

THE TIMING AND SIGNIFICANCE OF DENSITY-DEPENDENT AND DENSITY-INDEPENDENT MORTALITY OF AMERICAN SHAD, *ALOSA SAPIDISSIMA*

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ABSTRACT

We used stock-recruitment, pre- and postrecruitment mortality data for American shad, *Alosa sapidissima*, in the Connecticut River to estimate density-dependent and density-independent mortality rates at the prejuvenile (age 1–100 days) and postjuvenile (age 101 days to 5 years) phases. Total postjuvenile mortality rates from 1967 through 1982 were dominated by density-independent mortality, with only 6% ($Z_{D\text{ post}} = 0.30$) of the mean total ($Z = 4.85$) being ascribed to density-dependent processes. By contrast, 23% ($Z_{D\text{ pre}} = 1.13$) of the total prejuvenile mortality was compensatory, of which nearly all took place during the embryonic and early larval periods. Egg and early larval mortality rates from 1979 through 1987 were positively correlated to June river flows, and inversely related to mean June temperature, whereas mortality rates of all other life stages showed no such relationships. Daily egg and early larval mortality rates from 1979 through 1987 were usually higher and more variable than mortality rates during later stages. There were significant negative correlations between egg and early larval mortality rates and the strength of 1979–87 year classes in the adult stock, whereas mortality rates of late larvae and juveniles were independent of year-class strength. Density-dependent mortality during the egg and early larval stages comprised over 40% of the total mortality at those stages, resulting in the number of midlarvae and juveniles being positively correlated to adult recruitment. These data suggest that year-class strength of American shad in the Connecticut River is established after the egg and larval stages.

It is generally accepted that year-class strength of most fishes is established prior to the juvenile stage from density-independent (climatic factors) and density-dependent (competition, predation, cannibalism) processes (Cushing 1974; May 1974; Goodyear 1980). Although density-dependent mortality is believed to be the mechanism that keeps fish populations stable under low to moderate exploitation (McFadden 1977; Cushing 1980), density-dependent processes such as inter- and intraspecific competition, predation, and cannibalism are difficult to measure. This is particularly so for many highly fecund fishes, whose population sizes undergo wide fluctuations that often cannot be predicted by conventional stock-recruitment models (Parrish and MacCall 1978; Bakun 1984). Despite the acknowledged importance of density-dependent mortality to stock-recruitment theory (Ricker 1975; Ware 1980), few studies have been able to quantify density-dependent mortality, or determine the life stages at which compensation occurs.

Density-dependent mortality may be confined to the prejuvenile stage (Cushing 1974, 1980) or the

postjuvenile oceanic stage (Peterman 1978, 1982), or may occur throughout the prerecruitment period (Gulland 1965). The testing of these hypotheses has proceeded slowly because of environmental noise surrounding many stock-recruitment relationships, measurement errors associated with recruitment estimates (Ludwig and Walters 1981), and the lack of long-term mortality data on eggs and larvae.

One species, for which accurate and long-term stock-recruitment and prerecruitment mortality data exist, is the American shad, *Alosa sapidissima*, an anadromous clupeid that spawns in many Atlantic coast rivers (Walburg and Nichols 1967). Previous studies on American shad in the Connecticut River have demonstrated that larval and juvenile mortality rates decline with age (Crecco et al. 1983, 1986) and that growth and survival rates among discrete larval cohorts are significantly affected by short-term hydrographic and meteorological events (Crecco and Savoy 1985b, 1987a). Although previous stock-recruitment studies of Connecticut River shad (Leggett 1977; Lorda and Crecco 1987) found evidence of density-dependent mortality before the juvenile stage, no studies have attempted to estimate density-dependent mortality during the egg and larval stages, or quantify density-dependent and

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density-independent mortality after the juvenile stage.

In this study we used stock-recruitment, pre- and postrecruitment mortality data for American shad in the Connecticut River from 1967 through 1987 to 1) estimate egg mortality rates for the 1979–87 year classes; 2) measure the contribution of density-dependent and density-independent mortality before and after the juvenile stage; and 3) determine the life stage(s) at which most of the density-dependent mortality takes place.

METHODS

Data Source

Estimates of adult recruitment and parent stock size (\pm SE) from 1967 to 1982 (Table 1) were based on annual population estimates derived by earlier mark-recapture studies (Leggett 1976; Crecco and Savoy 1987²) and by the annual mean number of American shad lifted over the Holyoke Dam (Crecco and Savoy 1985a). The parent stock size (PAR_t) from 1967 through 1987 was the annual population estimate of female shad minus that year's commer-

cial catch of female shad. Parent stock (PAR_t) was separated into the parent stock that spawned above the Holyoke Dam (P_a) (Moffitt et al. 1982; O'Leary and Booke 1986³, 1987⁴) and the spawning stock that spawned below the dam ($P_b = PAR_t - P_a$).

Since female American shad mature between ages four and six, female shad recruitment from the 1967–82 year classes was the sum of virgin 4-, 5-, and 6-yr-old female shad in the 1970–87 runs based on the age-class structure from previous studies (Jones et al. 1976; Leggett 1976; Crecco et al. 1984⁵). Since the sex ratio of mature progeny from each year class is close to 1:1 (Leggett 1976), total recruitment (R_t) from the 1967–82 year classes was estimated by doubling the female shad recruitment estimates. Direct estimates of male shad recruitment are biased by gill net selectivity and differential culling practices of commercial fishermen (Crecco et al. 1984⁶).

³O'Leary, J., and H. E. Booke. 1986. Connecticut River anadromous fish investigations. Mass. Coop. Fish. Res. Unit Proj. Performance Rep., F-45-R-2, 37 p.

⁴O'Leary, J., and H. E. Booke. 1987. Connecticut River anadromous fish investigations. Mass. Coop. Fish. Res. Unit Proj. Performance Rep., 32 p.

⁵Crecco, V. A., T. Savoy, and L. Gunn. 1984. Population dynamics studies of American shad in the Connecticut River. CT Dep. Environ. Prot. Final Rep. AFC 13, 76 p.

⁶Crecco, V. A., L. Gunn, and T. Savoy. 1981. Connecticut River shad study, a progress report. Unpubl. manuscr., 87 p. Connecticut Department of Environmental Protection, Hartford, CT 06106.

²Crecco, V. A., and T. F. Savoy. 1987b. Fishery Management Plan for American shad in the Connecticut River. Unpubl. manuscr., 117 p. Connecticut Department of Environmental Protection, Hartford, CT 06106.

TABLE 1.—Estimates of total female American shad parent stock, female spawning stock above and below the Holyoke Dam, mean June flows from 1967 to 1987, and total number of adult recruits from the 1967–82 year classes. SE = standard errors about the estimates $\times 10^3$.

