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Dept: BiologyEmail Address: **Jeff.Wesner@usd.edu****Document Delivery uses Odyssey****Date Needed:** 10/25/2019**RAPID request held locally (Main Library)**

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# Feeding Ecology of Coexisting Larvae of American Shad and Blueback Herring in the Connecticut River

VICTOR A. CRECCO AND MARK M. BLAKE

Connecticut Department of Environmental Protection, Marine Fisheries Office  
Post Office Box 248, Waterford, Connecticut 06385

## Abstract

Food-habit, niche-breadth, and diet-overlap analyses were conducted for larvae of American shad *Alosa sapidissima* and blueback herring *Alosa aestivalis* collected from the Connecticut River from June 3 to July 15, 1981. River zooplankton densities (numbers·m<sup>-3</sup>) were used to assess the influences of prey availability on niche-breadth and diet-overlap indices for the species. Niche-breadth values were consistently higher for blueback herring than for American shad larvae. American shad fed mostly on the less-abundant crustaceans and immature insects, whereas blueback herring larvae usually utilized the numerically dominant rotifers. The cladoceran *Bosmina* sp. was utilized extensively by American shad of all sizes and by 13–16-mm blueback herring larvae, and was the only prey for which interspecific competition between the larval predators might occur. The mean mouth gape of American shad larvae was always larger than that of blueback herring larvae at a given length, and American shad larvae of all sizes generally selected the larger cyclopoid copepodites and chironomid larvae. The diet-overlap indices varied over time, but were generally higher among length groups within species than between species, suggesting that intraspecific competition for food may be more severe than interspecific competition.

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It is well established that planktivorous fish can alter freshwater zooplankton communities by size-selective grazing (Brooks and Dodson 1965; Janssen 1976). Much of the evidence for this phenomenon has come from studies of juvenile and adult alosids, particularly blueback herring *Alosa aestivalis* (Burbridge 1974), alewives *Alosa pseudoharengus* (Wells 1970; Warshaw 1972), and American shad *Alosa sapidissima* (Levesque and Reed 1972). These studies suggest that through size-selective grazing, planktivorous fishes may change the way in which food resources are partitioned among species of the same trophic level, resulting in increased interspecific competition. Size-selective predation among alosids would be especially important during the larva stage, given that year-class strength may be affected by predation and food availability during the period of larva drift (May 1974; Lasker 1978). In this paper, we compare prey-size selection and food habits between larvae of the American shad and blueback herring where they co-occur in the Connecticut River. We also use biweekly zooplankton densities and dietary-overlap indices to assess temporal changes in diet partitioning and potential competition between American

shad and blueback herring larvae of various length groups.

Both American shad and blueback herring are anadromous and their spawning runs support important recreational and commercial fisheries in rivers from Florida to Newfoundland (Walburg and Nichols 1967). Both species spawn in the Connecticut River during May and June (Loesch 1968; Leggett 1976), and larvae of both species hatch during June and July within similar riverine habitats (Cave 1978). Blueback herring and American shad larvae exhaust their yolk 3–5 days after hatching and become particulate feeders on zooplankton. The larva stage lasts about 25–35 days before larvae metamorphose into filter-feeding juveniles (Watson 1968).

## Methods

American shad and blueback herring larvae were collected weekly by haul seine at 12 stations in the Connecticut River from June 3 to July 15, 1981. All sampling sites were located between the Enfield Dam, Connecticut (km 85), and the Sunderland bridge, Sunderland, Massachusetts (km 182). Seine sites were chosen within eddies and backwater areas where larvae

of both species are known to co-occur (Cave 1978). Collections were made during daylight hours with a 6.1-m plankton bag seine (2.4 m deep, wing and bag mesh of 0.25 mm) and 30.5-m lead ropes. The seine was set from a boat about 30 m offshore, towed in a downstream arc toward shore and hauled with the lead ropes. Larvae were washed into a plankton bucket and immediately fixed in 4% formalin.

