Recruitment and spawning-stock biomass distribution of bay anchovy (*Anchoa mitchilli*) in Chesapeake Bay*

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Abstract—Recruitment of bay anchovy (*Anchoa mitchilli*) in Chesapeake is related to variability in hydrological conditions and to abundance and spatial distribution of spawning stock biomass (SSB). Midwater-trawl surveys conducted for six years, over the entire 320-km length of the bay, provided information on anchovy SSB, annual spatial patterns of recruitment, and their relationships to variability in the estuarine environment. SSB of anchovy varied sixfold in 1995–2000; it alone explained little variability in young-of-the-year (YOY) recruitment level in October, which varied ninefold. Recruitments were low in 1995 and 1996 (47 and 31×10^9) but higher in 1997–2000 (100 to 265×10^9). During the recruitment process the YOY population migrated upbay before a subsequent fall-winter downbay migration. The extent of the downbay migration by maturing recruits was greatest in years of high freshwater input to the bay. Mean dissolved oxygen (DO) was more important than freshwater input in controlling distribution of SSB and shifts in SSB location between April–May (prespawning) and June–August (spawning) periods. Recruitments of bay anchovy were higher when mean DO was lowest in the downbay region during the spawning season. It is hypothesized that anchovy recruitment level is inversely related to mean DO concentration because low DO is associated with high plankton productivity in Chesapeake Bay. Additionally, low DO conditions may confine most bay anchovy spawners to the downbay region, where production of larvae and juveniles is enhanced. A modified Ricker stock-recruitment model indicated density-compensatory recruitment with respect to SSB and demonstrated the importance of spring-summer DO levels and spatial distribution of SSB as controllers of bay anchovy recruitment.

Recruitment for marine fishes is variable and is regulated or controlled by a combination of density-dependent and density-independent processes. It has been hypothesized that density-independent processes dominate from the egg to larval stages whereas density-dependent control by predation may be more important in the juvenile stage (Sissenwine, 1984; Houde, 1987). Density-dependent processes may be stock dependent, regulated by adult abundances, or dependent on abundances of the early-life stages (Ricker, 1975). In estuarine systems, where hydrological conditions (e.g. dissolved oxygen, temperature, and circulation) vary widely, the roles of density-independent physical factors on fish recruitments may be dominant, making it difficult, but still important, to partition density-dependent and density-independent processes, particularly for short-lived small pelagic fishes such as anchovies and sardines.

Bay anchovy (*Anchoa mitchilli*) (Engraulidae) is a coastal species distributed broadly in the western Atlantic from Maine to Mexico. This small fish is the most abundant and ubiquitous fish in Chesapeake Bay, the largest estuary on the east coast of North America (Houde and Zastrow, 1991; Able and Fahay, 1998). It is not fished, yet there is evidence that recruitment is variable (Newberger and Houde, 1995). It feeds on zooplankton—primarily copepods and other small crustacea—and is a major prey of piscivores, including several economically important fishes (Baird and Ulanowicz, 1989; Luo and Brandt, 1993;

Hartman and Brandt, 1995). Male and female bay anchovy in Chesapeake Bay mature at 40–45 mm fork length (44–50 mm total length) at about 10 months of age, and peak spawning occurs in July (Zastrow et al., 1991). Most eggs are produced by age-1 individuals (Luo and Musick, 1991; Zastrow et al., 1991). Bay anchovy may survive to age 3+ and reach approximately 100 mm length and 5 g wet weight (Newberger and Houde, 1995; Wang and Houde, 1995).

Newberger and Houde (1995) noted large differences in annual survey abundances of bay anchovy that apparently resulted from variability in annual recruitments. In Chesapeake Bay, abundance, growth, and mortality rates of bay anchovy eggs and larvae vary temporally and spatially (Dorsey et al., 1996; MacGregor and Houde, 1996; Rilling and Houde, 1999a, 1999b). Individual-based models were developed to test the hypothesis that recruitment of bay anchovy is determined by variable growth and mortality during early-life stages that are regulated by density-dependent processes (Wang et al., 1997; Cowan et al., 1999; Rose et al., 1999). In previous research, there was little knowledge of levels of spawning stock biomass or density-independent environmental factors that may control recruitment through their effects on spatial and temporal variability in growth and mortality of prerecruit anchovy.
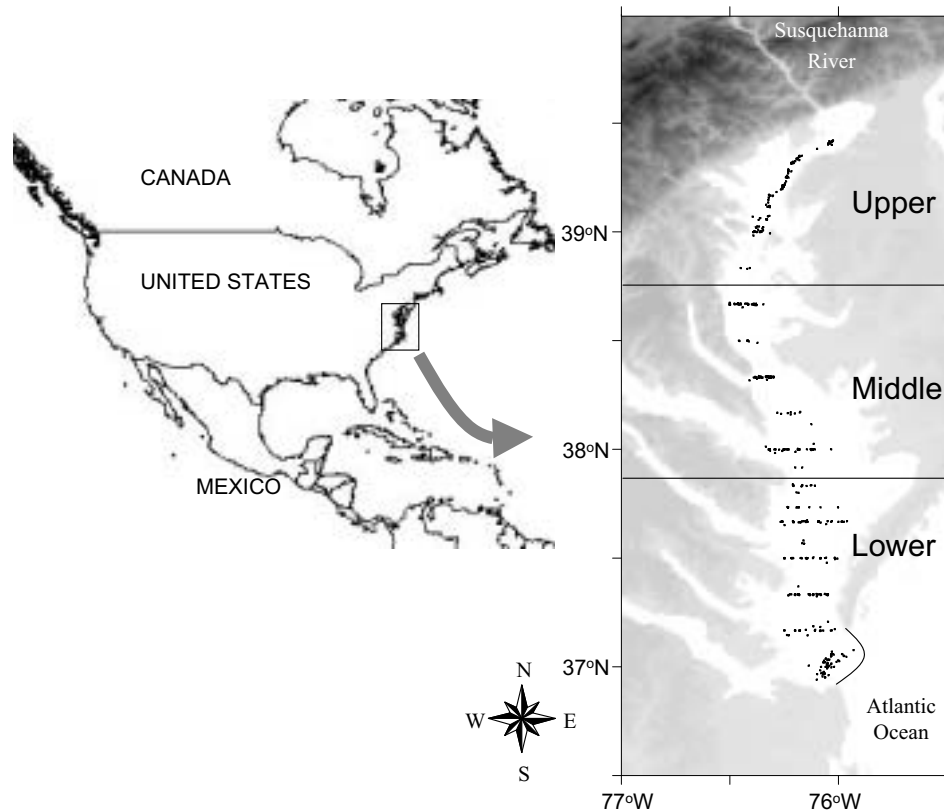
Figure 1

Chesapeake Bay and stations sampled by the midwater trawl in the 1995–2000 surveys. Horizontal lines indicate boundaries of three designated regions.

We evaluated environmental factors, spatial distribution of spawning stock biomass (SSB), and possible ontogenetic migrations of prerecruits (Dovel, 1971; Loos and Perry, 1991; Wang and Houde, 1995; Kimura et al., 2000) with respect to bay anchovy recruitment variability. Our objectives were 1) to estimate annual and regional variability in bay anchovy recruitment, 2) to evaluate effects of hydrological conditions (mainly, freshwater input, and dissolved oxygen concentration) on stage-specific distribution, ontogenetic migration, and recruitment, and 3) to identify mechanisms and describe patterns or trends in the bay anchovy recruitment process. Data were obtained in a six-year, multidisciplinary research program conducted throughout Chesapeake Bay.

