also, young-of-year largemouth bass were extremely abundant in early summer. This high density of young-of-year largemouth bass, coupled with poor recruitment of juvenile bluegills as prey (after mid-August), likely reduced largemouth bass growth in 1988 compared with 1987. When young-of-year largemouth bass densities were reduced, such that they were similar across years (after mid-August), growth rates during 1988 continued to be lower than during 1987. Though young-of-year largemouth bass fed on littoral invertebrates, they could not compensate for the lack of fish in their diets as fish did in Clark Lake, perhaps because abundant young-of-year largemouth bass reduced littoral invertebrate density. Without estimates of macroinvertebrate densities from Clark and Stonelick lakes, we are unable to test this hypothesis.

Thus, interactions between limnetic young-of-year threadfin shad and bluegills may have a pronounced negative effect on young-of-year largemouth bass growth if they lead to reduced survival of young-of-year bluegills in the limnetic zone and then to reduced recruitment of bluegills to the littoral zone. Additionally, slower growth may reduce overwinter survival of young-of-year largemouth bass if overwinter survival depends on body size and fat reserves (Adams et al. 1982a, 1982b; reviewed in Adams and DeAngelis 1987). As a consequence, the very management practice intended to enhance the fishery for adult piscivores may reduce survival of the target species. Although these negative effects are not direct (unlike the positive effects of increased prey availability), they could have substantial consequences over several years of such management manipulation.

Indirect effects, mediated through other species or even through other trophic levels, thus can determine the ultimate outcome of any manipulation. Our results support the hypothesis that interactions involving young-of-year fishes can have dramatic consequences for sport fishes (as at Stonelick Lake), but that these interactions are not

always the primary factor regulating community structure (as at Clark Lake). Determination of the factors responsible for influencing the relative importance of interactions among larvae represents a critical step toward successful management of inland lakes.

Acknowledgments

This work would not have been possible without the cooperation of M. Austin, S. Hurley, and D. B. Apgear of the Ohio Department of Natural Resources and G. Buynak and others of the Kentucky Department of Natural Resources. We thank J. Ballinger, P. Crane, D. Gleason, C. Habicht, L. Harper, H. Irvin, M. Knierim, E. Lewis, C. Mallison, L. Ryan, and J. Zablony for their help in the field and laboratory; E. Lewis, in particular, counted more zooplankton samples and looked at more fish guts than seems humanly possible. Helpful comments were provided on a previous draft of this manuscript by P. L. Chesson, J. M. Dettmers, R. W. Drenner, X. Lazzaro, W. M. Masters, E. L. Mills, J. A. Rice, and D. H. Wahl. This work was funded in part by National Science Foundation grants NSF BSR-8705518 to R. A. Stein and NSF BSR-8715730 to G. G. Mittelbach, and by Federal Aid in Fish Restoration Project F-57-R awarded to R. A. Stein and administered through the Ohio Division of Wildlife.

References

- Adams, S. M., and D. L. DeAngelis. 1987. Indirect effects of early bass-shad interactions on predator population structure and food web dynamics. Pages 103-117 in W. C. Kerfoot and A. Sih, editors. Predation: direct and indirect impacts on aquatic communities. University Press of New England, Hanover, New Hampshire.
- Adams, S. M., R. B. McLean, and M. M. Huffman. 1982a. Structuring of a predator population through temperature-mediated effects on prey availability. *Canadian Journal of Fisheries and Aquatic Sciences* 39:1175-1184.
- Adams, S. M., R. B. McLean, and J. A. Parrotta. 1982b. Energy partitioning in largemouth bass under conditions of seasonally fluctuating prey availability. *Transactions of the American Fisheries Society* 111: 549-558.
- Austin, M. R., and S. T. Hurley. 1989. Evaluation of a threadfin shad introduction on crappie growth in an Ohio lake(s). Ohio Department of Natural Resources, Federal Aid in Fish Restoration, Annual Performance Report, Project F-29-R-28, Study 21, Columbus, Ohio.
- Baglin, R. E., Jr., and R. V. Kilambi. 1968. Maturity and spawning periodicity of the gizzard shad, *Doro-*