One of the major aims of this study was to examine temporal changes in food habits between species and among various length groups. Therefore, gut contents of at least 30 American shad and 10 blueback herring were analyzed within each of three length groups (5–12, 13–15, and 16+ mm total length) for the 2-week intervals June 3–16, June 17–30, and July 1–15. Only stomachs containing at least one zooplankton were used in this analysis. A larger sample size was required for American shad because their stomachs usually contained fewer prey than those of blueback herring. Stomachs of larvae taken prior to June 3 were not examined because only small (5–12 mm) and intermediate-size (13–15 mm) American shad larvae were encountered. By contrast, few American shad larvae were collected after July 15 so these data were likewise omitted. It was necessary to pool larvae over 2-week intervals to ensure that the proper sample size was available within each length group.

All ingested organisms were identified to the lowest possible taxon and their body widths were measured to the nearest 0.01 mm with an ocular micrometer. Because larvae of both species ate small prey (usually less than 0.5 mm wide), it was difficult to estimate accurately the relative volumes or weights of each prey taxon as recommended by Wallace (1981). In this study, the percent composition ( $R_{iA}$  for American shad,  $R_{iB}$  for blueback herring) by number was determined for each prey taxon  $i$ .

The relative mouth gape ( $b$ ) of each larva was estimated from Shirota's (1970) expression:

$$b = T\sqrt{2};$$

$T$  = length of the maxillary bone.

The relationship between mouth gape and body length of larvae was examined graphically for both species. The mean, minimum, and maximum prey widths also were determined for each species. Paired  $t$ -tests were performed to com-

pare mean widths of the principal prey found in larvae of each length group with those found in river samples. This analysis provided insight about the degree of size-selective predation by both species.

River zooplankton was sampled weekly at the 12 seine sites from May 14 to July 15, 1981 with a 130-mm-diameter Clark-Bumpus plankton sampler fitted with an 80- $\mu\text{m}$ -mesh net and calibrated flowmeter. Triplicate 1-minute tows were made parallel to shore; each sample was filtered from 1–2  $\text{m}^3$  of river water. All zooplankton samples were taken a few minutes after seine sampling was completed. Each zooplankton tow was made downstream with the net 2 m below the water surface, well within the strata sampled by the seine. Zooplankton samples were immediately stored in 4% formalin.

Maximum widths of zooplankton (appendages excluded) were measured to the nearest 0.01 mm with an ocular micrometer. Cladocerans, adult copepods, and most female rotifers were identified to genus (Pennak 1953; Edmondson 1959; Smith and Fernando 1978). Male and soft-bodied rotifers were classified as "Rotifera spp." and immature copepods and insects were identified to the lowest taxon possible. The mean number of organisms counted from 2–3 aliquots (1 ml) was used to estimate zooplankton abundance (number  $\cdot \text{m}^{-3}$ ). The percent composition  $R_{iR}$  of river zooplankton was determined, allowing direct comparisons between resource availability and prey composition of the diet. The percent compositions of prey in the river were pooled into 2-week intervals (June 3–16, June 17–30, July 1–15), as was the percent in larva stomachs.

The degree of prey preference between species and among length groups was determined with the linear food selection index (Strauss 1979):

$$L = R_{iA} - R_{iR}; \quad L = R_{iB} - R_{iR}.$$

The range of  $L$  is  $-1.0$  to  $+1.0$ ; positive values suggest preference, and negative values, avoidance. The  $L$  value was calculated only for those zooplankton taxa which made up at least 5% of the river samples. The standard error of  $L$  was estimated by the method of Strauss (1982) and  $t$ -tests were conducted to determine whether or not  $L$  differed significantly ( $P < 0.05$ ) from 0.

In this study, niche breadth was defined as the degree of similarity between the percent

composition ( $R_{iA}, R_{iB}$ ) of prey taxa in larva stomachs and that ( $R_{iR}$ ) for river zooplankton (Hurlbert 1978). Dietary niche breadth among length groups and between species was computed for each collection period by the  $PS$  value of Feinsinger et al. (1981):

$$PS = 1 - 0.5 \sum_{i=1}^y |R_{iA} \text{ or } iB - R_{iR}|;$$

$y$  = total number of zooplankton taxa.

This index was preferred over others (Levins 1968; Colwell and Futuyma 1971) because it considers resource availability and permits the computation of standard errors. The  $PS$  values may vary from 1.0, when the predators use prey in exact proportion to prey abundance, to a value approaching 0 when the predators specialize exclusively on the rarest prey in the environment.