Year	Total spawning stock		Spawning stock above		Spawning stock below		Recruitment		June flow	
	$\times 10^3$	SE	$\times 10^3$	SE	$\times 10^3$	SE	$\times 10^3$	SE	m^3/s	m^3/s
1967	167	35	4	0.8	163	34	444	112	437	
1968	202	38	5	0.9	197	37	236	59	603	
1969	384	70	10	1.8	374	68	490	116	375	
1970	413	95	12	2.8	401	92	550	126	243	
1971	424	111	14	3.7	410	107	982	205	203	
1972	167	40	8	1.9	159	38	430	87	616	
1973	111	30	3	0.8	108	29	308	70	534	
1974	306	62	10	2.0	296	60	652	139	334	
1975	247	65	16	4.2	231	61	560	101	379	
1976	435	80	166	31.0	269	49	650	105	286	
1977	207	39	112	21.0	95	18	1,240	191	250	
1978	210	51	45	12.0	165	42	711	110	422	
1979	248	51	87	18.0	161	33	882	127	445	
1980	341	58	196	33.0	145	25	1,256	196	201	
1981	293	50	143	24.0	150	26	758	132	316	
1982	501	67	109	15.0	392	52	282	49	643	
1983	423	77	185	34.0	238	43			386	
1984	610	67	245	27.0	365	40			661	
1985	555	96	219	38.0	336	58			311	
1986	392	71	175	32.0	217	39			439	
1987	235	37	136	14.0	146	23			250	

American shad larvae (10–30 mm TL) were sampled during daylight hours in the Connecticut River with a 6.1 m plankton bag seine (2.4 m deep, wing and bag mesh of 0.505 mm) and 30 m lead ropes from 15 May to 20 July 1979–84, 1986, and 1987. No larval sampling was conducted in 1985. One seine haul was taken weekly at 8–12 fixed stations located throughout the major spawning areas (Fig. 1). Further details on sampling and methods of estimating larval abundance from net samples are contained in Crecco et al. (1983).

Juvenile American shad (40–90 mm TL) were collected weekly from 20 July through 15 October 1967–87 at 7–14 fixed stations located above and below the Holyoke Dam (Fig. 1) based on weekly and biweekly seine surveys (Scherer 1974; Foote 1976; Marcy 1976; Crecco and Savoy 1984). The annual

juvenile index of relative abundance (IND_t) from 1967 to 1987 was the mean juvenile catch per seine haul (\pm SE) from all stations and collection dates (Table 2).

The Timing of Density-Dependent Mortality

Analysis

One of the primary objectives of this study was to determine the magnitude and timing of density-dependent mortality for American shad. Peterman (1978, 1982) found that density-dependent mortality for some stocks of the anadromous sockeye salmon, *Oncorhynchus nerka*, was confined mainly to the 4–5 yr oceanic postjuvenile phase. Given that the Ameri-

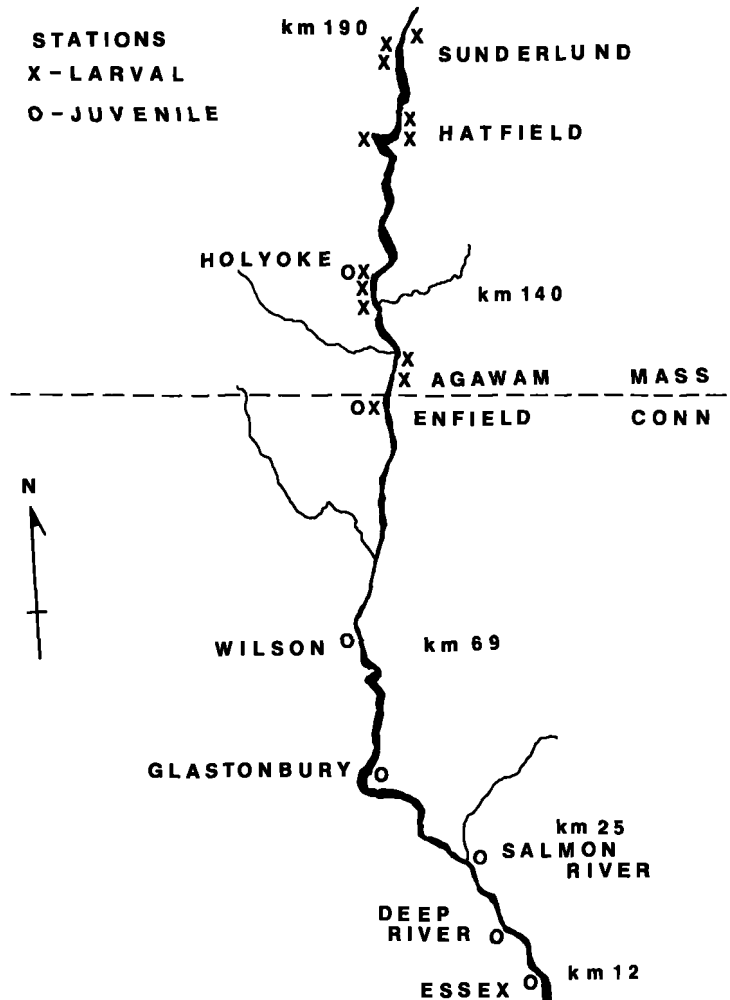


FIGURE 1.—Location of larval and juvenile American shad sampling stations on the Connecticut River.

TABLE 2.—Mean juvenile indices, scaled juvenile abundance from Equation (2) and total egg production for American shad in the Connecticut River from 1967 through 1987. SE = standard errors about the estimates.

Year	Juvenile index	SE	Juvenile abundance $\times 10^3$	SE $\times 10^3$	Total egg production $\times 10^6$	SE $\times 10^6$
1967	20.2	9.4	71,070	33,072	334	70
1968	11.1	1.7	39,053	5,981	404	76
1969	19.0	3.8	68,848	13,770	768	140
1970	27.8	8.2	97,809	28,850	826	190
1971	65.7	14.1	231,151	49,608	848	222
1972	15.3	2.9	53,830	10,203	334	80
1973	12.7	3.4	44,682	11,962	222	60
1974	21.4	6.3	75,292	22,165	612	124
1975	23.7	5.7	83,384	20,054	494	130
1976	22.4	5.9	78,810	20,760	870	160
1977	- - N O T A V A I L A B L E - -				414	78
1978	27.2	5.9	95,698	20,758	420	108
1979	19.6	3.2	68,959	11,259	496	102
1980	42.7	11.0	150,231	38,701	682	116
1981	16.0	2.7	56,293	9,499	586	100
1982	4.7	1.1	16,536	3,970	1,002	134
1983	26.3	6.6	92,531	23,221	846	154
1984	13.0	2.1	45,738	7,388	1,220	134
1985	17.8	2.7	62,626	9,499	1,110	192
1986	17.0	2.8	59,811	9,851	784	142
1987	44.7	15.1	157,268	53,126	470	74

can shad has a similar 4–6 yr postjuvenile phase as sockeye salmon, we tested Peterman's hypothesis for American shad with key factor analysis (Bellows 1981; Rosenberg and Doyle 1986). We fixed the postjuvenile period for American shad in the Connecticut River between 101 days and 5 years, corresponding to the average age (101 days) at which juvenile shad leave the river (Crecco and Savoy 1985b) and the average age (5 years) when they return to the river as mature adults. The total postjuvenile (age 101 days to 5 years) mortality rates (Z_A) for the 1967–82 year classes were related to the scaled juvenile indices (J_t) for those year classes (Table 2) in a linear model:

$$Z_A t = a + b(J_t), \quad (1)$$

where $Z_A t = -\log_e(R_t/J_t)$. If significant density-dependent mortality is present during the postjuvenile stage, the slope (b) of Equation (1) would be positive and differ significantly ($P < 0.05$) from zero.

