

Abstract.—Eggs and yolk-sac larvae of bay anchovy, *Anchoa mitchilli*, were surveyed at seven sites in Chesapeake Bay on 12 days in July 1991 to estimate abundances and mortality rates of daily cohorts and the relative biomasses of adults that spawned them. An objective was to determine variability in abundance and mortality rates among sites and survey dates. Estimated abundances of eggs spawned each day and their hourly mortality rates were considered in relation to 1) in situ predator abundances, 2) environmental factors, and 3) initial egg and yolk-sac larval abundances. The mean initial abundance of bay anchovy eggs on each day during the 12 experiments was 6,630 eggs/m² (427.0/m³). Mean initial abundance of yolk-sac larvae was 385 larvae/m² (24.6/m³). Mean adult biomass at the survey sites, estimated from the egg productions, was 18.0 g/m² (1.16 g/m³). A correlation analysis indicated that spawning by bay anchovy may be most intense in areas with high zooplankton biomass and where the ctenophore *Mnemiopsis leidyi*, a potential predator on eggs and larvae, was least abundant. Mean cohort instantaneous egg mortality was 0.066 eggs/h; on average, 73% of spawned eggs died before hatching. Yolk-sac larvae incurred a mean cohort instantaneous mortality of 0.053/h, i.e. 64% mortality during the first 24-h posthatch. Together, the mean egg and yolk-sac larval mortality rates indicated that >93% of bay anchovy daily cohorts die within 2 days after egg fertilization and before larvae reach the first-feeding stage. The range of cohort-specific mortality rates at a single station sampled on five consecutive days was equal to that observed at the seven sites. The high abundances, combined with high and variable cohort mortality rates, emphasize the probable importance of the egg and yolk-sac larval stages in the recruitment process of bay anchovy.

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Cohort abundances and daily variability in mortality of eggs and yolk-sac larvae of bay anchovy, *Anchoa mitchilli*, in Chesapeake Bay

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Most marine and estuarine fishes are highly fecund and spawn pelagic eggs that suffer high mortalities (Dahlberg, 1979; McGurk, 1986; Pepin, 1991). Historically, an estimation of in situ mortality rates of fish eggs and yolk-sac larvae has been problematic because of their temporally and spatially patchy distributions (Fortier and Leggett, 1985; Heath, 1992). However, it is important to obtain such estimates because the magnitude and variability of mortalities potentially can affect recruitment levels and contribute to fluctuations in stock abundance (Houde, 1989a).

Bay anchovy, *Anchoa mitchilli*, is the most abundant fish in estuar-

ies and bays along the east coast of the United States (Hildebrand and Schroeder, 1928; Bigelow and Schroeder, 1953; Houde and Zastrow, 1991). The species is euryhaline and occurs in habitats as diverse as tidal freshwater tributaries and continental shelf waters. In most estuaries, including the Chesapeake Bay, the bay anchovy is an important trophic link between plankton and piscivores (Baird and Ulanowicz, 1989; Luo and Brandt, 1993). Its eggs and larvae dominate summer ichthyoplankton collections from Chesapeake Bay, accounting for 99% of the

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eggs and ~70% of the larvae (Dovel, 1971; Olney, 1983).

Recruitment variability in anchovies is hypothesized to result from variable stage-specific mortality (Lasker 1985b; Smith 1985). If bay anchovy egg and yolk-sac larvae experience both high and variable stage-specific mortalities, the effect on annual recruitment could be substantial. Crude estimates of daily mortality of eggs and yolk-sac larvae ranged from 26% to 97% in Biscayne Bay, Florida, whereas mortality rates of feeding-stage larvae were lower, averaging 30%/d (Leak and Houde, 1987). To obtain reliable estimates of mortality during the short egg and yolk-sac larval stages (about two days total) of bay anchovy, it is necessary to sample repeatedly a daily cohort of eggs or yolk-sac larvae throughout a 24-h period. Our surveys followed that plan during twelve days on Chesapeake Bay in which mortalities were estimated in relation to biotic or abiotic factors that may have affected the rates. By restricting the study to cohorts of eggs and prefeeding yolk-sac larvae, the calculated mortalities must, therefore, have resulted primarily from causes other than starvation.

In Chesapeake Bay, bay anchovy is sexually mature at 40 mm fork length (FL), 10 months after hatching (Zastrow et al., 1991), and seldom lives beyond age 2 (Wang, 1992; Newberger and Houde, 1995). It is a serial spawner (Luo and Musick, 1991; Zastrow et al., 1991) and has a reproductive season in Chesapeake Bay that extends from May until September. Peak spawning occurs in July (Dalton, 1987) when virtually all females spawn nightly (Zastrow et al., 1991). Age-1 females produce most eggs (Zastrow et al., 1991), which hatch into yolk-sac larvae at approximately 20–24 h after fertilization. The yolk-sac larval stage also is short, with a duration of about 24 h (Houde and Zastrow, 1991).

The high abundances, serial spawning, and the presence of a single cohort of eggs on each day for this species allowed for repeated estimates of cohort-specific mortality rates within one season and for investigations into the factors that may affect variability in the rates. The four objectives of the study were as follows: 1) to estimate daily-cohort abundances and variability of bay anchovy eggs and yolk-sac larvae in selected areas of Chesapeake Bay; 2) to estimate mortality rates and variability of daily cohorts of bay anchovy eggs and yolk-sac larvae; 3) to relate densities of two potential predators—the scyphomedusan *Chrysaora quinquecirrha*, and the ctenophore *Mnemiopsis leidyi* (as well as environmental variables)—to anchovy egg and yolk-sac larval mortality rates; and 4) to estimate relative spawning-stock biomasses of bay anchovy at the experimental sites.

