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Blue-Crab Population-Dynamics In Chesapeake Bay - Variation In Abundance (York River, 1972-1988) And Stock-Recruit Functions

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BLUE CRAB POPULATION DYNAMICS IN CHESAPEAKE BAY: VARIATION IN ABUNDANCE (YORK RIVER, 1972–1988) AND STOCK-RECRUIT FUNCTIONS

Romuald N. Lipcius and Willard A. Van Engel

ABSTRACT

Blue crab abundance in the York River, Virginia was analyzed for interannual, monthly and spatial variation at two stations sampled by bottom trawl from 1972–1988. Various stock-recruitment and recruit-stock functions were derived from trawl abundance and commercial fishery landings statistics. The key component of variation was due to interannual fluctuations in abundance, which remained consistently high or low for two or more years before changing, suggesting internal population feedback mechanisms, such as cannibalism, or long-term climatic control. In addition, significant cyclic patterns in residuals from stock-recruitment functions further indicated the existence of long-term variability in abundance. Peak seasonal abundance and lowest variation occurred from June–August. A significant year × month interaction effect was due to shifts in the time of highest seasonal abundance from summer during high-abundance years to late summer and fall in low-abundance years, suggesting differential dominance of successive year classes. Spatial variation was appreciable such that an upriver station had consistently higher catches than a downriver station, except for 2 of 17 years. A key finding concerned the significant and dome-shaped stock-recruitment relationship (Ricker model) for the trawl data. Re-examination of previous empirical and conceptual arguments against the existence of a significant stock-recruitment relationship for the blue crab indicates their invalidity. Significant surrogate effects were incorporated into the stock-recruitment relationship, including components representing prior recruiting year classes and spawning stocks, which may impact recruitment through alterations in food availability, growth and survival. A recruit-stock function was significant and indicated a correlation between juvenile abundance and a measure of spawning stock size. In concert with the preceding models, other recruit-stock functions indicate various biologically meaningful inter-relationships between different segments of the blue crab population in Chesapeake Bay.

Blue crab abundance in Chesapeake Bay fluctuates greatly, as indicated by commercial catch statistics (Hurt et al., 1979; Tang, 1985; Van Engel, 1987) and research surveys (Hines et al., 1987). Such population variation is due to numerous biotic and environmental sources, which are difficult to identify and quantify without long-term fishery-independent data sets, as are the functional relationships between different segments of a population. For instance, conflicting views exist regarding the existence (Applegate, 1983; Tang, 1985) or absence (Pearson, 1948; Sulkin et al., 1983; Van Engel, 1987) of a spawning stock-recruitment relationship for the blue crab. Thus, despite the ecological and economic significance of the blue crab in Chesapeake Bay, its population dynamics remain poorly understood due in part to the lack of documented analyses of long-term abundance data exclusive of the commercial catch.

The Virginia Institute of Marine Science (VIMS) has been conducting a fishery-independent trawl survey of blue crab abundance for over three decades in the York River, Virginia, and for a shorter duration in the James and Rappahannock rivers, Virginia. The data set is the longest of its kind, and contains quantitative information on blue crab abundance over several temporal and spatial scales. A thorough analysis of this data set will be extremely useful in advancing our understanding of blue crab population dynamics in Chesapeake Bay. In this report
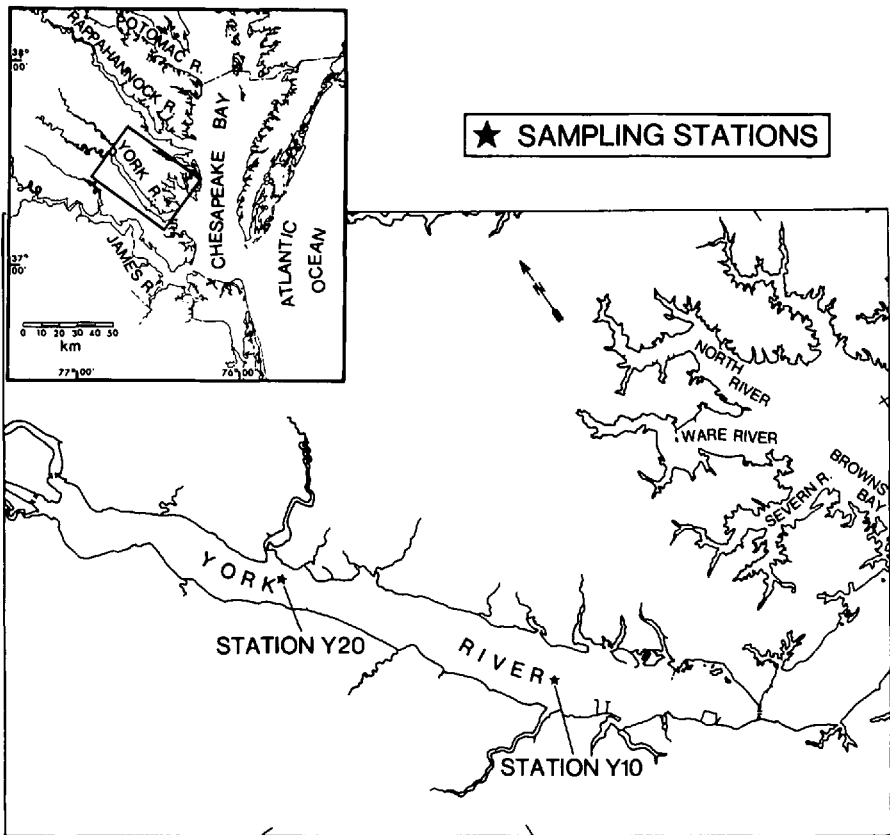
Figure 1.   VIMS trawl survey sampling stations in the York River, Virginia portion of Chesapeake Bay.

we present the results of an *exploratory* statistical analysis using selected trawl samples collected in the York River, Virginia from 1972–1988. These samples were selected to provide a replicated, balanced full-factorial experimental design incorporating year, month and station as factors. The analysis portrays (1) inter-annual, monthly and spatial variation in blue crab abundance, and (2) various basic stock-recruitment and recruit-stock functions encompassing data sets from the trawl survey and commercial fisheries.

