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Factors Affecting Abundance, Growth, and Survival of Age-0 Gizzard Shad

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Abstract.—Factors affecting abundance, growth, and survival of age-0 gizzard shad *Dorosoma cepedianum* were examined in Pomme de Terre and Stockton lakes, Missouri, during 1987–1991. Otolith ages were used to assign larvae (≤ 25 mm total length, TL) and juveniles (> 25 mm TL) to weekly cohorts so that cohort-specific estimates of abundance, growth, and survival could be made. The distribution of initial abundances of larvae among weekly cohorts was influenced by water temperature and reservoir water level but not by characteristics of adult females (abundance, size, condition, fecundity). Intense periods of spawning activity during rising water levels resulted in high peaks in larval abundance and relatively few large weekly cohorts (e.g., 1990). In the absence of water level rises, peaks in larval abundance were much lower and abundances of larvae were more evenly distributed among several cohorts (e.g., 1988). Spring warming also affected spawning; early cohorts in warm springs (1987 and 1991) were relatively more abundant than those during cool springs (1989 and 1990). The initial distribution of larvae among weekly cohorts influenced subsequent interactions between the larvae and their environment. Growth of larvae was positively affected by water temperature and, to a lesser degree, food abundance. Early cohorts grew slower because of lower water temperatures, and they suffered higher mortality than did late cohorts. Survival was also density dependent; weekly cohorts with high initial densities experienced lower survival than cohorts with small initial densities. High survival of larvae occurred in 1988 when densities of larvae were low and evenly distributed among weekly cohorts and food abundance was high. Growth and instantaneous mortality of juveniles were not closely tied to any single variable. Growth was positively related to food abundance and negatively related to gizzard shad density. Mortality was not significantly related to any measured variable. Overall, findings indicate that cohort dynamics of age-0 gizzard shad are initially driven by climatic factors and later by a combination of climatic and biotic factors.

Gizzard shad *Dorosoma cepedianum* are important prey for many sport fish in reservoir ecosystems (Noble 1981; Storck 1986; Johnson et al. 1988; Michaletz 1997, this issue), but they are also potentially detrimental competitors of young sport fish and other planktivores (Kirk and Davies 1987; DeVries and Stein 1992; Welker et al. 1994). Age-0 gizzard shad can be especially forceful competitors because they are more zooplanktivorous than their older counterparts (Bodola 1965; Cramer and Marzolf 1970; Baker and Schmitz 1971). Also, age-0 gizzard shad are often the most important age-group as prey, because older individuals often outgrow vulnerability to most predators (Noble 1981). Larvae and early juveniles can severely reduce zooplankton populations (DeVries and Stein 1992) and so reduce recruitment rates of fish such as bluegill *Lepomis macrochirus*. This may, in turn, indirectly affect recruitment of other fishes, such as largemouth bass *Micropterus salmoides*, that rely on bluegills as prey (DeVries et al. 1991). Because age-0 gizzard shad are important prey, changes in their abundance and size structure may affect diet composition and overlap, as well as growth rate of predator fish species (Hartman and Margraf 1992; Michaletz 1997).

Despite their importance, factors affecting abundance, growth, and survival of age-0 gizzard shad are not well documented. Initial abundances of larvae have been related to condition of adult females (Stock 1971; Kampa 1984; Willis 1987). Also, larger females may spawn earlier (Miranda and Muncy 1988) and over a shorter time (Willis 1987) than smaller counterparts, affecting temporal aspects of larval hatching and abundance. Environmental factors such as water-level change and water temperature also affect the timing and duration of spawning (Shelton et al. 1982; Willis 1987). Growth and survival of young appear to be negatively related to fish density (Stock 1971; Kampa 1984; Buynak et al. 1992; Welker et al. 1994) and positively related to food abundance (Welker et al. 1994). Matthews (1984) and Kashuba and Matthews (1984) reported high mortality rates for larvae due to starvation. Because piscivorous fishes feed heavily on juvenile gizzard shad (Noble 1981; Storck 1986; Johnson et al. 1988; Michaletz 1997), predation is likely an important mortality factor.

The objectives of this study were to identify factors affecting abundance, growth, and survival of age-0 gizzard shad in two large reservoirs.

Based on previous studies, I predicted that the initial abundances of larvae and their temporal distribution would be affected by both characteristics of adult females (size, condition, abundance, fecundity) and by changes in water temperature and water level. I also predicted that growth and survival of larvae (≤ 25 mm total length, TL) and juveniles (> 25 mm TL) would be positively related to temperature and food abundance, and negatively related to age-0 gizzard shad abundance. To test these predictions, I used otolith ages (d) to assign larval and juvenile gizzard shad to weekly cohorts and track first-year abundance, growth, and survival of these cohorts. Initial abundances of weekly cohorts were compared with characteristics of adult females, water temperature, and water level. Because larval gizzard shad are produced over a relatively long period, up to 15 weeks in this study, those that hatch earlier in the season can experience quite different environmental conditions than those that hatch later. By examining weekly cohorts, I was able to study the effects of these temporal changes on growth and survival of age-0 gizzard shad. The effects of temperature, prey abundance, and age-0 gizzard shad abundance on growth and survival were examined separately for larvae and juveniles. In previous studies, all age-0 gizzard shad were treated as a single cohort, except for the work of Welker et al. (1994), who used otoliths to estimate growth of larval gizzard shad for separate sampling dates.

The direct effect of predation on survival could not be assessed because the abundance of predators and their consumption rates were unknown. Piscivorous fish in the study reservoirs were not observed to feed heavily on age-0 gizzard shad until they reached the juvenile stage (Michaletz 1997), indicating that predation mortality was likely more important for juveniles than larvae. Predation on larvae by invertebrates is possible (Hartig et al. 1982; Hartig and Jude 1984) but its extent is unknown.

Methods

The study was conducted in the Lindley Creek arm of Pomme de Terre Lake (PDT) and the Sac River arm of Stockton Lake (STK), both in southwestern Missouri. The study areas constituted approximately one-third of the total surface area of each reservoir. These reservoirs were initially chosen for study because of their close proximity to each other (50 km apart) and their apparently different predator growth rates and gizzard shad abundance (Michaletz 1997). Pomme de Terre

Lake is a 3,167-ha Corps of Engineers reservoir used for flood control. Stockton Lake is a 10,072-ha Corps of Engineers reservoir used for both flood control and hydropower generation. Both systems are steep-sided, fairly deep (mean, about 10 m), relatively clear (seasonal mean secchi depths, > 1.5 m), and moderately productive (chlorophyll *a* averages 16.1 and 11.4 $\mu\text{g/L}$ and daily primary production averages 3.9 and 2.9 $\text{mg O}_2/\text{L}$, in PDT and STK, respectively; Knowlton 1989). Usually, both reservoirs are thermally stratified from late May through early September. Thermoclines develop at depths of 4–8 m and their hypolimnia become oxygen deficient in mid summer.

Study areas were divided into three (PDT) or four zones (STK) to account for potential longitudinal gradients in gizzard shad densities (Siler et al. 1986). For all zooplankton sampling and some trawling, the two lower zones (zones 1 and 2) in each reservoir were further subdivided into littoral or pelagic areas at the 6-m depth contour. Upper zones (zone 3 in PDT and zones 3 and 4 in STK) were not subdivided because depths usually did not exceed 6 m. In this paper, "strata" refer to the sampling units: zone 1–pelagic, zone 1–littoral, zone 2–pelagic, zone 2–littoral, zone 3, and zone 4 (zone 4 in STK only). For sampling that did not use subdivided zones, strata were simply zones 1, 2, 3, and 4 (zone 4 in STK only). Water volumes for each stratum were estimated from topographic reservoir maps and estimates were adjusted for changes in reservoir water levels at each sampling date. The volume of water deeper than 9 m was not included in the calculations. Sampling was not conducted below that depth because the water there was usually anoxic and fish were not detected by echo sounding.

