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Spatial and Temporal Patterns
in Recruitment Process

SCALE AND PATTERN IN RECRUITMENT PROCESSES OF BAY ANCHOVY IN CHESAPEAKE BAY

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ABSTRACT

Recruitment of bay anchovy (Anchoa mitchilli) varies annually in Chesapeake Bay, and levels and patterns are related to variability in hydrological conditions and the spatial distribution of spawning stock biomass. Midwater-trawl surveys, conducted three times annually from 1995-1999, over the entire 320-km length of the Bay, provided information on annual and regional patterns of recruitment, and their relationships to variability in the estuarine environment. Adult biomass of anchovy within the Bay at the beginning of spawning seasons in 1995-1999 varied six-fold, but it alone was not directly related to the young-of-the-year (YOY) recruitment level. Levels of recruitment in October were low in 1995 and 1996 (6 to 7 X 10^9) but higher in 1997-1999 (19 to 52 X 10^9). An important feature of the recruitment process is an ontogenetic migration in which YOY bay anchovy tended to move upbay until they are approximately 45 mm TL, after which they begin to move downbay. The strong salinity gradient may act as a partial barrier to upbay or downbay migration, the effect being more pronounced for small (<60 mm TL) anchovy. However, seasonal water temperature was more important in determining the latitudinal distribution of spawning stock biomass. Late-summer recruitment of YOY anchovy was high when water temperature was low in April-May, inhibiting upbay migration of adults at the onset of the spawning season, and insuring that most spawning occurred in the lower and middle region of the Bay. A modified Ricker stock-recruitment model that included the latitudinal range of adult migration between April and July, explained 98% of recruitment variability.

INTRODUCTION

Bay anchovy Anchoa mitchilli (Engraulididae) is a coastal species distributed in the western Atlantic from Maine to the Gulf of Mexico, and is the most abundant and ubiquitous fish in Chesapeake Bay, the largest estuary on the east coast of North America (Houde & Zastrow, 1991; Able & Fahay, 1998). Bay anchovy is not a target of fishing activity. It feeds on zooplankton, primarily copepods and other small crustacea, and is predated by piscivores including several economically important fish species (Baird & Ulanowicz, 1989; Luo & Brandt, 1993; Hartman & Brandt, 1995). Males and females can mature at 40-45 mm FL (44-50 mm TL) at ca 10 months posthatch, and peak spawning occurs in July (Zastrow et al. 1991). Most eggs are produced by age 1 individuals (Luo & Musick, 1991; Zastrow et al, 1991). Bay anchovy can survive to age 3+ and reach 5 g wet weight. Mean total lengths of age-specific bay anchovy were reported to be age 1 = 55 mm, age 2 = 74 mm, and age 3 = 88 mm (Newberger & Houde, 1995). Temporal and spatial variability in abundance, growth, and mortality rates were reported for Chesapeake Bay (Wang & Houde, 1995; Dorsey et al., 1996, MacGregor & Houde, 1996, Rilling & Houde, 1999ab). Dovel (1971) and Loos & Perry (1991) hypothesized ontogenetic migration to explain regional variability in abundance.

Newberger & Houde (1995) noted the large difference in abundances of bay anchovy among years, apparently a result of variability in annual recruitments. However, there was little knowledge about factors that control levels of recruitment, and its spatial and temporal variability. We hypothesize that recruitment of bay anchovy is at least partially determined by the spatial distribution of spawners, and not only by variable growth and mortality during early-life stages.

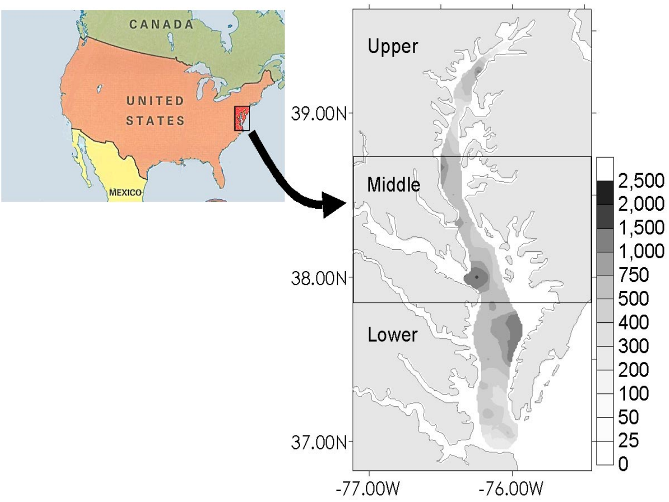


Fig. 1. Chesapeake Bay, and mean annually-aggregated bay anchovy catch-per-unit-effort (wet weight in gram/20 min tow) from 1995 to 1999. Horizontal lines indicate boundaries of the three regions.

Chesapeake Bay is the largest estuary in the United States. Geomorphically, it is a typical coastal plain estuary (Day et al., 1989). Its mainstem is 320 km long, varying in width from about 6.4 km to 50 km (Fig. 1). Chesapeake Bay is shallow. Less than 10% of the Bay area is > 18 m deep, and approximately 50% is < 6 m deep. Fifty tributaries enter the Chesapeake Bay. Physically, the Bay is a partially-mixed estuary (Day et al., 1989). Eighty to 90% of the freshwater entering the Bay is from tributaries on its northern and western sides. The Bay receives about half its water volume from the Atlantic Ocean, and the remainder drains into the Bay from a 166,000-km^2 drainage basin (Chesapeake Bay Program, 2000). The Bay's salinity grades from near-full seawater at its mouth to freshwater at its head, the mouth of Susquehanna River. Water temperatures may be as high as 28^o to 30^oC in mid summer, and may fall to 1^o to 4^oC in late winter (Murdy et al., 1997). Despite shallow depth, the Bay's mainstem usually has a strongly developed pycnocline with sharp gradients in vertical temperature and salinity profiles.

Objectives of this paper are 1) to evaluate effects of hydrological conditions on stage-specific distribution, ontogenetic migration, and recruitment, and 2) to delineate patterns in the bay anchovy recruitment process.

METHODS

Cruises

Research cruises for the Land Margin Ecosystem Research (LMER) program, "Trophic Interactions in Estuarine Systems (TIES)" (http://www.chesapeake.org/ties/) surveyed the entire Bay and were conducted three times annually (April-May, June-August and October) from 1995 to 1999 (Fig. 1). Plankton and fish collections, in addition to observations of environmental variables, were made. Net collections (midwater trawl) and hydroacoustic surveys in TIES cruises were conducted at three or four stations per transect in the lower-Bay (37^o55'N-37^o05'N), mid-Bay ($38\,^o$ 45'N-37^o55'N), and upper-Bay ($39\,^o$ 25'N-$38\,^o$ 45'N). The lower bay includes 51% of total baywide water volume, the middle bay 32%, and the upper bay 17% (Fig. 1). Numbers of midwater-trawl stations per TIES cruise ranged from 24 to 52. Additional cruises provided information in some periods when there were no TIES surveys; for example, in June 1997, August 1997, 1998, and September 1998.

An 18-m^2 mouth-opening midwater trawl (MWT), with 6-mm codend meshes was deployed to collect fish. The net was fished from the stern A-frame of 38-m RV Henlopen. Oblique tows were of 20-min duration. The net was fished in 2-min stepped intervals from surface to bottom to fish the entire water column. Fish catches (or samples) were counted, measured and weighed on deck immediately after a tow.

The MWT was effective in catching bay anchovy > 30 mm total length. The amount of water fished by a 20-min MWT tow was approximately 5,000 m^3. Based on this information, we expanded the CPUE values to estimate regional anchovy abundances and wet weights by multiplying water volumes of each region (Cronin, 1971).

Environmental factors

Depth profiles of temperature and salinity were determined from CTD casts. Because temperature and salinity in this partially mixed estuary show distinct features between surface and bottom, they were integrated over the entire depth after dividing the water column into a surface and bottom layer based on estimations of pycnocline depths. The following steps were applied to derive homogenous (randomly distributed) parameter values for environmental conditions.

For each station, the pycnocline depth was estimated from the derivative of the third-order polynomial regression fitted to salinity on depth:

$$s = ax^3 + bx^2 + cx + d,$$

Where s: salinity; x: depth (m); $a < 0$, $b > 0$.

After defining pycnocline depth at each station, the mean water-column temperature and salinity in each region (lower, middle, and upper Bay) were estimated for each cruise. The differences of temperature and salinity between cruise periods (spring, summer, and fall), and differences between two adjacent regions (gradients) also were summarized.

Exploratory statistical analysis

Spatial data usually show strong correlations between sites similar to auto-correlation in time-series data (Cressie, 1993). A variogram can be derived to interpolate values (abundances and biomasses) for grids or stations where no measurements were made. Anisotropic (both latitudinal and longitudinal) linear variogram functions without 'nugget' effect were used to estimate bay anchovy abundances and biomasses by interpolation of values for unsampled grids of 1 x 1 nautical mile to generate distribution maps. The variogram functions were derived by proc variogram of SAS 6.11, and the grid data files were generated by proc krige2d to produce distribution maps of bay anchovy number and biomass, and hydrological variables such as temperature and salinity (SAS, 1998).