MATERIALS AND METHODS

Data Collection. — TRAWL SAMPLING. Trawling was conducted in the channel of the York River, Virginia at two stations located 16.1 km (Y10) and 32.2 km (Y20) from the river mouth (Fig. 1). The York River is a tidally influenced tributary with salinity in the channel bottom near the sampling stations generally ranging from 13–20‰, temperature from 4–30°C, depths of about 10 m at mean low water, and sediments of fine sand (sandy-silty clay) and mud. A semi-balloon otter trawl (9.1 m wide) was towed twice within 30 min at each station for 5 min at approximately 2.5 knots, resulting in two monthly tows per station from May through November each year (1972–1988). Different gear and vessel combinations were deployed throughout the survey, but the resultant abundance estimates were standardized with conversion factors derived from previous gear comparisons (Table 1). The present gear configuration comprises a lined, semi-balloon otter trawl (9.1 m wide with 38-mm stretch mesh net and 13-mm cod-end liner) with a tickler chain and 18.3-m bridle, towed for 5 min at about 2.5 knots. Although all blue crabs were enumerated, sexed and measured, only abundance is analyzed herein.

Table 1. Gear combinations, vessels and conversion factors used to standardize blue crab abundance estimates from the VIMS trawl survey in the York River, Virginia

Original gear (time period)	Gear change (time period)	Conversion factor
9.1 m bridle (1972–1979)	18.3 m bridle (1980–1988)	(1980–1988 data) × 0.88*
Pathfinder vessel (1972–1979)	Other vessels (1980–1988)	(1972–1979 data) × 1.50*
No tickler chain (June, 1977)	Tickler chain (All else)	(June 1977 data) × 2.71†

* W. A. Van Engel, unpublished data.
† Chittenden and Van Engel, 1972.

FISHERY STATISTICS. The Virginia Marine Resources Commission (VMRC) prints annual summaries of monthly hard blue crab landings (pounds) in the state. We generated annual landings statistics from these summaries for the winter dredge fishery (December, year t through March, year t + 1) and for the hard crab fisheries from the spring through fall (May–November). The annual dredge fishery landings serve as an index of the spawning stock because most blue crabs caught in the area of the fishery are mature females (77–98%: Pearson, 1948; Van Engel, 1962; Schaffner and Diaz, 1988) of a single year class (Van Engel, 1958). The blue crab fishery in the spring through fall is composed of differing percentages of two or more year classes, with new recruits primarily occurring from September to November (Orth and van Montfrans, 1987; Van Engel, 1987). Whereas landings from this fishery cannot be standardized by effort due to the lack of catch per unit effort (CPUE) data, those from the dredge fishery need not be standardized because the available stock is reduced to a small fraction of the initial stock by the end of the dredge fishery season, irrespective of effort (Pearson, 1948; Applegate, 1983).

Statistical Analysis.—VARIATION IN ABUNDANCE. Each set of two monthly tows per station provided the dependent measure of blue crab abundance. These values were analyzed as a function of year (1972–1988), month (May–August and May–November) and station (Y10 and Y20) in multi-way analyses of variance (ANOVA). The dependent variables were log-transformed to meet assumptions of normality and homogeneity of variance. In all cases, either the variances were homogeneous as determined by Hartley's F_{max} test (Sokal and Rohlf, 1981), or the null hypotheses were rejected at alpha values lower than the P values of the test for heterogeneity of variance (Underwood, 1981).

STOCK-RECRUITMENT AND RECRUIT-STOCK FUNCTIONS. Various basic functions relating recruits-recruits, recruitment-spawning stock and spawning stock-recruitment were generated using data from the VIMS trawl survey and commercial fisheries. The relationships between the different segments and cohorts of the blue crab in Chesapeake Bay are depicted in Figure 2. We use the following terminology for stock-recruitment models, whereby statistical relationships are described as X-Y (e.g., a stock-recruitment function relates recruitment (Y) to spawning stock (X)).

In general, we proceeded by employing simple linear regression models and various transformations (i.e., log(Y), log(X), $(Y)^{1/2}$, 1/X and 1/Y) to achieve linearity and random, normally distributed residuals. Fit of the models was also tested with an experimental lack-of-fit test for regressions without replication (Burn and Ryan, 1983). When these models were statistically inadequate, we fit Ricker (1975), Beverton and Holt (1957) and Shepherd (1982) stock-recruitment functions. Table 2 details these stock-recruitment functions and their methods of analysis. In addition, we employed modifications of the Ricker curve:

$$R = a(S_1)exp(-b_1S_1 - b_2S_2) \tag{1}$$

analyzed with linear least squares regression as:

$$ln(R/S_1) = ln(a) - b_1S_1 - b_2S_2 \tag{2}$$

where R is recruitment in year t, S_1 and S_2 are stock sizes in years t − 2 and t − 3, respectively, a is a scaling parameter related to density-independent mortality, and b_1 and b_2 are scaling parameters related to density-dependent mortality as a function of stock size. The extra lag term (b_2S_2) serves as a surrogate for the additional effects of predation, cannibalism and food limitation due to a previous year class (Larkin, 1971; Collie and Walters, 1987).