Temperature and dissolved oxygen were measured from the surface to 9 m at 1-m intervals and secchi depths were also measured at a midreservoir location in each zone during each trawling trip. Water surface elevation data were acquired from the U.S. Army Corps of Engineers.

Adult spawning stock.—To assess characteristics of the spawning stock, adult (≥ 180 mm TL) gizzard shad were collected during two or three sampling trips during April and May, 1987–1991, by nighttime DC electrofishing. Sampling was carried out for usually 20 min per site at six sites (two per zone) on PDT and at eight sites (two per zone) on STK. Catch per unit effort (CPUE) was expressed as the number of fish caught per hour of electrofishing. All gizzard shad were measured

(nearest mm, TL) and individuals within a subsample used for aging were weighed (nearest g). Additionally, for each sampling trip, all adult gizzard shad were sexed and weighed until a sample of at least 20 females were obtained. The ovaries of these fish were removed and immediately preserved in 10% formalin. Relative weights (W_r) were computed by using the standard weight (W_s) equation from Willis (1987). For particular length categories, $W_r = 100$ (measured weight)/ W_s .

Preserved ovaries were weighed and gonadosomatic index (GSI) values were expressed as the percent of ovary weight within the total body weight. Ovaries collected in April (prior to most spawning) were subsampled by taking a transverse cross section from the middle of the ovary. The subsample was weighed and all eggs at least 0.15 mm in diameter were counted. Eggs of this size were considered stage-4 or larger oocytes (Bodola 1965), which, though not all mature, may mature and be released during the current year (Cox and Willis 1987). Fecundity was estimated by expanding the number of eggs counted in the weighed subsample to the weight of the entire ovary, and it was related to wet weight of females by linear regression. Because slopes did not differ among years within reservoirs (F -tests, $P > 0.05$), but differed between reservoirs (F -tests, $P < 0.05$), a distinct weight (WT)–fecundity (FE) equation was used over all years for each reservoir. For PDT, $FE = 1,164(WT) - 5,710$; $N = 109$, $r^2 = 0.52$, $P = 0.0001$. For STK, $FE = 1,076(WT) - 29,383$; $N = 97$, $r^2 = 0.53$, $P = 0.0001$.

An index of population fecundity (FE_p) was calculated as

$$FE_p = C \cdot P_s \cdot FE_i;$$

C is the average adult CPUE from all sampling trips in either reservoir per year, P_s is the proportion of all fish collected that were female, and FE_i is the average fecundity per female. The estimated mean proportion of females was 0.15 for PDT and 0.12 for STK over all years.

Zooplankton.—Zooplankton were collected with vertical tows of an 80- μ m-mesh Wisconsin plankton net (12-cm mouth diameter) and preserved in 10% formalin. One tow was made at each of two randomly selected sites in each stratum. Tows were made from either 9 m or the bottom, whichever was shallower.

In the laboratory, zooplankton samples were rinsed and concentrated into a 10–45-mL sample volume. Usually, three 1-mL subsamples were withdrawn with a large-bore pipette and all zoo-

plankton in each subsample were identified and counted. When densities of zooplankton were extremely low, I used 2-mL subsamples. Zooplankton were identified as rotifers, copepod nauplii, cyclopoid copepods, calanoid copepods, or to genus for cladocerans. Subsample counts were averaged to estimate zooplankton density (number/ m^3) of the sample; net efficiency was assumed to be 100%. Mean zooplankton densities in each reservoir's study area were estimated by averaging mean density estimates for each stratum weighted by the volume within each stratum (≤ 9 m).

One hundred randomly selected zooplankters from samples collected in zones 1 (pelagic) and 3 in PDT and in zones 1 (pelagic) and 4 in STK were measured (nearest 0.1 mm) as in Culver et al. (1985). Because most measurements were for rotifers and copepod nauplii due to their relatively high abundance, an additional 100 individuals, exclusive of rotifers and copepod nauplii, were randomly chosen from these same samples and measured so that length distributions for other zooplankters could be more adequately estimated. Zooplankton length measurements from the two zones were pooled by taxa to estimate the length distribution for each zooplankton taxon within the study area. Measured individuals usually were identified further to species. Their dry weights were estimated from length–dry weight equations for the same species or nearest congener (Dumont et al. 1975; Rosen 1981; Culver et al. 1985), and they were adjusted for preservation effects with equations from Giguère et al. (1989). Average individual dry weights for each taxon were multiplied by the corresponding mean density estimates to determine biomass of each taxon. Wet weight of zooplankton (g/m^3) was estimated by multiplying dry weight by 10 (Hewett and Johnson 1987).

Abundance and size of age-0 gizzard shad.—Sampling for age-0 gizzard shad was done once per week during May through mid-June, and then biweekly until late September or early October, 1987–1991. Larvae and juveniles were sampled from May to August with paired 500- μ m-mesh (small mesh), 1- m^2 frame trawls, and from July through late September or early October with either a 2.44- m^2 midwater trawl with a 3-mm-mesh cod end liner (Houser and Netsch 1971) or paired 6-mm-mesh (large mesh), 1- m^2 frame trawls (1990–1991 only), or both. An exception occurred in 1987 when small-mesh frame trawls were only used through late June. All trawl sampling was done at night in stair-step fashion from the surface to 2–3 m off bottom in shallow areas, or to 9 m

in deep areas. This sampling included the entire epilimnion of both reservoirs where gizzard shad are usually concentrated (Netsch et al. 1971; personal observation). Towing times depended on depth, but usually ranged from 2 to 6 min for frame trawling and from 3 to 9 min for midwater trawling. Towing speeds averaged 1 m/s for the small-mesh frame trawl, 2 m/s for the midwater trawl, and 1.6 m/s for the large-mesh frame trawl. Water volumes filtered per tow were estimated with flowmeters for the frame trawls and calculated from mouth opening, tow speed, and tow duration for the midwater trawl. Samples taken simultaneously with each of the two frame trawls were processed and analyzed separately.

A stratified random sampling design was used to estimate abundance and length distribution of age-0 gizzard shad. For frame trawls, 4–12 samples were collected from each stratum, yielding 20–22 samples for PDT and 36 samples for STK on each sampling date. For the midwater trawl, 2–8 samples were collected from each stratum, yielding to 10–22 samples for PDT and 12–18 samples for STK on each sampling date. Sample sizes for each stratum depended upon the size of the stratum and the past average variability of gizzard shad density estimates. Except for frame trawling in STK, sample sizes were increased during the study in an attempt to increase precision of the abundance estimates. Zones 1 and 2 were subdivided into littoral and pelagic areas for sampling with the small-mesh frame trawls but not for the large-mesh frame trawls or the midwater trawl because of the greater difficulty of maneuvering at higher speeds in shallow water.

Trawl samples were preserved in 10% formalin or 95% ethanol (fish for otolith analysis). Some samples with large numbers of juvenile gizzard shad were weighed in the field and a subsample was weighed and preserved. In the laboratory, samples from small-mesh frame trawling were subsampled with a Folsom plankton splitter if the resulting subsample contained at least 100 age-0 gizzard shad. Otherwise all fish within the trawl samples were identified and counted. At least 100 age-0 gizzard shad from small-mesh frame trawl samples and 200 from the other samples were measured to the nearest 1 mm TL for each stratum, when possible. Individual wet weights (g) were estimated from total lengths with a regression equation reported by Michaletz (1997).

Total number of age-0 gizzard shad and the number in each 1-mm length group were estimated for each study area for each sampling date. The num-

TABLE 1.—Correction factors (Y) for relative gear bias for small-mesh frame trawls (SFT), large-mesh frame trawls (LFT), and a midwater trawl (MWT) for total lengths (mm, X) of gizzard shad.