Materials and methods

Sampling design

After determining that anchovy eggs were present in test lifts of a plankton net, daily experiments were conducted at seven sites (Fig. 1) to estimate mortality rates of bay anchovy. Once a site had been selected, samples were obtained at 2-h intervals to estimate abundances of eggs and yolk-sac larvae. The sites were defined by the drift patterns of concurrent free-drifting mesocosm studies (Houde et al., 1994), which were initiated when the sites were selected. Each sample for this study was taken adjacent to free-drifting mesocosms. The mesocosms, which were 5 m in length and 1 m in diameter, acted as drogues and were assumed to drift with the water mass that was originally sampled. Each experiment consisted of 8 to 12 duplicate lifts of a plankton net. Water depths at the seven sites generally ranged from 10 to 25 m. Based upon the mesocosm drift tracks (Fig. 2), the mean area of the Bay included in an individual experiment was 59.8 km².

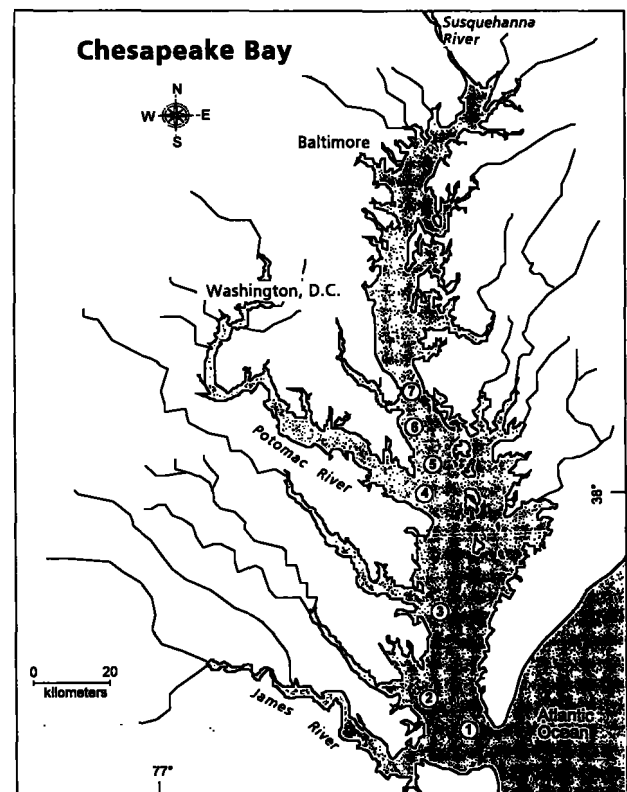


Figure 1
Chesapeake Bay and the seven sampling sites.

Collections

Collections were made from the research vessel *RV Henlopen* during the periods 2–9 July and 18–24 July 1991, the peak of the spawning season for bay anchovy. The lower Chesapeake Bay (sites 1–4) was surveyed on the first cruise and the mid-Bay (sites 5–7) was surveyed on the second cruise (Fig. 1).

Anchovy eggs and larvae were collected in a 40-cm diameter plankton net with 280- μm meshes. A flowmeter in the net mouth was used to determine the volume of water sampled. Vertical lifts of the net from near bottom (never deeper than 25 m) to the surface were made at 1 m/sec. The mean volume sampled in 312 net lifts was 3.00/m³ (SD=1.38/m³). Upon collection, samples were immediately preserved in 5% formalin-seawater. At each experimental site, sampling began between 0000 and 0400 h local time, shortly after peak spawning had occurred on each day. Duplicate samples were collected at 2-h inter-

vals until approximately 2100 h. By sampling at 2-h intervals we documented declines in abundances of eggs and yolk-sac larvae from which mortality rates of daily cohorts were estimated. In this way, the level of mortality and its variability were determined for 12 daily cohorts.

Abundances of gelatinous predators were estimated from collections in a 60-cm, 280- μm mesh, opening and closing net. Collections were made in partitioned oblique tows: 1) from near-bottom to the pycnocline; and 2) from the pycnocline to the surface. They were made ~12 times daily adjacent to the drifting mesocosm array and concurrent with collections of anchovy eggs and larvae. Total biovolumes of *C. quinquecirrha* and *M. leidy* >10 mm diameter in each sample were measured immediately upon collection.

Salinity, temperature, dissolved oxygen, and chlorophyll *a* fluorescence were determined from surface-to-bottom casts of a conductivity-temperature-depth (CTD) probe. Mean values during each 24-h experiment were based upon three to five CTD casts. Position data for plankton samples and CTD casts were logged by the vessel's navigation system to delineate drift tracks of the mesocosm deployments and the locations of sampling stations.