Another means of incorporating the impact of a previous year class is to use the recruit abundance of that year class, rather than its spawning stock:
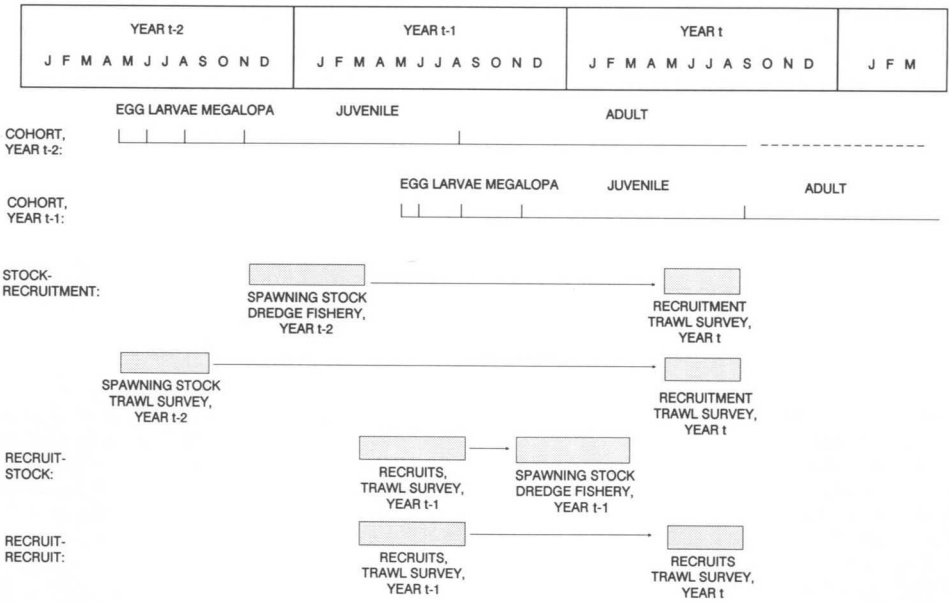
Figure 2.   Schematized life-history stages and stock-recruit relations for the blue crab in Chesapeake Bay.

$$R_1 = a(S)\exp(-b_1 S - b_2 R_2) \tag{3}$$

analyzed in the same manner as Equation 1, but where R_2 is the abundance of the previous year's recruits. In addition, the absolute abundance of the previous year's recruits may not be as important as the relative abundance of each pair of year classes. This was incorporated as:

$$R_1 = a(S)[\exp(-b_1 S)](R_2/R_1)^{-b_2} \tag{4}$$

and analyzed with linear least squares regression as:

$$\ln(R_1/S) = \ln(a) - b_1 S - b_2 \ln(R_2/R_1) \tag{5}$$

where R_1 and R_2 are recruitment in years t and t − 1, respectively.

Although linearized stock-recruitment models are computationally convenient to analyze with least-squares regression, they can be statistically biased when residuals are non-random and autocorrelated (Draper and Smith, 1981; Collie and Walters, 1987). We determined that residuals were random and not autocorrelated, after visual inspection of the residuals plotted against the independent variable and time, if the following were not significant: (1) Durbin-Watson test for first-order autocorrelation (Chaterjee and Price, 1977); (2) an experimental lack-of-fit test for regressions without replication (Burn and Ryan, 1983); and (3) a Monte Carlo simulation of the residuals run through the autocorrelation function up to lag 12 (Box and Jenkins, 1976). The Monte Carlo simulation involved randomizing (without replacement) the residuals generated by least squares regression 1,000 times, and running these through the autocorrelation function. Examination of the autocorrelation values generated a frequency distribution against which to compare the observed values. An observed autocorrelation value was deemed significant if it was in the upper 5% of simulated values.

Table 2.   Stock-recruit functions and methods of analysis

Model	Equation	Linearized equation	Method
Ricker	$R = a(S)\exp(-bS)$	$\ln(R/S) = \ln(a) - bS$	L*, N†
Beverton-Holt	$R = 1/(a + b/S)$	$1/R = a + b/S$	L*, N†
Shepherd	$R = aS/[1 + (S/b)^c]$	—	N†

* Linear least squares regression on linearized equation (Ricker, 1975).
† Non-linear least squares regression on untransformed equation using Marquardt algorithm in FISHPARM program (Prager et al., 1987).

Table 3. Three-way analysis of variance with year (1972–1988), month (May–November) and station (Y10 and Y20) as factors, and log-transformed catch per tow of blue crabs as the dependent variable

Source of variation	df	SS	Percentage of variation	MS	F	P<
Year	16	60.72	30.1%	3.80	40.60	0.0005
Month	6	17.48	8.7%	2.91	31.16	0.0005
Station	1	12.33	6.1%	12.33	131.86	0.0005
Year × month	96	58.48	29.0%	0.61	6.52	0.0005
Year × station	16	6.49	3.2%	0.41	4.34	0.0005
Month × station	6	2.17	1.1%	0.36	3.86	0.001
Year × month × station	96	21.83	10.8%	0.23	2.43	0.0005
Error	238	22.25	11.0%	0.09		

When the residuals of a particular stock-recruitment or recruit-stock function were significantly autocorrelated, we fit a sinusoidal term (of a period indicated by the autocorrelation function) to the dependent variable. The residuals from this regression were substituted for the autocorrelated recruitment values, similarly to the method employed in other stock-recruitment analyses (Phillips, 1986). Subsequently, the residuals from these analyses were examined as described previously. In some cases (Figs. 7, 8 and 9), a single outlier (1982) was deleted from the final analyses due to its extremely large residual error (more than three standard deviations from the mean).

RESULTS

Variation in Abundance. — YEAR, MONTH AND STATION EFFECTS. We provide separate analyses for May–November (Table 3) and May–August (Table 4) because the new year class of blue crab juveniles begins to recruit in September (Orth and van Montfrans, 1987; Van Engel, 1987). Significant interaction effects between Year, Month and Station (Tables 3, 4) precluded singular conclusions about main effects, and necessitated examination of effects within levels of main factors (Underwood, 1981).