Materials and methods

Study area

Chesapeake Bay is a coastal plain estuary of partially mixed fresh water and sea water. Its 320-km mainstem varies in width from about 6 to 50 km (Fig. 1). The Bay is shallow; less than 10% of its area is >18 m deep and approximately 50% is <6 m deep. More than 80% of the freshwater entering the bay is from tributaries on its northern and western sides

(Chesapeake Bay Program[1]). Salinity grades from near-full seawater at the mouth of the bay to freshwater near its head. Water temperatures reach 28–30°C in mid summer, and fall to 1–4°C in late winter (Murdy et al., 1997). Despite shallow depth, the bay usually has a strongly developed pycnocline, and has seasonally strong vertical gradients in temperature, salinity, and dissolved oxygen.

Surveys

Trawl surveys were conducted three times annually over the entire bay (April–May, June–August, and October), 1995–2000 (Table 1, Fig. 1). Midwater-trawl (MWT) fish collections[2] were made on transects in three regions: the lower bay (37°05′N–37°55′N), middle bay (37°55′N–38°45′N), and upper bay (38°45′N–39°25′N). As defined, the lower bay contains 51% of water volume, the middle bay 32%, and the upper bay 17% (Fig. 1). The number of midwater trawl sta-

Table 1

Cruise dates, mean temperatures (°C), salinities (psu), and dissolved oxygen (mg/L), integrated from surface to bottom, and pooled standard errors for individual cruises, years, seasons, and regions of Chesapeake Bay, 1995–2000. CV = coefficient of variation for annual means.

	Temperature	SE	Salinity	SE	Oxygen	SE
Cruise date (departure)						
28 Apr 95	13.88	0.11	15.01	0.42	8.53	0.13
23 Jul 95	28.13	0.12	15.48	0.44	6.50	0.14
28 Oct 95	17.26	0.12	17.39	0.45	7.59	0.14
28 Apr 96	13.87	0.10	10.84	0.36	10.21	0.11
17 Jul 96	24.66	0.11	11.80	0.41	7.43	0.13
22 Oct 96	16.10	0.10	11.26	0.36	8.55	0.11
20 Apr 97	10.93	0.13	11.41	0.50	10.01	0.16
11 Jul 97	25.28	0.13	13.59	0.51	7.10	0.16
29 Oct 97	14.64	0.13	18.19	0.51	8.01	0.16
11 Apr 98	12.26	0.12	8.90	0.44	9.95	0.14
04 Aug 98	26.15	0.12	12.89	0.46	7.01	0.15
19 Oct 98	18.60	0.13	16.64	0.49	8.64	0.15
19 Apr 99	11.97	0.13	13.51	0.49	10.04	0.16
26 Jun 99	23.52	0.15	16.02	0.56	5.75	0.18
23 Oct 99	16.30	0.14	17.38	0.53	8.87	0.17
29 Apr 00	12.95	0.17	12.51	0.64	8.98	0.20
25 Jul 00	24.26	0.14	14.06	0.53	5.17	0.17
17 Oct 00	17.89	0.15	16.73	0.56	7.63	0.18
Year						
1995	19.76	0.07	15.96	0.25	7.54	0.08
1996	18.21	0.06	11.30	0.22	8.73	0.07
1997	16.95	0.08	14.40	0.29	8.37	0.09
1998	19.00	0.07	12.81	0.27	8.53	0.08
1999	17.26	0.08	15.64	0.30	8.22	0.10
2000	18.36	0.09	14.43	0.33	7.26	0.11
CV	5.8%		12.5%		7.2%	
Season						
April–May	12.64	0.05	12.03	0.20	9.62	0.06
June–August	25.33	0.05	13.97	0.20	6.49	0.06
October	16.80	0.05	16.27	0.20	8.22	0.06
Region of bay						
Lower	18.40	0.04	21.19	0.16	8.15	0.05
Middle	18.33	0.05	14.06	0.19	8.33	0.06
Upper	18.04	0.06	7.02	0.23	7.85	0.07

tions per survey ranged from 24 to 52 (six-year total=597). Additional baywide surveys (August 1997 and September 1998) and partial surveys (June 1997, July 1998, and July 1999) also provided data (total stations =146).

An 18-m² mouth-opening midwater trawl (MWT), with 3-mm codend mesh was deployed from the stern of the 37-m research vessel *Cape Henlopen*. All trawling was conducted at night. Standardized tows of 20-min duration were conducted and the trawl was deployed at graded depth intervals from surface to bottom (2 minutes at each depth interval) in order to provide a sample of fish from the entire water column. Fish catches (or subsamples) were counted, measured (to the nearest 1.0 mm), and weighed on deck immediately after a tow.

Abundance and biomass of bay anchovy recruits and spawners

We separated bay anchovy catches into YOY and spawners based on total length (TL). The minimum length of bay anchovy retained by the MWT was 21 mm TL, which we also defined as the minimum TL for recruited YOY bay

anchovy. Modal lengths of young-of-the-year (YOY) bay anchovy cohorts were determined from length-frequency distributions in MWT catches and a modal analysis (Bhattacharya, 1967; King, 1995). Based on the modal analysis of summer and fall survey data, the maximum TL of YOY bay anchovy and, therefore, the minimum TL of spawners, were estimated (Table 2).

Length-dependent gear selectivity for bay anchovy was adjusted by comparing catches of the MWT and a 2-m² Tucker trawl with catches from 707-μm meshes at the same stations during a September 1998 baywide survey. The length-specific MWT:Tucker-trawl catch ratios (N_{MWT}/N_{TT}=catch per unit of effort MWT ÷ catch per volume of water Tucker trawl) for anchovies 21–70 mm TL indicated that both gears fished with a consistent selectivity for bay anchovy of 30–48 mm TL, and with a slight decrease in N_{TT} for 48–70 mm TL. However, the values of N_{MWT}/N_{TT} were lower by factors of 1~7 for 21–30 mm TL fish, indicating that small anchovies were collected less efficiently by the MWT. We concluded that length classes of anchovies >30 mm TL were equally vulnerable to the MWT and those >48 mm TL were less vulnerable to the Tucker trawl. Accordingly, we adjusted MWT catches of ≤30 mm TL anchovy by multiplying them by a weighting factor estimated from the regression of values of N_{MWT}/N_{TT} for 21–30 mm TL bay anchovy.

$$(\textit{Weighting factor}) = -0.59 \ TL + 19.08, \qquad (r^2=0.96)$$

where TL = total length.

The weighting factor equals 1.0 for anchovy >30 mm TL because MWT selectivity is constant for anchovy >30 mm TL. To estimate water sampled in a 20-min MWT tow,

$$D_N = N_{MWT}/V_{MWT} = (1/s) \times N_{TT}/V_{TT}$$

and

$$V_{MWT} = s \times (N_{MWT}/N_{TT}) \times V_{TT},$$

where D_N = the concentration of 31–48 mm TL bay anchovy at a station (i.e. number/m³);
N_{MWT} = the number of 31–48 mm TL bay anchovy collected per 20-min MWT tow at a station;
V_{MWT} = the effective water volume sampled by a 20-min MWT tow (m³);
N_{TT} = the number of 31–48 mm TL bay anchovy collected by the 2-m² Tucker trawl at the same station;
s = vulnerability to the Tucker trawl (s=1 if all bay anchovies in water volume, V_{TT}, are collected); and V_{TT} is the volume filtered by the Tucker trawl (m³) estimated from a flowmeter in its mouth.