- soma cepedianum*, (LeSueur), in Beaver Reservoir. Arkansas Academy of Science 22:38-43.
- Barger, L. E., and R. V. Kilambi. 1980. Feeding ecology of larval shad, *Dorosoma*, in Beaver reservoir, Arkansas. Pages 136-145 in L. A. Fuiman, editor. Proceedings of the Fourth Annual Larval Fish Conference. U.S. Fish and Wildlife Service, Ann Arbor, Michigan.
- Beard, T. D. 1982. Population dynamics of young-of-the-year bluegill. Wisconsin Department of Natural Resources Technical Bulletin 127.
- Buynak, G. L., B. T. Kinman, and R. V. Jackson. 1989. Purse seining to capture large numbers of adult threadfin shad. North American Journal of Fisheries Management 9:121-123.
- Chesson, J. 1978. Measuring preference in selective predation. Ecology 59:211-215.
- Chesson, J. 1983. The estimation and analysis of preference and its relationship to foraging models. Ecology 64:1297-1304.
- Cramer, J. D., and G. R. Marzolf. 1970. Selective predation on zooplankton by gizzard shad. Transactions of the American Fisheries Society 99:320-332.
- Cushing, D. H. 1975. Marine ecology and fisheries. Cambridge University Press, Cambridge, UK.
- Dendy, J. S. 1946. Food of several species of fish, Norris Reservoir, Tennessee. Journal of Tennessee Academy of Science 21:105-127.
- DeVries, D. R. 1989. The influence of an open-water planktivore on reservoir communities: the importance of trophic-level interactions and ontogenetic niche shifts. Doctoral dissertation. Ohio State University, Columbus.
- DeVries, D. R., and R. A. Stein. 1990. Manipulating shad to enhance sport fisheries in North America: an assessment. North American Journal of Fisheries Management 10:209-223.
- DeVries, D.R., and R. A. Stein. 1991. Comparing three zooplankton samplers: a taxon-specific assessment. Journal of Plankton Research 13:53-59.
- Downey, P., and D. Toetz. 1983. Distribution of larval gizzard shad (*Dorosoma cepedianum*) in Lake Carl Blackwell, Oklahoma. American Midland Naturalist 109:23-33.
- Ellison, D. G. 1984. Trophic dynamics of a Nebraska black crappie and white crappie population. North American Journal of Fisheries Management 4:355-364.
- Gardner, M. B. 1981. Effects of turbidity on feeding rates and selectivity of bluegill. Transactions of the American Fisheries Society 110:446-450.
- Gilliam, J. F. 1982. Foraging under mortality risk in size-structured populations. Doctoral dissertation. Michigan State University, East Lansing.
- Guest, W. C., R. W. Drenner, S. T. Threlkeld, F. D. Martin, and J. D. Smith. 1990. Effects of gizzard shad and threadfin shad on zooplankton and young-of-year white crappie production. Transactions of the American Fisheries Society 119:529-536.
- Haney, J. F., and D. J. Hall. 1973. Sugar-coated *Daphnia*: a preservation technique for Cladocera. Limnology and Oceanography 18:331-333.