Gear	Length (mm)	Correction factor
SFT	<33	1.0
	33–65	$\log_e Y = 0.095X - 3.113$
LFT	19–35	$\log_e Y = 8.139 - 0.230X$
	>35	1.0
MWT	<20	150.2 ^a
	≥20	$\log_e Y = 2.566 - 0.020X$

^a This correction factor was only used for three sampling trips in July and August 1987 when small-mesh frame trawl data were not available.

ber of age-0 gizzard shad within each stratum was estimated by averaging the density estimates (fish/m³) and multiplying the average by the stratum volume. Total number in the study area was the sum of fish numbers over all strata. The number of fish in each 1-mm length-group for each stratum was estimated by multiplying the number of fish in each stratum by the proportion in each length-group for that stratum. The number of fish in each length-group for the entire study area was estimated by summing fish numbers for each length-group over all strata.

When necessary, the total number and number of fish in 1-mm length-groups were adjusted for relative gear bias with correction factors (Table 1). Data from the most effective gear (small-mesh frame trawl data for fish smaller than 33 mm TL and large-mesh frame trawl data for larger fish) were not adjusted for gear bias (correction factor = 1). When these data were not available, the best available data were adjusted for relative gear bias. In 1987–1989, when large-mesh frame trawls were not used, I used data from small-mesh frame trawls for fish smaller than 60 mm TL and midwater trawl data for larger fish, when available. Relative gear biases were estimated from at least eight pairwise comparisons among all gear types. For a given sampling trip and gear, fish number estimates were first summed over 10-mm length-groups (but broader length-groups were necessary for the largest juveniles to ensure sufficient sample sizes). Estimates of numbers in a length-group from one gear were divided by the same from another gear to provide a gear bias estimate. The median relative bias value across all comparison dates was used as the correction factor between two gears for a given length-group. Regressions between these correction factors and fish length were developed for some length ranges when significant

relations occurred; otherwise, single correction factor values were used.

Otolith aging and cohort assignment.—Sagittal otoliths were removed from five age-0 gizzard shad per 5-mm length-group for each sampling date in 1987, 1990, and 1991, except no otoliths were removed from fish collected after June within 1987. Fish were not separated by strata because Pitts (1992) found no consistent differences in growth rates between upper and lower zones (strata) in either reservoir. Otoliths were mounted on a slide with thermoplastic cement and polished as necessary to observe the innermost rings. Ring counts were made at 100 or 400 \times magnification under a compound microscope. Initially, two independent counts of growth rings were made for each otolith by one observer. If these counts differed by more than three rings or 15%, the otolith was read one (47% of the otoliths) or two more times (10%) by the same observer. When the two or more counts per otolith met the acceptance criteria, these were averaged to estimate the actual ring count. If the criteria for acceptance was not met after four readings, the otolith was not included in the data set (<1%). Fish age was assumed to be the ring count plus 3 d, given that the first ring is deposited on the fourth day after hatching (Davis et al. 1985).

Ages of age-0 gizzard shad from PDT and STK during 1988 and 1989 were supplied by P. Pitts (University of Missouri, Columbia) and were determined with procedures described by Pitts (1992). To ensure consistency between age determinations made by Pitts and my observer, a subsample of juvenile otoliths from 1988 and 1989 was aged by my observer. Age agreement was good in most cases. When the estimated ages did not agree, the otolith was aged again by my observer and the closest readings were averaged, provided the readings varied by less than 15% as described above.

Aged fish were assigned to weekly cohorts based on their estimated hatch date. Hatch dates were determined by subtracting a fish's estimated age from its capture date (day of year). Fish were assigned to weekly (7-d) cohorts beginning with cohort 0, which represented fish that were hatched during the first full week of April in each year.

The total number of fish (N) in each cohort (c) on a given sampling date (j) was estimated as

$$N_{cj} = \sum_{k=1}^m L_{jk} P_{cjk};$$

L_{jk} is the total number of fish in the k th length group on the j th sampling date, P_{cjk} is the proportion of fish in the k th length-group in the c th cohort on the j th sampling date, and m is the total number of length-groups. Length-groups were the same as those used for otolith analysis. Individual lengths were not adjusted for preservation effects because Pitts (1992) found no consistent differences in shrinkage between specimens stored in ethanol or formalin.

Peak abundance within cohorts was used as an index of initial cohort abundance. In 1987, unaged larvae collected after June were assigned to cohorts based on an age-length key for larvae collected in May and June so that estimates of initial abundances could be made.

Growth.—Growth for each weekly cohort was described separately for larvae (≤ 25 mm TL) and juveniles (> 25 mm TL) by the Gompertz growth equation

$$L_t = L_{\infty} e^{-e^{\beta - \delta t}};$$

L_t is the length of fish at t days of age, L_{∞} is the theoretical asymptotic length at the end of either the larval phase or the growing season, and β and δ are growth coefficients. The Gompertz model has been recommended for larval and juvenile growth analysis (Zweifel and Lasker 1976), and it fit my gizzard shad growth data better than simple linear models. Parameters were estimated with regression techniques described by Ratkowsky (1983). An iterative approach was used to maximize r^2 by changing values of L_{∞} . Weekly cohorts that were represented by fewer than 10 aged individuals, or by individuals that were all similar in length, were excluded from analysis.

Regression models (PROC REG, STEPWISE option, SAS Institute 1989) were used to assess independent variables that explained differences across cohorts in lengths of larvae at ages 14 and 28 d. Initially, models were developed for every 7 d during the larval phase. I present only the 14- and 28-d models because they adequately represent the other models. Larval lengths at 14 and 28 d were predicted from Gompertz models, and independent variables included epilimnetic temperature, total zooplankton (including rotifers) density and biomass, crustacean zooplankton density and biomass, and age-0 gizzard shad density and biomass. Independent variables were mean study-area-wide values over either the first 14 or 28 d of life, for each cohort. Total zooplankton and crustacean zooplankton densities and biomasses were adjusted to exclude zooplankton that ex-

ceeded mouth gape limits of larvae. Mouth gapes were estimated from total lengths of larvae and juveniles with the equation of Michaletz et al. (1987), and estimates of gape-available zooplankton were updated for each week of each cohort's life. Calanoid copepods were not considered in these analyses because they were rarely consumed ($\leq 1.5\%$ of diet by numbers; Michaletz, in press) by gizzard shad larvae.

The same procedures were used to determine variables that significantly explained size variation among juveniles in the different cohorts at 28 and 56 d after fish reached 25 mm TL (considered the beginning of the juvenile stage). As before, initially more models were developed (for every 14 d) but only 28- and 56-d models are presented. Because juvenile gizzard shad were not precluded from eating zooplankton due to mouth gape limits, all sizes of zooplankton were considered available to them as food, except, as for larvae, calanoid copepods.

Survival.—Instantaneous daily mortality rates (Z) were computed for each larval and juvenile cohort by regressing the natural logarithm of fish abundance in a cohort against successive collection dates (time). Only the descending portions of the catch curves were used because small larvae (< 10 mm TL) were not fully recruited to the gear. Because a cohort's abundance on a given sampling date was determined from a relatively small number of aged fish, occasionally certain cohorts were not represented on a given date. In such cases no value was assigned as opposed to a zero value. Only fish up to 60 d old were used to calculate Z s for larvae and only fish at least 40 d old were used for juveniles. The average duration of the larval phase was about 40 d, but it was as long as 66 d for some cohorts. I used fish up to 60 d old for larval analysis so that at least one abundance estimate for fish reaching the juvenile stage would be included for most cohorts.