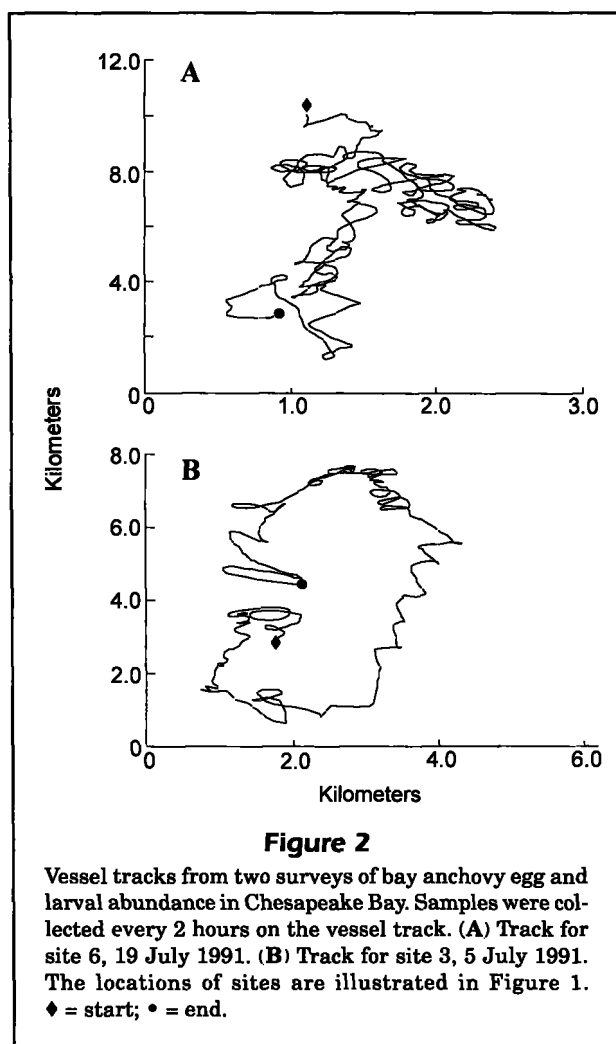
In the laboratory, fish eggs and larvae (yolk-sac and older) were removed from all samples. Eggs were identified and counted. Yolk-sac larvae were sorted, identified, and separated on the basis of ≥ 6 samples from each day's collections.

Settled volumes of zooplankton from the 40-cm net collections, determined from a minimum of three samples each day, were recorded and expressed as mL under 1 m² of bay surface. The zooplankton in the 280- μm mesh net potentially represented prey of adult bay anchovy, rather than prey of first-feeding larvae.

Egg and yolk-sac larval abundance

Densities (number/m³) and abundances (number under 1.0/m²) of anchovy eggs and yolk-sac larvae in each sample were estimated. Duplicate samples, collected between 0000 and 0600 h, were examined to determine the sample pair on each day which had the maximum abundance of eggs or yolk-sac larvae. Those samples provided an estimate of the mean "initial abundance" for each experiment. The decline in abundance over the next 18 to 20 h was a measure of mortality.

Some yolk-sac larvae are extruded through 280- μm meshes. However, abundances of yolk-sac larvae, which are of uniform length (approximately 2.0 mm), were not adjusted for extrusion in this analysis be-



cause mortality estimates presumably were not affected by consistent proportional losses. Adjustments to estimate actual yolk-sac larval abundances could be obtained by multiplying the uncorrected abundances by 2.3, the adjustment factor derived from paired collections in 280- μm and 53- μm mesh nets (MacGregor, 1994).

Mortality

Because bay anchovy eggs are abundant in Chesapeake Bay and hatch <24 h after being spawned, an intensive ichthyoplankton survey could derive mortality estimates for a daily cohort of eggs or yolk-sac larvae on the basis of the decline in their abundances on a single day. By using this approach, daily mortality rates were estimated. Hourly instantaneous mortality rates of eggs and yolk-sac larvae were estimated from a log-linear fit of the exponential model: $N_t = N_0 e^{-Zt}$, where N_t is the abundance (number under $1/\text{m}^2$) of a cohort at time t , N_0 is its initial abundance (number under $1/\text{m}^2$), Z is the instantaneous mortality coefficient (per h), and t is the time elapsed (h) since the initial abundance estimate.

Estimates of daily cohort abundances and mortality rates of eggs and yolk-sac larvae were compared among days, an approach seldom possible in research on species with eggs that have longer development times. Some losses due to diffusion or transport of eggs and larvae out of the sampling areas may have occurred. However, such losses were minimized by the short period over which each cohort was sampled (≤ 1 d) and because sampling was directed by the drift of mesocosms that tracked the initially sampled water mass.

Egg production and adult biomass

We obtained an estimate of adult biomass from estimates of egg production, knowledge of adult fecundity, and spawning frequency. Egg production, when divided by relative fecundity (mean number of eggs spawned per gram of female), provides an estimate of adult female biomass (Saville, 1964). Biomass of serial-spawning fishes such as bay anchovy can be estimated by single-survey methods of egg production (Lasker, 1985a; Parker, 1985; Eltink¹). Parker's (1985) formulation to estimate adult biomass is

$$B = E_d / (F_{bw} \times S \times R),$$

where B = adult biomass (g);
 E_d = daily egg production;
 F_{bw} = mean batch fecundity per female;
 S = spawning fraction (i.e. the fraction of females that spawned on the sampling date); and
 R = the proportion of the population that is female.

Batch fecundities and spawning fraction of bay anchovy were based upon estimates by Zastrow et al. (1991) who reported that batch fecundity (F_{bw}) was 687.1 ova per gram of ovary-free female weight and that spawning fraction (S) was 1.0 during July in Chesapeake Bay. We assumed that the proportion of adult females (R) was 0.5, on the basis of trawling data (Newberger and Houde, 1995), which indicated a mean female:male ratio of 1.02:1.00. Thus, relative adult biomass (g/m^2) at each site was about twice the relative female biomass.

Predators and other factors

Egg and yolk-sac larval abundances were examined in relation to environmental variables. Possible correlations between egg or yolk-sac larval abundances and biovolumes (mL/m^2) of two gelatinous predators (ctenophore *M. leidyi* and scyphomedusa *C. quinquecirrha*) were analyzed because Cowan and Houde (1992, 1993) and Purcell et al. (1994) indicated that these dominant species were important predators on bay anchovy eggs and larvae. Bay anchovy apparently is not cannibalistic (Klebasco, 1991), and other major predators have not been identified. Possible correlations between egg or yolk-sac larval abundances and zooplankton biomasses also were examined.