The mean of N_{MWT}/N_{TT} for 30–48 mm TL bay anchovy during the September 1998 survey indicated that V_{MWT} = 4961 m³, if 30–48 mm TL bay anchovy did not significantly avoid the mouth of the 2-m² Tucker trawl (i.e. s=1). Assuming s=1 (i.e. V_{MWT}=4961 m³), we estimated "relative" bay-

Table 2
Estimated maximum total lengths of young-of-the-year bay anchovy (mm) from Chesapeake Bay, based on analysis of length-frequency distributions.

Year	Date	Length (mm)
1995	23 Jul	52
	28 Oct	69
1996	17 Jul	57
	22 Oct	68
1997	11 Jul	30
	2 Aug	56
	29 Oct	66
1998	4 Aug	50
	7 Sep	62
	19 Oct	69
1999	26 Jun	30
	23 Oct	65
2000	25 Jul	52
	17 Oct	67

wide abundance and biomass of YOY and spawners for the 18 surveys from 1995 to 2000.

To coarsely estimate a typical value of s, "absolute" baywide spawner biomasses in June–August were estimated for 1995–2000 according to an egg production method (Parker, 1985; Rilling and Houde, 1999a). Bay anchovy eggs had been collected in a 1-m² Tucker trawl during the same surveys and provided estimates of egg abundance. The coverage of stations and sampling design for the Tucker trawl was comparable to that of the MWT, but the Tucker trawl was deployed during both day and night. We presumed that all eggs collected between 00:00 and 20:00 h had been spawned near a midnight peak (00:00 h) (Zastrow et al., 1991) and decreased in abundance at a mean instantaneous mortality (reported for bay anchovy eggs in Chesapeake Bay as M = 0.066/h; Dorsey et al., 1996). Based on the estimated number of eggs spawned at 00:00 h for each station, the regional mean weight of individual spawners (defined by the minimum TL in Table 2) in MWT catches, and the reported fecundity-weight relationship for females (Zastrow et al., 1991), we were able to coarsely estimate "absolute" baywide spawner biomass. We assumed that the spawning fraction of adult females per day was essentially 1.0 (i.e. all adult females participated in spawning, Zastrow et al., 1991) and the fecundity-weight relationship was constant over years.

Comparison of the baywide estimates of spawner biomass in June–August based on the egg production method ("absolute" biomass) with estimates based on the MWT catch-per-unit-of-effort ("relative" biomass) indicated that, on average, for 1995 to 2000, s is equal to 0.20. Therefore, the mean effective water volume fished by a 20-min MWT tow was 4961×0.20 = 989 m³.

Because N_{MWT} of bay anchovy was highly variable, even at stations on the same sampling transect, and a mixed model (SAS version 6.12, SAS Inst. Inc., Cary, NC) including spatial covariance (variogram) did not significantly improve precision in annual, seasonal, and regional means or differences of N_{MWT}, a stratified sampling design (Steel and Torrie, 1980), i.e. stratum = region, was adopted. Based on the mean effective water volume (= $s \times V_{MWT}$), we estimated regional "absolute" abundance and biomass (number and wet weight) and related standard errors of the linear combination by regional subvolumes (Samuels, 1989) of bay anchovy ≥21 mm TL for all MWT surveys from 1995 to 2000 by multiplying regional mean MWT catch by $V_r/989$, where V_r represents the water volume (m³) in each bay region (Cronin, 1971):

$$N_{total} = (N_l \times V_l + N_m \times V_m + N_u \times V_u)/(s \times V_{MWT}) \times V_{total}$$

$$SE_N = Sc_N \sqrt{V_l^2 / n_l + V_m^2 / n_m + V_u^2 / n_u},$$

where N_{total} = baywide absolute abundance;
N_l, N_m, N_u = mean values of N_{MWT} for the lower (l), middle (m), and upper (u) bay;
V_l, V_m, V_u = bay subvolumes for the lower (l), middle (m), and upper (u) bay (from Cronin, 1971), $V_l = 26.7 \times 10^9$ m³, $V_m = 16.8 \times 10^9$ m³, $V_u = 8.7 \times 10^9$ m³, $V_{total} = V_l + V_m + V_u = 52.1 \times 10^9$ m³;
SE_N = standard error of N_{total};
n_l, n_m, n_u = number of midwater trawl stations for the lower (l), middle (m), and upper (u) bay;
Sc_N = pooled standard deviation of N_{MWT} = square root of mean squares within groups in analysis of variance table = $\sqrt{(SS_l + SS_m + SS_u)/(n_{total} - 3)}$, where SS_l, SS_m, SS_u = sum of squares of N_{MWT} for the lower (l), middle (m), and upper (u) bay, and $n_{total} = n_l + n_m + n_u$.

Environmental factors

Depth profiles of temperature, salinity, and dissolved oxygen (DO) concentration were determined from conductivity-temperature-depth (CTD) casts at sampling stations. DO data were adjusted by calibrating against Winkler titration data from water samples collected in Niskin bottles deployed with the CTD cast. However, DO data from the CTD could not be adjusted for the 1999 summer and all calendar year 2000 cruises because Winkler titrations were not conducted. To estimate regional means for the water column, we averaged temperature, salinity, and DO values by integrating the observed values with respect to depth, after dividing the water column into "above pycnocline" and "subpycnocline" layers.

Ontogenetic migration

We analyzed length-frequency distributions along the south-north axis of the bay (i.e. by latitude) to delineate possible ontogenetic migrations of YOY and adult bay anchovy. To parameterize the distribution of YOY and adult abundance and biomass, we estimated the biomass-weighted mean latitudes of occurrence for each length class (3-mm interval).

$$\overline{L}_{B,l} = \sum_k B_{k,l} L_k / \sum_k B_{k,l},$$

where $\overline{L}_{B,l}$ = biomass-weighted mean latitude of a length class, *l*;
L_k = latitude of the station, *k*; and
B = biomass (g, wet weight) per 20-min tow.

We devised a metric to parameterize the location of bay anchovy SSB. We assumed that the baseline boundary for SSB distribution during the spring was at the mouth of the bay (37°00′N). Then, the upbay difference between biomass-weighted mean latitude of SSB (in decimal units) in Jun–August and the baseline for SSB during the spring (ΔL) was calculated:

$$\Delta L = \left(\begin{array}{c} \text{biomass-weighted mean latitude of} \\ \text{SSB in June – August} \end{array} \right) - 37.00.$$

Recruitment model

As an exploratory step, a correlation analysis was undertaken to examine the relationships between bay anchovy SSB, migration patterns, and recruitment levels with respect to regional and depth-layer-specific mean temperature, mean salinity, mean DO, their gradients, and monthly mean freshwater flow from the Susquehanna River. Cross-correlations revealed that SSB migration pattern (ΔL), regional mean DO concentrations, and October YOY recruitment level were closely correlated. Regional mean DO concentration provided the best fit to YOY recruitment level in October when baywide SSB also was included as an explanatory variable in multiple regressions. However, because there is uncertainty in the uncalibrated DO measurements in 1999 and 2000, we did not use regional mean DO in our recruitment model. Instead, we developed a modified Ricker-type stock-recruitment model (Ricker, 1975) that included ΔL as an explanatory variable:

$R_y = a S \exp(-\beta_1 S - \beta_2 \Delta L) + \varepsilon_y$ (modified Ricker model)

where R_y = recruitment level = October YOY abundance in each year (1995–2000);
y; a, β_1 and β_2 = regression coefficients;
S = estimated baywide SSB (male+female) in metric tons for April–May; and
ε_y = the error term.

In this model, if ΔL is held constant, R_y is maximum at $S = 1/\beta_1$. Although no abiotic factor was included explicitly in the model, ΔL is strongly correlated with regional mean DO and serves as a proxy for it. For the modified Ricker model, collinearity, and jackknife influence diagnostic tools were

Table 3

Seasonal mean freshwater flow entering Chesapeake Bay from the Susquehanna River (m^3/s). Data source: http://va.water.usgs.gov/chesbay/RIMP/adaps.html.