Most variation in abundance was associated with Year (30.1–38.5%, Tables 3, 4); lowest abundance was observed in 1974–1977 and 1985–1988, and highest abundance in 1972–1973 and 1978–1984 (Fig. 3). The interannual pattern in abundance did not fluctuate greatly from year to year, but rather it remained high or low for 2 or more years in succession before increasing or decreasing (Fig. 3). More variation in abundance was associated with Month for the May–November data (8.7%, Table 3), than for May–August (2.9%, Table 4), because of the generally higher abundance in May–August than September–November (Fig. 4). The least variable months were those with highest abundances (June–August; CV's: 35–46%), whereas May, October and November exhibited the highest variability

Table 4. Three-way analysis of variance with year (1972–1988), month (May–August) and station (Y10 and Y20) as factors, and log-transformed catch per tow of blue crabs as the dependent variable

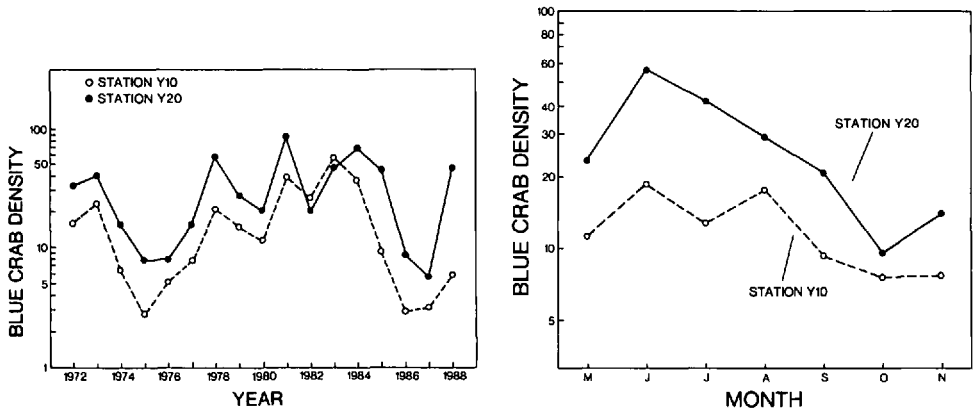| Source of variation	df	SS	Percentage of variation	MS	F	P<
Year	16	40.92	38.5%	2.56	27.52	0.0005
Month	3	3.12	2.9%	1.04	11.18	0.0005
Station	1	10.00	9.4%	10.00	107.63	0.0005
Year × month	48	25.00	23.5%	0.52	5.60	0.0005
Year × station	16	3.50	3.3%	0.22	2.35	0.005
Month × station	3	0.99	0.9%	0.33	3.56	0.05
Year × month × station	48	10.08	9.5%	0.21	2.26	0.0005
Error	136	12.64	11.9%	0.09		

Figure 3 (left).   Annual blue crab abundance at stations Y10 and Y20 in the York River. Blue crab density represents the mean annual catch per station plotted on a logarithmic scale.
Figure 4 (right).   Monthly blue crab abundance at stations Y10 and Y20 in the York River. Blue crab density represents the mean monthly catch per station plotted on a logarithmic scale.

(CV's: 60–72%). A key interaction effect for Year × Month was associated with substantial variation in abundance (23.5–29.0%, Tables 3, 4), and was due to the shift in peak monthly catches from May–August in years of high abundance to August–November in years of low abundance (Table 5).

Although Station was associated with relatively little variation (6.1–9.4%, Tables 3, 4), there were consistently higher catches at the upriver station (Y20, Figs. 3, 4). A significant Year × Station effect (Tables 3, 4) was caused by the switch in higher catches to station Y10 in 1982–1983 (Fig. 3). In addition, monthly peak catches in those years switched in station dominance, causing a weakly significant Month × Station interaction effect (0.9–1.1% of variation, Tables 3, 4). The

Table 5.   Peak monthly abundance of blue crabs in York River trawl collections at stations Y10 and Y20

Year	Month						
	May	June	July	August	September	October	November
1972			Y20			Y10	
1973†		Y10–Y20					
1974*		Y10	Y20				
1975*			Y20		Y10		
1976*				Y20		Y10	
1977*		Y20					Y10
1978†	Y20			Y10			
1979			Y20	Y10			
1980		Y20	Y10				
1981†		Y10			Y20		
1982†	Y20				Y10		
1983†	Y10–Y20						
1984†		Y10–Y20					
1985†	Y10–Y20						
1986*				Y10			Y20
1987*		Y20		Y10			
1988	Y20			Y10			
All		Y10–Y20					

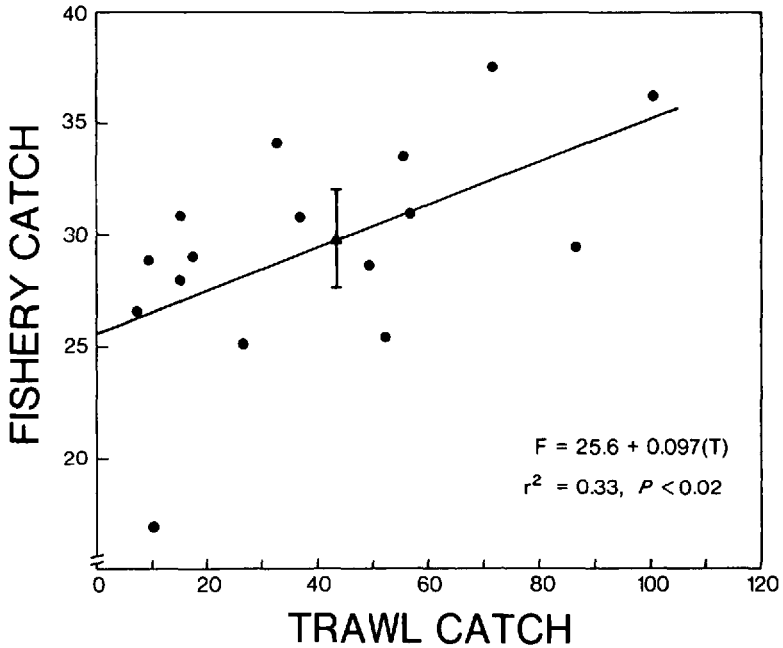* Lowest annual abundance values.
† Highest annual abundance values.