Comparisons of relative diet overlap were made with Hurlbert's (1978) index:

$$B = \sum_{i=1}^z (R_{iA} R_{iB} / R_{iR});$$

$z$  = total number of prey taxa common to both predators.

For each collection period, the diet-overlap index was calculated within and between species. This index was chosen because it considers the availability of prey. The  $B$  value assumes a value of 0 when no prey are shared by two predators, a value of 1.0 when both predators utilize each prey type in proportion to its abundance in the environment, and a value approaching infinity if both predators only utilize the rarest prey in the environment.

## Results

### River Zooplankton Abundance

Rotifers, dominated by *Keratella* spp. and soft-bodied species, were numerically the most diverse and abundant taxonomic group, making up 79–96% of the river zooplankton during June and July 1981 (Table 1). Cladocerans always were less than 2% of the total, *Bosmina* spp. being the most abundant and persistent among them. Immature and adult copepods were less diverse but more abundant than cladocerans, constituting 2.5–6.0% of the total zooplankton. Mussel glochidia made up nearly 12% of the zooplankton standing crop during

early June, but declined sharply thereafter. Midge (chironomid) larvae, mayfly nymphs, and caddis fly larvae were encountered in low numbers throughout June and July.

Temporal changes in zooplankton density were evident (Fig. 1). These were chiefly due to rotifers, whose abundance peaked in early June and varied around  $10^4 \cdot m^{-3}$  thereafter.

### Prey Preference

Obvious differences in prey preference were evident between American shad and blueback herring larvae (Table 1). Gut contents of 372 American shad larvae revealed that chironomid larvae, cyclopoid copepodites, and, to a lesser extent, *Bosmina* spp. made up 95% of this species' diet. Rotifers, the most abundant taxonomic group in river samples, were found in only two American shad stomachs. By contrast, 67% of the diet among 196 blueback larvae was composed of the rotifers *Keratella* spp. and "Rotifera" spp., an additional 27% consisting of *Bosmina* spp.

Chironomid larvae were an important food item among larval American shad, and the proportion ( $R_{iA}$ ) of this taxon in the diet increased over time despite the low occurrence of chironomids in river samples (Table 1). The food selection index ( $L$ ) was always positive and significant for this taxon. The relative abundance of cyclopoid copepodites in American shad stomachs greatly exceeded that found in river samples. The  $L$  values indicated that American shad larvae of all sizes selected for cyclopoid copepodites from June 3 to 30. American shad larvae of all sizes showed a significant preference for *Bosmina* spp. from June 17 to June 30, whereas all American shad larvae exhibited significant avoidance of *Keratella* spp. and "Rotifera" spp." The  $L$  values for copepod nauplii and mussel glochidia were always negative but only occasionally significant.

Temporal changes in prey selection among blueback herring larvae generally followed changes in river zooplankton (Table 1). *Keratella* spp. were the most-selected prey among all length groups of larvae from June 3 to 16, during which this taxon was most abundant in the river. Likewise, blueback herring larvae fed extensively on "Rotifera" spp." from July 1 to 15, when this taxon clearly dominated the river samples. However, the proportion of "Rotifera" spp." in their diet was always much less than

TABLE 1.—Percent composition of river zooplankton in the Connecticut River  $R_{IR}$  and in stomachs of larval American shad ( $R_{IA}$ ) and blueback herring ( $R_{IB}$ ), June 3–July 15, 1981. Decimal fractions are rounded; + denotes less than 0.005; 0 denotes not found. L = linear selection index. Asterisks (\*) denote significant ( $P < 0.05$ ) L values.