Modal lengths of bay anchovy cohorts were determined from length-frequency distributions. Baywide relative abundance of each cohort was estimated by Bhattacharya plots (Bhattacharya, 1967; King, 1995). Criteria of maximum total length of YOY bay anchovy are shown in Table 1.

Table 1. Maximum total length of young-of-the-year bay anchovy (mm).

Year	Date	Length (mm)
1995	23-Jul	57
	28-Oct	78
1996	17-Jul	57
	22-Oct	77
1997	11-Jul	-
	02-Aug	57
	29-Oct	69
1998	04-Aug	57
	07-Sep	62
	19-Oct	69
1999	26-Jun	-
	23-Oct	75

We produced length frequencies by latitude to delineate possible ontogenetic migration of YOY and adult bay anchovy. To parameterize the distribution of YOY and adult biomass, we estimated biomass-weighted and abundance-weighted mean latitudes of occurrence for each length by the following formula.

$$L_{bl} = \sum B_{nl}\, V_n\, L_n / \sum V_n\, B_{nl}$$
$$L_{al} = \sum A_{nl}\, V_n\, L_n / \sum V_n\, A_{nl}$$

where, L_{bl}: biomass-weighted mean latitude of a length, l; L_{al}: abundance-weighted mean latitude of a length, l; B: Biomass (g in wet weight) per 20-min tow; A: Abundance (number) per 20-min tow; n: station; V_n: water volume (m^3) of the region where station n is located,
$\sum V = V_{\text{lower bay}} + V_{\text{middle bay}} + V_{\text{upper bay}} = 26.668 + 16.840 + 8.664 = 52.112\ (\times 10^9\ m^3)$.

In an exploratory step, correlation analysis was used to examine relationships of bay anchovy spawning and migration patterns with regional- and depth-layer-specific mean temperature, mean salinity, their gradients or differences from the previous cruise, and monthly mean stream flow from the Susquehanna River. The parameters of temperature and salinity were related to mean latitudes of occurrence and baywide abundance/biomass for YOY and adult bay anchovy.

Ontogenetic migration

A General Linear Model (proc GLM in SAS) was used to evaluate the importance of environmental factors on size-dependent migration:

$$L_{ljk} = C_j + \tau_{lj} + \beta_j\, x + \varepsilon_{ljk}$$

where, L: mean latitude of occurrence for bay anchovy weighted by abundance or biomass; l: length (mm) of bay anchovy; j: season (= 1, 2, 3); k: year (= 95, 96, 97, 98, 99); C: constant term; β: slope coefficient; τ: effect of body-size; x: values for each environmental factor (salinity, temperature, their gradient, freshwater input, etc.); ε: error term.

After determining the most important factor for distribution of YOY and adult bay anchovy, regression analysis based on sequential sums of squares (type I SS) was applied to fit the relationship between the factor and length-specific mean latitude of distribution, after filtering out the size-dependency by polynomial equations (proc REG and GLM in SAS 6.11: SAS, 1990; Littell et al., 1991). The statistical model is:

$$L_{jk}(l) = \beta_0 + \beta_1\, l + \beta_2\, l^2 + \beta_3\, l^3 + \beta_4\, x + \beta_5\, (x\, l) + \varepsilon_{ljk}\ \text{(cubic)}$$

where, β_0: intercept; β_1, β_2, β_3: slope coefficenits for the polynomial equation; l: total length (mm) of bay anchovy; x: values for the environmental factor; (x l) : interaction term; β_5: slope coefficient for the interaction term; ε: error term.

If the highest order term or the interaction term was not significant at $\alpha = 0.05$, we fit again after removing those terms from the model equation, until all terms were significant.

Recruitment models

To test whether there is a significant relationship between bay anchovy spawning stock biomass (SSB) in April-May and YOY recruitment in October, we initially ran cross-correlation analysis. The relationship between the seasonal changes in the spatial distribution pattern of adult bay anchovy and YOY recruitment levels in October was tested by regression analysis, after examining the distribution maps of YOY and adult bay anchovy distribution for each cruise.

Finally, two different recruitment models were tested based on the estimated SSB in April-May and the differences in biomass-weighted mean latitude of spawner distribution between April-May and June-August. First, the log-transformed YOY recruitment level in October was fitted by a statistical model:

$$\mathrm{Log}(R_y) = \beta_0 + \beta_1 S + \beta_2 \Delta L + \varepsilon_y$$

where R_y: recruitment level = October YOY abundance in the year, y; B_0: intercept; β_1 and β_2: slope coefficients; ΔL: difference in biomass-weighted mean latitude of SSB in decimal units between April-May and June-August; S: baywide spawning stock biomass (male + female) in tons for April-May, or for June-August; ε_y: error term.

The statistical model fit the observed recruitment levels quite well, but was biologically unacceptable, because it did not include density-dependence. To include a density-dependent term, a modified Ricker model was applied (Ricker, 1954, 1975):

$$R_y = aS \exp(-\beta_1 S - \beta_2 \Delta L + \varepsilon_y)$$
$$\log(R_y) - \log(S) = \log(a) - \beta_1 S - \beta_2 \Delta L + \varepsilon_y$$

For this multivariate recruitment model, collinearity diagnostic tools available in proc REG of SAS, such as variance inflation factor (VIF) and condition index (CI), were applied. A common rule of thumb was adopted: if VIF > 10 or CI > 15, collinearity was judged to be problematical.

RESULTS

Environmental factors

Monthly stream flow from the Susquehanna River (Table 2) showed high annual and seasonal variability. Stream flows were high in 1996 and1998, and low in 1995, 1997 and 1999.

Table 2. Seasonal mean stream flow (m^3/s)

Period\Year	1995	1996	1997	1998	1999
Jan.-Mar.	1,289	2,495	1,474	2,563	1,325
Apr.-Jun.	728	1,702	920	1,625	791
Jul.-Sep.	238	768	239	334	294
Oct.-Dec.	923	2,230	746	194	642
Annual mean	795	1,799	845	1,179	763

Water temperature and salinity varied annually, seasonally, and regionally (Table 3). Annually, temperature was highest in 1995, and lowest in 1997. Salinity was highest in 1995 and lowest in 1996. Regionally, salinity was more variable than temperature. Seasonally, temperature was more variable than salinity. Temperature was highest in the June-August, the spawning season of bay anchovy, and lowest during the April-May surveys. Salinity increased progressively from April-May to October. Salinity was lowest in April-May in all years. The coefficient of variation (CV) for annual mean salinities was about 2 times higher than that for temperatures.

Trends in abundance and recruitment

Annual bay anchovy recruitment levels were highly variable. Levels of YOY recruitment in October were low in 1995 and 1996 (6 to 7 X 10^9) but higher in 1997-1999 (19 to 52 X 10^9). Baywide estimates of bay anchovy biomass for fish > 30 mm TL increased from April to October (Fig. 2). October baywide biomass was highest in 1998 (mean ± SE = 38,000±4,100 tons), and lowest in 1996 (5,000±1,100 tons).

Spawning stock biomass (SSB), estimated as the baywide biomass in April-May, was lowest in 1995 (663 tons), and highest in 1997 (4,010 tons). The SSB, at first glance, did not show any apparent relationship with October YOY abundance (Fig. 3-a). The SSB in June-August, estimated from age 1+ bay anchovy biomass, also did not show any obvious relationship with October YOY abundance (Fig. 3-b).

Table 3. Mean temperatures (°C) and salinities (psu) integrated over surface to bottom, with pooled standard errors

Period	Temperature	SE	Salinity	SE
Cruise date				
28-Apr-95	14.08	0.09	17.60	0.41
23-Jul-95	28.04	0.19	17.77	0.46
28-Oct-95	17.71	0.09	20.43	0.38
28-Apr-96	13.24	0.13	13.01	0.39
17-Jul-96	24.57	0.15	14.55	0.56
22-Oct-96	16.61	0.15	14.13	0.42
20-Apr-97	10.96	0.08	13.52	0.64
11-Jul-97	25.46	0.18	15.57	0.47
29-Oct-97	15.00	0.06	20.59	0.35
11-Apr-98	12.20	0.08	11.45	0.46
04-Aug-98	25.86	0.07	15.65	0.40
19-Oct-98	19.08	0.08	18.80	0.42
19-Apr-99	12.09	0.11	15.72	0.45
26-Jun-99	23.23	0.14	18.22	0.48
23-Oct-99	16.31	0.10	19.59	0.46
Year				
1995	19.95	0.07	18.60	0.24
1996	18.14	0.09	13.90	0.26
1997	17.14	0.06	16.56	0.28
1998	19.05	0.05	15.30	0.25
1999	17.21	0.07	17.84	0.27
CV	6.6%		11.5%	
Season				
April-May	12.52	0.05	14.26	0.21
June-August	25.43	0.07	16.35	0.22
October	16.94	0.05	18.71	0.19
Region				
Lower	18.40	1.44	20.94	0.74
Middle	18.29	1.52	14.09	0.77
Upper	17.99	1.57	7.17	0.78

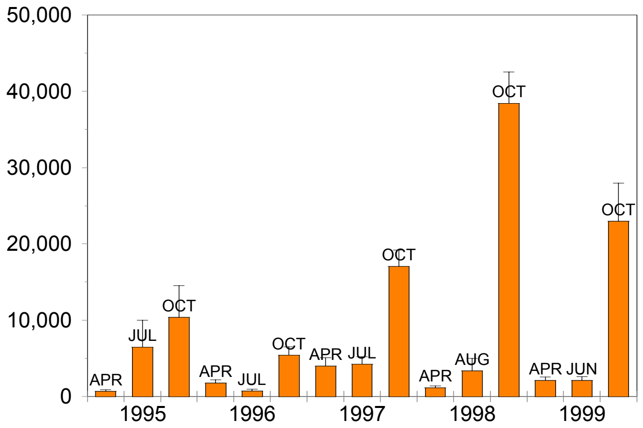


Fig. 2. Baywide estimate of > 30 mm TL bay anchovy biomass (YOY + adult) in tons.