Survival of larvae from 10 mm TL to the juvenile phase (25 mm TL) was determined for each weekly cohort by predicting the number of fish that reached the juvenile phase from

$$N_t = N_0 e^{-Zt};$$

N_0 was the initial number of fish at 10 mm TL, and N_t was the number of fish on day t when fish reached 25 mm TL. The ages of fish at 10 and 25 mm TL were predicted from the Gompertz growth equation. Survival (S) was then estimated as

$$S = \frac{N_t}{N_0}.$$

Regression models, similar to those for growth, were used to evaluate factors that accounted for the variation in S among weekly cohorts of larvae. Survival values were linearized with an $S/(1-S)$ transformation. Independent variables were the mean epilimnetic temperature, total zooplankton density and biomass, crustacean zooplankton density and biomass, and age-0 gizzard shad density and biomass, all throughout the larval period of each cohort, and the initial number of fish at 10 mm TL for each cohort. Because Z values were very imprecise for juveniles (see "Results: Survival"), I did not attempt to explain variation in survival among weekly cohorts of juveniles.

To determine whether relationships existed between larval and juvenile abundances among years, correlation analysis was used to compare densities of 10-mm and 25-mm TL larvae and the average density of juveniles (July–October). To estimate yearly values of S for larvae, I used the ratio of the total number of 25-mm to 10-mm larvae across all weekly cohorts within years.

Among-year correlations for juveniles.—I observed that ages of older juveniles were increasingly underestimated from otoliths with age, based on changes in estimated mean age over time. Because of this, juvenile growth and mortality rates were also estimated from changes in mean lengths and densities within annual populations from late July through early October. This period was chosen because the majority of spawning had occurred and most age-0 gizzard shad were juveniles. Growth rates (mm/d) were estimated by simple linear regressions of mean length against time. Instantaneous daily mortality rates were also estimated from the slope of regressions of \log_e (density) versus time. No attempt was made to separate populations into cohorts based on length modes. Correlation analysis was used to assess relations among growth and mortality of juveniles, and mean temperature, densities and biomasses of total zooplankton (excluding calanoid copepods), and densities, biomasses, and mean weights of age-0 gizzard shad.

Results

Temporal Distribution in Initial Abundance of Cohorts

Temporal distributions of initial weekly cohort abundance appeared to be influenced by water temperature and changes in water level (Figure 1) but

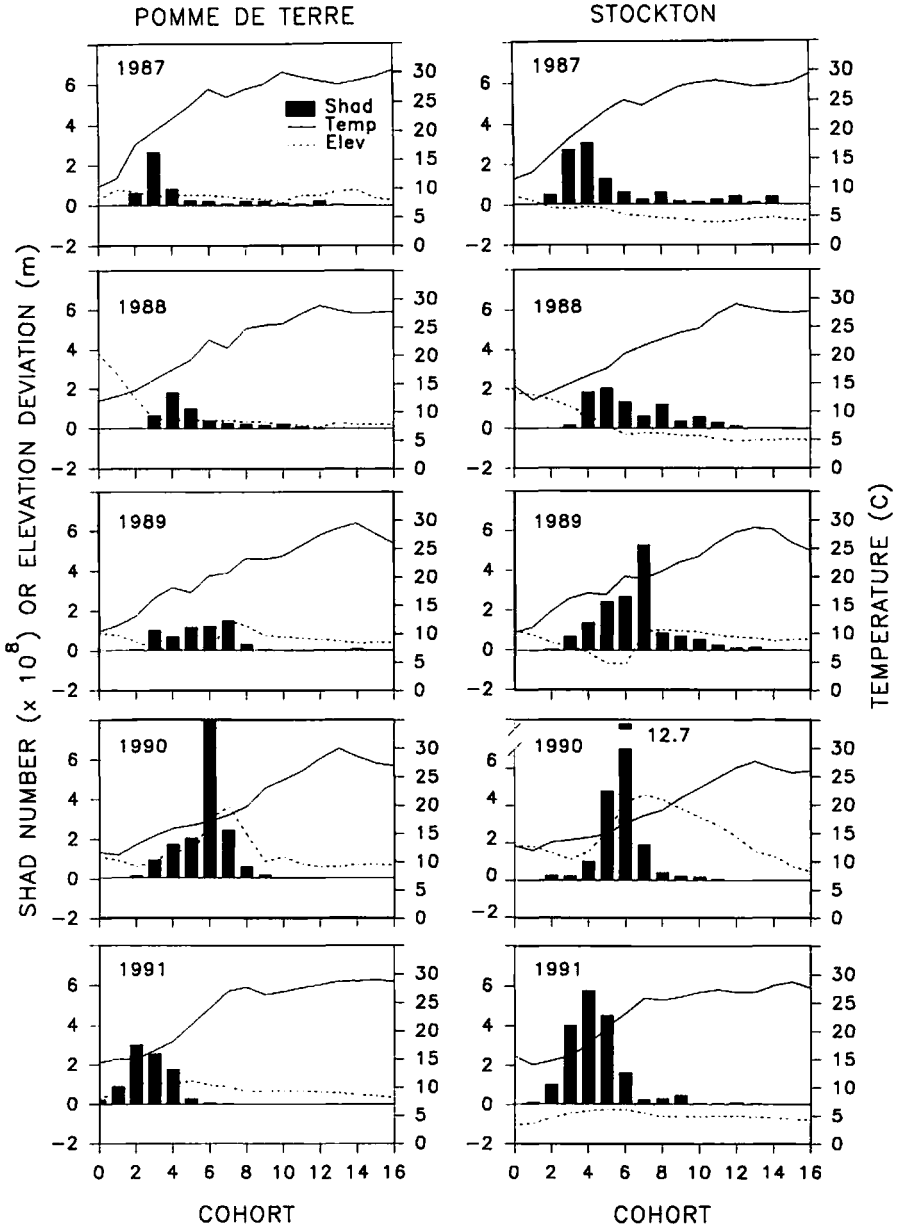


FIGURE 1.—Peak abundances of weekly cohorts of age-0 gizzard shad, mean epilimnetic water temperatures ($^{\circ}\text{C}$), and deviations of water levels from normal pool (m) for Pomme de Terre and Stockton lakes, 1987–1991. Cohort 0 began the first full week of April each year.

not characteristics of the spawning stock. The spawning season, based on the presence of cohorts, lasted from 12 to 15 weeks. Spawning usually began when mean epilimnetic water temperatures reached 13°C . The strongest cohorts were produced earlier in the warm springs of 1987 and 1991

than in the cool springs of 1989 and 1990. Rises in water levels also affected initial cohort strength. Strong cohorts were produced in 1989 and 1990 during 2- to 3-m rises in lake levels. In 1990, a single cohort made up over 50% of the initial abundance of all larvae in both reservoirs. In contrast,

stable or falling lake levels produced more even distributions of weekly cohort abundance, as in 1988 for STK.

Characteristics of the spawning stock had no measurable effect on the initial number of larvae produced or on the distributions of weekly cohort abundances. None of the cumulative initial abundance of larvae, the coefficient of variation ($CV = SD/mean$) of larval abundance among cohorts, nor the modal hatching date (assumed to be the Wednesday of the peak hatching week) were significantly correlated with W_t , CV of W_t , CV of TL , GSI , CV of GSI , $CPUE$, or population fecundity of adult females ($P > 0.05$). Only the mean TL of adult females was significantly correlated (negatively) with the cumulative initial abundance of larvae for STK ($r = -0.90$, $P = 0.04$). However, this relationship yielded a positive correlation for PDT ($r = 0.74$, $P = 0.15$), suggesting that it was either reservoir specific or had no causal basis.