- Heidinger, R. C. 1983. Life history of gizzard shad and threadfin shad as it relates to the ecology of small lakes fisheries. Pages 1-18 in D. Bonneau and G. Radonski, editors. Pros and cons of shad. Iowa Conservation Commission, Des Moines.
- Heidinger, R., and F. Imboden. 1974. Reproductive potential of young-of-the-year threadfin shad (*Dorosoma petenense*) in southern Illinois lakes. Transactions of the Illinois State Academy of Science 67: 397-401.
- Johnson, J. E. 1970. Age, growth, and population dynamics of threadfin shad, *Dorosoma petenense* (Günther), in central Arizona reservoirs. Transactions of the American Fisheries Society 99:739-753.
- Kashuba, S. A., and W. J. Matthews. 1984. Physical condition of larval shad during spring-summer in a southwestern reservoir. Transactions of the American Fisheries Society 113:199-204.
- Keast, A. 1980. Food and feeding relationships of young fish in the first weeks after the beginning of exogenous feeding in Lake Opinicon, Ontario. Environmental Biology of Fishes 5:305-314.
- Kimsey, J. B. 1958. Possible effects of introducing threadfin shad (*Dorosoma petenense*) into the Sacramento-San Joaquin Delta. California Department of Fish and Game, Inland Fisheries Administrative Report 58-16, Sacramento.
- Kirk, J. P. 1984. Competitive influences of gizzard shad introductions on balanced largemouth bass-bluegill populations. Doctoral dissertation. Auburn University, Auburn, Alabama.
- Kirk, J. P., and W. D. Davies. 1987. Competitive influences of gizzard shad on largemouth bass and bluegill in small impoundments. Proceedings of the Annual Conference Southeastern Association of Fish and Wildlife Agencies 39(1985):116-124.
- Kissick, L. A. 1988. Early life history of the gizzard shad in Acton Lake, Ohio: feeding ecology and drift of stream-spawned larvae. Master's thesis. Miami University, Oxford, Ohio.
- Lasker, R. 1975. Field criteria for survival of anchovy larvae: the relation between inshore chlorophyll maximum layers and successful first feeding. U.S. National Marine Fisheries Service Fishery Bulletin 73:453-462.
- Mallin, M. A., L. J. Birchfield, and W. Warren-Hicks. 1987. Food habits and diet overlap of larval *Lepomis* spp. and gizzard shad in a Piedmont reservoir. Proceedings of the Annual Conference Southeastern Association of Fish and Wildlife Agencies 39(1985):146-155.
- Mayhew, J. 1977. The effects of flood management regimes on larval fish and fish food organisms at Lake Rathbun. Iowa Conservation Commission, Iowa Fisheries Technical Series 77-2, Des Moines.
- Mills, E. L., and J. L. Forney. 1988. Trophic dynamics and development of freshwater pelagic food webs. Pages 11-29 in S. R. Carpenter, editor. Complex interactions in lake communities. Springer-Verlag, New York.
- Mills, E. L., J. L. Forney, and K. J. Wagner. 1987. Fish predation and its cascading effect on the Oneida