Sampling dates, total length of larvae (number of stomachs)	Statistic	Principal prey taxa <sup>a</sup>								
		Rotifers			Cladocerans		Copepods		Chironomid larvae or pupae	Mussel glochidia
		Kera- tella spp.	Poly- arthra spp.	"Rotifera spp." <sup>b</sup>	Bosmina spp.	Daphnia spp.	Nauplii	Cope- podites		
<i>River zooplankton</i>										
Jun 3–16	$R_{IR}$	0.37	0.04	0.33	0.02	+	0.04	0.01	0.01	0.12
Jun 17–30	$R_{IR}$	0.04	0.01	0.76	0.01	+	0.05	0.01	0.02	0.02
Jul 1–15	$R_{IR}$	0.02	+	0.93	+	0	0.02	+	0.01	+
<i>American shad stomachs</i>										
Jun 3–16	$R_{IA}$	0.03	0	0	0.10	0	0	0.30	0.37	0
	L	-0.34*	-0.04	0.33*	+0.08*	0	-0.04	+0.29*	+0.36*	-0.12*
10–12 mm	$R_{IA}$	0	0	0	0.11	0.06	0	0.42	0.21	0
(41)	L	-0.37*	-0.04	-0.33*	+0.09*	+0.06	-0.04	+0.41*	+0.20*	-0.12*
13–15 mm	$R_{IA}$	0	0	0	0.23	0.06	0	0.23	0.38	0
(30)	L	-0.04	-0.01	-0.76*	+0.22*	+0.06*	-0.05*	+0.22*	+0.36*	-0.02
16+ mm	$R_{IA}$	0	0	0	0.33	0.03	0	0.18	0.27	0
(50)	L	-0.37*	-0.04	-0.33*	+0.01	+0.10	-0.04	+0.40*	+0.17*	-0.12*
Jun 17–30	$R_{IA}$	0	0	0	0.08	0.02	0	0.28	0.49	0
	L	-0.04	-0.01	-0.76*	+0.07*	+0.02	-0.05*	+0.27*	+0.47*	-0.02
10–12 mm	$R_{IA}$	0	0	0	0.23	0.06	0	0.23	0.38	0
(47)	L	-0.04	-0.01	-0.76*	+0.22*	+0.06*	-0.05*	+0.22*	+0.36*	-0.02
13–15 mm	$R_{IA}$	0	0	0	0.33	0.03	0	0.18	0.27	0
(30)	L	-0.04	-0.01	-0.76*	+0.32*	+0.03	-0.05*	+0.17*	+0.25*	-0.02
Jul 1–15	$R_{IA}$	0	0	0	0.08	0.02	0	0.13	0.53	0
	L	-0.02	0	-0.93*	+0.08*	+0.02	-0.02	+0.13*	+0.52*	0
10–12 mm	$R_{IA}$	0	0	0	0.02	0.02	0	0.30	0.54	0
(43)	L	-0.02	0	-0.93*	+0.02	+0.02	-0.02	+0.30*	+0.53*	0
13–15 mm	$R_{IA}$	0	0	0	0.01	0.01	0	0.10	0.65	0
(30)	L	-0.02	0	-0.93*	0	+0.01	-0.02	+0.10*	+0.64*	0
16+ mm	$R_{IA}$	0	0	0	0.01	0.01	0	0.05	0	0
(50)	L	-0.02	0	-0.93*	0	+0.01	-0.04	+0.04	-0.01	-0.12*
<i>Blueback herring stomachs</i>										
Jun 3–16	$R_{IB}$	0.77	0	0.03	0.10	0	0.07	0	0	0
	L	+0.40*	-0.04	-0.30*	+0.08*	0	+0.03	-0.01	-0.01	-0.12*
5–12 mm	$R_{IB}$	0	0	0.04	0.19	0	0	0	0.07	0
(24)	L	+0.33*	-0.04	-0.29*	+0.17*	0	-0.04	-0.01	+0.06*	-0.12*
13–15 mm	$R_{IB}$	0.70	0	0.04	0.19	0	0	0	0.07	0
(11)	L	+0.33*	-0.04	-0.29*	+0.17*	0	-0.04	-0.01	+0.06*	-0.12*
16+ mm	$R_{IB}$	0.61	0	0.02	0.23	0.02	0	0.05	0	0
(12)	L	+0.24*	-0.04	-0.31*	+0.21*	+0.02	-0.04	+0.04	-0.01	-0.12*
Jun 17–30	$R_{IB}$	0.68	0	0.17	0.13	0	0	0	0.01	0
	L	+0.64*	-0.01	-0.59*	+0.12*	0	-0.05*	-0.01	-0.01	-0.02
5–12 mm	$R_{IB}$	0.22	0	0.03	0.71	0	0	0	0.02	0
(24)	L	+0.18*	-0.01	-0.73*	+0.70*	0	-0.05*	-0.01	0	-0.02
13–15 mm	$R_{IB}$	0.06	0	0.05	0.72	+	+	0.08	0.03	0
(30)	L	+0.02	-0.01	-0.71*	+0.71*	0	-0.05*	+0.07*	+0.01	-0.02
Jul 1–15	$R_{IB}$	0.19	0	-0.54*	0	0	0	0.02	0.05	0
	L	+0.17*	0	-0.39*	0	0	-0.02	+0.02	+0.04	0
5–12 mm	$R_{IB}$	0.52	0	0.37	0.07	0.01	0	0.02	0	0
(20)	L	+0.50*	0	-0.56*	+0.07*	+0.01	-0.02	+0.02	-0.01	0
13–15 mm	$R_{IB}$	0.09	0	0.41	0.32	+	0.01	0.05	0.04	0
(10)	L	+0.07*	0	-0.52*	+0.32*	0	-0.01	+0.05	+0.03	0
16+ mm	$R_{IB}$	0.09	0	0.41	0.32	+	0.01	0.05	0.04	0
(44)	L	+0.07*	0	-0.52*	+0.32*	0	-0.01	+0.05	+0.03	0