Abundance of Age-0 Gizzard Shad and Zooplankton

Seasonal patterns in abundance of age-0 gizzard shad were similar between reservoirs within years despite considerable among-year variation (Figure 2). Time of peak abundance varied by as much as 1 month among years, being earliest in 1987 and latest in 1989 and 1990. Abundances declined rapidly after the high peaks in 1990 but declined much more slowly after low peaks in 1988. The prominent secondary peak in 1989 for PDT was caused by extremely large catches in two trawl tows which severely inflated the overall estimate of abundance. I detected a "zig-zag" pattern in abundances of juvenile gizzard shad from midsummer to fall in most years that coincided with the lunar cycle. Density estimates were lower during full than during new moon periods (sign test, $P < 0.05$, $n = 25$ samples, new moon versus preceding full moon, all years and reservoirs included), presumably because fish were better able to detect trawls when light intensity was higher.

Seasonal zooplankton abundance patterns were also quite similar between reservoirs within years, despite marked among-year variation (Figure 2). Abundance of crustacean zooplankton was much higher in 1987 and 1988 than in 1989 and 1990. Rotifer abundance was highest in 1988 and lowest in 1990 and 1991.

Growth

Gompertz growth parameter values were determined for 68 larval and 65 juvenile cohorts; parameter values were not determined for juveniles

in 1987 because otoliths were not collected from fish after June. The Gompertz model usually provided good fits to cohort growth data, especially for larvae (r^2 median, range: larvae, 0.87, 0.42–0.98; juveniles, 0.79, 0.40–0.95). Maximum length L_∞ was fixed at 27 mm for larvae and at 150 mm for all juveniles; these L_∞ values produced the highest r^2 values for the majority of cohorts. The r^2 values were relatively insensitive to changes in values of L_∞ of ± 5 mm for larvae and ± 20 mm for juveniles.

Overall, growth rates averaged 0.67 mm/d (range, 0.44–1.01 mm/d) for larvae between 0 and 21 d of age and declined to 0.41 mm/d (0.30–0.54 mm/d) for larvae between 21 and 35 d as they approached metamorphosis to the juvenile stage. Juveniles averaged 0.66 mm/d (0.39–1.00) but showed substantial size variation. Duration of the larval phase (to 25 mm TL) ranged from 28 to 66 d among all cohorts, averaging 46 d as predicted from cohort-specific Gompertz larval growth models. When mean age was estimated directly from actual age determinations of 25-mm fish, the average age was 39 d, possibly indicating that survivors to the juvenile stage grew faster than average. Growth of juveniles was also quite variable, the mean length of a 91-d-old juvenile ranging from 49 to 78 mm. Initially, late cohorts grew significantly faster than early cohorts, but their length advantage became less pronounced with age (Figure 3).

Growth rates of larval cohorts were positively related to the mean temperature and food abundance they experienced, but not significantly negatively related to gizzard shad biomass (Table 2). Temperature explained about 70% of the variation in length at age among larval cohorts for the 14-d model but less than 50% for the 28-d model. Crustacean zooplankton biomass, the best food variable, explained an additional 0–10% of the variation. Gizzard shad biomass entered the 28-d model for STK with a negative coefficient but was not significant. Other zooplankton and gizzard shad abundance variables were not included in the models because of potential intercorrelation.

Growth rates of juvenile cohorts were positively related to food abundance and negatively related to gizzard shad density (Table 3). In contrast to larvae, temperature was never a significant variable in models explaining differences in growth of juveniles. Independent variables (zooplankton biomass and temperature) for 28-d growth models explained little variation in length among juvenile cohorts for PDT; no independent variable was sig-

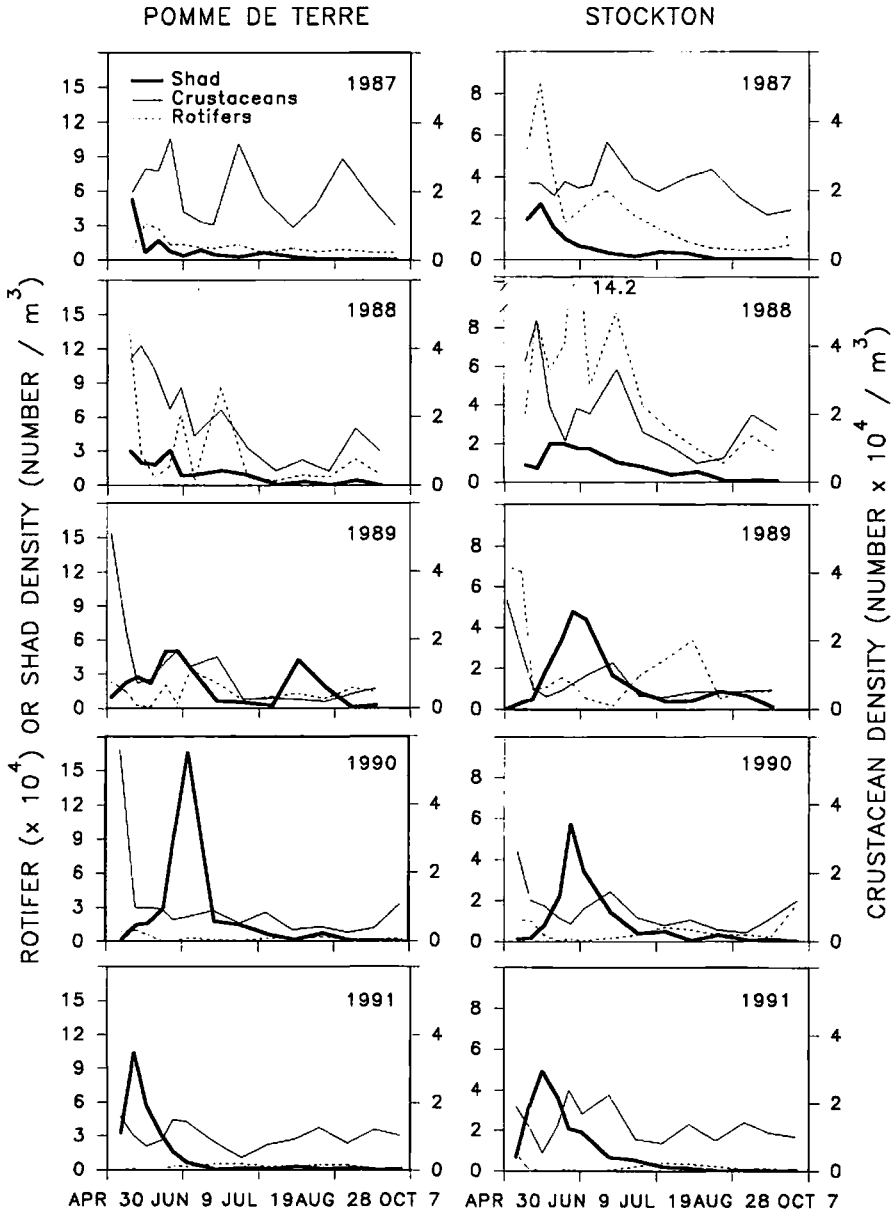


FIGURE 2.—Densities (number/m³) of age-0 gizzard shad, crustacean zooplankton (exclusive of calanoid copepods), and rotifers for Pomme de Terre and Stockton lakes, 1987–1991. Note that the vertical scales differ between lakes.

nificant for STK. Models for 56-d growth accounted for greater proportions of length variation among cohorts, zooplankton biomass and gizzard shad density being most important. Unlike for larvae, total zooplankton biomass explained more variation than crustacean biomass, consistent with my observation that rotifers are more important in the diets of juveniles than of larvae (Michaletz, in

press). As with larvae, other zooplankton and gizzard shad abundance variables were not included in the model because of potential intercorrelation.