Correlations

Correlation coefficients of biomass-weighted mean latitude of YOY and adult bay anchovy distribution with salinity, temperature, and Susquehanna River stream flow are provided in Table 4. Salinity gradients did not show significant correlations with the mean latitude of YOY and adult bay anchovy biomass or number in October. It was difficult to interpret the high correlation coefficients between YOY and adult bay anchovy abundances in October with salinity change in the lower Bay from April-May to June-August, but it suggested that October recruitment might be fixed in the April to August period (Fig. 4). Although some variables were significantly correlated, we were unable to detect any consistent patterns with respect to season, or life-stage of bay anchovy. Also, SSB in April-May was not significantly correlated with the previous year's YOY recruitment level, probably because of variable winter migrations out of the Bay. The simple correlations alone were not sufficient to test the hypothesis, because there were only 5 years of observations, and significant correlations could have occurred by chance.

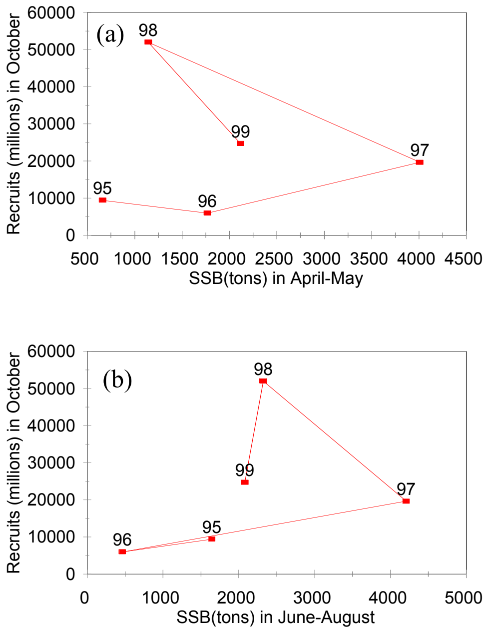


Fig. 3. YOY recruitment vs. spawning stock biomass of bay anchovy in Chesapeake Bay.

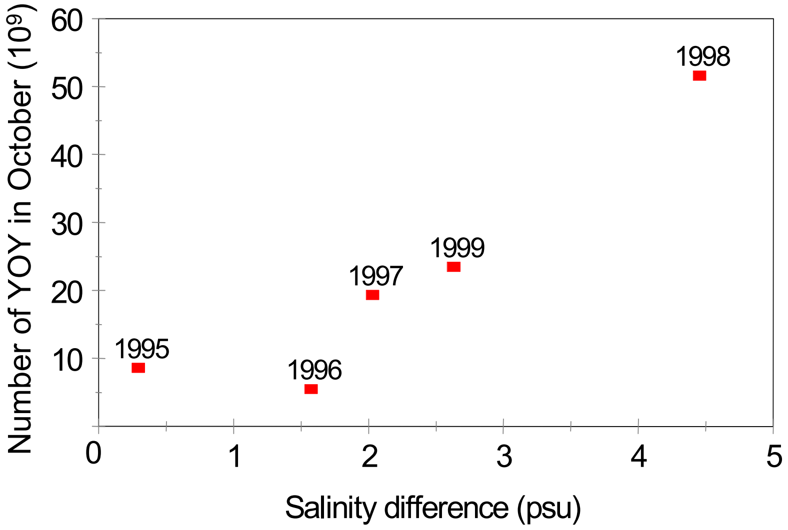


Fig. 4. YOY recruitment of bay anchovy in October plotted on salinity change in the lower Bay from April-May to June-August.

Table 4. Correlation coefficients for bay anchovy distribution and abundance with temperature, salinity and stream flow from 1995 to 1999. Row variables that did not show any significant correlation at α = 0.05 are not shown here.

Explanation of the abbreviations for variable names:
1) Column variable names
The first character: L = mean latitude of occurrence weighted by biomass, N = baywide abundance, B = biomass
The third character: Y = young-of-the-year bay anchovy. A = age 1+ bay anchovy
The fourth and fifth digit: 04 = April-May, 07 = June-August, 10 = October
2) Row variable names
The first three characters: SAL = salinity, TEM = water temperature,
D_S = salinity difference from the previous cruise, D_T = temperature difference
G_S = salinity gradient between two regions, G_T = temperature gradient
The fourth and fifth digit: 04 = April-May, 07 = June-August, 10 = October
The sixth character: L = lower Bay, M = middle Bay, U = upper Bay
The last character: S = surface, B = bottom layer
FLOW: monthly mean stream flow from the Susquehanna River from January (01) to October (10)
3) * = Significant at alpha = 0.05, ** = significant at alpha = 0.01

Variable	L_Y07	L_Y10	N_Y07	N_Y10	L_A04	L_A07	L_A10	B_A04	B_A07	B_A10
SAL04LS	0.86	0.43	0.50	-0.76	0.58	0.72	0.60	-0.07	-0.18	**-0.88***
SAL04US	0.32	-0.31	0.37	-0.17	**0.91***	0.09	0.02	0.12	0.41	-0.36
SAL04UB	0.27	-0.32	0.28	-0.13	**0.93***	0.04	0.04	0.15	0.42	-0.33
SAL10MB		**-0.89***		0.47			-0.71			0.38
SAL10UB		**-0.94****		0.60			-0.71			0.51
TEM04LS	0.79	0.24	0.86	-0.19	0.16	0.70	0.07	**-0.93***	-0.66	-0.22
TEM04MS	0.91	0.68	0.65	-0.53	-0.03	**0.93***	0.52	-0.78	**-0.89***	-0.54
TEM04US	0.48	0.74	0.16	-0.30	-0.60	0.62	0.44	-0.59	**-0.92***	-0.19
TEM04LB	0.93	0.35	**0.90***	-0.48	0.35	0.83	0.27	-0.73	-0.55	-0.54
TEM04MB	**0.98***	0.51	0.88	-0.63	0.15	**0.91***	0.35	-0.65	-0.60	-0.64
TEM07MS	0.61	-0.13	**0.91***	-0.06		0.33	-0.45		-0.14	0.02
TEM07US	0.49	-0.29	**0.92***	-0.04		0.24	-0.49		0.08	-0.02
D_S07LS	-0.82	-0.71	-0.28	**0.91***		-0.79	-0.82		0.33	**0.99****
D_S07MS	-0.93	-0.86	-0.55	**0.88***		**-0.95***	-0.62		0.66	0.81
D_S07LB	-0.49	-0.59	-0.27	0.14		-0.59	-0.34		**-0.95***	0.08
D_S07MB	**-0.98***	-0.48	**-0.90***	0.64		-0.87	-0.26		0.52	0.62
D_S10UB		**-0.90***		0.62			-0.70			0.58
D_T07MS	-0.22	-0.65	0.50	0.33		-0.34	**-0.88***		0.52	0.43
D_T07LB	**-0.96***	-0.14	0.17	0.13		-0.21	-0.60		0.14	0.38
G_S04US	0.80	0.87	0.41	-0.62	-0.35	**0.89***	0.62	-0.59	**-0.93***	-0.55
G_T04UB	0.02	-0.58	0.26	0.14	**0.92***	-0.19	-0.22	0.13	0.56	-0.05
G_S07UB	**-0.96***	-0.36	-0.67	0.37		-0.51	0.13		0.40	0.18
FLOW01	0.17	0.53	-0.03	-0.02	-0.73	0.32	0.21	-0.52	-0.79	0.12
FLOW02	-0.65	-0.06	-0.60	0.55	-0.71	-0.47	-0.23	0.00	-0.15	0.67
FLOW03	-0.88	-0.42	-0.47	0.72	-0.62	-0.71	-0.62	0.10	0.21	0.86
FLOW04	-0.45	0.07	-0.56	0.51	-0.51	-0.28	0.00	-0.21	-0.40	0.56
FLOW05	-0.27	0.30	-0.31	0.20		-0.06	-0.03		-0.47	0.38
FLOW06	-0.44	0.15	0.02	-0.02		-0.07	-0.33		-0.08	0.24
FLOW07	0.18	0.42	0.12	-0.01		0.27	-0.02		-0.64	0.18
FLOW08		0.73		-0.36			0.41			-0.17
FLOW09		0.84		-0.46			0.83			-0.43
FLOW10		**0.97****		-0.68			0.79			-0.61

Ontogenetic migration

The length-specific mean latitudes of occurrence of bay anchovy, weighted by their abundance, revealed an apparent ontogenetic migration. 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. 5). In April-May, small age 1 bay anchovies < 60 mm TL, apparently recruited from the previous year, varied annually in their mean latitude of occurrence in the Bay, whereas large (> age 1) bay anchovy had relatively stable latitudinal locations near the lower-middle Bay boundary (Fig. 5-a). Compared to April-May, age 1+ bay anchovy in June-August were more variable in their annual mean latitudes of occurrence, but both YOY and adult bay anchovy tended to move upbay (Fig. 5-b). In 1997 and 1999, when annual mean temperatures were lowest (Table 3), YOY bay anchovy were too small to be sampled by the MWT in June-August. The mean latitudes for 30-60 mm TL bay anchovy in April-May showed not only additive, but also interactive (size x latitude) annual differences. October mean latitudes (Fig. 5-c) indicated consistent ontogenetic migration patterns, although there were significant additive, annual differences, but without interactive differences. The most probable explanation is that YOY bay anchovies tended to move upbay, and began to move downbay at ca. 45 mm TL.