Statistical analyses

When assumptions for parametric tests were met, Analysis of Variance (ANOVA) was used to test for differences among daily surveys in initial egg abundances, zooplankton biomasses, and gelatinous predator biovolumes. An ANOVA also was used to determine if means of those variables differed among the five surveys carried out at site 5 (Fig. 1). When ANOVA results were significant, individual means were compared by using the a posteriori Student-Newman-Keuls (SNK) multiple-comparison procedure.

The estimates of hourly instantaneous mortality rates of eggs and yolk-sac larvae were the regression coefficients in the log-linear models relating \log_e abundance to elapsed time. Egg mortality was calculated from collections made between 0200 and 2000 h because eggs hatch in ~20 h. Yolk-sac larval mor-

¹ Eltink, A. 1991. Horse mackerel egg production and spawning stock size in the North Sea in 1990. Int. Coun. Explor. Sea, Council Meeting 1991/H:27, 14 p.

tality was calculated from collections made between 0000 and 2400 h. Each of the duplicate samples was treated as a separate data point in regression analysis. An SNK test was applied following the regression analyses to determine which of the instantaneous mortality rates of eggs and yolk-sac larvae differed significantly from each other. In several cases the estimated mortality coefficients did not differ significantly from zero at the $P = 0.05$ level. These coefficients were retained in our overall analysis of mortality rates and comparisons among sites because we assumed that low, near-zero rates may occur and that such estimates did characterize low rates of loss at some sites.

Pearson product-moment correlation coefficients were calculated for mortality rates and selected biotic variables. Possible correlations between egg or yolk-sac larval mortality rates and initial abundances, zooplankton biomasses, and gelatinous predator biovolumes, were examined.

Results

Hydrography

Mean values of temperature, salinity, oxygen, and chlorophyll *a* fluorescence at 3-m depth are summarized in Table 1. Chlorophyll *a* fluorescence tended

to increase in a south-to-north direction. Both temperatures and chlorophyll *a* fluorescence peaked at site 5 (Fig. 1). Depth profiles of salinity and oxygen, although not illustrated, indicated increasing stratification in a south-to-north direction and nearly anoxic conditions near-bottom at sites 5, 6, and 7.

Initial egg abundance and adult biomass

Initial egg abundances of daily cohorts during each of the 12 experiments were high and variable, ranging from 935 to 18,277 eggs/m² (Table 2). The mean initial abundance was 6,630 eggs/m² (427.0/m³). The initial abundances of eggs differed significantly among experiment dates (ANOVA, $P < 0.0002$) and probably among sites, although most sites were sampled on only one day. The highest initial egg abundance, 18,277 eggs/m², was observed at site 7, the northernmost site (Fig. 1).

The mean relative adult biomass (± 2 standard error [SE]), estimated from the initial cohort abundances of eggs, was 18.0 g/m² (± 8.0 SE). Biomass estimates varied widely among experiments and sites, ranging from 2.5 to 49.3 g/m² (Table 2).

Initial yolk-sac larval abundance

The mean initial abundance of cohorts of yolk-sac larvae was approximately 17 times less than initial

Table 1

Summary of sampling data for bay anchovy, *Anchoa mitchilli*, in Chesapeake Bay, 3–24 July 1991. Data include estimated relative biomass (B) of adult bay anchovy; mean daily biovolumes (mL/m²) of *Mnemiopsis leidyi* (CTV), *Chrysaora quinquecirrha* (CHV), and zooplankton (ZP), mean daily temperature (TMP); salinity (SLT); oxygen concentration (OXY); and chlorophyll *a* fluorescence (FLR) at 3-m depth. Identical superscripts on means indicate no significant ($P > 0.05$) difference (SNK pairwise comparison procedure). Locations of sites are indicated in Figure 1.

July date	Site	B g/m ²	CTV mL/m ²	CHV mL/m ²	ZP mL/m ²	TMP °C	SLT PSU	OXY mg/L	FLR mg/m ²
3	1	33.1	0.0 ^b	0.0 ^b	15.3 ^{ab}	26.4 ^a	22.3 ^a	8.04 ^a	0.82 ^b
4	2	15.0	0.0 ^b	0.0 ^b	16.4 ^{ab}	26.2 ^a	20.9 ^{ab}	7.87 ^a	1.53 ^b
5	3	10.6	0.0 ^b	0.0 ^b	17.1 ^{ab}	26.5 ^a	18.3 ^{bc}	9.35 ^a	1.10 ^b
7	4	2.5	484.4 ^a	128.4 ^a	7.2 ^b	26.6 ^a	14.6 ^{cd}	7.47 ^a	1.47 ^b
8	4	5.3	470.8 ^a	36.6 ^b	6.8 ^b	26.6 ^a	14.8 ^{cd}	6.44 ^a	0.90 ^b
18	7	49.3	32.5 ^b	41.8 ^b	20.3 ^a	27.3 ^a	14.3 ^{cd}	6.63 ^a	15.7 ^{ba}
19	6	15.5	24.4 ^b	35.7 ^b	15.0 ^{ab}	25.2 ^a	13.0 ^d	8.26 ^a	15.8 ^{ba}
20	5	19.6	30.6 ^b	6.8 ^b	10.6 ^{ab}	28.0 ^a	15.4 ^{cd}	6.01 ^a	11.0 ^{ba}
21	5	35.9	49.39 ^b	18.6 ^b	13.4 ^{ab}	28.0 ^a	15.4 ^{cd}	6.42 ^a	18.4 ^a
22	5	5.7	129.0 ^b	19.5 ^b	12.2 ^{ab}	28.5 ^a	15.3 ^{cd}	6.92 ^a	15.9 ^{ba}
23	5	9.2	278.6 ^{ab}	39.8 ^b	10.6 ^{ab}	26.6 ^a	13.9 ^{cd}	7.85 ^a	23.7 ^a
24	5	13.7	368.9 ^{ab}	22.3 ^b	18.8 ^{ab}	28.7 ^a	15.6 ^{cd}	5.41 ^a	25.3 ^a
Mean		18.0	155.7	29.1	13.6	27.1	16.1	7.22	11.0
Standard error		4.0	52.8	10.1	1.2	0.3	0.8	0.31	2.6

mean egg abundance. In the 12 experiments, initial yolk-sac larval abundances ranged from 56 to 781/m² with a mean of 385/m² (24.6/m³ SE) (Table 2). Mean abundances differed significantly among ex-

periments (ANOVA, $P < 0.002$). The highest abundance of yolk-sac larvae was observed at site 7, where eggs also were most abundant (Table 2).