Figure 5. Correlation between annual trawl survey abundance in the York River and hard crab landings from the commercial hard-crab fisheries in Chesapeake Bay, both from May through November. The triangle represents the projected estimate for 1988 with a 95% confidence interval.

significant Year × Month × Station interaction effect was associated with substantial variation (9.5–10.8%, Tables 3, 4), and was caused by the shift in monthly and station dominance between years of low and high catches. Variation due to error was relatively high (11.0–11.9%, Tables 3, 4), indicating a need to increase the number of tows per station.

COMPONENT CORRELATIONS. Blue crab abundance peaked most often in June each year (Fig. 4, Table 5), with little variability (CV = 42%). We correlated annual abundance with June abundance to assess the efficacy of June abundance as an index of trawl survey abundance and commercial fishery catches.

Annual abundance from May–August correlated significantly with June abundance:

$$Y = -104 + 78.4 \log(X), \qquad r^2 = 0.80, \qquad P < 0.0005$$

where Y is cumulative abundance from May–August, and X is June abundance. In addition, the form of the relationship was hyperbolic, as indicated by a significant fit of a Beverton-Holt model (Table 2):

$$Y = 1/[0.0082 + (1.652/X)], \qquad r^2 = 0.73, \qquad P < 0.0005.$$

Trawl survey abundance from May–November correlated significantly with the Virginia commercial fishery catch of hard blue crabs from May–November (Fig. 5), though with substantial variability (i.e., $r^2 = 0.33$). The simple regression model provided a combined best fit and residuals than any transformations or recruit-stock models, and projected a Virginia commercial fishery catch of 29.81 million pounds for May–November, 1988. In addition, the fishery catch (Y) also correlated
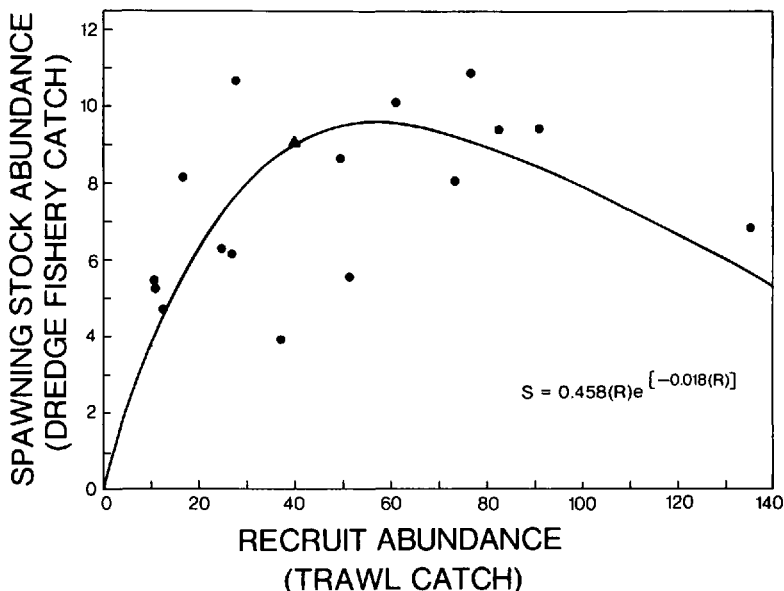
Figure 6. Blue crab recruit-stock relationship between abundance of recruits (untransformed mean annual trawl survey catch from May–August) and the subsequent spawning stock (annual landings in the dredge fishery from December–March). The Ricker model was significant with the coefficient of determination equal to 80% ($P < 0.0005$). The triangle represents projected landings for the 1988–1989 dredge fishery.

significantly with trawl survey abundance in June (X), but again with high variability:

$$\log(Y) = 1.26 + 0.106 \log(X), \qquad r^2 = 0.28, \qquad P < 0.035.$$

Stock-recruitment and Recruit-stock Functions. — RECRUIT-STOCK RELATIONSHIPS. We correlated trawl survey blue crab abundance from May–August (year t), which excludes the new year class, with the corresponding dredge fishery catch (December, year t–March, year t + 1). This provides a recruit-spawning stock relationship since most of the crabs caught from May–August in the trawl survey will enter the dredge fishery as mature crabs.

The recruit-stock relationship was highly significant and modelled best by a Ricker function (Fig. 6). The estimated maximum spawning stock occurs when R = 1/b (Table 2; Ricker, 1975), and was calculated as that when R = 56.82 in the Ricker equation (Fig. 6). The projected dredge fishery catch for the 1988–1989 season (December, 1988–March, 1989) was 9.05 million pounds (Fig. 6) given the May–August, 1988 trawl survey mean abundance of 39.9. Although the Durbin-Watson statistic was non-significant, suggesting an absence of first-order autocorrelation, the simulation analysis of residuals indicated significant autocorrelation at longer periods. Consequently, we examined a recruit-stock model using residuals from a regression analysis with sinusoidal terms.

After examining various periodicities with the regression analysis of sinusoidal terms, a periodicity of 14 years was used to remove the autocorrelation in the residuals. The resulting recruit-stock model (Fig. 7) was qualitatively similar to the version with autocorrelated residuals, though it explained more of the variation in stock abundance (88% vs. 80%) and projected a slightly higher stock value (13.01 million pounds) in 1988–1989 than the preceding model. Nonetheless,
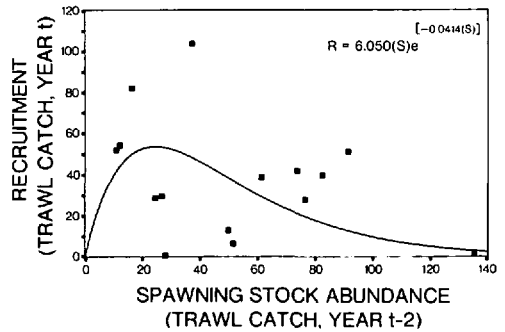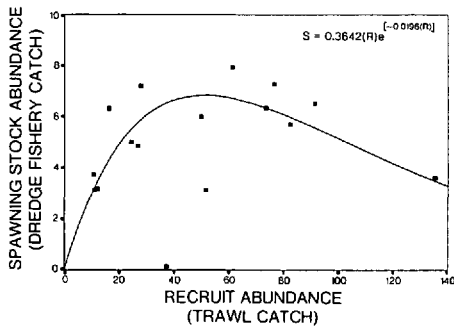
Figure 7.   Blue crab recruit-stock relationship between abundance of recruits (residuals from sinu-soidal regression with period length of 14 years on trawl survey catch from May–August) and the subsequent spawning stock (annual landings in the dredge fishery from December–March). The Ricker model was significant with the coefficient of determination equal to 88% ($P < 0.0005$).