<sup>a</sup> Principal prey taxa made up at least 5% of one or more river samples (pooled biweekly) or one composite stomach sample (pooled biweekly by species and larva length). Other taxa encountered in the river and stomachs of American shad or blueback herring were: (rotifers) *Asplanchna*, *Kellicottia*, *Lecane*, *Monostyla*, *Pleosoma*, *Synchaeta*, *Trichotria*, *Trichocerca*, *Euchlanis*; (cladocerans) *Alona*, *Chydorus*, *Leydigia*, *Sida*, *Pleuroxus*, *Euryercus*, *Diaphanosoma*, *Ilyocryptus*, *Holopedium*; (copepods) calanoid copepodites, *Diacyclops*, *Eucyclops*; (insects) *Ephemeroptera*, *Trichoptera*.

<sup>b</sup> "Rotifera spp." comprises male and soft-bodied rotifers.

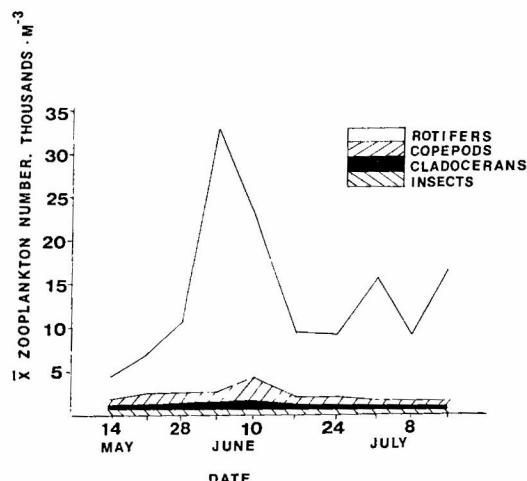


FIGURE 1.—Temporal changes in zooplankton density in the Connecticut River, May 14–July 15, 1981.  $\bar{X}$  = mean.

that in river samples, resulting in negative values for this taxon. *Bosmina* spp. was a major food item among blueback herring larvae especially from June 17 to July 1. The *L* values for *Bosmina* spp. were always positive and significant for 13–15- and 16+ mm larvae, indicating preference for this taxon. The food selection index rarely differed from 0 for the rotifer *Polyarthra* spp., cyclopoid copepodites, and chironomid larvae, and was negative (but only occasionally significant) for copepod nauplii and mussel glochidia.

#### Size Selection

There was a linear relationship between mouth gape and body length among blueback herring larvae (Fig. 2). Mouth gape and body length were also linear for American shad, but mouth size appeared to increase at a faster rate as American shad larvae approached metamorphosis. Mouth size was always larger at body length for American shad than blueback herring larvae, indicating that American shad potentially can consume larger prey.