The juvenile indices were scaled to thousands of fish (J_t) so that the y -axis intercept in Equation (1) directly estimates the mean density-independent mortality ($Z_{I\text{post}}$), and the slope (b) times the geometric mean juvenile abundance (GM) from 1967 through 1987 is the mean density-dependent mortality rate ($Z_{D\text{post}}$). Total juvenile abundance (J_t)

was estimated by multiplying the juvenile indices (IND_t) by a scalar (SC):

$$SC = [GR \exp(-EZA) \cdot GM] = 3,518.3, \quad (2)$$

where GR is the geometric mean total adult recruitment for 1967 through 1982; GM is the geometric mean juvenile index from 1967 through 1987; EZA (4.85) is the mean total instantaneous mortality among postjuveniles from 1967 through 1982. We estimated EZA as the sum of mortality during the late juvenile period (age 101–365 days), and the subadult stage (age 1–5 years). The mean total instantaneous mortality rate during the late juvenile stage was estimated as 2.65 (0.01 · 265 days), using a mean daily mortality rate of 0.01 (SE = 0.002) extrapolated from the 1979–84 larval and juvenile survivorship curves (Crecco and Savoy 1985b). The mean total instantaneous mortality rate of subadult shad was 2.2, based on an annual instantaneous natural mortality rate of 0.45 from the method of Pauly (1980) plus 0.10 to reflect oceanic fishing mortality (2.2 = 4(0.45 + 0.10)). We estimated the annual natural mortality rate (0.45) by substituting the K (0.25, SE = 0.03) and L (55 cm FL, SE = 3 cm) parameters of the von Bertalanffy equation for male and female shad combined and preferred ocean temperature (14°C) of American shad (Leggett and Whitney 1972) into Pauly's multiple regression model. The oceanic fishing mortality estimate (0.10) was based on tagging studies in Delaware Bay (White et al. 1969; Zarbock 1969) and off the New York-New Jersey coast (Nichols 1958).

To determine if density-dependent mortality takes place during the egg and larval stages as Cushing (1980) hypothesized, we related total prejuvenile mortality rates (ZEJ_t) to annual egg production ($Eggs_t$), and to both egg production (Table 2) and mean June river flow ($JFLOW$) from 1967 to 1987 (Table 1) in linear regression models:

$$ZEJ_t = a + b(Eggs_t) \quad (3a)$$

and

$$ZEJ_t = a + b(Eggs_t) + c(JFLOW_t), \quad (3b)$$

where $ZEJ_t = -\log_e(J_t/Eggs_t)$. Mean June river flows (m^3/s) were included in Equation (3b) because previous studies (Crecco and Savoy 1985b, 1987a) have shown that high June flows reduced prejuvenile survival rates, leading to a significant inverse correlation ($r = -0.74$, $P < 0.01$) between the juvenile indices of abundance from 1967 through 1980 and

mean June river flow (Crecco and Savoy 1984, 1985b). Mean June flows (m^3/s) were measured within the major spawning areas (Leggett 1977) by the United States Geological Survey (U.S. Geological Survey 1967-84). We estimated total egg production ($Eggs_t$) in Equations (3a) and (3b) as the product of the mean fecundity of a female American shad times that year's parent stock (PAR_t) of female shad (Table 1). The average fecundity was reduced from 269,000 ova (Leggett 1969) to 200,000 to reflect the average rates of egg retention and incomplete fertilization (Watson 1970; Reed and Russo 1976⁷). Since Leggett (1969) showed that the average fecundity of American shad varied by less than 10% from 1966 through 1973, we were justified in using an average fecundity for all years.

The mean density-independent mortality rate (Z_{Ipre}) present during the prejuvenile stage was the y -axis intercept (a) in Equation (3b) plus the slope (c) times the overall geometric mean June flow

($GJFLOW$) from 1967 through 1987:

$$Z_{Ipre} = a + c(GJFLOW), \quad (4)$$

The mean density-dependent mortality rate (Z_{Dpre}) was the slope (b) of Equations (3a) and (3b) times the geometric mean egg production ($GEgg$) from 1967 through 1987. A positive and statistically significant slope (b) of prejuvenile mortality on egg abundance would support the Cushing hypothesis that density-dependent mortality takes place before the juvenile stage. If the b estimates of Equations (1), (3a), and (3b) were all positive and significant, our results would support Gulland's (1965) hypothesis that density-dependent mortality occurs over the entire prerecruitment phase.

Results

Although total juvenile abundance varied 14-fold from 1967 through 1982 (Table 2), the total postjuvenile mortality rates (ZA_t) exhibited relatively low variability (95% C.I.: 4.70-5.00) about the estimated mean ($EZA = 4.85$) (Fig. 2). The slope of the linear regression between total postjuvenile mortal-

⁷Reed, R. J., and A. Russo. 1976. American shad research Connecticut River, Massachusetts, 1976. I. Fecundity, egg retention, sex ratio, and age class composition. Unpubl. manuscript, 16 p. Massachusetts Cooperative Fisheries Research Unit, University of Massachusetts, Amherst, MA 01003.