Survival

Instantaneous mortality rates (*Z*) were estimated for 61 larval and 79 juvenile cohorts. Values of *Z* averaged 0.12 (range, 0.02–0.29) for larvae and

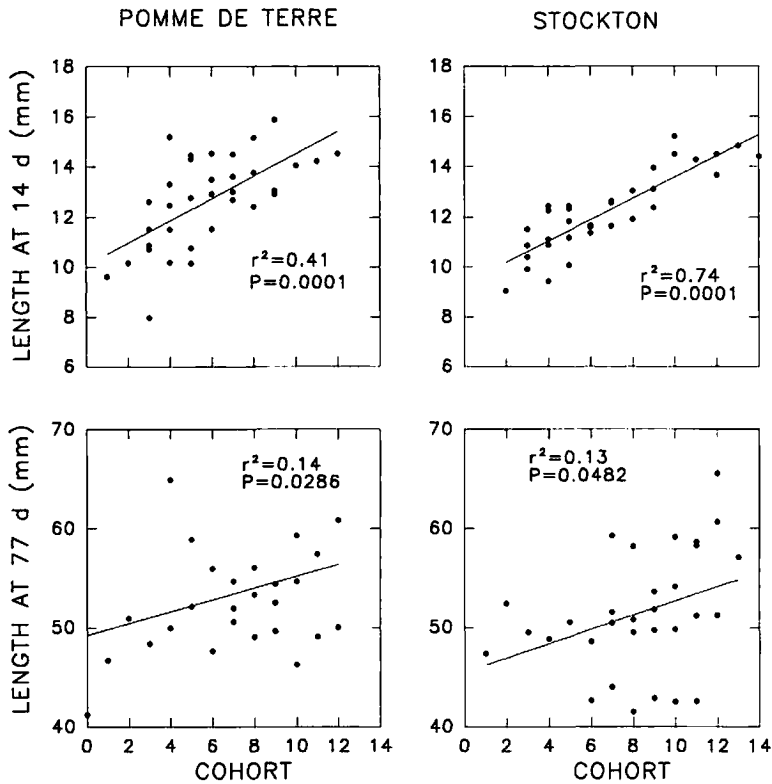


FIGURE 3.—Relationships between cohort order and predicted total length (mm) at ages of 14 and 77 d for gizzard shad in Pomme de Terre and Stockton lakes, 1987–1991.

0.04 (0.00–0.22) for juveniles. Coefficients of determination for linear regressions used to estimate Z were usually much higher for larvae (median, 0.88; range, 0.37–1.00) than for juveniles (median,

TABLE 2.—Coefficients of regression equations relating temperature (T), crustacean zooplankton biomass (CB), and age-0 gizzard shad biomass (GB) to length of larval gizzard shad at 14 d (TL14) and 28 d (TL28) in Pomme de Terre (PDT) and Stockton (STK) reservoirs, 1987–1991; $n = 34$ samples for each reservoir. Asterisks denote variables that are significant at $P \leq 0.05$. Only independent variables that were significant at $P \leq 0.15$ were included.

Dependent variable	Lake	Intercept	Independent variable			R^2
			T	CB	GB	
TL14	PDT	4.224*	0.380*			0.72
		3.950*	0.358*	11.227*		0.80
	STK	4.656*	0.345*			0.74
		4.090*	0.356*	4.540*		0.78
TL28	PDT	11.619*	0.389*			0.45
		11.035*	0.358*	10.263*		0.55
	STK	12.202*	0.344*			0.48
		9.942*	0.465*		-12.359	0.54

0.49; range, 0.00–1.00). Few Z values (9% at $P \leq 0.05$, 16% at $P \leq 0.10$) were significantly different from zero for juvenile cohorts. More estimates of Z for larvae differed significantly from zero (41% at $P \leq 0.05$, 64% at $P \leq 0.10$).

Larval survival averaged 6.8% and ranged from 0.01–60.5% among cohorts. Survival ($S/[1 - S]$ -transformed), was positively related to cohort order and length at age (Table 4), indicating that later and faster-growing cohorts survived better. In step-wise regression models, the initial number of larvae (10 mm TL) in cohorts was negatively related to S in both reservoirs (Table 5). Temperature was positively related to S in models for PDT. Age-0 gizzard shad density, crustacean zooplankton density, and crustacean zooplankton biomass were sometimes significant but were of less importance in explaining variation in S .

Among years, S averaged 1.8% and ranged from 0.04 to 4.2%. Survival was high in 1988 and low in 1991 for both reservoirs. The lowest survival occurred in STK during 1987. The density of 10-mm larvae was not significantly correlated with

TABLE 3.—Coefficients of regression equations relating temperature (T), total zooplankton biomass (ZB), and age-0 gizzard shad densities (GD) to length of gizzard shad after 28 d (TLJ28) and 56 d (TLJ56) of juvenile growth in Pomme de Terre (PDT) and Stockton (STK) reservoirs, 1988–1991. Asterisks denote variables that are significant at $P \leq 0.05$. Only independent variables that were significant at $P \leq 0.15$ were included. For PDT, sample size $n = 33$ for TLJ 28 and 30 for TLJ56; for STK, $n = 31$ for TLJ28 and 27 for TLJ56. No independent variables met significance criteria for the TLJ28 model for STK.

Dependent variable	Lake	Intercept	Independent variable			R^2
			T	ZB	GD	
TLJ28	PDT	42.848*		11.711		0.09
		-7.640	1.745	20.238*		0.19
TLJ56	PDT	48.616*		62.221*		0.44
	STK	65.999*			-7.378	0.11
		44.168*		97.032*	-20.624*	0.59

either the density of 25-mm larvae or the average density of juveniles for either reservoir ($P > 0.11$), indicating that survival of larvae after 10 mm TL was variable among years. The density of 25-mm larvae was marginally significantly correlated with the average density of juveniles in STK ($r = 0.86$, $P = 0.06$) but not in PDT ($r = 0.10$, $P = 0.87$). However, the juvenile estimate for PDT in 1989 was severely inflated by a single density estimate from August. When 1989 data were excluded, the density of 25-mm larvae was strongly correlated with average juvenile densities ($r = 0.98$, $P = 0.02$), suggesting that juvenile survival was less variable among years than larval survival and that events during the larval stage exerted a greater influence on the relative year-class strength.

Among-year Correlations for Juveniles

Among years, growth rates of juveniles averaged 0.54 mm/d and ranged from 0.20 to 1.11 mm/d. Growth rates were not significantly correlated with mean temperature, total zooplankton density and biomass, or density, biomass, and mortality of age-0 gizzard shad for either reservoir. Although not significant, likely because of low sample sizes ($n = 5$), correlation coefficients were relatively strong for temperature (PDT, $r = 0.71$, $P = 0.18$; STK, $r = 0.73$, $P = 0.16$) and gizzard shad density (PDT, $r = -0.68$, $P = 0.21$; STK, $r = -0.71$, $P = 0.18$).

Values of Z for juveniles after mid-July averaged 0.04 and ranged from 0.01 to 0.09. Mortality rates were not significantly related to mean temperature, total zooplankton density and biomass, or density,

TABLE 4.—Coefficients for correlation of survival ($S/(1 - S)$ -transformed) from 10 to 25 mm total length with cohort order and length at age (d) of age-0 gizzard shad in Pomme de Terre (PDT) and Stockton (STK) reservoirs, 1987–1991; $n = 32$ samples for PDT and 29 for STK. Asterisks denote significant correlations at $P \leq 0.05$.

Lake	Cohort order	Length at age (d)				
		7	14	21	28	35
PDT	0.60*	0.49*	0.68*	0.63*	0.59*	0.56*
STK	0.71*	0.39*	0.44*	0.37*	0.30	0.25

biomass, or mean weight of age-0 gizzard shad for either reservoir. However, correlation coefficients exceeded 0.7 (PDT, $r = 0.73$, $P = 0.16$; STK, $r = 0.82$, $P = 0.09$) with temperature for both reservoirs, indicating a possible relationship.