The SSB, i.e., spawning stock biomass of bay anchovy (excludes YOY), from 1995 to 1999 was centered between 37.30' N – 38.00'N in April-July (Fig. 6-a). However, in June-August 1995-1996, the SSB shifted toward the upper Bay, whereas its mean latitudinal positions hardly differed between April-May and June-August in 1997-1999. The June-August latitude of SSB was strongly and significantly related to surface temperature in the middle Bay in April-May (r^2 = 86%, p=0.0233; Fig. 6-b). The regression equation is:

$$\text{Latitude} = 33.93 + 0.35\,T$$

where, T = Temperature for 10.5-14.5 ^{o}C.

Contour plots of adult abundance with respect to surface temperature and salinity showed that spawners were mostly distributed at 10-12^{o}C in April-May (Fig. 7-a). In July 1995, when adults were distributed over the entire Bay, the surface temperature exceeded 26^{o}C throughout the Bay, and adults were mostly distributed at 27-30^{o}C and 5-6 psu salinity. The upper-left concentration in the lower panel of Fig. 7-a corresponds exclusively to adult SSB in July 1995. In 1996-1999, the spawner distribution in June-August coincided with the 24 - 26^{o}C temperature area (Fig. 7-a). In 1996, the lowest recruitment year, adults moved far upbay in July (Fig. 8), probably because the 25-26^{o}C temperature range occurred there (Fig. 7-b). Thus, the latitudinal range of adults was broad in July-August 1996 (Fig. 8). In contrast, in July-August 1998, the 25-26^{o}C temperatures occurred only in the lower Bay (Fig. 7-b), and most adults did not move far upbay between April and July-August (Fig. 8). Thus, water temperature, rather than the salinity gradient, may be more important variable to define latitudinal range of spawning activity. April-May temperature in the middle Bay was high in

1995-1996, but low in 1997-1999, and the low April mid-Bay temperature was associated with higher YOY recruitment in October.

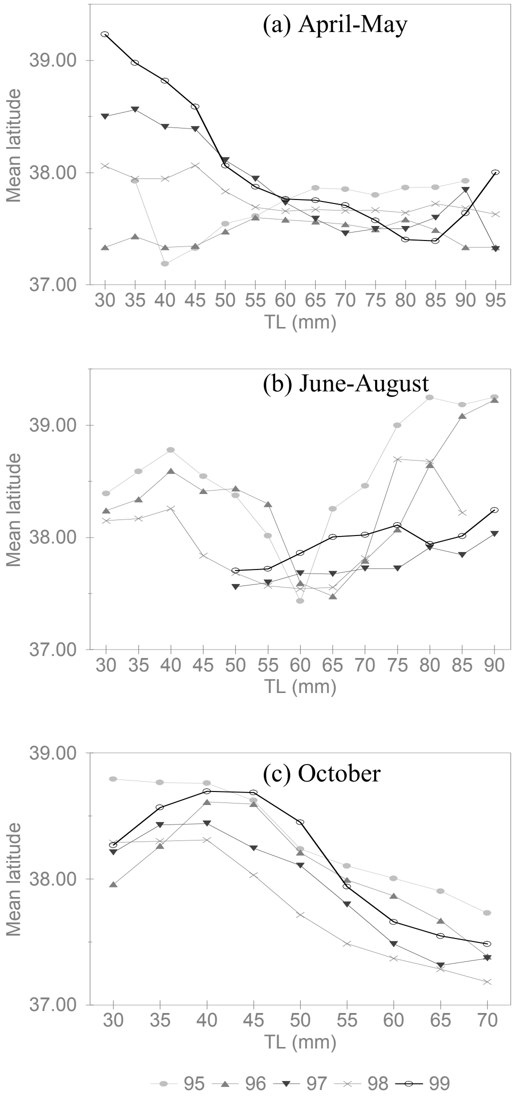
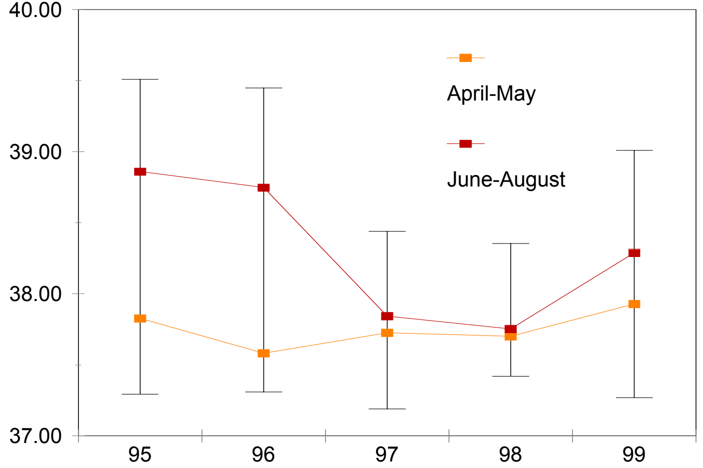


Fig. 5. Abundance-weighted mean latitude of occurrence of bay anchovy, 1995-1999.

(a) Mean latitude of adults



(b) Mean latitude of adults in June-August

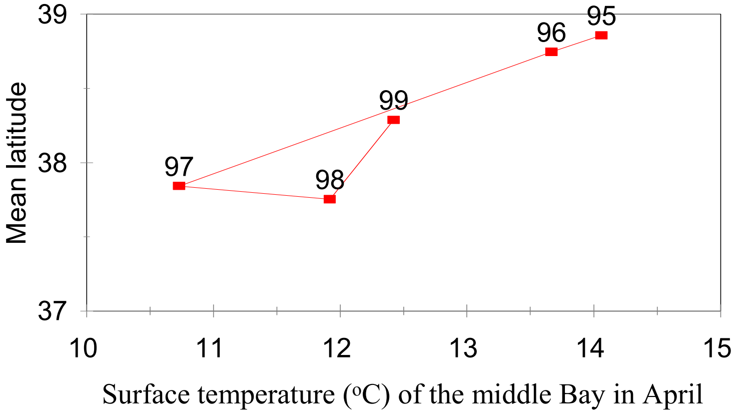


Fig. 6. Mean latitude of occurrence of adult bay anchovy. The upper vertical bar represents mean + STD of June-August, and the lower vertical bar represents mean – STD of April-May.

For small (<60 mm TL) or YOY bay anchovy, correlation and regression analyses revealed that salinity gradients were consistently related to the length-specific mean latitudes of occurrence of bay anchovy (Fig. 9). In April-May, the length-specific mean latitude weighted by abundance moved upbay as the salinity gradient (the difference between the middle and the upper Bay mean salinity) decreased (Fig. 9-a). As bay anchovy length increased, the mean latitudes of occurrence decreased, e.g., larger bay anchovies generally were distributed toward the lower Bay. Because there was strong interaction between the size (x-axis) and salinity gradient (y-axis) in April-May, length differences mostly disappeared, if the salinity gradient is larger than approximately 7 psu. The smallest bay anchovy experienced the most pronounced salinity gradient effect in April-May.

In June-August and October, the length-specific mean latitudes of occurrence of YOY bay anchovy did not show a significant interaction effect (length x salinity gradient), and the salinity-gradient effect was additive for all size classes (Fig. 9-b and c). The direction of the salinity-gradient effect was opposite during the two periods. Under low salinity gradients in June-August, YOY bay anchovy distributions were displaced upbay, whereas in October a low salinity gradient was associated with downbay distributions. The result indicates that steep salinity gradients discourage upbay YOY bay anchovy migration from April to August, and downbay migration from July to October. A steep salinity gradient apparently would inhibit ontogenetic migration of small or YOY bay anchovy in either an upbay or downbay direction.