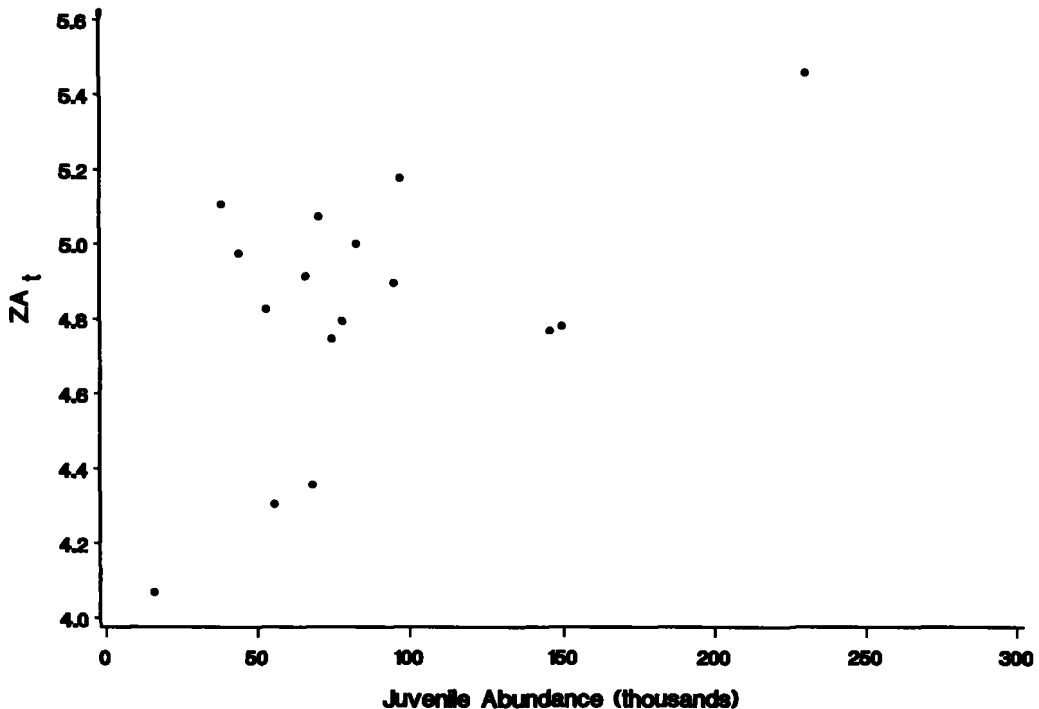


FIGURE 2.—Relationship between American shad postjuvenile mortality (ZA_t) and relative abundance of juveniles (J_t) from 1967 through 1982.

ity rates (ZA_t) and scaled juvenile abundance (J_t) was positive and statistically significant ($P < 0.04$) (Table 3). Since the average density-dependent mortality ($Z_{D\text{ post}} = 0.30$) present during the postjuvenile stage comprised only 6% of the mean total postjuvenile mortality rate ($ZA = 4.85$), density-dependent mortality is not large enough to alter the significant linear correlation ($r = 0.78$, $P < 0.01$)

between the juvenile indices (J_t) and adult recruitment (R_t) for the 1967 through 1982 year classes (Fig. 3).

The prejuvenile mortality rates (ZEJ_t) from 1967 through 1987 were positively correlated ($r = 0.70$, $P < 0.0004$) to total egg production (Eggs_t) (Fig. 4). Egg production alone explained 49% of the variation in prejuvenile mortality (Table 3) and the slope

TABLE 3.—Estimates of density-dependent (Z_D), density-independent mortality (Z_I) and the fraction of density-dependence ($Z_D/(Z_I + Z_D)$) during the postjuvenile (1967–82) and prejuvenile (1967–87) mortality phases for American shad in the Connecticut River. SE = standard error, and numbers in parentheses = 95% C.I. for Z_D . ZEJ_t = prejuvenile mortality, ZA_t = postjuvenile mortality.

Model	Parameters	SE	Z_D	Z_I	$Z_D/(Z_I + Z_D)$
Prejuvenile					
$ZEJ_t = a + b(\text{Eggs}_t)$	$a = 5.466$	0.313	1.13	5.47	0.17
	$b = 1.88 \times 10^{-8}$	4.43×10^{-9}	(0.862–1.392)		(0.136–0.203)
	$r^2 = 0.49$				
$ZEJ_t = a + b(\text{Eggs}_t) + c(J\text{Flow}_t)$	$a = 4.287$	0.303	1.18	5.34	0.18
	$b = 1.97 \times 10^{-8}$	2.87×10^{-9}	(1.007–1.351)		(0.158–0.202)
	$c = 0.0028$	0.0005			
	$r^2 = 0.80$				
Postjuvenile					
$ZA_t = a + b(J_t)$	$a = 4.53$	0.15	0.30	4.53	0.062
	$b = 3.49 \times 10^{-6}$	1.51×10^{-6}	(0.035–0.560)		(0.008–0.110)
	$r^2 = 0.275$				

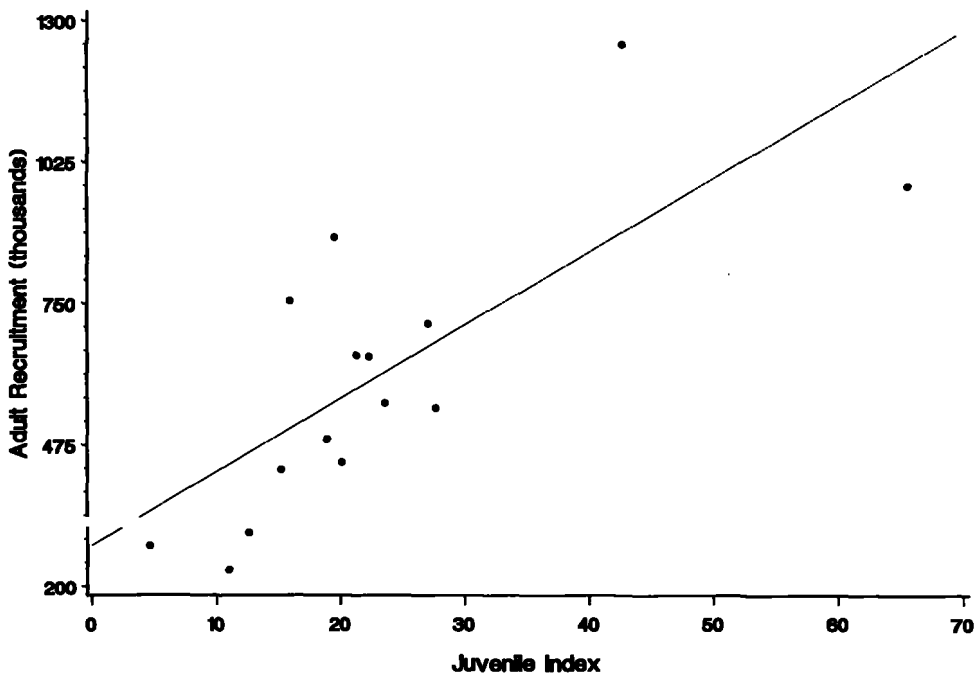


FIGURE 3.—Relationship between total adult recruitment (R_t) and the juvenile abundance indices (IND_t) of American shad from 1967 through 1982.

of the regression differed significantly from zero, indicating the presence of significant density-dependent mortality during the prejuvenile stage. When prejuvenile mortality rates were related to both egg production ($Eggs_t$) and mean June river flow, ($JFLOW_t$), the multiple regression model accounted for 80% of the variability in prejuvenile mortality (Table 3), and the slope estimates for egg production (b) and June flow (c) were positive and highly significant. Note that the standard error (SE) about the slope estimate (b) was reduced by 60% when June flow effects were considered. These results suggest that prejuvenile mortality rates are affected by a combination of density-dependent (egg production) and density-independent (June river flow) factors.

The mean density-dependent mortality rate during the prejuvenile phase ($Z_{D_{pre}} = 1.18$) from the multiple regression model was four times greater than the mean $Z_{D_{post}}$ value (0.30) for postjuveniles (Table 3), suggesting that 80% ($1.18/1.18 + 0.30$) of the total compensatory reserve for American shad occurs before the juvenile stage. Whereas compensatory density-dependent mortality may play a significant role in regulating egg and larval abundance during years of high egg production, it is clear that

most of the variability (82%) in egg and larval abundance is ascribed to density-independent factors.