Period	1995	1996	1997	1998	1999	2000
Jan–Mar	1289	2495	1474	2563	1325	1379
Apr–Jun	728	1702	920	1625	791	1627
Jul–Sep	238	768	239	334	294	393
Oct–Dec	923	2230	746	194	642	504
Annual mean	795	1799	845	1179	763	976

applied to evaluate reliability of the regression model (Belsley et al., 1980; SAS, 1989).

Results

Environmental factors

Stream flows from the Susquehanna River (Table 3) varied annually and seasonally. Freshwater stream flows were higher in 1996 and 1998 than in other years. Baywide mean values of water temperature, salinity, and DO concentration, averaged from surface to bottom, varied annually, seasonally, and regionally (Table 1). Annually, mean temperature was highest in 1995 and lowest in 1997. Mean salinity was highest in 1995 and lowest in 1996. Mean DO concentration was highest in 1996 and lowest in 2000. Regionally, salinity was more variable than temperature and DO concentration. Seasonally, temperature and DO concentration were more variable than salinity. Temperature was highest in the June–August period, the spawning season of bay anchovy. Seasonally, salinity increased progressively from April–May to October. Mean DO concentration was consistently lowest in June–August.

Trends in abundance and recruitment

Estimates of bay anchovy abundance reported in our study are for the entire mainstem of Chesapeake Bay. The estimated recruitment levels (baywide abundance of YOY bay anchovy >30 mm TL in October) varied ninefold and were low in 1995 and 1996 (47.5 ±16.6 and 30.6 ±8.6 × 10^9 individuals) but much higher in 1997–2000 (99.6 ±12.4 to 264.8 ±32.6 × 10^9). Baywide estimates of bay anchovy biomass for individuals >30 mm TL increased from April to October in each year (Table 4). October baywide biomass varied sevenfold from 27.1 ±5.5 × 10^3 to 192.9 ±20.4 × 10^3 tons and was highest in 1998 and lowest in 1996.

Estimated spawning stock biomass (SSB) in April–May was lowest in 1995 (3.3 ±1.1 × 10^3 tons), and highest in 1997 (20.1 ±5.3 × 10^3 tons), indicating sixfold variability. SSB in June–August was lowest in 1996 (2.4 ±0.2 × 10^3 tons), and highest in 1997 (21.1 ±2.3 × 10^3 tons). The SSBs in April–May and June–August did not show any obvious relationship to YOY abundance (recruitment) in October.

Ontogenetic migration

The length-specific mean locations (latitudes of occurrence) of bay anchovy revealed an apparent ontogenetic migration. Small juveniles of bay anchovy tended to move upbay and were located primarily upbay until they were approximately 45 mm TL, after which they began to move downbay (Fig. 2). In April–May, age-1 bay anchovy <60 mm TL, consisting of individuals recruited from the previous year, varied annually in their mean latitude of occurrence, whereas large (≥age 1, ≥60 mm TL) bay anchovy had relatively stable locations near the boundary between the lower and middle bay regions, centered at latitude 37°40′N (Fig. 2A). Compared to April–May, age-1+ bay anchovy in June–August were more variable in their annual mean locations, but both YOY and adult bay anchovy tended to occur upbay of latitude 38°00′N, except in year 2000 (Fig. 2B). In 1997 and 1999, when annual mean temperatures were lowest (Table 1), YOY bay anchovy were too small to be sampled by the MWT in June–August and are not represented in Figure 2B. In October, mean latitudes of occurrence (Fig. 2C) indicated a consistent distribution pattern and an apparent ontogenetic migration by YOY anchovy. The most probable explanation for the observed latitudinal distributions was that small YOY bay anchovy tended to move upbay initially, but then downbay at about 45 mm TL. Distribution of age-1+ individuals in October was variable.

The SSB of bay anchovy (excludes YOY) from 1995 to 2000 was centered near 38°00′N in April–August except in June–August of 1995 and 1996, when the SSB was centered farther upbay (Fig. 3A). In 2000, the migration pattern differed from other years. Spawning bay anchovy in 2000 were located farther downbay in July than in April (Fig. 3A). The April–May location of prespawning SSB was mostly explained by the mean flow of the Susquehanna River from June of the previous year to February of the current year (r^2=0.94, P=0.0012; Fig. 3B). But, in June–August, the mean location of spawning fish was more strongly and significantly related to the subpycnocline-layer mean

Table 4

Baywide abundance and biomass estimates for bay anchovy >30 mm TL (young-of-the-year + adult). SE = standard error.

Year	Period	Abundance ($\times 10^9$)		Biomass ($\times 10^3$ metric tons)	
		Estimate	SE	Estimate	SE
1995	April–May	2.1	0.7	3.3	1.1
	June–August	57.8	28.1	32.6	17.5
	October	47.5	16.6	51.9	21.0
1996	April–May	4.9	1.1	8.9	2.0
	June–August	5.3	1.6	3.7	1.3
	October	30.6	8.6	27.1	5.5
1997	April–May	11.8	3.3	20.1	5.3
	June–August	9.4	2.3	21.1	5.0
	October	99.6	12.4	85.6	10.8
1998	April–May	3.5	0.7	6.1	1.3
	June–August	14.4	4.5	17.0	7.9
	October	264.8	32.6	192.9	20.4
1999	April–May	6.9	1.4	10.6	2.2
	June–August	5.5	1.2	10.6	2.4
	October	124.5	28.3	115.3	25.0
2000	April–May	6.2	4.1	13.0	6.6
	June–August	144.6	51.2	56.0	17.0
	October	169.1	43.7	152.9	40.0

DO during that same period in the middle bay (r^2=0.75, P=0.02; Fig. 3C).

Correlations

Correlation analyses suggested that regional mean DO concentrations are the most important environmental correlate associated with spatial distribution of SSB and recruitment processes of bay anchovy. The mean locations (latitudes of occurrence), abundances, and biomasses for YOY and adult bay anchovy were analyzed with respect to environmental variables (Table 5). Recruitment levels (YOY abundance) in October were consistently inversely correlated with DO concentrations in the lower and middle bay in June–August (r=–0.13 to –0.89). Biomass-weighted mean latitude of SSB (age 1+) in April–May was consistently and positively correlated with regional salinities in April–May (r=0.30 to 0.88). On the other hand, in June–August, surface-layer mean salinity in the lower Bay and subpycnocline-layer mean DO in the lower and middle bay were significantly and positively correlated with mean latitude of SSB or ΔL (r=0.82 to 0.91). Baywide SSB in April–May and June–August tended to be negatively correlated with water temperature in April–May (r=–0.45 to –0.90).

Recruitment model

Although SSB alone did not correlate significantly with recruitment level, mean DO in June–August was signifi-

cantly related to the mean latitude of SSB in June–August (or ΔL) and bay anchovy recruitment level in October (Figs. 3C and 4). ΔL was selected as the explanatory variable, rather than DO, because DO data were uncalibrated in 1999 and 2000. The correlation observed between ΔL and DO (Fig 3C) suggested that ΔL can serve as a proxy for DO in the stock-recruitment model. Including ΔL and SSB for April–May in a modified Ricker model provided a good fit to bay anchovy recruitment levels observed from 1995 to 2000 (Fig. 5). The model is

$$R_y = 365\ S \exp\ (-0.19\ S\ 1.35\ \Delta L) \quad \text{(modified Ricker model)}.$$

In the model, if ΔL is held constant, predicted recruitment level of bay anchovy is maximum when baywide SSB in April–May is approximately 5.3×10^3 tons. Collinearity and influence diagnostic statistics did not indicate collinearity between the two independent variables (S and ΔL), or that an observation in any year had a dominating influence on parameter estimates.