The relationship between prey width and body length was asymptotic for both species, although prey widths were consistently larger for American shad than for blueback herring larvae (Fig. 2). The standard error of prey widths also increased in magnitude with body length for both species, because maximum prey

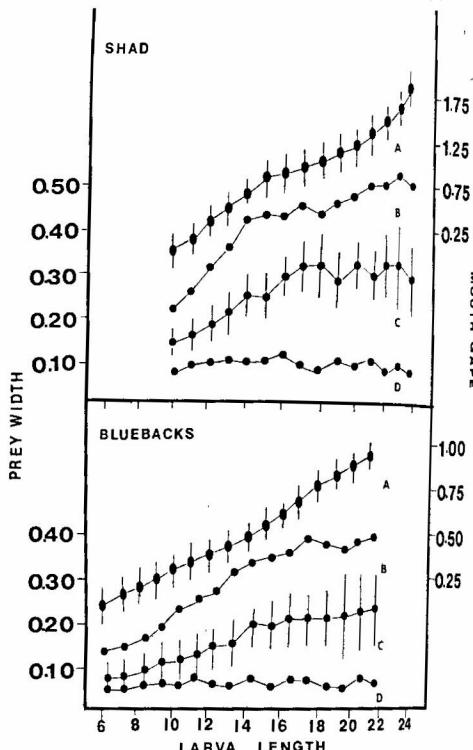


FIGURE 2.—Relationships of mean mouth gapes  $\pm 2$  SE (A), maximum prey widths (B), mean prey widths  $\pm 2$  SE (C), and minimum prey widths (D) with total lengths of larval American shad and blueback herring.

widths for both species increased with larva length, and minimum widths remained nearly constant. Therefore, the larger standard error of prey widths among larger larvae was due primarily to an increase in the upper range of prey size.

Mean widths of the five principal prey taxa (*Keratella* spp., "Rotifera" spp., chironomid larvae, *Bosmina* spp., and cyclopoid copepodites) were compared between river and stomach samples to determine size-selective predation (Table 2). Advanced blueback herring larvae (16+ mm) significantly selected larger *Keratella* spp. and "Rotifera" spp., as well as smaller cyclopoid copepodites. There was no evidence that blueback herring larvae select larger or smaller *Bosmina* spp. Nevertheless, the standard deviation for *Bosmina* spp. widths among small (5–12-mm) blueback herring was much less than that for river samples, suggesting that these larvae select for average-sized *Bosmina* spp. Bi-

TABLE 2.—Mean zooplankton widths (mm  $\pm$  SD) in Connecticut River samples and in stomachs of larval American shad and blueback herring, June 3–July 15, 1981. Zooplankton sample sizes are in parentheses. Asterisks (\*) denote significant differences in zooplankton widths between stomachs and river (t-tests; P < 0.05).

	River	American shad			Blueback herring		
		10–12 mm	13–15 mm	16+ mm	5–12 mm	13–15 mm	16+ mm
Keratella spp.	49 $\pm$ 10 (1,107)				48 $\pm$ 9 (78)	48 $\pm$ 9 (130)	54 $\pm$ 11* (157)
"Rotifera spp." <sup>a</sup>	102 $\pm$ 21 (875)				93 $\pm$ 20 (28)		117 $\pm$ 34* (447)
Bosmina spp.	220 $\pm$ 59 (917)	231 $\pm$ 33 (18)	215 $\pm$ 63 (27)	261 $\pm$ 85* (63)	201 $\pm$ 36 (12)	231 $\pm$ 60 (181)	215 $\pm$ 78 (622)
Cyclopoid copepodite	164 $\pm$ 36 (275)	168 $\pm$ 32 (50)	190 $\pm$ 59 (65)	215 $\pm$ 73* (88)			152 $\pm$ 31* (36)
Chironomid larvae	98 $\pm$ 49 (265)	113 $\pm$ 59 (97)	140 $\pm$ 52 (86)	159 $\pm$ 85* (148)		82 $\pm$ 33 (6)	96 $\pm$ 68 (55)

<sup>a</sup> Male and soft-bodied rotifers.

contrast, advanced American shad larvae ate significantly larger *Bosmina* spp., cyclopoid copepodites, and chironomid larvae, whereas intermediate-sized American shad larvae showed no selection for larger *Bosmina* spp. Like the small blueback herring larvae, small American shad larvae selected for averaged-sized *Bosmina* spp. because their standard deviation for prey width was considerably smaller than that for river samples.

#### Dietary Niche-Breadth and Overlap Analysis

Because American shad larvae rarely utilized the dominant rotifers, niche-breadth indices (PS) for American shad never exceeded 0.13 (Table 3). The PS values for blueback herring larvae varied greatly among collection periods and were affected by the degree of predation on the dominant rotifers. They were always significantly ( $P < 0.05$ ) greater than corresponding values for American shad.