Egg, Larval, and Juvenile Mortality, 1979–87

Analysis

To examine how larval and juvenile mortality rates varied with year-class strength, survivorship curves for 19,000–180,000 American shad larvae and 800–3,500 juveniles were developed annually from 1979 to 1987 following the techniques of Lough (1976) and Hewitt et al. (1985). Mortality rates could not be estimated directly for prolarvae because American shad yolk-sac larvae (7–9 mm TL) remain in deep water (Marcy 1976) and were only partially susceptible to the plankton seine.

All larvae and juveniles collected annually were separated into four length intervals: 1) 10–13 mm TL, reflecting first-feeding larvae with undeveloped pelvic fins (Wiggins et al. 1984); 2) 14–19 mm TL, associated with the onset of pelvic fin development (Lippson and Moran 1974); 3) 20–28 mm TL, representing larvae approaching metamorphosis, characterized by invagination of the gut (Maxfield 1953);

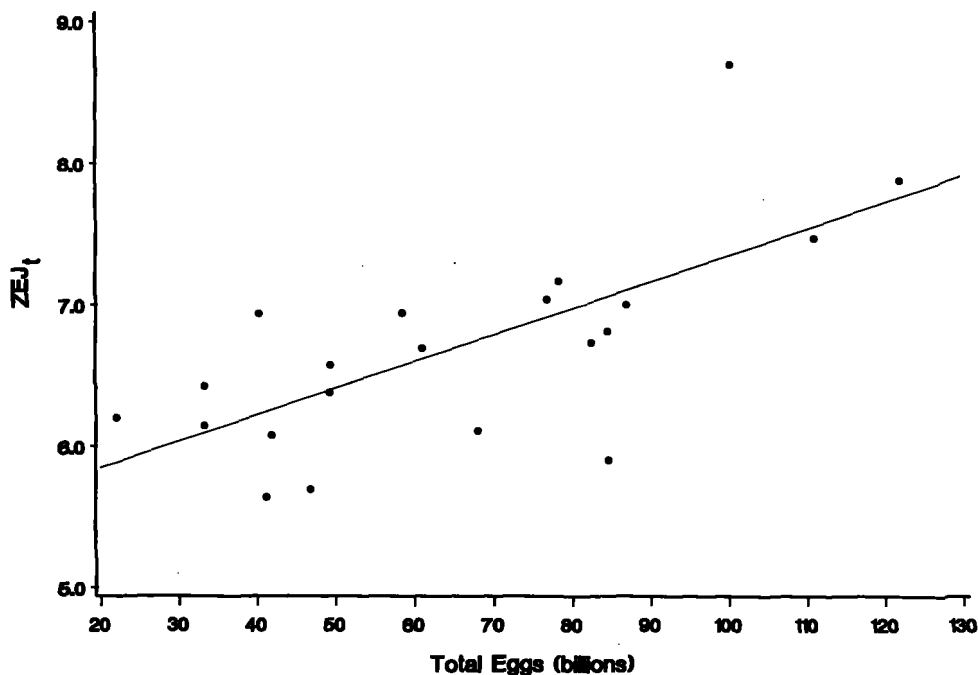


FIGURE 4.—Relationship between American shad prejuvenile mortality (ZEJ_t) and the number of eggs produced ($Eggs_t$) from 1967 through 1987.

and 4) 29–80 mm TL, corresponding to the juvenile stage and the onset of scale development (Marcy 1976). These four groups are hereafter referred to as early larval, midlarval, late larval, and juvenile stages, respectively.

We used otolith increment counts (Savoy and Crecco 1987) to age a subsample of 100–400 American shad larvae and 80–200 juveniles annually from 1979 to 1987. The age-length relationship for larvae and juveniles in all years was well described by the Gompertz growth equation (Crecco et al. 1983; Crecco and Savoy 1985b) so we used a pooled Gompertz equation to describe larval and juvenile growth. The average age (t) of each of the four length groups was estimated by rearranging the Gompertz equation:

$$t = \log_e[K/K - \log_e(L_t/L_0)]/a \quad (5)$$

where L_t = total length (mm); L_0 = length at hatching (8.0 mm); K = growth rate at the inflection point; and a = rate of exponential decay.

The daily instantaneous mortality rates (d) for each stage and their standard errors from 1979 through 1987 were estimated by an exponential model,

$$N_t = A \exp(-dt), \quad (6)$$

that related abundance (N_t) and age (t) by nonlinear regression methods (SAS 1982). The total instantaneous mortality rates of early (ZEL_t), mid (ZML_t), and late (ZLL_t) larvae and juveniles (ZJ_t) were estimated by multiplying the corresponding daily mortality rate (d) by the average duration (D_s = days) within each stage. Previous studies (Crecco and Savoy 1985a; Savoy and Crecco 1987) found that the growth rates of early (10–13 mm) and midlarvae (14–19 mm) were positively correlated with June water temperatures, whereas the growth of late larvae and juveniles were independent of river temperatures. As a result, we adjusted the stage duration (D_s) of early and midlarvae with the mean June temperatures (U.S. Geological Survey 1979–87) from 1979 through 1987 and the larval growth-

subtracting the sum of larval (ZEL_t , ZML_t , ZLL_t), juvenile (ZJ_t) and postjuvenile (ZA_t) mortality rates from the total prerecruitment mortality rate ($ZTotal_t$):

$$ZE_t = ZTotal_t - (ZEL_t + ZML_t + ZLL_t + ZJ_t + ZA_t), \quad (7)$$

where $ZTotal_t = -\log_e(R_t/Eggs_t)$. However, since the 1983 through 1987 year classes have not been fully recruited to the spawning population, we estimated total adult recruitment (Rp_t) for those year classes by the following environment-dependent stock-recruitment model:

$$Rp_t = 24.29 (PAR_t) \exp(-0.0052 \cdot P_b) \exp(-0.0032 \cdot P_a) \exp(-0.0025 \cdot JFLOW_t) \quad (8)$$

Adult recruitment was estimated independently of the juvenile indices by substituting each year's parent stock size (PAR_t), mean June flow ($JFLOW$), female parent stock lifted over the Holyoke Dam (P_a), and female parent stock below the Holyoke Dam (P_b) (Table 1) into the model. This nonlinear model was shown (Loda and Crecco 1987) to be a good predictor ($r^2 = 0.81$, $P < 0.001$) of adult recruitment (R_t) for the 1966 through 1982 year classes. Moreover, the predicted recruitment levels (R_t) of the 1983 through 1987 year classes from Equation (8) were closely correlated ($r = 0.92$, $P < 0.01$) with the corresponding juvenile abundance (J_t) for those years (Table 4) which is consistent with the positive correlation ($r = 0.78$, $P < 0.01$) between adult recruitment and the 1967–82 juvenile indices (Fig. 2). This justifies the use of Equation (8) to predict adult recruitment, total mortality, and postjuvenile mortality rates for the 1983–87 year classes.