Discussion

Complex environmental processes and biological interactions control bay anchovy recruitment in Chesapeake Bay. Dissolved oxygen (DO), freshwater flow, salinity, and temperature acting on prerecruits and adults are important factors affecting bay anchovy distribution and levels of recruitment. Spawning stock size also is related to recruit-

ment level. Our results have demonstrated that there is a strong spatial component in the recruitment dynamics of bay anchovy. Although fish recruitment processes historically have been difficult to understand, our six-year, spatially extensive research has provided new insights into processes that control bay anchovy recruitment.

Ontogenetic migration pattern

It is apparent that ontogenetic migration plays a role in the spatial and temporal patterns in abundance, biomass, and production of bay anchovy. There are several lines of evidence. Rilling and Houde (1999a), in a baywide analysis, reported that mean density of eggs and larvae in June and July 1993 was very high in the lower Chesapeake Bay compared to more upbay sites. Dovel (1971) and Loos and Perry (1991) reported possible upbay or upriver migration of bay anchovy larvae and juveniles in the mainstem and tributaries of the Bay. Recent otolith microchemical analyses have strongly supported the hypothesis that an upbay ontogenetic migration by small YOY anchovy (≥25 mm, late larvae and small juveniles) occurs (Kimura et al., 2000). In the middle Hudson River estuary (Schultz

Figure 2

Abundance-weighted mean latitude of occurrence of bay anchovy (*Anchoa mitchilli*) in Chesapeake Bay, 1995–2000.

et al., 2000) and Chesapeake Bay (North and Houde, in press), selective tidal-stream transport was suggested as a mechanism for up-estuary movements of bay anchovy larvae. Our conceptual model of the bay anchovy life cycle includes migration patterns in the bay based on available knowledge and evidence (Fig. 6).

It is uncertain what benefits YOY bay anchovy derives from upbay migration in summer and whether the migration is passive or active before a subsequent reverse migration in the fall. To explain upbay movements of estuarine fishes, Dovel (1971) proposed that there is a "critical zone" of low salinity and high prey production in the upper bay, which is important as a nursery for bay anchovy and other fish species. In late spring and early summer, age-1 and age-1+ bay anchovy mature and move upbay while spawning, although the year 2000, when mean freshwater streamflow during the previous fall-winter was lowest, was an exception. Recruited YOY bay anchovy apparently overwinter primarily, but not entirely, downbay until spring.

There remains a possibility of significant immigration to the bay by adult bay anchovy in some years from the coastal ocean or tidal tributaries of the bay. Without such immigration, baywide adult abundance would decrease continuously during the April–October period through natural mortality. However, in two years of our six-year study, 1995 and 1998, estimated adult abundance increased substantially from April to July, and in 1999 adult abundance increased from June to October, implying significant immigration to the bay in those years (Jung, 2002).

Recruitment control and regulation

The modified Ricker recruitment model that included SSB and ΔL as explanatory variables provided a good fit to bay anchovy recruitments. Although the model fitted well, there were only six years of data, and the underlying mechanisms explaining relationships between the distribution and level of SSB, hydrological conditions, and density-dependent regulatory processes in recruitment of bay anchovy are not yet clear. Nevertheless, correlations and the recruitment model clearly indicated a density-dependent effect of SSB level and also implicated environmental factors (at the mesoscale) that are related to mean DO concentration, latitudinal distribution of SSB (ΔL), and the recruitment level of bay anchovy (Fig. 4).

The modified Ricker model for bay anchovy (Fig. 5) indicates a density-compensatory stock-recruitment relationship (Ricker, 1975), although we do not know at what life stages density-dependent processes are most important. Without accounting for the controlling effect of ΔL and mean DO on a regional scale, the density-dependence might have gone undetected (Fig. 4). Recent individual-based models suggest that density-dependent processes during early-life stages could stabilize bay anchovy recruitments (Wang et al., 1997; Cowan et al., 1999; Rose et al., 1999). At the small scales of several meters modeled by Wang et al. (1997) and Cowan et al. (1999), larval-stage feeding
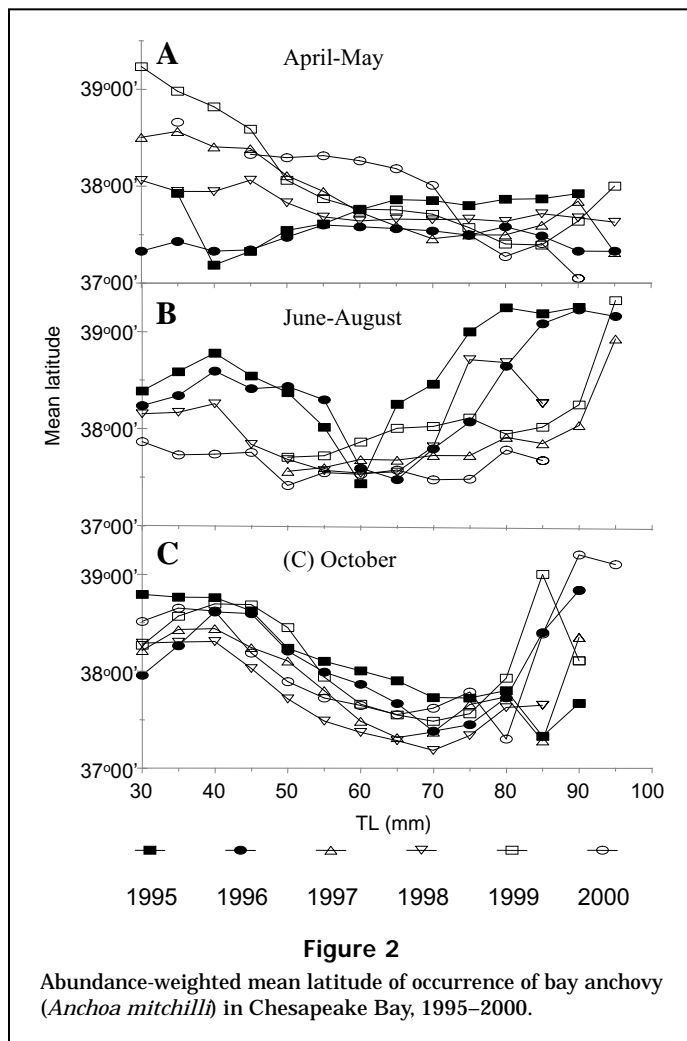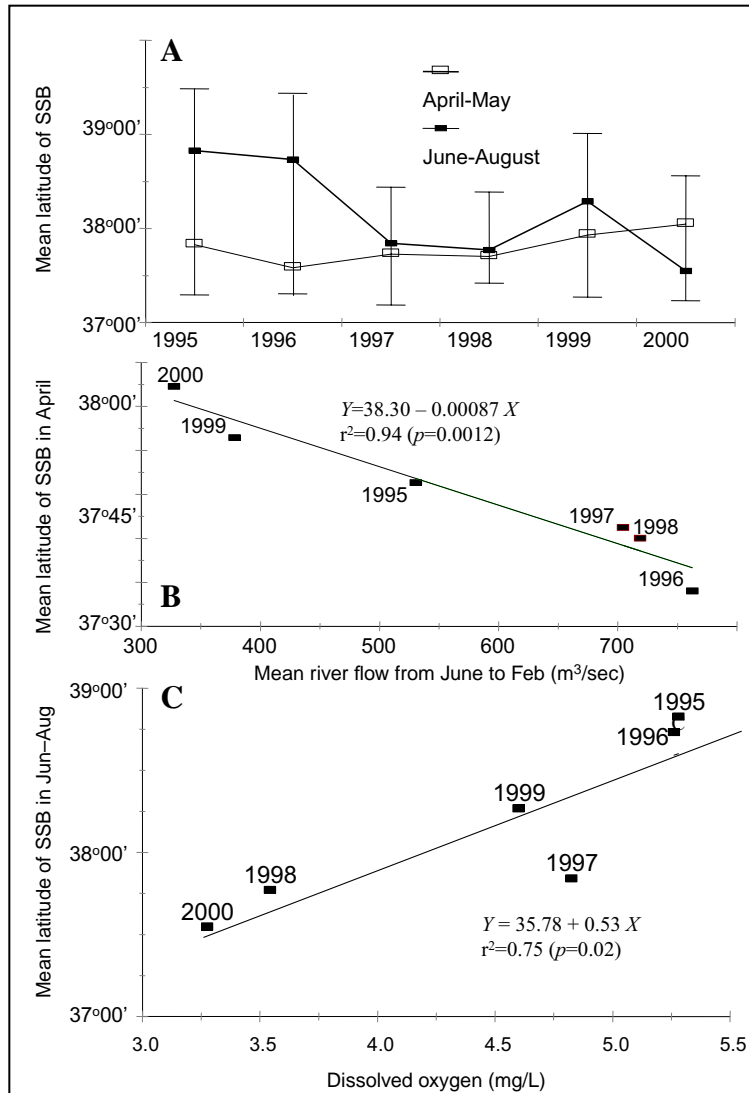
Figure 3