Figure 8.   Blue crab stock-recruitment relationship between a measure of stock abundance in year t − 2 (untransformed mean annual trawl survey catch from May–August) and recruit abundance in year t (residuals from sinusoidal regression with period length of 14 years on trawl survey catch from May–August). The Ricker model was significant with the coefficient of determination equal to 73% ($P < 0.0005$).

both models describe highest stock abundance at recruit levels of 40–70 (Figs. 6, 7). In addition, low recruit abundance (trawl survey) values produced low spawning stock (dredge fishery) catches, and high values produced high catches, except for a single extreme value at the highest recruit abundance. However, at intermediate values of recruit abundance, spawning stock catches spanned the full range of observed variation.

STOCK-RECRUITMENT RELATIONSHIPS. We examined spawning stock-recruitment relationships using trawl survey data correlated with itself. In the regression analyses, we progressively examined simple linear regressions, linear regressions with transformed data, linearized and non-linear versions of stock-recruitment models (Table 2), and modifications of the Ricker stock-recruitment function (Eqs. 1–5) that accommodate effects of previous year classes and spawning stocks. In all cases, the final analyses presented for the linearized versions of each model resulted in regressions with random, normally distributed residuals lacking significant auto-correlation, with non-significant lack-of-fit tests, and with the highest correlation coefficients.

The relationship between spawning stock in year t − 2 and recruitment in year t was best modelled by a dome-shaped (Ricker) function (Fig. 8). Recruitment was represented by the residuals from a sinusoidal regression with period length of 14 years, and not the raw data, due to autocorrelated errors in the regression using raw recruitment values. The resulting Ricker model explained 73% of the variance, and did not exhibit autocorrelated errors (Fig. 8).

A significant effect upon recruitment in year t by the recruitment level in year t − 1 was incorporated into the stock-recruitment relationship for the trawl survey data (Fig. 9) with a modified Ricker function (Eq. 4):

$$R_t = 4.63(S_{t-2})\exp[-0.038(S_{t-2})]\,(R_{t-1}/R_t)^{-0.268}, \quad r^2 = 0.82, \quad P < 0.0005.$$

As for the preceding model, residuals from the sinusoidal regression term with period length of 14 years represented recruitment to eliminate autocorrelated errors. This significant effect ($P < 0.050$) incorporated the *relative* abundance of

recruiting year classes (Eq. 4), whereas incorporating the *absolute* abundance of a previous year class (Eq. 3) or the corresponding spawning stock (Eq. 1) did not significantly enhance the stock-recruitment relationship ($P > 0.050$). Thus, the relative abundance of the preceding year class (year $t - 1$) reduces the amplitude of recruitment in year t as a function of spawning stock in year $t - 2$ (Fig. 9).

DISCUSSION

Variation in Abundance. — Blue crab abundance in the York River exhibited significant interannual, seasonal and spatial variation with quantifiable main and interaction effects. These effects would likely be undetectable had the data set been shorter than 10–15 years, indicating the importance of long-term, fishery-independent data collection to the accurate portrayal of blue crab population dynamics, as for other species (Holland et al., 1987; Wolfe et al., 1987). Furthermore, the significance of interactive factor effects underscores the need for broad spatial and temporal coverage in abundance surveys that attempt to characterize blue crab population fluctuations effectively.

The most significant component of variation in blue crab abundance within the York River was due to interannual fluctuations, differing over an order of magnitude from 1972–1988. Such fluctuations have been observed elsewhere in Chesapeake Bay (Ulanowicz et al., 1982; Abbe, 1983; Tang, 1985; Hines et al., 1987), and probably result from interannual differences in recruitment of larval and postlarval stages (McConaugha, 1988; van Montfrans et al., in press), or physicochemical conditions and food availability (Holland et al., 1987). In addition, population abundance did not generally vary greatly from year to year, rather it appeared to remain consistently high or low for two or more years before changing. This type of pattern suggests internal feedback mechanisms within the population, such as cannibalism, or environmental control through periodic climatic factors (Hassell, 1978; Cushing, 1982). Thus, the blue crab population in Chesapeake Bay is not simply varying erratically about some average level (e.g., equilibrium value; Hassell, 1978), but fluctuating in response to long-term or periodic sources of variation (e.g., environmental cycles or alternate population states; Steele and Henderson, 1984) superimposed over yearly variation.

Seasonal (monthly) variation in blue crab abundance was considerable, with peak abundance in the summer (June through August). In our study, which spanned May through November, lowest abundance was in the fall (October and November), though blue crabs are least abundant in trawl catches during winter and early spring (December–April). Such a seasonal abundance pattern is characteristic of the blue crab (Hines et al., 1987) and macrobenthos (Holland et al., 1987) in Chesapeake Bay, being caused by seasonal movements, mortality, food availability or physicochemical conditions. Furthermore, the summer months of peak abundance were least variable. This contrasts the large variance during late spring (May) and autumn, which is most likely due to temperature-associated movements and to variability in recruitment by the new year class, respectively.