Gelatinous predator biovolumes

The above-pycnocline biovolumes of gelatinous zooplankters were highly variable among experiments, ranging from 0 to 612.8 mL/m² (Table 1). Ctenophore *M. leidy* biovolumes ranged from 0 to 484.4 mL/m² and scyphomedusan *C. quinquecirrha* biovolumes ranged from 0 to 128.4 mL/m². The mean biovolume of *M. leidy* was 4 times higher than that of *C. quinquecirrha*. Biovolumes of each species were highest at site 4 (ANOVA, $P < 0.0001$), near the mouth of the Potomac River (Table 1; Fig. 1).

Zooplankton biomass

Zooplankton biovolumes from the 280- μ m net ranged from 6.8 to 20.3 mL/m², mean = 13.6 mL/m². The two lowest zooplankton biovolumes (ANOVA, $P < 0.02$) were observed at site 4 (Table 1; Fig. 1), where gelatinous zooplankton biovolumes were highest. The highest zooplankton biovolume occurred at site 7, coincident with highest anchovy egg and yolk-sac larvae abundances.

Egg and yolk-sac larvae mortality rates

The overall mean instantaneous mortality rate for eggs was 0.066/h. The estimates, which ranged from 0.001 to 0.185/h, represent stage-specific (20-h) mortalities of 2% to 98%. The highest egg mortality rates (>0.10/h) were estimated on 3, 22, and 24 July (Figs. 3 and 4; Table 2). If only the seven rates judged to be significantly different from zero ($P < 0.05$) are included in the analysis, the mean mortality was 0.094/h (SE=0.017).

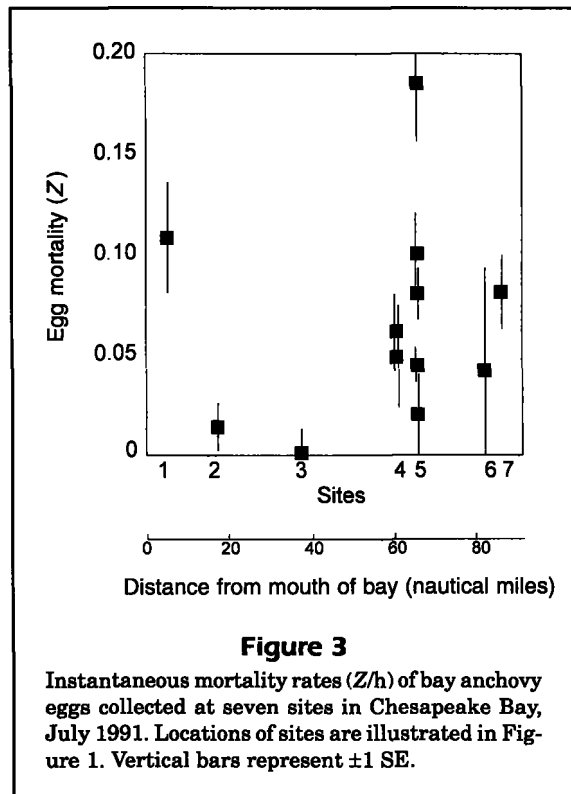
The overall mean mortality rate of yolk-sac larvae was 0.053 larva/h. The yolk-sac larval rates, which ranged from 0.017 to 0.177/h, represent daily mortality rates of 33.5 to 98.6%. The highest yolk-sac larval mortality rates (>0.07/h) were estimated on 5, 7, and 22 July. If only the four rates judged to be significantly different from zero ($P < 0.05$) are included in the analysis, the mean mortality rate was 0.077/h (SE=0.035/h).

The mortality estimates differed among the daily surveys. Rates were estimated with low precision, possibly because the eggs and larvae were distributed in patches within each sampling site. The standard errors of yolk-sac larval mortality rates were relatively high at sites between the mouth of the Chesapeake Bay and the Potomac River (sites 1–4)

Table 2

Estimated hourly mortality rates and standard errors (SE) for egg (Z) and yolk-sac larvae (Z_L), initial egg abundances (N_0) and initial yolk-sac larval abundances (NL) of bay anchovy, *Anchoa mitchilli*, on 12 days during the period 3–24 July 1991. Identical superscripts on mortality rates and initial abundances indicate no significant ($P > 0.05$) difference (SNK pairwise comparison procedure). Asterisks indicate that regression coefficients of \log_e abundances regressed on time (h), from which Z and Z_L estimates were obtained, differed significantly from zero at $P = 0.05$ level.