The standard errors about the egg mortality rates (ZE_t) were derived as the sum of the variances of all other terms (Cochran 1965):

$$SE_{ZE}^2 = \sqrt{SE_{ZEL}^2 + SE_{ZML}^2 + SE_{ZLL}^2 + ZJ^2 + SE_{ZA}^2 + SE_{ZTotal}^2} \quad (9)$$

temperature equations (Crecco and Savoy 1985b: table 7).

We estimated total egg and prolarval mortality rates (ZE_t) indirectly from 1979 through 1987 by

The standard errors about the total prerecruitment ($ZTotal_t$) and postjuvenile (ZA_t) mortality rates (Table 5) were based on the same principle as Equation (9) (App. 1).

TABLE 4.—Predicted total adult recruitment of American shad from the environmental dependent stock-recruitment model (Equation (8)), 95% confidence limits about the recruitment values and juvenile abundance for the 1983–87 year classes.

Year	Predicted adult recruitment $\times 10^3$	95% C.I.	Juvenile abundance $\times 10^3$
1983	634	362–906	92,531
1984	196	112–280	45,738
1985	555	317–793	62,626
1986	587	335–839	59,811
1987	955	547–1,363	157,268

TABLE 5.—Estimates of the total (Z_{Total}) and postjuvenile (Z_A) instantaneous mortality rates and their standard errors (SE) for American shad from 1979 through 1987.

Year	Z_{Total}	SE	Z_A	SE
1979	10.94	0.26	4.36	0.23
1980	10.90	0.24	4.78	0.32
1981	11.26	0.25	4.31	0.25
1982	13.00	0.27	4.77	0.34
1983	11.80	0.30	4.98	0.36
1984	13.34	0.26	5.45	0.28
1985	12.21	0.29	4.72	0.28
1986	11.80	0.30	4.62	0.29
1987	10.80	0.28	5.10	0.47

Given that ZE represents total mortality throughout the egg and prolarval period, daily egg mortality rates were determined by dividing ZE by the average duration (D_s) of the egg and prolarval stages of American shad in the Connecticut River. Watson (1968) reported an inverse relationship between the incubation period (D) of shad eggs and water temperature (T) by the expression:

$$D = 120.95 \exp(-0.154 \cdot T). \quad (10)$$

To determine the duration (D_s) of the egg stage from 1979 through 1987 we substituted the mean June temperatures for the Connecticut River (U.S.G.S. Annual Water Year Reports 1979–87) into Equation (10).

The total number of prolarvae (age 2 days) and early larvae (age 10 days) for the 1979 through 1987 year classes was estimated by

$$NE_t = \text{Eggs}_t \cdot \exp(-ZE_t) \quad (11)$$

and

$$NF_t = \text{Eggs}_t \cdot \exp(-ZE_t - ZEL_t) \quad (12)$$

respectively, where NE_t is the estimated number of prolarvae larvae and NF_t is the number of early larvae. The abundance of older larvae and juveniles from each year class was estimated by adding their respective total mortality rates to Equation (12). To determine the life stage(s) at which year-class strength is established, we related the stage-specific total mortality rates and abundance estimates to the number of adult recruits (R_t or Rp_t) from the 1979–87 year classes in several linear models. If year-class strength is established early, there should be a significant positive correlation between the number of prolarvae (NE) and early larvae (NF) and adult recruitment, and total mortality rates during these early stages (ZE and ZEL) should be inversely related to adult recruitment.

To determine the extent of density-independent mortality at the egg, larval, and juvenile stages, we correlated the stage-specific total mortality rates from 1979 through 1987 to mean May and June river flows (m^3/s) and water temperatures ($^{\circ}C$) in several linear models. May and June hydrographic and meteorological parameters were used because they coincide with egg, larval, and juvenile development in the Connecticut River (Leggett 1977) and were the only monthly abiotic variables that were significantly linked to adult shad recruitment from 1966 to 1980 (Crecco and Savoy 1984, 1987c). May and June water flows and temperatures were recorded by the U.S. Geological survey (U.S. Geological Survey 1966–1980) within the major spawning areas (river km 89) of American shad (Leggett 1977).

Results

The mean daily mortality rates from 1979 through 1987 declined by an order of magnitude from the egg through the juvenile stages (Table 6). Total egg mortality rates were relatively high (mean $ZE = 2.584$, $cv = 18.5\%$) and were inversely correlated ($r = -0.76$, $P < 0.03$) with adult recruitment (R_t or Rp_t) from those year classes (Table 7). These data indicate that shad eggs and prolarvae (age 1–2 days) from 1979 through 1987 experienced high (85–96%) mortality that was directly linked to year-class success.

The total mortality rates (ZEL) among early larvae were slightly lower and more variable (mean $ZEL = 1.608$, $cv = 31.5\%$) than the egg mortality rates (Table 6), and were also inversely related ($r = -0.83$, $P < 0.01$) to adult recruitment from 1979 through 1987. By contrast, the total mortality rates of older larvae (ZML and ZLL) and juveniles (ZJ)

TABLE 6.—Stage-specific total instantaneous mortality rates of egg, larval, and juvenile American shad from 1979 to 1987. SE = stage-specific standard errors; cv = coefficient of variation, Days = duration of each stage.

Year or statistic	Instantaneous total mortality									
	Egg + pro-larvae (day 2)		Early larvae (day 3-9)		Mid-larvae (day 10-18)		Late larvae (day 19-29)		Juvenile (day 30-100)	
	mean	SE	mean	SE	mean	SE	mean	SE	mean	SE
1979	2.481	0.554	1.323	0.245	1.116	0.189	0.330	0.110	1.330	0.280
1980	1.853	0.819	1.218	0.186	1.096	0.336	0.693	0.099	1.260	0.280
1981	2.580	0.684	1.836	0.108	0.408	0.328	0.726	0.154	1.400	0.210
1982	2.940	0.501	2.144	0.152	1.160	0.210	0.726	0.187	1.260	0.210
1983	3.012	0.785	1.400	0.546	0.522	0.234	0.836	0.143	1.050	0.140
1984	2.706	0.601	2.520	0.352	0.640	0.330	0.484	0.242	1.540	0.280
1985	N O D A T A									
1986	3.158	0.652	1.323	0.196	1.206	0.261	0.374	0.066	1.120	0.280
1987	1.944	0.852	1.098	0.180	0.864	0.128	0.464	0.088	1.330	0.210
Z	2.584		1.608		0.877		0.579		1.286	
SE	0.169		0.179		0.111		0.066		0.051	
cv	0.185		0.315		0.359		0.325		0.120	
Days	7.2		6.9		8.9		11.0		70.0	
Daily Z	0.359		0.233		0.099		0.053		0.018	

TABLE 7.—Correlations between stage-specific total mortalities and adult recruitment and several abiotic factors from 1979 to 1987 for American shad. P = probability levels.