Discussion

Cohort dynamics of age-0 gizzard shad in PDT and STK appeared to be driven initially by climatic factors and later by a combination of climatic and biotic factors. Water temperatures controlled the onset of spawning. Once a minimum temperature was reached (about 13°C mean epilimnetic temperature in this study), changes in water level and temperature appeared to regulate the duration and intensity of spawning activity. Intense periods of spawning activity during rising water levels resulted in high peaks in larval abundance and relatively few large weekly cohorts, such as in 1990 for both reservoirs. The timing of water level rises was important. Rises earlier in the spawning season (1990) had a greater effect on abundance distributions than those nearer the end (1989) when most spawning had already been completed. In the absence of water level rises, peaks in larval abundance were much lower and the abundance of larvae more evenly distributed among several cohorts (e.g., STK in 1988). Spring warming also affected spawning; early cohorts in the warm springs of 1987 and 1991 were relatively more abundant than those in the cool springs of 1989 and 1990. Similarity in the initial cohort distribution between the two reservoirs within years demonstrates the importance of climatic conditions in regulating the timing and duration of spawning. The reservoirs experienced similar temperature and precipitation patterns because of their close proximity.

Spawning stock characteristics had no measurable influence on either the total number of larvae produced or the distribution of larvae among weekly cohorts. No stock-recruitment relationships were evident, probably because recruitment

TABLE 5.—Coefficients of regression equations relating temperature (T), crustacean zooplankton density (CD) and biomass (CB), age-0 gizzard shad density (GD), and log_e-transformed initial number of 10-mm TL larvae (IN) to survival ($S/[1 - S]$ -transformed) from 10 to 25 mm total length for weekly cohorts of larval gizzard shad in Pomme de Terre (PDT) and Stockton (STK) reservoirs, 1987–1991; $n = 32$ samples for PDT and 29 for STK. Asterisks denote variables that are significant at $P \leq 0.05$. Only independent variables that were significant at $P \leq 0.15$ are listed.

Lake	Intercept	Independent variable					R^2
		T	CD	CB	GD	IN	
PDT	–10.600*	0.280*					0.37
	–8.925*	0.216*				–0.443*	0.53
	–8.929*	0.182*	0.00005			–0.406*	0.56
	–10.940*	0.196*	0.00009*		0.454*	–0.758*	0.63
STK	–3.947*					–1.361*	0.57
	–2.321*			–10.296		–1.178*	0.61
	–7.256*	0.257		–17.080*		–0.778*	0.66

variability is more often related to environmental fluctuations than to parent stock size (Cushing 1977). Admittedly, the index of adult female abundance was rather crude and may not adequately represent actual fluctuations in stock size. It is also possible that fluctuations in stock size were not large enough to substantially affect recruitment during this study. However, I found no evidence that the size distribution of adult gizzard shad affected the duration of spawning or the relative distribution of abundance among cohorts, as suggested by Miranda and Muncy (1988) and Willis (1987). The relative condition of adult females also did not appear to affect the number of larvae produced but W_r values were moderately high (85–97) and did not vary much among years. Poor condition ($W_r < 85$) of female gizzard shad in other studies reduced reproductive success (Stock 1971; Kampa 1984; Willis 1987).

The initial distribution of larvae among weekly cohorts influenced subsequent interactions between the larvae and their environment. Early cohorts grew slower because of lower water temperatures and suffered higher mortality than late cohorts. Similar results have been reported for American shad *Alosa sapidissima* (Crecco and Savoy 1985) and bloater *Coregonus hoyi* (Rice et al. 1987b). Because warmer temperatures usually increase growth (Comyns et al. 1989; Mooij and van Tongeren 1990; Fechtel et al. 1992; Griffiths et al. 1992; this study), early cohorts, experiencing cooler water, took up to two times longer to reach the juvenile stage than did late cohorts. The prolonged larval stage enabled mortality factors to act over a longer time, causing early cohorts to experience lower survival than faster-growing late cohorts. Slow-growing fish are probably more susceptible to starvation because foraging abilities dramatically increase with body size (Miller et al.

1988, 1992). They may also be more susceptible to predation (Rice et al. 1987a; Miller et al. 1988) for longer periods.

Cohorts with high initial densities also experienced higher mortality than cohorts with small initial densities. Mayhew (1977), Crecco and Savoy (1987), and Welker et al. (1994) also documented density-dependent mortality. DeAngelis et al. (1993) suggested that high age-0 densities may result in a massive die-off of fish or a mortality “overshoot,” so that the population may crash to low levels more quickly than an initially smaller age-0 population. They suggested that the strength of this event will depend on the resilience of the prey populations to bounce back after they had been depressed by fish predation. There was no clear evidence that high densities of larvae depressed zooplankton populations in this study. Cyclopoid copepods and nauplii, which were preferred prey for small larvae (Michaletz, in press), did not decline rapidly during periods of high larval densities. However, estimated densities of cyclopoid copepods and nauplii were low ($< 15,000/\text{m}^3$) throughout much of the study and were considerably less than the estimated prey densities required for high survival of fish larvae in laboratory studies (Houde 1978; Buckley et al. 1987; Hart and Werner 1987; Goshorn and Epifanio 1991) even if actual net efficiency had been low (40–50%). Fewer prey would have been available to individual larvae at high larval densities. Because larvae are also patchily distributed, localized prey depletion may have occurred. Small larvae are inefficient foragers and may not have been able to successfully locate other concentrations of food.

Although, I could not document that food abundance influenced survival of larvae, R. S. Hayward (University of Missouri, personal communication), in a closely related study in PDT, found that

many larvae were feeding below maintenance rations in both 1989 and 1990. Duration of sub-maintenance feeding periods appeared to be positively related to gizzard shad densities and negatively related to zooplankton abundance. His data were site specific and sensitive to localized conditions, whereas I used average values across a large area, which may have masked relationships that vary spatially. I did find that food abundance affected growth of larvae, which would indirectly affect their survival. This suggests that food abundance may have affected survival of larvae and that larvae were competing for food resources.

The combined effects of environmental factors on larvae were that more larvae from late cohorts survived and that initially large cohorts did not maintain their numerical dominance into the juvenile stage. High survival of larvae occurred in 1988, when the densities of larvae were low and evenly distributed among weekly cohorts and food abundance was high. That year, production of young from mid June to early October was also highest in both reservoirs (Michaletz 1997). Survival of larvae was much lower in 1990, when larval densities were high and food abundance was low.

The exceptionally low survival of larvae in STK during 1987 cannot be explained from the data collected. Water temperatures warmed quickly and food abundance was relatively high, which resulted in fast growth of larvae. Densities of larvae never reached high levels. Despite these apparently favorable conditions, mortality was very high. Perhaps other factors such as disease or parasitism were important causes of mortality.

Compared with the larval stage, the juvenile stage was far less dynamic. Mortality rates among cohorts were low and less variable than those for larvae. The abundance of larvae reaching the juvenile stage was correlated with the average densities of juveniles after mid-July (exclusive of 1989 for PDT), indicating that relative year-class strength was set by the end of the larval stage.

Growth and mortality of juveniles were not closely tied to any single environmental variable. Neither growth of individual cohorts nor average annual juvenile growth rates were significantly related to temperature, likely because the range in average temperatures experienced by juveniles was relatively small, about 4°C, compared with as much as 14°C for larval cohorts. However, coefficients for temperature in regression and correlation models were positive, indicating that growth generally increased with temperature. Mortality

rates of juveniles among years were the most closely correlated with temperature. However, gear avoidance may have been greater during warm years because juveniles attained larger sizes, which may have caused positive bias of Z estimates. Growth among juvenile cohorts was positively related to zooplankton biomass, but average annual juvenile growth and mortality rates were not. Although juveniles rely more on detritus and algae for food than do larvae (Bodola 1965; Cramer and Marzolf 1970), inclusion of more zooplankton in their diets may result in faster growth (Mundahl and Wissing 1987). In comparison with larvae, juveniles probably suffered less from starvation because of their larger size (Miller et al. 1988, 1992) and more omnivorous diet (Bodola 1965; Cramer and Marzolf 1970). Evidence that growth of juveniles was density dependent was found in other studies (Stock 1971; Kampa 1984; Buynak et al. 1992), but this was seen only for STK. The relationships between density and average annual growth of juveniles, although negative, were not significant. Juvenile density had no apparent effect on mortality.