Mean location (latitude) of adult bay anchovy (*Anchoa mitchilli*) spawning stock biomass (SSB) in Chesapeake Bay. (**A**) Mean latitude and standard deviation in April–May and in June–August. The upper vertical bar represents mean + standard deviation for June–August, and the lower vertical bar represents mean–standard deviation for April–May, (**B**) Mean latitude in April–May and mean Susquehanna River flow from June of the previous year to February of the current year. (**C**) Mean latitude in June–August and mean dissolved oxygen in the subpycnocline layer of the middle bay in June–August.

processes were important and high adult SSB could produce abundant first-feeding larvae with subsequent density-dependent food competition. In Tampa Bay, Florida, Peebles et al. (1996) hypothesized that bay anchovy's size-specific fecundity is directly related to prey availability for adults. Modeled results of Rose et al. (1999) suggested that density-dependent growth of bay anchovy larvae and juveniles in Chesapeake Bay would lead to density-dependent survival of these stages. Hunter and Kimbrell (1980) and Alheit (1987) proposed that cannibalism by adults on

eggs and larvae provides a degree of density-dependent regulation in anchovies of the genus *Engraulis*. Analyses of feeding by adult bay anchovy did not indicate that pelagic fish eggs were a significant part of bay anchovy diet (Vazquez-Rojas, 1989; Klebasko, 1991), although no specific study of cannibalism has been undertaken.

We propose three hypotheses that may explain the relationships among regional DO concentration, the latitudinal shift in SSB distribution during the spawning season (ΔL), and recruitment levels of bay anchovy in October. The

hypotheses are the following: 1) averaged DO concentration is inversely related to levels of plankton productivity in a region and high plankton productivity favors high recruitments of planktivorous bay anchovy; 2) low dissolved oxygen concentrations can restrict spatial distribution of bay anchovy SSB to the lower bay insuring high egg and
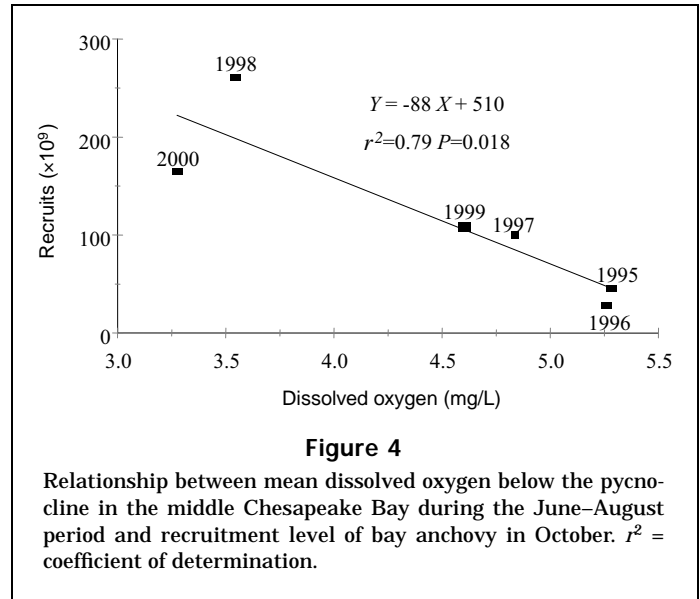
Table 5

Cross-correlation coefficients for bay anchovy distribution and abundance with respect to region- and layer-specific means of temperature, salinity, and dissolved oxygen from 1995 to 2000. Mean latitude is biomass-weighted mean latitude of occurrence of bay anchovy. Abundance and biomass are baywide total estimates. ΔL = (mean latitude in June–August) –37.00. Abbreviations are as follows: SAL = salinity, TEM = water temperature, OXY = dissolved oxygen; the fourth and fifth digits: 04 = April–May, 07 = June–August; the sixth character: L = lower bay, M = middle bay, U = upper bay; The last character: S = layer above the pycnocline, B = layer below the pycnocline. * = significant at α = 0.05.