Stage	Adult recruitment	May flow	May temperature	June flow	June temperature
Egg	-0.76	0.38	-0.08	0.66	-0.59
P	0.03	0.35	0.85	0.08	0.13
Early	-0.83	0.42	-0.21	0.81	-0.64
P	0.01	0.29	0.62	0.01	0.09
Mid	0.16	-0.41	0.49	0.09	-0.34
P	0.71	0.32	0.22	0.83	0.42
Late	-0.02	0.20	-0.51	-0.13	0.18
P	0.96	0.64	0.20	0.75	0.68
Juv	-0.19	0.05	0.02	0.26	-0.08
P	0.65	0.91	0.97	0.53	0.86

were highly variable, but showed no relationship to adult recruitment.

Given that high (94-99%) egg and early larval mortality rates were inversely related to year-class strength, the abundance of first-feeding larvae (age 10 days) was closely correlated ($r = 0.84$, $P < 0.01$) with adult recruitment (Rp_t) from 1979 through 1987 (Table 8). Because year-class strength from 1967 through 1987 was independent ($r = -0.15$, $P < 0.46$) of egg production ($Eggs_t$), our results suggest that year-class strength of American shad is determined by the number of shad that survive the embryonic and early larval stages.

Early larval mortality rates from 1979 to 1987 were positively correlated with mean June river

flows. No such relationships were evident for any other stage-specific mortalities (Table 7). The high egg and early larval mortality rates (Table 6) and relative failure of the 1982 and 1984 year classes coincided with major storm events in mid-June 1982 and late May 1984 (Crecco and Savoy 1984) which increased river flows and kept water temperatures below 17°C until late June. The high river flows in 1982 and 1984 were also coupled with the highest parent stocks on record since 1967 (Table 1). By contrast, the relatively low egg and early larval mortality rates for the dominant 1980 and 1987 year classes were associated with low June river flows, a steady rise in June water temperatures (Crecco and Savoy 1984) and low to moderate size parent stocks (Table 1). These results suggest that dominant year classes of American shad are most likely to occur when lower than normal June flows are coupled with relatively small spawning stocks.

Prejuvenile Density-Dependent Mortality: A Closer Look

Analysis

Having estimated that 82% of the density-dependent mortality for American shad takes place before the juvenile stage (Table 3), we attempted to estimate the relative contribution of density-dependent mortality during the egg, early, mid-, and late larval and juvenile stages from 1979 through 1987. We related egg mortality rates (ZE_t) from

TABLE 8.—Relationship between the number ($\times 10^6$) of American shad at each life history stage and adult recruitment from each year class. r = correlation coefficient and P = probability levels from 1979 to 1987.

Year-class	Stage						
	Egg	Pro-larvae	Early larvae	Mid-larvae	Late larvae	Juvenile	Adult ¹
1979	496	41.5	11.0	3.6	2.6	0.7	882
1980	682	106.9	31.6	10.6	5.3	1.5	1,256
1981	586	44.4	7.1	4.7	2.3	0.6	758
1982	1,002	53.0	6.2	1.9	0.9	0.3	282
1983	846	41.6	10.3	6.1	2.6	0.9	634
1984	1,220	81.5	6.6	3.5	2.1	0.5	196
1985	1,110	----- N O D A T A -----					555
1986	784	33.3	8.9	2.7	1.8	0.6	587
1987	470	67.3	22.4	9.5	5.9	1.6	955
$r =$	-0.15^2	0.33	0.84	0.80	0.79	0.82	
$P =$	0.46	0.43	0.01	0.02	0.02	0.01	

¹Predicted or observed recruitment in thousands.

²Correlation coefficient for egg abundance and recruitment was based on the 1967–87 data (Tables 1, 2).

1979 to 1987 to total egg production ($Eggs_t$) in a linear model:

$$ZE_t = a + b(Eggs_t). \quad (13)$$

As before, significant density-dependence would be shown if the slope (b) in Equation (13) was positive and differed significantly from zero.

The cumulative amount of density-dependent mortality during the egg and early larval stages combined was estimated by summing the instantaneous total mortality rates of early larvae (ZEL_t) and eggs (ZE_t) and then regressing the total ($ZE_t + ZEL_t$) against egg production as in Equation (13). This procedure was repeated for each subsequent stage by adding their respective instantaneous total mortality rates. We then estimated the relative magnitude of density-dependent mortality (Z_D) at each stage by multiplying the slope (b) of each regression equation by the geometric mean egg pro-

duction ($GEgg$) from 1967 through 1987. The density-independent mortality rate (Z_I) at each stage was expressed by the y -axis intercept (a) of each regression equation. The percentage contribution of density-dependent mortality ($\%Z_D$) for each period was the ratio of Z_D to total mortality ($Z_D + Z_I$) times 100.

Results

Our results showed that significant density-dependent mortality first occurs during the early larval stage and persists for all stages thereafter (Table 9). The percentage contribution of density-dependent mortality ($\%Z_D$) rose from 24% of the total during the egg stage to 41% during the early larval stage, and then declined during the mid- and late larval stages as the magnitude of density-independent mortality increased. The mean density-dependent mortality rate for the egg and early larval

TABLE 9.—Relationship between the cumulative mortality rates and parent stock sizes ($Eggs_t$). The cumulative mortality rate was egg mortality (ZE) plus early larval mortality (Z_2), midlarval mortality (Z_3), late larval mortality (Z_4), and juvenile mortality (Z_5). Z_D = density-dependent mortality rate, Z_I = density-independent mortality rate, $\%Z_D$ = percentage density-dependent mortality, $\%Z_I$ = percentage density-independent mortality, t = student t -statistic.

Model	b parameter	SE(b)	t	Z_D	Z_I	$\%Z_D$	$\%Z_I$
$ZE = a + b(Eggs_t)$	9.89×10^{-9}	6.40×10^{-9}	1.55	0.59	1.83	24	76
$Z_2 = a + b(Eggs_t)$	2.57×10^{-8}	7.76×10^{-9}	13.31	1.54	2.24	41	59
$Z_3 = a + b(Eggs_t)$	2.44×10^{-8}	8.16×10^{-9}	12.99	1.46	3.21	31	69
$Z_4 = a + b(Eggs_t)$	2.60×10^{-8}	7.74×10^{-9}	13.36	1.55	3.67	30	70
$Z_5 = a + b(Eggs_t)$	2.69×10^{-8}	7.50×10^{-9}	13.59	1.61	4.88	25	75

¹Significant student t -statistic at the $P < 0.01$ level and SE(b) = standard error of b .

stages combined ($Z_D = 1.54$) between 1979 and 1987 was not significantly different (Table 9) from the total density-dependent mortality rate ($Z_{D_{pre}} = 1.18$) estimated during the prejuvenile period from 1967 to 1982 (Table 3), suggesting that nearly all of the density-dependent mortality for prejuvenile American shad occurs before the midlarval stage.