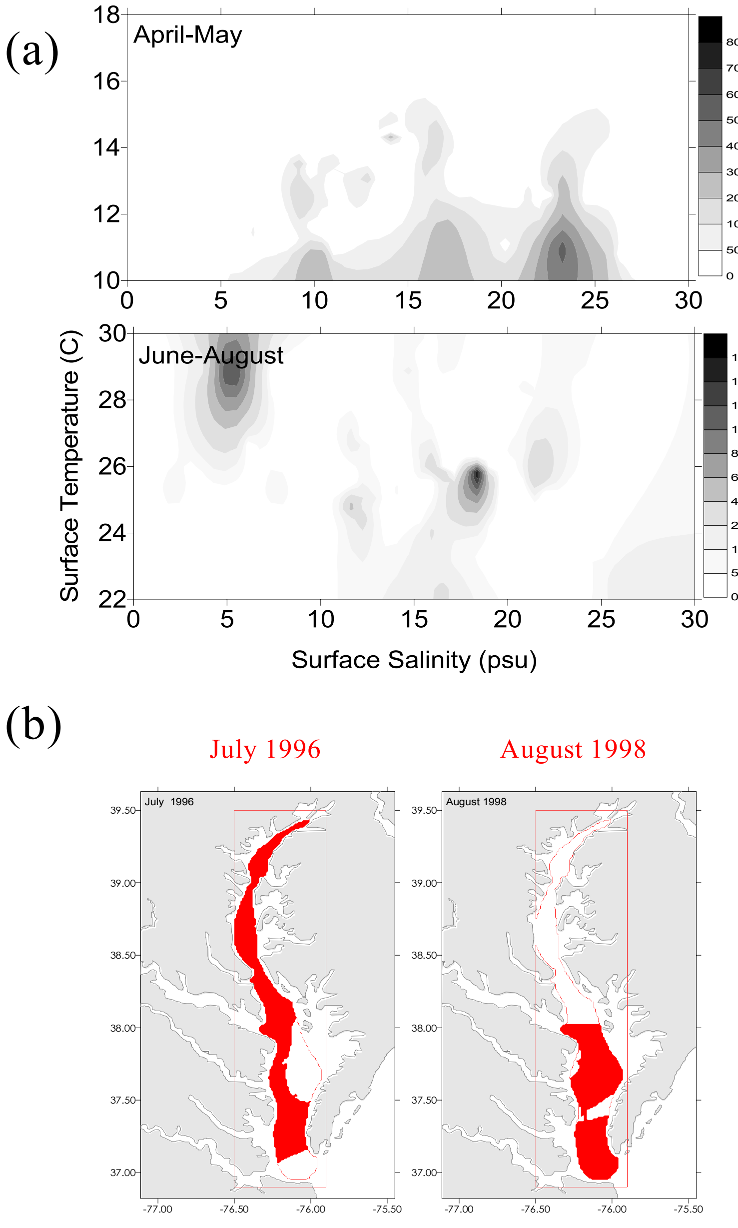


Fig. 7. Potential spawning areas and conditions in Chesapeake Bay. (a) adult abundance with surface salinity and temperature (1995-1999), (b) potential spawning area based on surface temperature (24-26^{o}C).

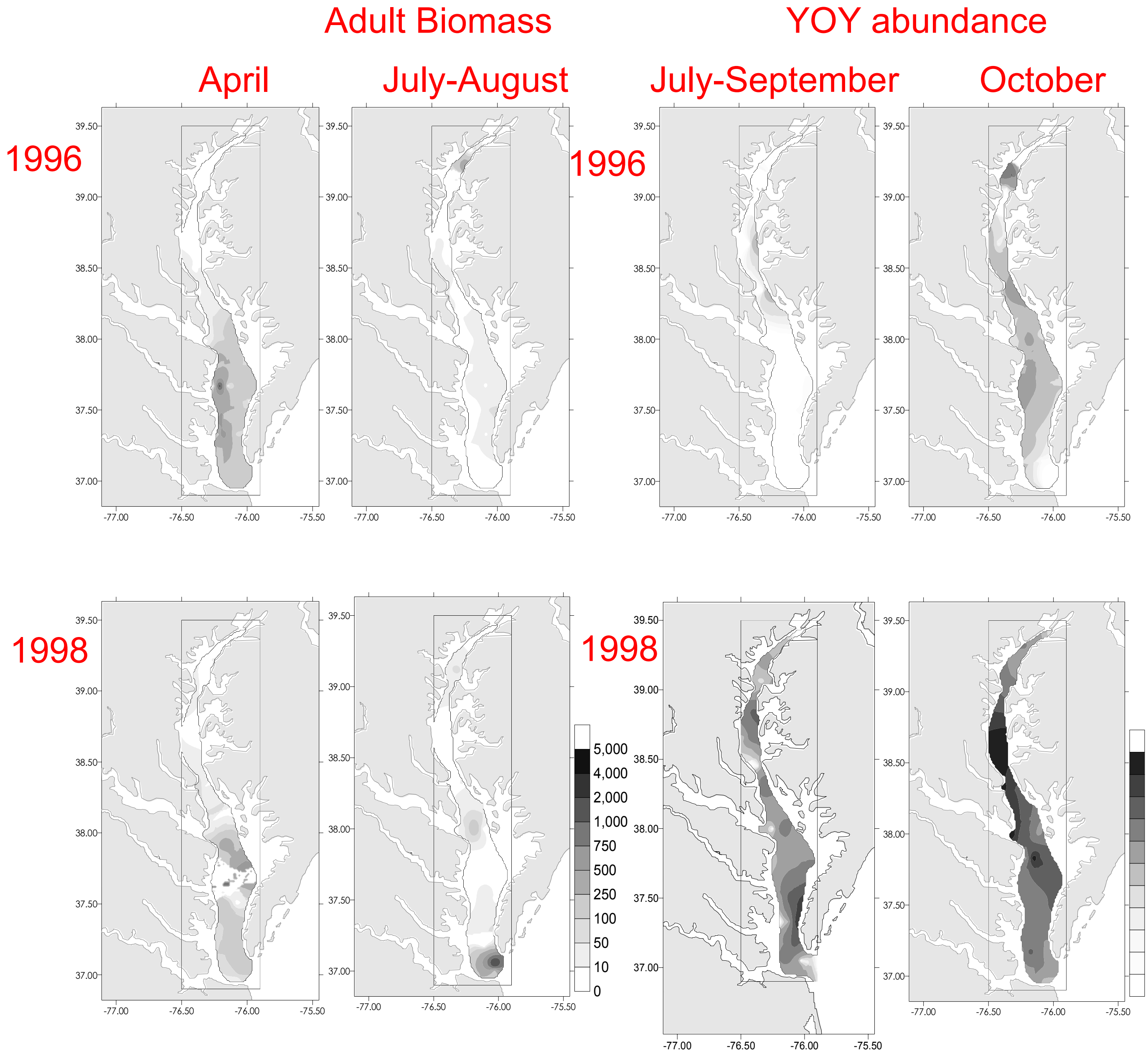


Fig. 8. Distribution of bay anchovy spawning stock biomass and YOY recruitment in 1996 and 1998, Chesapeake Bay.

Recruitment Models

Although SSB alone was not correlated with recruitment level, the shift in spatial distribution of adult spawners between April-May and June-August was strongly correlated with October YOY recruitment levels. In the regression analysis for the statistical model, the latitudinal shift alone explained 85% of recruitment variability from 1995 to 1999 (Fig. 10-a). The regression equation is:

$$\text{Log}(R) = 10.55 - 1.49\,\Delta L$$

Where, R: number of recruits in millions; ΔL: difference in mean location latitude of SSB, [(July latitude) – (April latitude)].

When a SSB term was included, the regression improved and explained 99.5% of recruitment variability (Fig. 10-b). The equation is:

$$\text{Log}(R) = 11.29 - 0.000285\,S - 1.83\,\Delta L$$

where, S: SSB (male + female) in tons.

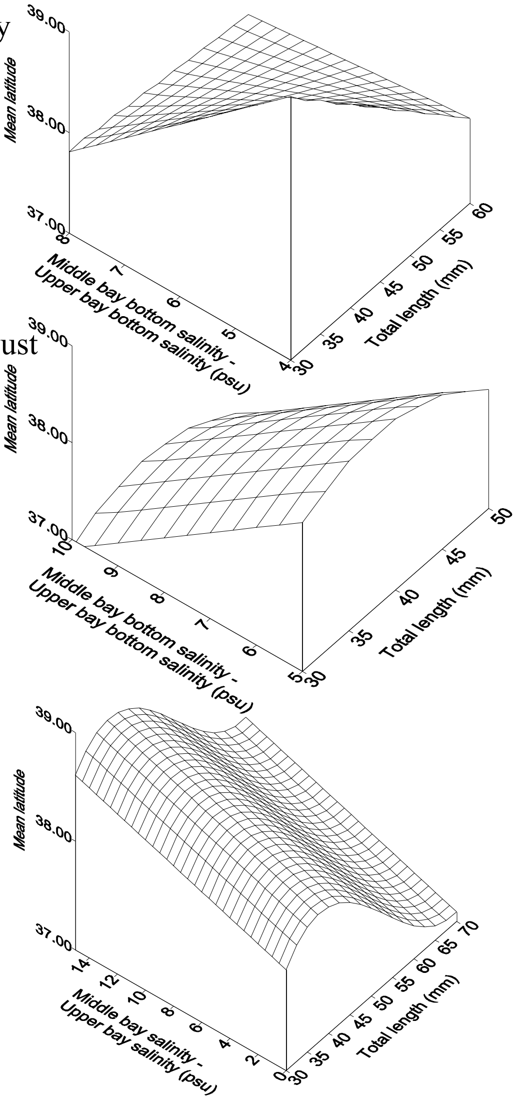
The latitudinal shifts in SSB still explained most of recruitment variability ($p < 0.0032$). Although SSB alone was not significantly correlated with recruitment, SSB was statistically significant in the model, if latitudinal shifts were held constant for the five years ($p=0.0180$). This statistical model indicates that recruitment level is maximized when SSB = 0, an obviously unrealistic outcome (Fig. 11-a). The unrealistic result apparently was generated because the negative slope of SSB implies a density-dependent recruitment process that is not accounted for by the statistical model.