A highly significant interaction effect between year and month was explained by differences in seasonal abundance between years of high and low abundance. Generally, peak blue crab abundance occurred in the summer when annual abundance was high, and in the late summer or fall when annual abundance was low. This reflects the differential dominance of a previous year's cohort in the summer, or the new year class in the late summer and fall. Thus, years of high abundance appear to be dominated by the previous year class, whereas those of low abundance are characterized by a reduced strength of the previous year class and concomitant
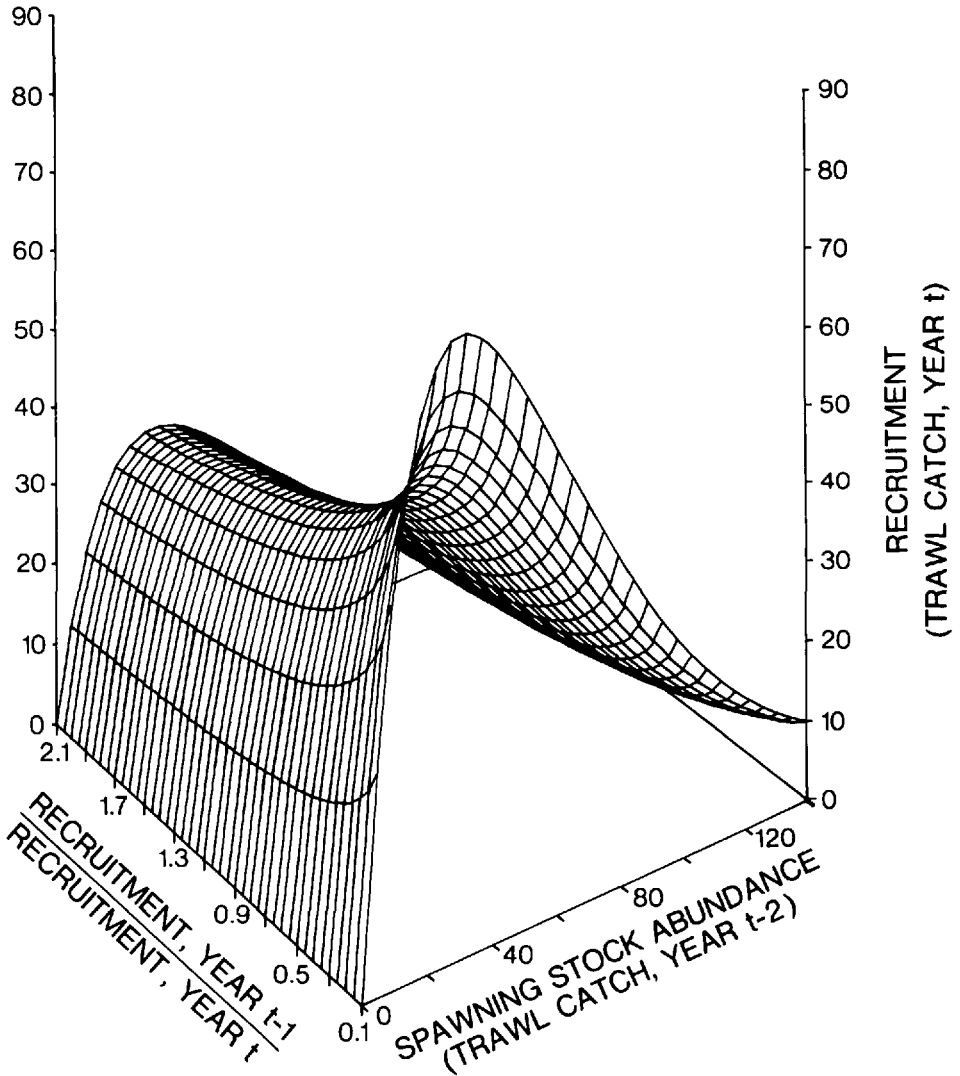
Figure 9. Blue crab stock-recruitment relationship incorporating the surrogate effect of a previous year class. Recruitment in year t (residuals from sinusoidal regression with period length of 14 years on trawl survey catch from May–August) is a function of stock in year t − 2 (untransformed mean annual trawl survey catch from May–August) and relative abundance of the recruiting year class in year t − 1 (untransformed mean annual trawl survey catches from May–August in years t − 1 and t). The modified Ricker model was significant with the coefficient of determination equal to 82% ($P < 0.0005$). The first component (stock) accounted for 88.9% of the regression variance, and the second component (relative recruit abundance) 11.1%.

dominance by the new year class. Although size-specific abundance information is needed to confirm this inference, the observation reinforces the hypothesis that recruitment may drive interannual population fluctuations in the blue crab.

Appreciable spatial variation in blue crab abundance was evident whereby catches at an upriver station in the York River were consistently higher than those at a downriver station, except during two years from 1972–1988. This inter-locality difference may be due to an ontogenetic shift upriver by crabs as they

feed and grow (Hines et al., 1987) after settlement near the mouth (van Montfrans et al., in press; Lipcius et al., in press), or to differences in habitat quality (e.g., refuge or food) between the two locations. Such habitat selection behavior is common in various blue crab stages, including larvae and postlarvae (Mc-Conaugha, 1988), juveniles (Hines et al., 1987; Olmi et al., in press; van Montfrans et al., in press), and adults (Pearson, 1948; Van Engel, 1958; Schaffner and Diaz, 1988). Further studies with replicated upriver and downriver sampling stations are needed to resolve this confounding between location and habitat quality.

Stock-recruitment and Recruit-stock Functions. — A key finding of this study concerns the significant and dome-shaped relationship (Ricker model) between measures of spawning stock and recruitment for the blue crab. The existence of a stock-recruitment relationship for the blue crab has been suggested recently (Applegate, 1983; Tang, 1985). Earlier views stressed the lack of a significant stock-recruitment relationship (Pearson, 1948; Sulkin et al., 1983; Van Engel, 1987). Arguments against a significant stock-recruitment relationship were based on two lines of evidence. The first was empirical, whereby Pearson (1948) analyzed dredge fishery landings from 1930–1944, and found a non-significant correlation between landings in year $t - 2$ (stock) and those in year t (recruitment). However, this conclusion was based on a simple correlation analysis, and not on curvilinear functions (e.g., Ricker and Beverton-Holt models). We re-analyzed the same data (Pearson, 1948: table 12, columns B and C), and found significant stock-recruitment relationships using simple Ricker models with the raw data ($r^2 = 0.52$, $P = 0.006$) or with residuals from a three-year sinusoidal component ($r^2 = 0.36$, $P = 0.040$), as well as the stated non-significant linear correlation ($r^2 = 0.02$, $P > 0.5$).