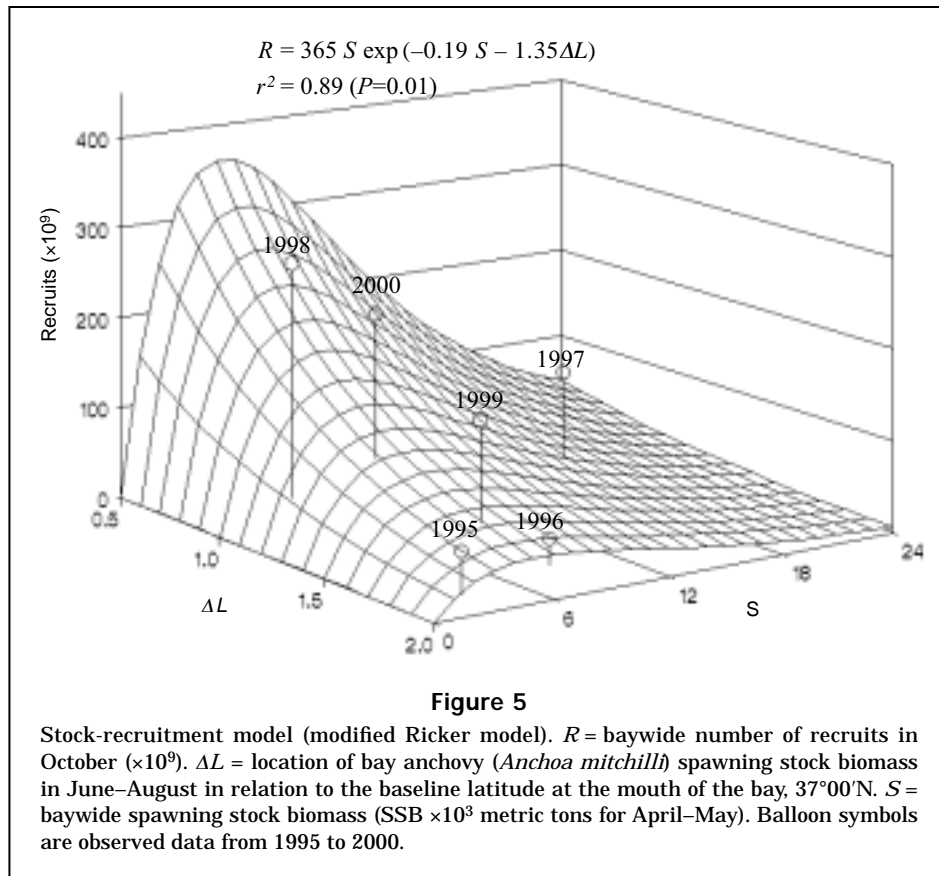| | Young-of-the-year | | Adult | | | |
| | Mean latitude | Abundance | Mean latitude | | Biomass | |
| | | | | June–August | | |
	October	October	April–May	(or ΔL)	April–May	June–August
SAL04LS	0.29	−0.43	0.74	0.26	−0.17	−0.52
SAL04MS	0.45	−0.63	0.30	0.71	−0.41	−0.22
SAL04US	0.27	−0.60	0.42	0.53	−0.18	−0.02
SAL04LB	−0.24	0.01	0.88*	−0.16	−0.14	−0.31
SAL04MB	0.08	−0.17	0.59	0.33	−0.39	−0.05
SAL04UB	0.29	−0.61	0.45	0.46	−0.03	0.05
SAL07LS	0.83*	−0.75		0.91*		−0.46
SAL07MS	−0.12	0.06		0.14		0.31
SAL07US	0.06	−0.03		−0.04		−0.33
SAL07LB	0.70	−0.75		0.64		−0.11
SAL07MB	−0.41	0.60		−0.31		0.19
SAL07UB	0.15	−0.20		0.01		−0.42
TEM04LS	0.16	−0.25	−0.03	0.65	−0.90*	−0.48
TEM04MS	0.50	−0.46	0.14	0.65	−0.71	−0.85*
TEM04US	0.53	−0.32	−0.36	0.52	−0.56	−0.85*
TEM04LB	0.29	−0.49	0.19	0.71	−0.72	−0.45
TEM04MB	0.22	−0.42	0.39	0.47	−0.55	−0.62
TEM04UB	0.40	−0.26	−0.39	0.48	−0.60	−0.77
TEM07LS	−0.49	−0.04		0.11		0.45
TEM07MS	−0.16	−0.21		0.47		0.14
TEM07US	−0.29	−0.08		0.39		0.38
TEM07LB	−0.68	0.24		−0.11		0.38
TEM07MB	−0.24	−0.10		0.37		−0.04
TEM07UB	−0.45	0.16		0.21		0.46
OXY04LS	0.63	−0.22	−0.80	0.39	−0.10	−0.30
OXY04MS	−0.27	0.56	0.23	−0.81	0.55	−0.04
OXY04US	−0.43	0.41	−0.30	−0.30	0.30	0.88*
OXY04LB	0.93**	−0.68	−0.59	0.63	0.04	−0.38
OXY04MB	0.47	−0.35	−0.31	−0.09	0.70	−0.12
OXY04UB	−0.57	0.65	−0.32	−0.46	0.21	0.78
OXY07LS	0.18	−0.30		0.29		0.32
OXY07MS	0.01	−0.13		0.29		0.56
OXY07US	0.23	−0.32		0.50		0.10
OXY07LB	0.67	−0.48		0.82*		−0.28
OXY07MB	0.72	−0.89*		0.87*		−0.04
OXY07UB	0.01	0.16		0.21		0.37

larval production there; and 3) density-depensatory predator satiation occurs when concentrations of bay anchovy larvae and juveniles at the mesoscale (10–100 km) are high in relation to satiation potential of predators, which favors larval production and high anchovy recruitments.

First, averaged DO level in the bay or its regions may be an indicator of ecosystem metabolism and secondary production. DO level in the subeuphotic layer is an indicator of respiration and secondary production by planktonic and benthic communities (Kemp and Boynton, 1980; Kemp et al., 1992). Recruitment levels of bay anchovy increased substantially in 1997 and in subsequent years. We speculate that enhanced detrital production potentially increased zooplankton prey abundances in the subsequent year and that associated elevated levels of respiration by detrital microorganisms and zooplankton contributed to low mean DO. Increased zooplankton prey abundances, in turn, may have promoted production of larval and juvenile bay anchovy in 1997 and 1998. Thus, increased prey availability, associated with low mean DO concentration, could have enhanced recruitment (Fig. 4).

The second hypothesis proposes that spatial restriction of SSB by low DO is a factor controlling bay anchovy recruitment. Based on our results, hypoxic conditions in the bay appear to define the distribution and potential for upbay migration of bay anchovy SSB (Fig. 3C). In years

Figure 4

Relationship between mean dissolved oxygen below the pycnocline in the middle Chesapeake Bay during the June–August period and recruitment level of bay anchovy in October. r^2 = coefficient of determination.

when the baywide subpycnocline mean DO level was low, spawning bay anchovy tended to be most concentrated in the lower bay (Table 5, Fig. 3, A and C), possibly because hypoxia in deeper waters of the mid-bay region discouraged upbay migration. The region selected by adult anchovy as the predominant spawning area and its variability played

Figure 5

Stock-recruitment model (modified Ricker model). R = baywide number of recruits in October ($\times 10^9$). ΔL = location of bay anchovy (*Anchoa mitchilli*) spawning stock biomass in June–August in relation to the baseline latitude at the mouth of the bay, 37°00′N. S = baywide spawning stock biomass (SSB $\times 10^3$ metric tons for April–May). Balloon symbols are observed data from 1995 to 2000.
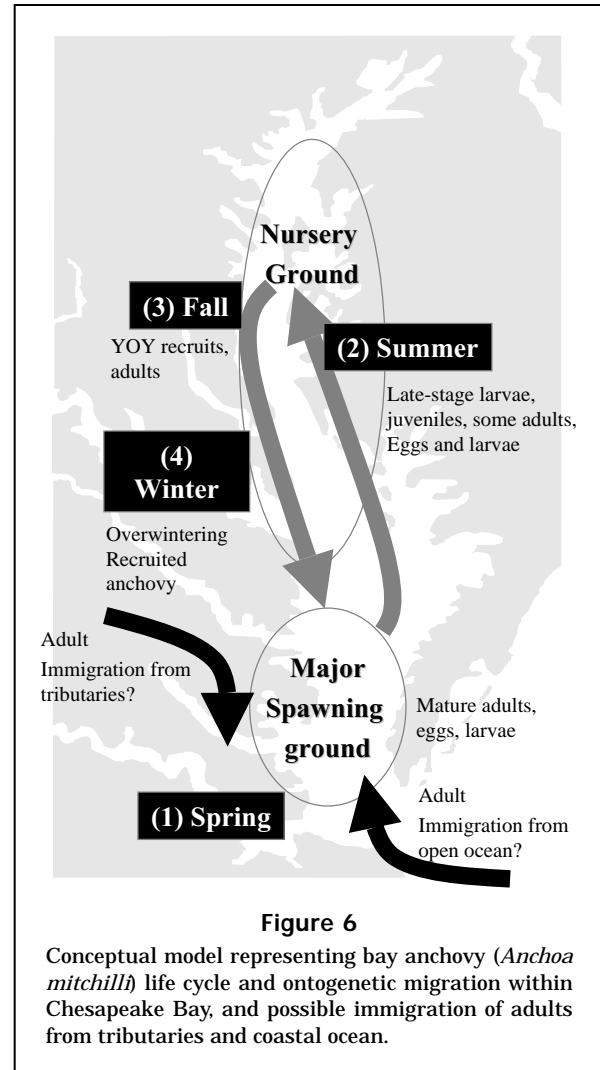
a strong role in controlling YOY recruitment levels. The four highest recruitment years in our series had the lowest mean subpycnocline DO levels and had distribution patterns of SSB that differed little between the prespawning April–May and spawning June–August periods (Fig. 4). Although we do not fully understand how DO, and possibly hypoxic conditions, affect migratory behavior and distribution patterns of bay anchovy, hypoxia in Chesapeake Bay has been demonstrated in other research to affect spatial and temporal patterns of fish abundance, including bay anchovy (Breitburg, 1992; Keister et al., 2000).