Despite a small decrease in r^2 and the possibility of collinearity among SSB, latitudinal shift, and recruitment, the modified Ricker model provided a good fit to the YOY recruitment data (r^2=98.2%, $p = 0.0176$), with a biologically realistic result (Fig. 11-b). The equation is:

$$R = 128\,S\exp(-0.000785\,S - 1.805\,\Delta L)$$

where, R: recruitment levels, millions of YOY in October; S: SSB (male + female, tons) in April-May.

This model maximizes recruitment level when baywide relative biomass of adults in April (SSB) is approximately 1,300 tons, if the latitudinal shift (ΔL) is held constant. If SSB is held constant, the model maximized recruitment level when ΔL = 0, i.e., if the SSB distribution is exactly the same between April-May and June-August. In 1998, the highest recruitment year, the estimated baywide adult biomass was 1,145 tons in April-May. Since the VIF was only 1.28 << 10 and all CIs were far smaller than 15, we assumed that collinearity was not a problem. We also included the interaction term (S x ΔL) and fit the model again, but without improvement because the interaction term was not significant ($p = 0.06$).


(a) April-May

(b) June-August

(c) October

Fig. 9. Mean latitude of occurrence of small (<60 mm TL) or YOY bay anchovy (1995-1999) with respect to salinity gradient between the upper and the middle Bay. (a) for < 60 mm TL bay anchovy, (b) and (c) for YOY ban anchovy.

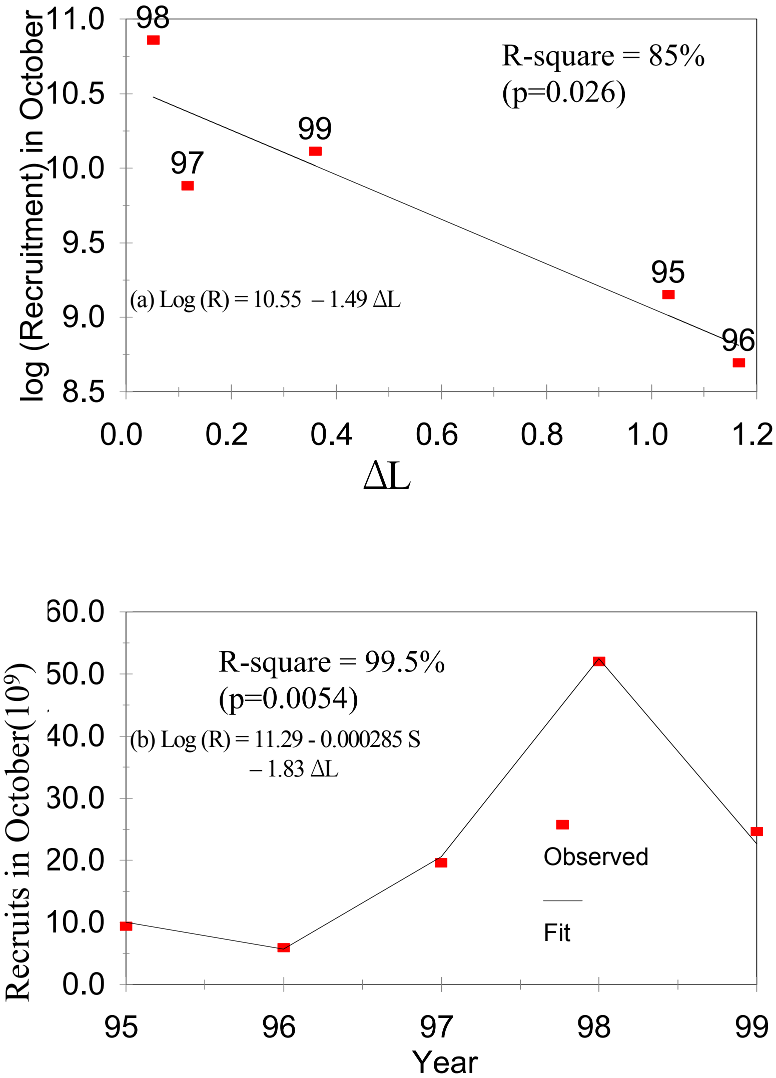
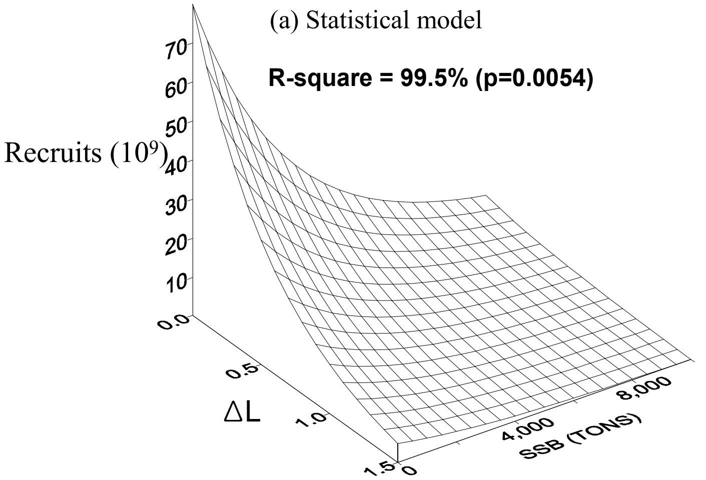


Fig.10. Regression analyses of YOY bay anchovy recruitment level for five years in Chesapeake Bay. R: YOY recruitment level; ΔL: difference in biomass-weighted mean latitude of SSB in decimal units between April-May and June-August; S: baywide spawning stock biomass (male + female) in tons for April-May. (a) ΔL alone included as explanatory variable, (b) ΔL and S included as explanatory variables.

DISCUSSION

Not only biological interactions, but also complex oceanographic processes control bay anchovy recruitment. Our results demonstrated that there is a strong spatial component in the recruitment dynamics of bay anchovy in Chesapeake Bay. Both salinity and temperature distributions are important to bay anchovy recruitment and distribution. In addition, spawning stock size also was related to recruitment level, mediated by hydrological conditions. Although fish recruitment processes have been difficult to understand, the spatially-extensive TIES program has provided valuable information on processes related to bay anchovy recruitment.


(a) Statistical model

(b) Ricker model

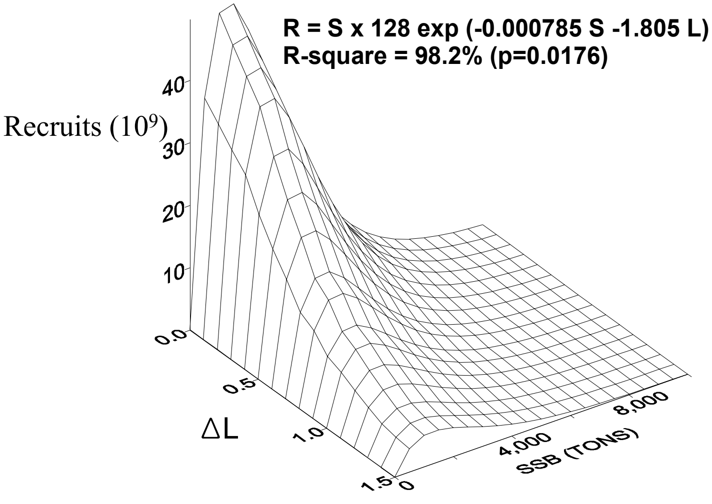


Fig. 11. Two stock-recruitment models. ΔL: difference in biomass-weighted mean latitude of SSB in decimal units between April-May and June-August; SSB: baywide spawning stock biomass (male + female) in tons for April-May. ΔL and SSB included as explanatory variables.

It is possible that the apparent ontogenetic migration pattern might have been caused by regional differences in growth and mortality rate. However, it is difficult to think that the smooth consistency from 1995 to 1999, and significant relationships between mean latitudes of bay anchovy distribution and salinity gradient and total length (Fig. 5 and 9) could have been generated by spatial differences in growth and mortality. But it is possible that small variances in the locations of bay anchovy could be explained by regional variability in growth and mortality. It seems probable that ontogenetic migration is the dominant feature determining spatial and temporal patterns in abundance, biomass, and production of bay anchovy at the mesoscale.

It is uncertain why YOY bay anchovy migrate upbay while growing in summer and then begin to move toward the lower Bay in late summer and fall. A steep salinity gradient seems to deter or diminish the ontogenetic migration of YOY bay anchovy. Kimura et al. (2000), based on otolith microchemical analysis, supported the hypothesis of an upbay ontogenetic migration by small YOY anchovy (late larvae and small juveniles). Adult bay anchovy probably is not influenced significantly by salinity barriers in the Bay (Houde & Zastrow, 1991), but may search for suitable spawning conditions in which water temperatures, and probably prey levels, are critical. It might be beneficial for juvenile bay anchovy to disperse widely to exploit food resources baywide if they are not significantly restricted by temperature or salinity ranges. However, when they approach the adult stage, they must return to suitable spawning areas that are defined by suitable temperature, salinity, or other hydrological and biological conditions to spawn successfully. Differences in physiological and ecological requirements among life stages of bay anchovy may control the distinctive ontogenetic migration pattern that has been observed, although little information is available to test for such differences.