DISCUSSION

Although American shad eggs and early larvae experience high mortality (15–40%/day) in the Connecticut River, the average density-dependent mortality rate ($Z_{D_{pre}} = 1.18$) during those stages comprised a relatively small percentage (18%) of the total prerecruitment mortality. This suggests that most of the annual variability in American shad recruitment is explained by density-independent factors, which is consistent with the significant positive correlation between mean June flow and egg and early larval mortality rates, and with the significant inverse correlation ($r = -0.74$, $P < 0.001$) between mean June river flow and adult recruitment from the 1967 through 1982 year classes (Crecco and Savoy 1984, 1987b). Whereas these data illustrate that density-dependent mortality plays a minor role in governing annual variability in American shad recruitment, this does not mean that compensatory processes are trivial. As pointed out by Ricker (1954) and others (Cushing 1974; Garrod and Horwood 1984), only a small amount of density-dependent mortality is required to stabilize the growth potential of fish populations because density-dependent effects become progressively more effective at higher egg and larval densities (Shepherd and Cushing 1980; Murray 1982).

Although our results on American shad support the Gulland (1965) hypothesis that density-dependent mortality persists throughout the prerecruitment period, most (82%) of the density-dependent mortality occurs during the egg and early larval stages. Our average estimate of density-dependent mortality ($Z_D = 1.54$) during the early larval periods does not differ significantly from the mean Z_D value (1.34) estimated among the 5-d larval cohorts in 1983 and 1984 (Crecco and Savoy 1987a), or from the mean density-dependent mortality rate Z_D (1.21) estimated by stock-recruitment methods for the entire prerecruitment period (Lorda and Crecco 1987). That year-class strength is established early in the ontogeny of American shad is supported further by the significant positive correlation ($r = 0.84$, $P < 0.009$) between the relative abundance of early larvae and all subsequent stages from 1979

through 1987 and adult recruitment from those year classes (Table 8).

The main causes of density-dependent mortality are thought to be predation, competition, and cannibalism (Ricker 1954). Since adult American shad are not thought to feed in freshwater (Walburg and Nichols 1967), we can probably eliminate cannibalism as a mechanism for significant density-dependent mortality during the egg and early larval stages. Therefore, density-dependent mortality among early American shad larvae is most likely caused by intraspecific competition for food or space and predation. The exact underlying density-dependent mortality mechanisms are difficult to quantify because the outcome of competition and predation may depend on June flow effects shown here (Table 3) and elsewhere (Crecco and Savoy 1987a, b) to be the principal density-independent factor. High June river flows have been shown to reduce June river temperatures (Crecco and Savoy 1984) and the growth rates of shad eggs (Watson 1968) and early larvae (Crecco and Savoy 1985b). Because slower growing larvae may be susceptible to predation for a longer period of time (Hunter 1976), periods of high flow may indirectly enhance egg and larval predation. Additionally, since high flows reduce the spatial patchiness (Crecco and Savoy 1987a), abundance and availability of river zooplankton (Whitton 1980; Threlkeld 1986), high flows may result in increased levels of competition among American shad larvae for available prey, especially if shad larvae are capable of depleting local aggregations of edible zooplankton. Periods of high runoff that coincide with peak larval production, such as in June 1982 and 1984, may advect larvae and their zooplankton prey from eddies and backwaters where they are normally found (Cave 1978) to areas of high predator abundance. In light of the many ways in which June flows potentially mediate larval mortality, it is unlikely that a single compensatory mechanism is responsible for the relatively high density-dependent mortality rate ($Z_{D_{pre}}$) among early larvae.

Since egg and prolarval shad have endogenous food reserves, density-dependent mortality of these stages is likely due to predation and competition for sites among spawning adults. As spawning stocks reach high densities, such as in 1982–84, crowding of adult fish on the spawning grounds may result in a reduction in the number of eggs released (Goodyear 1980). In addition, since the amount of spawning habitat in the Connecticut River can be considered fixed from year to year, larger spawning stocks are more apt to deposit an increasing percentage of eggs in unfavorable areas. Layzer (1974)

noted that the highest survival rates of American shad eggs occurred over gravel and rubble substrates. Since these areas generally have higher water velocities, eggs lodged within the interstices of the gravel and rubble are less likely to be eaten by predators or covered by silt. Dense aggregations of eggs may also be highly susceptible to fungal agents (Leach 1925), which could then act as efficient density-dependent predators. However, since predators of American shad eggs and larvae in the Connecticut River have not yet been identified, density-dependent losses are difficult to quantify. Also, predation mortalities in general may be either density-dependent or density-independent, depending on the functional response between the predator and the prey (Hassell 1978), and whether predators actively search for discrete aggregations of eggs and larvae or prey on randomly encountered eggs and larvae (Gulland 1987).

In the absence of direct egg mortality estimates of American shad, the accuracy of our egg mortality estimates (Z_E) from Equation (7) are difficult to evaluate, particularly since the standard errors about the estimates are highly variable (Table 6). To provide an independent estimate of daily egg mortality, we used the multiple regression method of McGurk (1987) to estimate the average daily egg mortality rate. This method requires an estimate of the patchiness and the mean dry weight of a shad egg. We derived Lloyd's patchiness index ($\bar{x} = 7.26$, $SE = 0.376$) for American shad eggs in the Connecticut River from the 1974-75 egg surveys in the Holyoke Dam impoundment (NUSCo 1977). Substituting the mean weight of a shad egg (0.00025 g, Leggett 1969) and the mean patchiness index into McGurk's equation 4, yields an instantaneous daily egg mortality rate of 0.34 which closely approximates our average estimate (0.36) from 1979 to 1987 (Table 6).

Lastly, since it is presently unknown if younger (smaller) virgin female American shad produce smaller, less viable eggs than older shad as was reported for cod, *Gadus morhua*, (Knutsen and Tilseth 1985), the contribution of the age structure to the parent progeny relationship (Rosenberg and Doyle 1986) should be considered. This issue and an examination of whether egg deposition rates are density-dependent should be addressed by monitoring egg retention rates among postspawning American shad.

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APPENDIX 1

The total prerecruitment (Z_{Total_t}) and postjuvenile (Z_{A_t}) mortality rates from 1979 through 1987 were estimated by

$$Z_{Total_t} = -\log_e(Par_t * 200,000) - \log_e(R_t)$$

and

$$Z_{A_t} = \log_e(J_t) - \log_e(R_t),$$

respectively. The standard errors about Z_{Total_t} and Z_{A_t} were estimated as the sum of the variances (Cochran 1965):

$$SE_{Z_{Total_t}} = \sqrt{\frac{S_{R_t}^2}{n_t} + \frac{S_{Par_t}^2}{n_t}}$$

and

$$SE_{Z_{A_t}} = \sqrt{\frac{S_{J_t}^2}{n_{J_t}} + \frac{S_{R_t}^2}{n_t}}$$

respectively. The variance estimates ($S_{R_t}^2$, $S_{Par_t}^2$) of adult recruitment and spawning stock size were calculated from the log transformed estimates from the daily lift rates at the Holyoke Dam, where n_t is the total number of days in which 99% of the American shad were lifted. The variance ($S_{J_t}^2$) about the juvenile abundance estimates (J_t) was based on the log transformed catches per seine haul from all stations and collection dates, where n_{J_t} is the total number of seine hauls made in that year.