July date	Site	Z/h	$SE_{Z/h}$	N_0/m^2	n	r^2
Eggs						
3	1	*0.108 ^{ab}	0.027	12,214 ^{bc}	16	0.54
4	2	0.014 ^{ab}	0.015	5,521 ^d	18	0.05
5	3	0.001 ^{ab}	0.012	3,891 ^d	19	0.10
7	4	0.049 ^a	0.027	935 ^d	20	0.15
8	4	*0.062 ^{ab}	0.021	1,966 ^d	20	0.32
18	7	*0.081 ^b	0.020	18,277 ^a	19	0.50
19	6	0.042 ^{ab}	0.055	5,708 ^{cd}	19	0.04
20	5	*0.080 ^{ab}	0.013	7,245 ^{bcd}	20	0.67
21	5	0.020 ^{ab}	0.027	13,237 ^{ab}	20	0.02
22	5	*0.100 ^a	0.021	2,118 ^d	20	0.55
23	5	*0.045 ^b	0.012	3,402 ^d	20	0.44
24	5	*0.185 ^b	0.028	5,044 ^{cd}	20	0.77
Mean		0.066		6,630		
Standard error		0.014		1,462		
July date	Site	Z_L/h	$SE_{Z_L/h}$	NL/m^2	n	r^2
Yolk-sac larvae						
3	1	*0.057 ^{ab}	0.049	422 ^{bc}	7	0.18
4	2	0.040 ^b	0.048	222 ^d	8	0.11
5	3	0.082 ^b	0.064	614 ^{ab}	9	0.19
7	4	*0.177 ^{ab}	0.018	162 ^{cd}	6	0.96
8	4	0.017 ^{ab}	0.052	56 ^d	7	0.02
18	7	*0.036 ^b	0.009	781 ^a	11	0.66
19	6	0.022 ^{ab}	0.019	605 ^{ab}	8	0.19
20	5	0.022 ^a	0.028	380 ^{bcd}	6	0.14
21	5	0.058 ^{ab}	0.027	430 ^{bc}	9	0.39
22	5	*0.072 ^{ab}	0.015	289 ^{bcd}	11	0.72
23	5	0.028 ^b	0.018	364 ^{bcd}	8	0.27
24	5	0.030 ^{ab}	0.021	299 ^{bcd}	8	0.25
Mean		0.053		386		
Standard error		0.012		56.7		



compared with sites farther north (Table 2; Fig. 1). Observed variability in mortality rates was approximately equal for eggs and yolk-sac larvae. Coefficients of variation (ratio of standard deviation to mean) were 0.73 and 0.79 for eggs and yolk-sac larvae, respectively.

The regression coefficients, which were the estimates of mortality rates, did not differ significantly from zero at the $\alpha = 0.05$ level in five of the twelve \log_e egg abundance-on-time regressions and eight of the twelve yolk-sac larva regressions. The yolk-sac larval regressions were based upon relatively few data points, which contributed to their lower precision (Table 2). The nonsignificant ($P > 0.05$) mortality coefficients corresponded to low, near-zero regression coefficients. Although not significantly different from zero, these coefficients were presumed to estimate mortality rates.

Correlations

There were several simple correlations among organism abundances, biovolumes, and mortality rates (Table 3). Most notable were 1) the positive correlation between yolk-sac larval mortality rate and *C. quinquecirrha* biovolume ($P < 0.01$); 2) the positive correlations between egg abundance, yolk-sac larval abundance, and zooplankton biovolume ($P < 0.05$); and

3) the negative correlations between both egg and yolk-sac larval abundances and *M. leidy* biovolume ($P < 0.05$).

Discussion

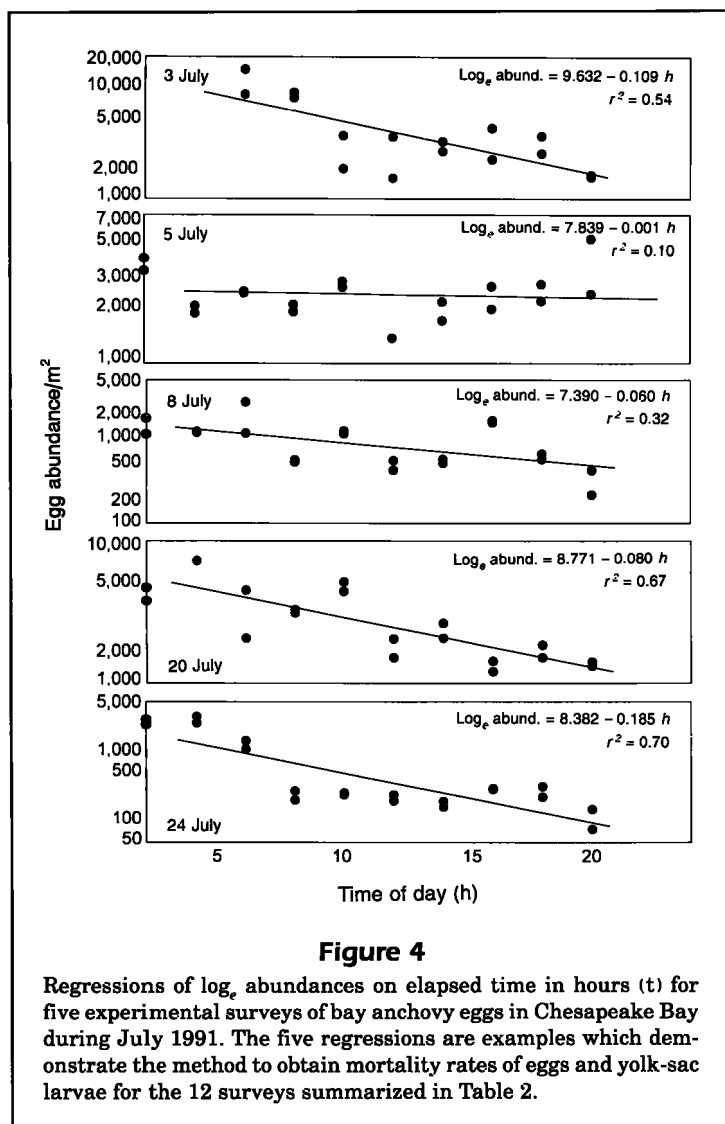
Daily cohorts of bay anchovy were demonstrated to suffer high and variable mortality during egg and yolk-sac larval stages. Our estimates of mortality rates indicate both day-to-day and regional variability in Chesapeake Bay. At site 5, which was sampled on five consecutive days, the range of egg mortality rates exceeded the range observed over all remaining sites. The high variability at a single site suggests that environmental conditions were changing daily. Variability in initial egg abundances indicated that numbers of adult spawners in the area also were changing on a daily basis.