Although the modified Ricker model for bay anchovy recruitment fit the data well, the number of years is only five, and the significant relationship could have originated by chance. However, we believe that possible statistical errors are minimal because diagnostics did not indicate significant collinearity. Moreover, considering the number of stations available to parameterize the values of each variable in the recruitment models, the baywide estimates of bay anchovy abundance and biomass are quite accurate and possible measurement error is relatively small. The number of CTD stations was near 100 for each cruise, and the surface and bottom temperature and salinity were not averaged based on an arbitrary fixed depth of pycnocline, but were carefully separated by the best estimate of pycnocline depth based on the depth profiles. The fishery-independent baywide estimate of abundance for each size class of bay anchovy also is believed to be unbiased and accurate.

The spawning area of adult anchovy in 1995-1999 was critical in determining YOY recruitment levels. The high recruitment years had similar distribution patterns of SSB between April-May and June-August. Rilling & Houde (1999a, b) reported high biomasses of adult anchovy predominantly in the lower Bay in June and July 1993, a high recruitment year, in agreement with the pattern proposed here that supports high recruitment. Zastrow et al. (1991) reported that the spawning season extended from mid-May to mid-August. The period for the latitudinal shift, ΔL, April-May to June-August, mostly coincided with the spawning season. However, It is uncertain why recruitment levels were higher when the latitudinal shifts were narrower.

Recent individual-based models suggested that density-dependent processes during early-life stages could stabilize bay anchovy recruitments (Wang et al., 1997; Rose et al., 1999; Cowan et al., 1999). Rilling & Houde (1999 a, b) reported that mean density of eggs and larvae in July 1993 was highest in the lower Bay and lowest in the upper Bay, whereas cumulative mortality from egg to 18-d-old larval stage was highest in the lower Bay, and lowest in the Upper Bay. In addition, other recruitment models that we fit, but for which results are not given, consistently indicated density-dependence (significant β_1

values). At small scales of several meters, considered by Wang et al (1997) and Cowan et al. (1999), feeding processes are important and high anchovy spawning stock biomass could induce density-dependent food competition on abundant first-feeding larvae because planktonic prey of bay anchovy are far smaller than anchovy, and certainly subject to control by small-scale processes. Peebles et al. (1996) hypothesized that bay anchovy's size-specific fecundity is related to prey availability in Tampa Bay, Florida, and Rose et al. (1999) suggested that density-dependent growth of larvae and juveniles would lead to density-dependent survival of these stages. Hunter & Kimbrell (1980) and Alheit (1987) proposed that cannibalism during egg and larval stages is responsible for density-dependence in anchovies. Our modified Ricker model accounted for the possible density-dependence, although we do not know at which stages such density-dependent processes are most important.

At first glance, the observed relationship between latitudinal shift of bay anchovy SSB distribution and YOY recruitment conflicts with the density-dependent hypothesis, because expected density-dependence would be more severe and recruitment would decrease as the range of the latitudinal shift decreases. But, we observed that recruitment increased as the shift decreased. This seemingly precludes prey distribution as a primary factor explaining the relationship between latitudinal shifts in SSB distribution and YOY recruitment.

The conflict may be explained by considering the spatial scale of processes and body-size issues. Predation has been suggested as an important controller of fish recruitment processes in early-life stages (Sissenwine, 1984; Bailey & Houde, 1989). At the mesoscale of 10-100 Km, which corresponds to ranges of the latitudinal shifts of adult bay anchovy, distribution of predators may be important because most predators are larger than bay anchovy and can move actively or vary in distribution and abundance at the scale of 10-100 Km. We speculate that an abundant and spatially concentrated supply of larvae or juvenile anchovy, especially in the middle Bay, could promote early-life survival, but more analyses of anchovy, their predators, and their prey are required.

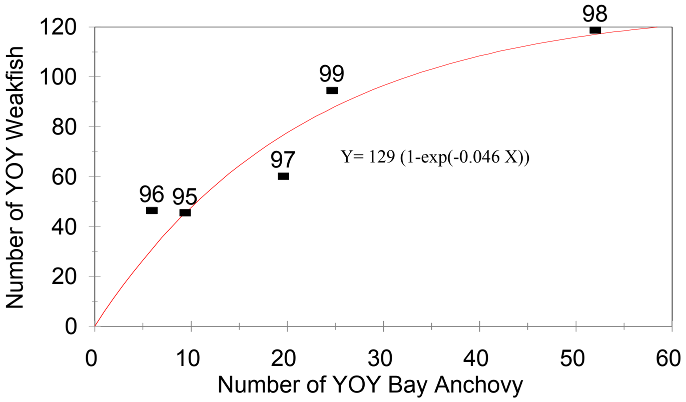


Fig.12. Exponential saturation relationship between number of YOY weakfish (x10^6) and YOY bay anchovy (x10^9) in October.

The abundance of YOY weakfish (Cynoscion regalis), a major predator of bay anchovy in Chesapeake Bay (Hartman & Brandt, 1995), showed an exponential saturation relationship with respect to YOY bay anchovy number (Fig. 12), and supported, at least circumstantially, the predator-satiation hypothesis. If the spawning area is narrow, the supply of larvae and juvenile fish to potential predators may be

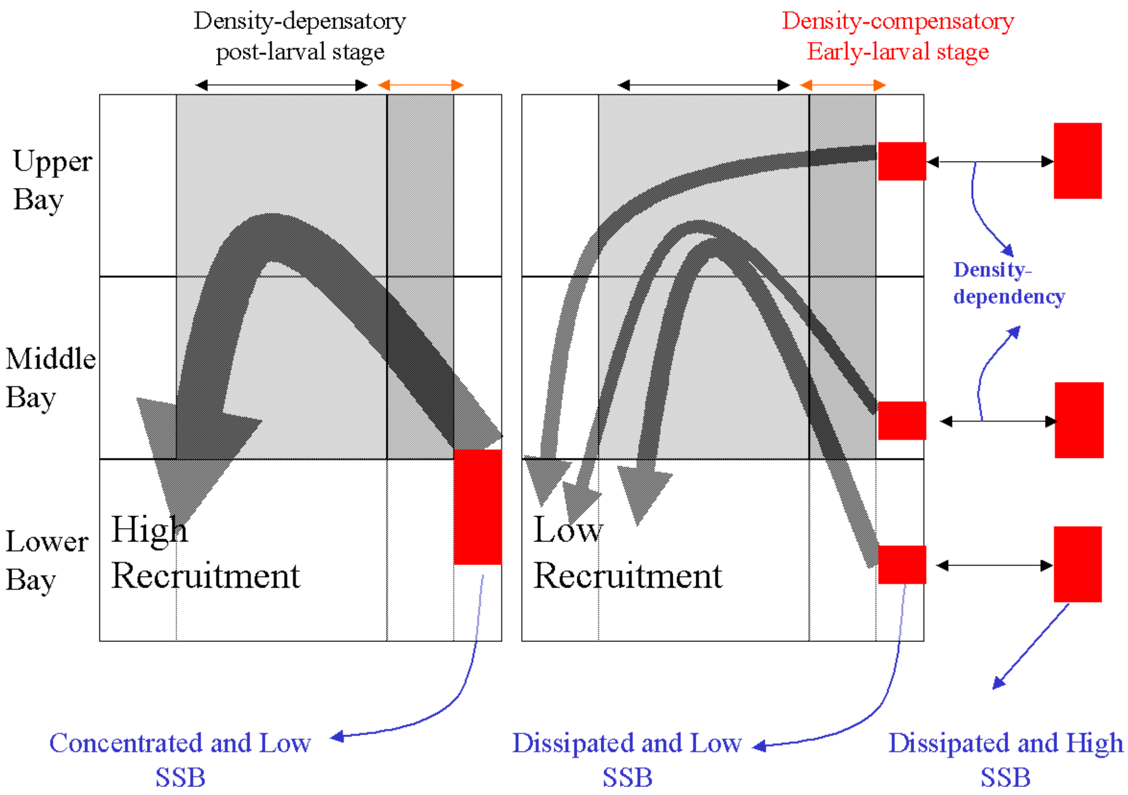


Fig. 13. A conceptual model of the bay anchovy recruitment process in Chesapeake Bay. Spawning biomass size is indicated by two sizes of black boxes. The latitudinal shift of spawners is explained by vertical positions of the black boxes. Horizontal arrows indicate density-compensatory and density-depensatory processes in early-larval and post-larval stages. Large black arrows indicate ontogenetic migration of YOY bay anchovy.

saturating. This mechanism for survival has been suggested for insects and plants (Gould, 1977), in which temporal sequence, i.e., periods in cyclic spawning activity, seems to be critical. The temporal sequencing also has been emphasized in fish recruitment processes, e.g., the match-mismatch hypothesis (Cushing, 1974). In the case of bay anchovy recruitment, however, we hypothesize that it is not the temporal sequence, but the spatial distribution of spawners that may be more important in controlling recruitment through predator satiation.

A conceptual model for hypothesized mechanisms of bay anchovy recruitment in Chesapeake Bay is outlined in Fig. 13. To summarize:

1) Low temperatures at a baywide scale in Chesapeake Bay during April-May will restrict distribution of most adults during the pending spawning season to a confined area in the lower Bay. If relatively low temperatures persist until the June-August spawning season, temperature-critical spawning activity will be confined to a relatively small area of the lower and lower-mid Bay.