The second line of evidence against the existence of a stock-recruitment relationship for the blue crab was conceptual and based on "r-selected" life-history features of the blue crab (Sulkin et al., 1983; Van Engel, 1987). Sulkin et al. (1983) argued that a stock-recruitment relationship was improbable due to density-dependent mortality of offspring, and domination by abiotic factors of recruitment success, although they also stated that ". . . there obviously must exist a theoretical threshold of spawning stock size below which inadequate numbers of larvae will be produced." The former argument does not preclude a stock-recruitment relationship, but implies high variance about such a relationship. The latter argument actually implies the existence of a stock-recruitment model such as the Beverton-Holt function, given the spawning stock threshhold and subsequent levelling of recruitment. Van Engel (1987) suggested that a stock-recruitment model was unlikely to be density-dependent given the various "r-selected" life-history characteristics of the blue crab, particularly the high fecundity, high interannual variation in production, rapid growth, early maturity, high mortality and relatively short life span. However, "r-selected" species (e.g., insects (Hassell, 1978) and shrimp (Rothschild and Brunenmeister, 1984)), can be regulated by density-dependent factors which do not eliminate the stock-recruitment relationship (Eberhardt, 1977; Pitcher and Hart, 1982; Rothschild, 1986). Population collapse due to recruitment overfishing (i.e., a sharp decline in recruitment at low stock sizes) may be more likely in such species with only one or two major year classes. Moreover, various authors (e.g., Ricker, 1954; Rothschild, 1986) have discussed the conceptual necessity for a stock-recruitment relationship in marine species, and consequently dismissed the idea that stock-recruitment relationships are non-existent in theory. However, in most arguments there is no clear objective and quantitative definition of a "non-existent" stock-recruitment relationship. We propose that a stock-recruitment relationship is non-significant, and thereby

"non-existent," if spawning success (i.e., proportional survival of recruits as a function of stock size) is constant at low and intermediate stock sizes. Thus, a significant stock-recruitment relationship implies either compensatory (e.g., Ricker model) or depensatory survival of recruits as a function of spawning stock size. Finally, the Ricker stock-recruitment relationship is also conceptually adapted to "r-selected" species (Eberhardt, 1977; Ware, 1980; Pitcher and Hart, 1982). Therefore, we conclude that there is neither empirical nor conceptual evidence against the existence of a blue crab stock-recruitment relationship.

The evidence in favor of a stock-recruitment relationship for the blue crab is based on statistically significant lagged autocorrelations of dredge fishery (Pearson, 1948—our re-analysis; Applegate, 1983; Tang, 1985) or fishery-independent trawl survey (this study) data with dome-shaped Ricker models. Various modifications of the simple Ricker model have been used to incorporate the effects of environmental and biotic factors. Applegate (1983) used a multiplicative model composed of the simple Ricker model times a linear sum of environmental variables affecting recruit survival—streamflow, incidence of light, wind magnitude and wind direction. However, none of these correlated significantly with the recruit survival index, calling into question the necessity of using these as components of a complex Ricker model. Tang (1985) also attempted to incorporate environmental factors into the simple Ricker model by substituting a linear sum of environmental variables—radiant energy, streamflow, salinity and water temperature—for the density-independent parameter. This modification produced a significant fit (Tang, 1985: $r^2 = 0.69$, $P = 0.01$), and suggested the use of a family of stock-recruitment curves derived from varying environmental conditions. However, the analysis was misleading in that Tang did not present the regression statistics for the simple Ricker model without the environmental variables. Our analysis of the data (Tang, 1985: table 1) with a simple Ricker model yielded equivalent parameter estimates (a = 10.3393, b = 0.026868) as those noted by Tang, and also a better fit ($r^2 = 0.75$, $P < 0.0005$) than the complex model. Therefore, the incorporation of environmental variables into the simple Ricker stock-recruitment model is unwarranted for the blue crab without further analyses.

We added other biologically meaningful and statistically significant components to the simple Ricker model, in a manner similar to Larkin (1971) and Collie and Walters (1987) for Pacific salmon. In particular, relative measures of recruitment of the previous year class (i.e., recruit abundance in year $t - 1$) enhanced the correlation between stock in year $t - 2$ and recruitment in year t for the blue crab. This effect is most likely mediated by the impact of a previous year class upon food supply, or growth and survival of the new recruits. For instance, benthic prey of the blue crab decline sharply in late summer (Lipcius and Hines, 1986; Hines et al., 1987) with concomitant decreases in feeding efficiency and increases in cannibalism rates. Furthermore, our analyses with these modified Ricker stock-recruitment models indicate that the relative abundance of the two year classes may be critical, suggesting an interactive effect due to the absolute and relative abundances of successive blue crab year classes.

Recruit-stock relationships of the blue crab were significant in addition to the aforementioned stock-recruitment functions. Significant correlations were found between (1) recruits (trawl survey abundance) and spawning stock (catch in the dredge fishery), and (2) recruits in the trawl survey and recruits in the commercial hard crab fishery. Furthermore, these correlations held when a single month (June) was used to represent trawl survey abundance. Such correlations between recruits and subsequent stock are expected given the characteristically reduced mortality rates of juveniles and adults in contrast to those of larvae and postlarvae (Roths-

child, 1986). We suspect that future analyses using size-specific measures of recruit and stock abundance will be enhanced in accuracy and precision, and thereby increase their utility in understanding and predicting population and fishery fluctuations of the blue crab in Chesapeake Bay.

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