Dietary-overlap indices ( $B$ ) were computed within and between species for each collection period (Table 3). The within-species  $B$  values for American shad were usually higher than those between species, suggesting that intraspecific competition for food is more probable than interspecific competition with blueback herring. The within-species  $B$  values for blueback herring larvae were always smaller than those for American shad. However, relatively high  $B$  values were evident between 16+-mm and 13–15-mm blueback herring larvae from June 17 to July 15 when both groups utilized the rarer *Bosmina* spp. The  $B$  values between species were

below 5.0 during June 3–16, but increased sharply from June 17 to July 15 between larger blueback herring (13–15, 16+ mm) and American shad larvae. This again was due mostly to co-utilization of *Bosmina* spp. as a food source.

#### Discussion

The various strategies with which sympatric fishes capture prey are important in partitioning food resources and minimizing potential interspecific competition (Confer and Blades 1975; O'Brien 1979). The results of this study indicate that American shad and blueback herring larvae coexist within the same habitat by utilizing different prey taxa, or by selecting different sizes of the same prey taxon. First-feeding (10–12-mm) American shad larvae ate mostly cyclopoid copepodites and chironomid larvae, whereas first-feeding (5–12-mm) blueback herring consumed mostly rotifers (Table 1). Because feeding success is often low among first-feeding larvae (Hunter 1972), complete partitioning of food resources at this stage may enhance food availability, and ensure that enough larvae of both species survive the critical first days of feeding (Blaxter and Staines 1971; Hunter 1977). It was also evident that larger (13+-mm) American shad and blueback herring larvae fed extensively on *Bosmina* spp. from June 17 to 30, suggesting a greater probability of interspecific competition for this taxon. However, the degree of diet overlap may have been minimized by size selection on the more robust *Bosmina* spp. by advanced American shad larvae (Table 2). That American shad

TABLE 3.—*Niche breadth and diet overlap matrices for American shad and blueback herring larvae in the Connecticut River, 1981.*

Date, total length	American shad			Blueback herring		
	10-12 mm	13-15 mm	16+ mm	10-12 mm	13-15 mm	16+ mm
<i>Niche breadth (mean ± SD)</i>						
Jun 3-16	0.130 ± 0.030	0.101 ± 0.001	0.101 ± 0.022	0.490 ± 0.039	0.440 ± 0.022	0.481 ± 0.029
Jun 17-30	0.120 ± 0.024	0.121 ± 0.004	0.121 ± 0.019	0.240 ± 0.044	0.180 ± 0.018	0.190 ± 0.026
Jul 1-15	0.028 ± 0.005	0.028 ± 0.016	0.027 ± 0.006	0.587 ± 0.031	0.402 ± 0.009	0.472 ± 0.006
<i>Diet-overlap matrix: species separately</i>						
Jun 3-16						
10-12 mm						
13-15 mm	21.57				2.41	
16+ mm	20.04	28.10			2.46	3.34
Jun 17-30						
10-12 mm						
13-15 mm	18.95				12.99	
16+ mm	15.20	18.90			10.41	15.50
Jul 1-15						
10-12 mm						
13-15 mm	71.02				5.68	
16+ mm	122.07	66.90			3.29	25.95
<i>Diet-overlap matrix: American shad versus blueback herring</i>						
<b>Blueback herring</b>						
Jun 3-16						
5-12 mm	0.66	0.65	0.29			
13-15 mm	3.59	2.52	1.55			
16+ mm	2.88	4.80	4.72			
Jun 17-30						
5-12 mm	1.30	3.19	4.45			
13-15 mm	6.20	16.74	23.75			
16+ mm	8.83	19.05	25.75			
Jul 1-15						
5-12 mm	8.35	10.20	8.25			
13-15 mm	8.35	7.48	2.15			
16+ mm	35.42	24.16	8.80			

larvae of all sizes eat mostly crustacean zooplankton and immature insects is well documented in the literature (Leim 1924; Mitchell et al. 1925; Maxfield 1953; Domermuth 1976). There are no food-habits studies of blueback herring larvae to which our results can be compared. Dietary studies of alewife larvae (Norden 1968; Heinrich 1981), a species closely related to the blueback herring, show that larvae of all sizes feed mostly on cladocerans and copepods, and ignore rotifers.