Our egg-stage mortality rates ranged from 2% to 98%, and averaged 73%. Recent experiments in free-drifting mesocosms (Houde et al., 1994) conducted at the same sites and dates of surveys reported here have also provided estimates of mortality of bay anchovy eggs and yolk-sac larvae. The mesocosms, which included gelatinous predators, provided mean estimates of mortality that were essentially identical to those reported here. In Great South Bay, New York, Castro and Cowen (1991) reported that seasonal mortality rates of combined bay anchovy eggs and yolk-sac larvae ranged from 70% to 98%/d. If eggs in Great South Bay hatched in 20 h, the mortality rates on eggs alone may have ranged from 63.0% to 96.5%/d. In Biscayne Bay, Florida, Leak and Houde (1987) compared seasonal abundances of eggs and yolk-sac larvae of bay anchovy and estimated that

Table 3

Matrix of correlation coefficients for bay anchovy, *Anchoa mitchilli*, where *Z* is hourly egg mortality rate, *ZL* is hourly yolk-sac larvae mortality rate, *N* is initial abundance of eggs, *NL* is initial abundance of yolk-sac larvae, *CTV* is biovolume in mL/m^2 of *M. leidy*, *CHV* is biovolume in mL/m^2 of *C. quinquecirrha*, *ZP* is zooplankton biovolume in mL/m^2 . Asterisks indicate significant correlation ($P < 0.05$).

	<i>Z</i>	<i>ZL</i>	<i>N</i>	<i>NL</i>	<i>CTV</i>	<i>CHV</i>
<i>ZL</i>	-0.19					
<i>N</i>	+0.07	-0.28				
<i>NL</i>	-0.12	-0.20	+0.66*			
<i>CTV</i>	+0.29	+0.30	-0.57*	-0.68*		
<i>CHV</i>	-0.04	+0.67*	-0.28	-0.26	+0.68*	
<i>ZP</i>	+0.22	-0.30	+0.58*	+0.70*	-0.59*	-0.49



mean daily egg mortality was 86%, with a range of 26% to 97%.

Egg mortality rates of bay anchovy obviously are high. But, they are lower than predicted at their temperature of development (27°C), based upon Pepin's (1991) temperature-dependent mortality model, $Z = 0.030 e^{0.187T}$, in which Z is the daily instantaneous mortality rate for marine fish eggs and T is temperature (°C). At 27°C the model predicts a mortality of $Z = 3.91$ (=0.16/h), a rate more than twice our mean estimate of $Z = 1.58/d$ (=0.066/h). Pepin's (1991) model for marine fish eggs predicts mortality rates of $Z = 2.81$ to 4.63/d for temperatures in the range 25.23°C to 27.99°C which were observed during this study. These predicted mortality rates are higher than all except one of our estimated rates and are also higher than rates estimated for bay anchovy eggs by Leak

and Houde (1987) in Biscayne Bay, Florida. Castro and Cowen (1991) determined mortality of bay anchovy eggs and yolk-sac larvae at lower average temperatures in Great South Bay. At their two-year mean of 23.4°C, they estimated a mean mortality rate of 2.36/d, a value rather close to Pepin's (1991) model-predicted 2.02/d. Pepin (1991) had suggested that species with short development times (i.e. high temperatures) may have lower than predicted daily mortality rates because of their relatively short exposure to predators.

Mortality rates for bay anchovy eggs are higher and perhaps more variable than rates reported for eggs of other anchovy species. Only the Peru anchoveta, *Engraulis ringens*, has been reported to experience similar daily egg mortality rates, a consequence of cannibalism by adult anchoveta and of high predation rates by other pelagic fish (Smith et al., 1989). The reported stage-specific egg mortalities of other anchovies, while high, probably do not exceed 50% to 60% (Dorsey and Houde²) and appear to be considerably lower than rates estimated for bay anchovy.

Instantaneous mortality rates for bay anchovy eggs also are higher than rates reported for most teleost fishes (Houde, 1989b; Houde and Zastrow, 1993). However, if stage-specific mortalities are compared, rather than daily rates, the bay anchovy resembles many fishes. For example, Harding et al. (1978) estimated that the mean mortality rate for plaice, *Pleuronectes platessa*, eggs was $Z = 0.075/d$ in the Southern Bight of the North Sea at mean temperature 5.65°C. Egg-stage duration of plaice is about 22 days (Coombs et al., 1990). Thus, the stage-specific egg mortality is $Z_{cum} = 1.65$, equivalent to 81%, and similar to that of bay anchovy ($Z_{cum} = 1.32$) despite the more than 20-fold difference in hourly rates (0.003 for plaice, 0.066 for bay anchovy).