2) Concentrated spawning activity that produces eggs and larvae in the confined area could satiate predators of bay anchovy larvae and YOY (spatial predator-satiation hypothesis).

3) Density-dependence suggested by the spawning stock-recruitment relationship might be a result of feeding constraints, cannibalism, and competition in the early-larval stages.

Ultimately, other hypotheses may explain better the relationships between latitudinal shifts of spawners and recruitment than does predation satiation. The latitudinal shifts of adults might have been controlled by the same common factor as the recruitment process, and the relationship might be the result of the common factors. We are still investigating other possible hypotheses to explain the relationship between the distribution of spawners and recruitment. Accepting results of our analyses and considering scaling issues, the density-compensatory process seems certain to act during early-larval stages at small spatial scales, whereas the possible density-depensatory processes explaining the effect of latitudinal shift might occur during the post-larval and juvenile stage at the mesoscale. It is apparent that spatially-explicit processes operating at the mesoscale, and affecting both adult and YOY, have important implications for bay anchovy recruitment in Chesapeake Bay. The nature of density-dependent mechanisms and physical processes operating at fine- and mesoscales are still poorly understood.

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REFERENCES

Able, K.W.; Fahay, M.P. (1998): The first year in the life of estuarine fishes in the Middle Atlantic Bight. Rutgers University Press, New Brunswick, New Jersey. 342 pages.

Alheit, J. (1987): Egg cannibalism versus egg predation: their significant in anchovies. S. Afr. J. Mar. Sci. 5, 467-470.

Bailey, K.M.; Houde, E.D. (1989): Predation on eggs and larvae of marine fishes and the recruitment problem. Adv. Mar. Bio. 25, 1-83.

Baird, D.; Ulanowicz, R.E. (1989): The seasonal dynamics of the Chesapeake Bay ecosystem. Ecol. Monogr. 59(4), 329-364.

Bhattachara, C.G. (1967): A simple method of resolution of a distribution into Gaussian components. Biometrics 23, 115-135.

Chesapeake Bay Program (2000): Chesapeake Bay: Introduction to an ecosystem. 30 p.

Cowan, J.H.; Rose, K.A.; Houde, E.D.; Wang, S.B.; Young, J. (1999): Modeling effects of increased larval mortality on bay anchovy population dynamics in the mesohaline Chesapeake Bay: evidence for compensatory reserve. Mar. Ecol. Prog. Ser. 185, 133-146.

Cressie, N.A.C. (1993): Statistics for spatial data. Revised edition. Wiley-Interscience publication, New York. 900 pages.

Cronin, W.B. (Ed.) (1971): Volumetric, areal, and tidal statistics of the Chesapeake bay estuary and its tributaries. Chesapeake Bay Institute. The Johns Hopkins University. Baltimore. 15 pages.

Cushing, D.H. (1974): The possible density-dependence of larval mortality and adult mortality in fishes. In: The early life history of fish. (Ed: Blaxter, J.H.) Cambridge University Press, Cambridge, 103-111.

Day, J.W.; Hall, C.A.S.; Kemp, W.M.; Yáñez-Arancibia, A. (1989): 3. Estuarine Chemistry. In: Estuarine Ecology. (Eds: Day, J.W.; Hall, C.A.S.; Yáñez-Arancibia, A.) John Wiley & Sons, Inc, New York, 79-143.

Dorsey, S.E.; Houde, E.D.; Gamble, J.C. (1996): Cohort abundances and daily variability in mortality of eggs and yolk-sac larvae of bay anchovy, Anchoa mitchilli, in Chesapeake Bay. Fish. Bull. 94, 257-267.

Gould, S.J. (1977): Ever since Darwin. W.W. Norton, New York.

Hartman, K.J.; Brandt, S.B. (1995): Predatory demand and impact of striped bass, bluefish, and weakfish in the Chesapeake Bay: applications of bioenergetics models. Can. J. Fish. Aquat. Sci. 52, 1667-1687.

Houde, E.D.; Zastrow, C.E. (1991): Bay anchovy. In: Habitat requirements for Chesapeake Bay living resources. (Eds: Funderburk, S.L.; Mihursky, J.A.; Jordan, S.J.; Riley, D.) Living Resources Subcommittee, Cheapeake Bay Program, Annapolis, 8.1-8.14.

Hunter, J.R.; Kimbrell, C.A. (1980): Egg cannibalism in the northern anchovy, Engraulis mordax. Fish. Bull. 78, 811-816.

Kimura, R.; Secor, D.H.; Houde, E.D.; Piccoli, P.M. (In press): Up-estuary dispersal of young-of-the- year bay anchovy Anchoa mitchilli in the Chesapeake Bay: Inferences from microprobe analysis of Sr in otoliths. Mar. Ecol. Prog. Ser.

Kimura, R.; Secor, D.H.; Houde, E.D.; Piccoli, P.M. (2000): Migration/dispersal patterns of YOY bay anchovy Anchoa mitchilli in the Chesapeake Bay: Sr:Ca analysis on a ubiquitous species. Manuscript submitted to ICES 2000 Annual Science Conference, Session N.

King, M. (1995): Fisheries biology, assessment and management. Fishing News Books, Oxford. 341 pages.

Littell, R.C.; Freund, R.J.; Spector, P.C. (Eds.) (1991): SAS system for linear models. 3rd ed. SAS Institute Inc., Cary, North Carolina. 329 pages.

Loos, J.J.; Perry, E.S. (1991): Larval migration and mortality rates of bay anchovy in the Patuxent River. In: NOAA Technical Report NMFS 95. Larval fish recruitment and research in the American: proceedings of the 13th annual fish conference; 21-26 May 1989, Merida, Mexico. (Ed: Hoyt, R.D.), 65-76.

Luo, J.; Brandt, S.B. (1993): Bay anchovy Anchoa mitchilli production and consumption in mid- Chesapeake Bay based on a bioenergetics model and acoustic measurement of fish abundance. Mar. Ecol. Prog. Ser. 98(3), 223-236.

Luo, J.; Musick, J. (1991): Reproductive biology of the bay anchovy in Chesapeake Bay. Trans. Am. Fish. Soc. 120, 701-710.

MacGregor, J.M.; Houde, E.D. (1996): Onshore-offshore pattern and variability in distribution and abundance of bay anchovy Anchoa mitchilli eggs and larvae in Chesapeake Bay. Mar. Ecol. Prog. Ser. 138, 15-25.

Murdy, E.O.; Birdsong, R.S.; Musick, J.A. (1997): Fishes of Chesapeake Bay. Smithsonian Institute Press, Washington, D.C. and London. 324 pages.

Newberger, T.A.; Houde, E.D. (1995): Population biology of bay anchovy Anchoa mitchilli in the mid Chesapeake bay. Mar. Ecol. Prog. Ser. 116(1-3), 25-37.

Peebles, E.B.; Hall, J.R.; Tolley, S.G. (1996): Egg production by the bay anchovy Anchoa mitchilli in relation to adult and larval prey fields. Mar. Ecol. Prog. Ser. 131, 61-73.

Ricker, W.E. (1954): Stock and recruitment. Fish. Res. Bd. Canada 11, 559-623.

Ricker, W.E. (1975): Computation and interpretation of biological statistics of fish population. Bull. Fish. Res. Bd. Can. 191, 1-382.

Rilling, G.C.; Houde, E.D. (1999a): Regional and temporal variability in distribution and abundance of bay anchovy (Anchoa mitchilli) eggs, larvae, and adult biomass in the Chesapeake Bay. Estuaries 22, 1096-1109.

Rilling, G.C.; Houde, E.D. (1999b): Regional and temporal variability in growth and mortality of bay anchovy, Anchoa mitchilli, larvae in Chesapeake Bay. Fish. Bull. 97, 555-569.

Rose, K.A.; Cowan, J.H.; Clark, M.E.; Houde, E.D.; Wang, S.B. (1999): An individual-based model of bay anchovy population dynamics in the mesohaline region of Chesapeake Bay. Mar. Ecol. Prog. Ser. 185, 113-132.

SAS (1990): SAS/STAT User's Guide. 4th ed. SAS Institude Inc., Cary, NC.

SAS (1998): SAS/STAT Technical report: spatial prediction using the SAS system. SAS publishing. 80 pages.

Sissenwine, M.P. (1984): Why do fish populations vary? In: Exploitation of marine communities. (Ed: May, R.M.) Springer-Verlad, Berlin, 59-94.

Wang, S.B.; Cowan, J.H.; Rose, K.A.; Houde, E.D. (1997): Individual-based modelling of recruitment variability and biomass production of bay anchovy in mid-Chesapeake Bay. J. Fish Biol. 51 (Supplement A), 121-134.

Wang, S.B.; Houde, E.D. (1995): Distribution, relative abundance, biomass and production of bay anchovy Anchoa mitchilli in the Chesapeake Bay. Mar. Ecol. Prog. Ser. 121, 27-38.

Zastrow, C.E.; Houde, E.D.; Morin, L.G. (1991): Spawning, fecundity, hatch-date frequency and young-of-the-year growth of bay anchovy Anchoa mitchilli in mid-Chesapeake Bay. Mar. Ecol. Prog. Ser. 73, 161-171.