- Lake food chain. Pages 118–131 in W. C. Kerfoot and A. Sih, editors. Predation: direct and indirect impacts on aquatic communities. University Press of New England, Hanover, New Hampshire.
- Mittelbach, G. G. 1981. Foraging efficiency and body size: a study of optimal diet and habitat use by bluegills. *Ecology* 62:1370–1386.
- Ney, J. J. 1981. Evolution of forage-fish management in lakes and reservoirs. *Transactions of the American Fisheries Society* 110:725–728.
- Noble, R. L. 1981. Management of forage fishes in impoundments of the southern United States. *Transactions of the American Fisheries Society* 110:738–750.
- Noble, R. L. 1986. Predator-prey interactions in reservoir communities. Pages 137–143 in G. E. Hall and M. J. Van Den Avyle, editors. Reservoir fisheries management: strategies for the 80's. American Fisheries Society, Southern Division, Reservoir Committee, Bethesda, Maryland.
- O'Brien, W. J., B. Loveless, and D. Wright. 1984. Feeding ecology of young white crappie in a Kansas reservoir. *North American Journal of Fisheries Management* 4:341–349.
- Persson, L. 1988. Asymmetries in competitive and predatory interactions in fish populations. Pages 203–218 in B. Ebenman and L. Persson, editors. Size-structured populations. Springer-Verlag, New York.
- Ploskey, G. R. 1986. Effects of water-level changes on reservoir ecosystems, with implications for fisheries management. Pages 86–97 in G. E. Hall and M. J. Van Den Avyle, editors. Reservoir fisheries management: strategies for the 80's. American Fisheries Society, Southern Division, Reservoir Committee, Bethesda, Maryland.
- Prophet, C. W. 1982. Zooplankton changes in a Kansas lake 1963–1981. *Journal of Freshwater Ecology* 1:569–575.
- Prophet, C. W. 1985. Calanoid population structure in a Kansas lake after introduction of threadfin shad. *Southwestern Naturalist* 30:162–163.
- Prophet, C. W. 1988. Changes in seasonal population structures of two species of *Diatomus* (Calanoida, Copepoda) subsequent to introductions of threadfin and gizzard shad. *Southwestern Naturalist* 33:41–53.
- Santucci, V. J., Jr. 1985. Comparison of the temporal and spatial distributions of larval gizzard shad, threadfin shad, and inland silverside in Rend Lake, Illinois. Master's thesis. Southern Illinois University, Carbondale.
- SAS Institute. 1985. SAS user's guide: statistics, version 5 edition. SAS Institute, Cary, North Carolina.
- Schoener, T. W. 1970. Non-synchronous spatial overlap of lizards in patchy habitats. *Ecology* 51:408–418.
- Storck, T. W. 1978. The distribution of limnetic fish larvae in a flood control reservoir in central Illinois. *Transactions of the American Fisheries Society* 107:419–424.
- Tisa, M. S., J. J. Ney, and D. K. Whitehurst. 1987. Spatial and temporal distribution of larval alewives and gizzard shad in a Virginia reservoir. *Proceedings of the Annual Conference Southeastern Association of Fish and Wildlife Agencies* 39(1985):65–73.
- Van Den Avyle, M. J., and J. R. Wilson. 1980. Food habits and feeding selectivity of larval *Dorosoma* spp. in Center Hill Reservoir. Pages 146–156 in L. A. Fuiman, editor. Proceedings of the Fourth Annual Larval Fish Conference. U.S. Fish and Wildlife Service, Ann Arbor, Michigan.
- Vinyard, G. L., and W. J. O'Brien. 1976. Effects of light and turbidity on the reactive distance of bluegill sunfish (*Lepomis macrochirus*). *Journal of the Fisheries Research Board of Canada* 33:2845–2849.
- VonGeldern, C., Jr., and D. F. Mitchell. 1975. Largemouth bass and threadfin shad in California. Pages 436–449 in H. Clepper, editor. Black bass biology and management. Sport Fishing Institute, Washington, D.C.
- Wallace, R. K., Jr. 1981. An assessment of diet-overlap indexes. *Transactions of the American Fisheries Society* 110:72–76.
- Ware, D. M. 1980. Bioenergetics of stock and recruitment. *Canadian Journal of Fisheries and Aquatic Sciences* 37:1012–1024.
- Werner, E. E., and J. F. Gilliam. 1984. The ontogenetic niche and species interactions in size-structured populations. *Annual Review of Ecology and Systematics* 15:393–425.
- Werner, E. E., and D. J. Hall. 1988. Ontogenetic habitat shifts in bluegill: the foraging rate-predation risk trade-off. *Ecology* 69:1352–1366.
- Werner, R. G. 1967. Intralacustrine movements of bluegill fry in Crane Lake, Indiana. *Transactions of the American Fisheries Society* 96:416–420.
- Willis, D. W. 1987. Reproduction and recruitment of gizzard shad in Kansas reservoirs. *North American Journal of Fisheries Management* 7:71–80.
- Wydoski, R. S., and D. H. Bennett. 1981. Forage species in lakes and reservoirs of the western United States. *Transactions of the American Fisheries Society* 110:764–771.
- Ziebell, C. D., J. C. Tash, and R. L. Barefield. 1986. Impact of threadfin shad on microcrustacean zooplankton in two Arizona lakes. *Journal of Freshwater Ecology* 3:399–406.