Yolk-sac larvae are essentially embryos free of the chorion, and their expected mortality may be more comparable to eggs than to feeding-stage larvae. Our estimated mortality rates of bay anchovy yolk-sac larvae ranged from $Z = 0.41$ to 4.24/d (33.5 to 98.5%/d). The mean rate was $Z = 1.27/d$ (72.0%/d), a value nearly equal to the egg-stage mortality rate. Because the yolk-sac larval stage of bay anchovy is approximately one day in duration, the daily mortality rate is

² Dorsey, S. E., and E. D. Houde. 1992. Daily variability in mortality of bay anchovy, *Anchoa mitchilli*, eggs in Chesapeake Bay. Int. Coun. Explor. Sea, Pelagic Fish Committee, Council Meeting 1992/H:17, 11 p.

equivalent to a stage-specific rate. At 27°C, the mean stage-specific mortality of bay anchovy yolk-sac larvae ($Z=1.27$) is higher than the mortality predicted ($Z=0.77$) from the temperature-dependent model of Pepin (1991) for yolk-sac larvae of marine fishes.

There was a high degree of spatial and temporal variability in the abundances of bay anchovy eggs. The initial abundances of eggs varied among days (i.e. experiments) and probably among sites. Because repeated experiments were carried out only at sites 4 and 5, it was not possible to critically analyze among-site differences in egg abundances or their mortality rates. Some of the variation may be explained by adult distributions and spawning strategy; Luo and Musick (1991) hypothesized that bay anchovy spawns preferentially in areas with plentiful adult food. Our study supports their hypothesis because zooplankton biovolumes were positively correlated with initial anchovy egg abundances. Additionally, the two lowest initial egg abundances in our study occurred at site 4, which also had lowest zooplankton biovolumes; the highest egg abundance was observed at site 7, where highest zooplankton biovolume occurred.

Our estimates of relative adult biomasses may be considerably higher than actual mean biomasses of bay anchovy in Chesapeake Bay because we had selected survey sites with high egg abundances. Our criterion for selecting sampling sites was the obvious presence of bay anchovy eggs in test tows. This criterion probably accounts for the high biomass estimates. Our mean biomass estimate, 1.16 g/m^3 (18.0 g/m^2), equates to approximately one adult anchovy per m^3 . In a concurrent study of bay anchovy in the mid and upper Chesapeake Bay, acoustics-adjusted trawl abundances in July 1991 indicated a mean adult biomass of 0.58 g/m^3 (Wang and Houde, 1995).

Initial mean abundance of cohorts of yolk-sac larvae, uncorrected for the extrusion of a fraction of larvae through the 280- μm net meshes, equaled $385.4/\text{m}^2$ ($24.6 [\pm 6.0]/\text{m}^3$). This unadjusted abundance was approximately 17 times lower than the initial mean abundance of egg cohorts. If yolk-sac larvae abundances were adjusted upward by the factor (2.3) required to correct them (MacGregor, 1994), the difference between initial egg and yolk-sac larvae abundances reduces to a factor of 5.8. The observed mean initial abundance of yolk-sac larvae, after adjustment, based upon our mean egg mortality rate ($0.066/\text{h}$), was still only 50% of that expected. However, because eggs hatch at ca. 2000 h and the initial yolk-sac larval abundance was estimated at ca. 0230 h, continuing mortality would have caused further declines in yolk-sac larval numbers for 6.5 h before samples were taken. Applying the mean yolk-sac larval mortality rate ($0.053/\text{h}$) to the 6.5-h period fur-

ther reduced the mean discrepancy, although initial numbers of yolk-sac larvae were still 30% lower than expected. The cause of the remaining discrepancy, if real, was not identified but could have resulted if a fraction of the sampled eggs were infertile or dead.

Estimated biovolumes of two gelatinous predators of bay anchovy eggs and larvae, *M. leidyi* and *C. quinquecirrha*, were variable, probably patchy on temporal and spatial scales. Both have been demonstrated to be major consumers of bay anchovy eggs and larvae (Cowan and Houde, 1993; Purcell et al., 1994). There was a significant correlation between mortality of yolk-sac larvae and *C. quinquecirrha* biovolume (Table 3). Biovolumes of the two jellyfishes were highest at site 4, where lowest zooplankton biovolumes and lowest anchovy egg and larval abundances occurred. At the three southernmost sites (sites 1, 2, and 3 in Table 1), neither *M. leidyi* nor *C. quinquecirrha* were present. Despite their absence, there was no evidence that mortality rates of anchovy eggs or yolk-sac larvae were lower there than at sites with jellyfish present.

Spawning intensity by bay anchovy, indexed by initial abundances of egg cohorts, was lowest at site 4 where the gelatinous predator biovolumes were highest, raising a possibility that anchovy adults might avoid areas where zooplankton have been depleted on account of consumption by gelatinous predators. This suggests a mechanism that may indirectly reduce baywide predation mortality on anchovy eggs and larvae; this, in turn, is supported by the negative correlations between both egg and yolk-sac larval abundances and jellyfish biovolumes. The combined densities of *C. quinquecirrha* and *M. leidyi* were extremely high at site 4, near the mouth of the Potomac River, and possibly caused the depressed zooplankton biovolumes. Purcell (1992) noted that consumption by *C. quinquecirrha* depleted zooplankton in tributaries of Chesapeake Bay, but she reported smaller effects in the mainstem of the Bay.

An important conclusion of our study is that bay anchovy suffers highest mortality during its first two days after being spawned; on average, 73% of all spawned bay anchovy eggs in Chesapeake Bay died before hatching. Of the surviving 27%, approximately 72% perished during the 24-h yolk-sac larval stage. In July 1991 only 7.6%, on average, of each night's egg production survived until the first-feeding stage, which commences 2 days after hatching. Lasker (1985b) and Smith (1985) pointed out that fluctuations in yearly recruitment in engraulids may result from variable stage-specific mortality rates, which can be a consequence of interannual variability in both biotic and abiotic factors. Results of our study suggest that such factors also vary significantly on

much shorter, day-to-day, temporal scales and that interannual recruitment differences in species with life histories similar to bay anchovy could depend upon the variable conditions faced by daily cohorts during each summer's spawning season.

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