Niche-breadth values (*PS*) for blueback herring larvae varied considerably among collection periods and appeared to be partially governed by prey-switching (Murdoch 1969). Blueback herring larvae from June 3 to 16 fed mostly on *Keratella* spp., the most abundant taxon in river samples. However, during the succeeding period (June 17-30), larger blueback

herring larvae switched their prey preference to *Bosmina* spp.; first-feeding larvae continued to feed on *Keratella* spp. despite the decline of these prey in the river zooplankton. In July, the small larvae fed on "Rotifera spp." and the rarer *Bosmina* spp. The ability of blueback herring larvae to utilize the abundant rotifer community may be instrumental in their numerical dominance over American shad in the Connecticut River (Marcy 1976), as well as in other east-coast rivers (Loesch and Kriete 1980). Werner and Hall (1979) have hypothesized that planktivorous fishes that feed on small prey and that can shift their preference to abundant prey should show a wider niche breadth than fishes whose choice of prey is more restrictive. Data presented here on American shad and blueback herring larvae support their hypothesis.

There is considerable evidence in the litera-

ture that the morphological limitations imposed by mouth size affect prey selectivity among larval clupeids (Blaxter 1965; Hunter 1977). In this study, mean mouth gape among American shad larvae was consistently larger than that for blueback herring of the same length. This would explain the tendency for larger American shad larvae to prefer the more robust cladocerans and copepods. It also represents an important morphological adaptation by which American shad and blueback herring coexist in the same habitat. Evidence supporting the hypothesis that mouth size affects prey selectivity in larvae has been obtained for the scaled sardine *Harengula pensacolae* (Detwyler and Houde 1970), rainbow smelt *Osmerus mordax* (McCullough and Stanley 1981), northern anchovy *Engraulis mordax* (Arthur 1976), and Pacific mackerel *Scomber japonicus* (Hunter and Kimbrell 1981).

The range of prey widths increased steadily with body length for both species mainly because larvae consumed larger prey as they grew. It is more difficult to explain why minimum prey widths remained nearly constant over a wide range of predator sizes. Brooks (1968) noted that planktivorous fish will continue to eat small prey even after larger prey become available. Perhaps one explanation is that reaction distance necessary to evoke an attack response is related to prey size (Confer et al. 1978) and prior experience (Ware 1971). Familiarity with small prey may be the reason American shad and blueback herring larvae continue to consume some small organisms even as their ability to take larger prey increases. It is also known that immature cladocerans and copepods are weaker swimmers than the adults (O'Brien 1979), so larger larvae may have a distinct predatory advantage over small zooplankton.

In this study, it was assumed that co-utilization of rare prey enhances diet overlap as well as the probability of competition between species (MacArthur 1972). Several authors (Pianka 1975; Hurlbert 1978; Abrams 1980) have questioned whether or not overlap indices are related to competition, and have strongly recommended that these indices be interpreted with caution. One major problem is that plankton samples from towed nets are horizontally integrated and thus may undersample certain taxa that avoid, or are extruded through, plankton nets (Tranter 1968). Another prob-

lem is that neither zooplankton nor their predators are likely to be randomly distributed throughout the river (Hutchinson 1967). It is possible that the plankton sampler underestimated the relative abundance of the more epibenthic organisms such as chironomid larvae (James 1959) on which American shad larvae extensively fed. Finally, the complete absence of soft-bodied rotifers in stomachs of American shad larvae may have been an artifact of differential digestion of certain organisms (Le-Bour 1921), or to a greater tendency for small larvae to void their gut contents during capture and preservation (Burdick 1969). The high dietary-overlap and low dietary-breadth indices reported here for American shad larvae of various length groups may have been biased by the aforementioned factors. As noted by Hurlbert (1978) and Abrams (1980), if prey resources are not in short supply, no competition will ensue regardless of the magnitude of diet overlap. Moreover, such ecological adaptations as character displacement among sympatric species are the result of evolutionary forces brought about by past competition (Bulmer 1974; Lewontin 1974). Thus, it is generally recognized that niche-overlap indices are related only indirectly to the degree of competition (Colwell and Futuyma 1971; Pianka 1975; Heck 1976).

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