Factors affecting survival among juvenile cohorts were not examined because Z-values for juvenile cohorts were very imprecise. This imprecision probably arose because of the apparent changes in catchability over the lunar cycle and the inherent patchiness in the distribution of pelagic fishes. Mortality rates were likely also biased because of the underaging of older juveniles.

Predation can be important in regulating the abundance and size structure of prey populations (Forney 1977; Tonn et al. 1992; Rice et al. 1993). Age-0 gizzard shad were not observed to be important in the diets of piscivorous fishes until they reached the juvenile stage (Michaletz 1997). But because larvae may be digested rapidly, making it difficult to observe them in stomach contents, I cannot discount fish predation as a mortality factor for larvae. Invertebrate predators are known to prey on small larval clupeids (Hartig et al. 1982), but because of their very low densities and small sizes in the two reservoirs (unpublished data), it is unlikely that they were responsible for the high mortality rates of larval gizzard shad. Predation by fish was likely a major source of mortality for juveniles. Piscivorous fishes fed heavily on juveniles throughout the growing season (Michaletz 1997). Small juveniles are more vulnerable to a wider array of predators than are large juveniles and should experience higher predation mortality (Tonn and Paszkowski 1986; Post and Prankevi-

cius 1987). However, average body weight of juveniles was not negatively correlated with Z , providing no evidence that faster-growing juveniles experienced higher survival than slower-growing individuals. Juveniles in STK during 1987 grew large yet experienced high mortality. Gear avoidance may have biased Z estimates, as previously discussed. Piscivorous fishes also may have consumed a larger portion of the juvenile population in 1987 because densities of juveniles were low.

Aging Bias

Daily rings on otoliths from young gizzard shad became progressively more difficult to identify with fish age. For 1990 and 1991 data, 20% of otoliths from larvae had to be counted a third time compared to 46% for juveniles. In addition to decreasing precision of the ring counts with age, estimated ages became increasingly biased. It appears that serious biases in aging began in late August when the mean age exceeded 70 d, which is at the upper limit of ages validated by Davis et al. (1985). Underaging was likely caused by the difficulty in distinguishing rings due to increased opaqueness of the otolith and decreased spacing of growth increments. Goodgame and Miranda (1993) reported underestimates of daily age for juvenile largemouth bass, and Parrish et al. (1994) reported this problem for juvenile walleyes *Stizostedion vitreum*. Underaging of older juveniles may be a common problem for other fish species as well.

Both growth and mortality rates of juveniles were biased by underaging. Underaging caused juveniles to be incorrectly assigned to later cohorts, resulting in overestimation of growth rates of both early and late cohorts. Bias was probably greater for late cohorts because juveniles were incorrectly assigned to them; for early cohorts, these juveniles were simply not included in growth rate calculations. Mortality rates were positively biased for early cohorts and negatively biased for late cohorts. Several estimates of Z for late cohorts were negative ($>100\%$ survival) because of this aging bias. Although these biases cannot be ignored, they probably did not seriously affect my conclusions about cohort dynamics of age-0 gizzard shad because the most important events appeared to occur in the larval and early juvenile periods.

Management Implications

Fisheries managers are interested in maintaining or developing an adequate prey base for sport fish to ensure their rapid growth. Age-0 gizzard shad

are the most important prey for sport fish in many reservoirs, and annual changes in their abundance and average size may affect growth of sport fish (Michaletz 1997). Consequently, it would be beneficial to manage gizzard shad populations to produce optimal densities and sizes of young. The results of this study indicate that the main factors controlling spawning and subsequent cohort dynamics of age-0 gizzard shad were largely climatic. Water elevation changes brought about by inflow from precipitation and water temperature increases in the spring greatly influenced gizzard shad spawning. Resulting temporal distributions of larvae, in turn, influenced growth and to a greater degree, survival of larvae. Temperature largely controlled growth rates of larvae, which also affected their survival to the juvenile stage. Thus, the abundance and sizes of juveniles available to sport fish were mostly regulated by water levels and temperatures.

Ideally, a broad size range of young gizzard shad should be present to ensure optimal prey sizes for the ambient size range of sport fish (Willis 1987). A larger size range of young was available to sport fish in 1988 than in 1990 in STK (Figure 4). These differences were a result of more prolonged and less intense spawning in association with more gradual changes in water levels in 1988 than in 1990, when rapid rises in water levels occurred along with a shorter-duration and more intense spawning. Production of juvenile gizzard shad was also highest in 1988, and age-2 and older largemouth bass, white crappies *Pomoxis annularis*, and black crappies *P. nigromaculatus* grew more that year than during 1990 in STK (Michaletz 1997). However, younger sport fish such as age-1 white crappies and black crappies grew faster in 1990, possibly because of the large numbers of small juveniles available as prey.

Despite a wide variety of environmental conditions, enough juvenile gizzard shad were usually produced each year to support good growth rates of sport fish except for STK in 1987 (Michaletz 1997). The low juvenile densities in STK during 1987 resulted in poor growth of sport fish. Causes for the poor survival of larvae and juveniles that year remain unknown. In PDT, juvenile densities were always high and growth of sport fish varied little over the 5 years of the study, likely because prey were in surplus. However, high densities of juveniles exceeding those necessary to support sport fish may not be beneficial. High densities of juvenile gizzard shad may reduce zooplankton populations and indirectly reduce recruitment of

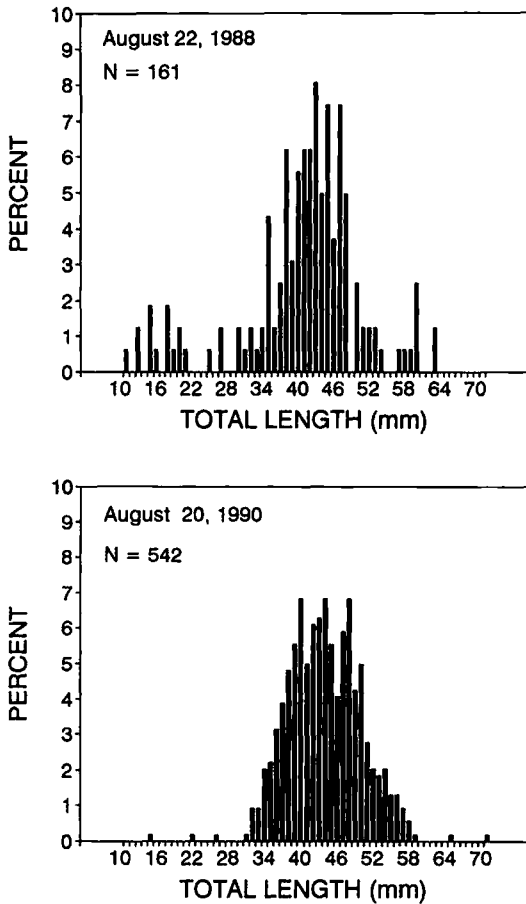


FIGURE 4.—Percent length frequencies of age-0 gizzard shad collected with small-mesh frame trawls from Stockton Lake during late August of 1988 and 1990.

sport fishes (DeVries et al. 1991; DeVries and Stein 1992). Regulating densities of larval and juvenile gizzard shad may be extremely difficult because climatic factors cannot be controlled. However, it may be possible to regulate water levels during the spawning season to indirectly manipulate densities and sizes of young gizzard shad.

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