Our third hypothesis proposes that predation is an important regulator of fish recruitment in early-life stages (Sissenwine, 1984; Bailey and Houde, 1989). We hypothesize that abundant and spatially concentrated larval or juvenile anchovy, as observed in the lower bay, could promote early-life survival by satiating predators, even if some predators migrate to areas where larval and juvenile anchovy are abundant. At mesoscale distances of 10–100 km, distribution of predators (e.g. YOY and age-1 weakfish [*Cynoscion regalis*]) may be important. If the maximum number of prey that can be eaten by predators is reasonably constant, the effect of predation can be density-depensatory (Hilborn and Walters, 1992), i.e. predation mortality rate decreases as prey density increases.
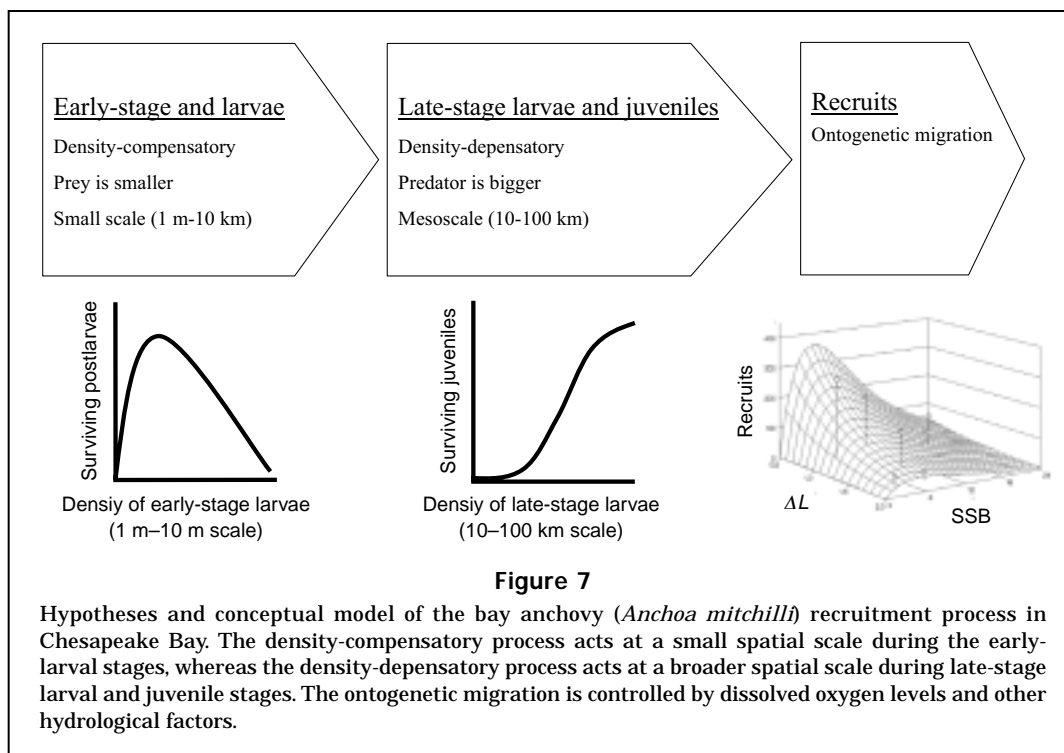
In support of the third hypothesis, a correspondence analysis on fish species assemblages by year, season, region, and life stage (Jung and Houde, 2003) indicated that distributions and abundances of YOY weakfish, a major predator of bay anchovy in Chesapeake Bay (Hartman and Brandt, 1995), and YOY bay anchovy were closely associated spatially, seasonally, and annually in our six-year study. The major spawning area of bay anchovy is spatially restricted. If predator migration to the area is limited, then as the supply of larvae and juveniles increases, it may saturate predator demand, the condition necessary for depensation to be important.

It may seem contradictory to propose that density-compensation with respect to SSB (the negative sign of β_1) and density-depensation with respect to ΔL (the second or third hypothesis) can act simultaneously during larval and juvenile stages. Under this circumstance, the number of surviving postlarval anchovies is hypothesized to decrease because of food limitation when larval abundance is high, reducing subsequent predation-related mortality rate on postlarvae and small juveniles. Low abundance of anchovy early-life stages will lead to the opposite effect (Fig. 7). The proposed opposing responses of the early-larval and late-larval–juvenile stages are explained by differences in the spatial scales of distribution and densities of life stages of bay anchovy (Fig. 7). The spatial scale of processes that affect distributions of late-stage larvae and juveniles is large compared to that for early-stage larvae because of the increased dispersal and swimming ability of juveniles. Comparing early-larval and late-larval–juvenile stages of bay anchovy, we propose that effects of prey concentration (the first hypothesis) and SSB level (density-compensation) act primarily on the dynamics of early-larval stages, whereas predation mortality and the inhibitory effects of low DO (density-depensation; the second and third hy-

Figure 6

Conceptual model representing bay anchovy (*Anchoa mitchilli*) life cycle and ontogenetic migration within Chesapeake Bay, and possible immigration of adults from tributaries and coastal ocean.

potheses) are more important regulators and controllers, respectively, during late-larval and juvenile stages.

The three hypotheses that relate DO, SSB distribution, and recruitment of bay anchovy are not mutually exclusive. If low mean DO level is an indicator of enhanced prey production and availability to larvae and juveniles, increased prey productivity in the lower bay could enhance bay anchovy recruitment potential by supplying enough zooplankton prey to spawning adults, larvae, and juveniles. At the same time, low mean DO in the mid-Bay could confine most spawning bay anchovy to the lower bay, thus increasing spawning and larval production there, and possibly enhancing survival of juveniles by predator satiation. Ultimately, other hypotheses may provide better explanations of the relationships between regional mean DO, latitudinal shifts in distribution of spawners, abundances of spawners, and recruitment of bay anchovy. For example, abundant gelatinous organisms, such as the scyphomedusa (*Chrysaora quinquecirra*) and the lobate ctenophore (*Mnemiopsis leidyi*), can be important predators on early-stage anchovy and competitors with juveniles and adults (Purcell et al.,

Figure 7

Hypotheses and conceptual model of the bay anchovy (*Anchoa mitchilli*) recruitment process in Chesapeake Bay. The density-compensatory process acts at a small spatial scale during the early-larval stages, whereas the density-depensatory process acts at a broader spatial scale during late-stage larval and juvenile stages. The ontogenetic migration is controlled by dissolved oxygen levels and other hydrological factors.

1994), but their potential role with respect to bay anchovy recruitment could not be defined in our study. For the present, it is clear that most spawning occurs in the lower and mid Chesapeake Bay, from which larval and juvenile anchovies disperse upbay. We hypothesize that food availability is the major factor controlling production of bay anchovy early-larval stages whereas predation becomes more important during late-larval and juvenile stages. Our results and hypotheses implicate density-related processes, operating at different spatial scales, as regulators of recruitment of bay anchovy in Chesapeake Bay.

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