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Fecundity of Blue Crab, *Callinectes Sapidus*, in Chesapeake Bay: Biological, Statistical and Management Considerations

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FECUNDITY OF BLUE CRAB, *CALLINECTES SAPIDUS*, IN CHESAPEAKE BAY: BIOLOGICAL, STATISTICAL AND MANAGEMENT CONSIDERATIONS

Michael H. Prager, John R. McConaugha, Cynthia M. Jones
and Patrick J. Geer

ABSTRACT

To study the fecundity of the blue crab (*Callinectes sapidus*) and its relationship to size, we collected 135 ovigerous blue crabs from the mouth of Chesapeake Bay during the 1986 and 1987 spawning seasons. Mean carapace width of these crabs was 14.7 cm; mean fecundity was $3.2 \cdot 10^6$ eggs. Fecundity was significantly related to carapace width, and did not vary significantly with developmental stage of the eggs. However, mean fecundities were different in the two years: $2.6 \cdot 10^6$ eggs in 1986, and $4.0 \cdot 10^6$ eggs in 1987. An additive model with year and size effects described the observed fecundities reasonably well, was compact, and was easier to interpret than a multiplicative model. Since the additive model did not result in homogeneous variances for the residuals, we used several alternative fitting methods to examine robustness of the parameter estimates. To fit a more general model without year effects, we took the mean of 1986 and 1987 results, and modeled fecundity as $\hat{E} = -2.25 + 0.38W$, where \hat{E} is predicted fecundity (10^6 eggs), and W is carapace width (cm). Within-season temporal patterns were also different between years. In 1986, the width-specific fecundity increased sharply during peak abundances on the spawning grounds. In 1987, when the density of crabs on the spawning grounds was more uniform, the width-specific fecundity did not exhibit a peak.

The blue crab, *Callinectes sapidus* Rathbun, supports important commercial and recreational fisheries along the central and southern Atlantic coast of the United States and in the Gulf of Mexico; the species is especially abundant in Chesapeake Bay and its tributaries. Despite its biological and economic importance, large gaps persist in our knowledge of its population biology. In a recent species synopsis, Millikin and Williams (1984) designated several items, including average abundance, age composition, average density, mortality rates, and reproduction rates, as having "no information available." In this paper, we report observations of fecundity (the number of eggs carried) and its relationship to the carapace width and time of year.

SAMPLING METHODS

During the spawning seasons of 1986 and 1987, we gathered blue crabs by otter trawl from the mouth of Chesapeake Bay, waters that are spawning grounds of the Chesapeake Bay stock of *Callinectes sapidus* (Van Engel, 1958; Jones et al., 1989). Since we used in addition crabs from a few unscheduled sampling opportunities, our collection numbers (Table 1) do not coincide with the cruise numbers of Jones et al. (1989), although about 90% of the crabs were collected on the same occasions. In 1986, we selected 74 ovigerous females at random for fecundity measurements; in 1987, we selected 61. The specimens were wrapped in heavy plastic bags and placed in iced coolers pending return to the laboratory. Details of collection are given in Jones et al. (1989).

Two different procedures were used to estimate fecundity; the first step in each was to remove the pleopod structure from the egg mass. Although some fine hairs inevitably remained, we estimate their contribution to the total weight or volume of the egg mass at no more than a few percent. In 1986, we used a method based on dry weight. A counted subsample of 500 eggs and the remaining egg mass were dried at 60°C to constant weight. The subsample was weighed to estimate the mean dry weight of a single egg; the estimated fecundity of the individual was the dry weight of the egg mass divided by the estimated mean dry weight of a single egg, plus 500.

Table 1. Collection numbers, dates, and sample sizes of ovigerous blue crabs taken from Chesapeake Bay mouth

Collection number	Dates	Sample size
1	9–10 July 1986	6
2	17–18 July 1986	16
3	24–26 July 1986	8
4	31 July–2 August 1986	20
5	15 August 1986	15
6	6 September 1986	3
7	11 September 1986	6
8	27 May 1987	10
9	11 June 1987	12
10	11 July 1987	5
11	24 July 1987	4
12	5 August 1987	9
13	20–21 August 1987	21

In 1987, we first measured the volume of each individual's total egg mass by displacement of water in a graduated cylinder. The mass was agitated gently to dislodge any trapped air. To estimate the mean volume of a single egg, we measured by ocular micrometer the diameter of 100 eggs from each collection of crabs, and computed the equivalent volume (assuming sphericity). We estimated fecundity of each crab by dividing the volume of its egg mass by the estimated mean volume of a single egg.

SUMMARY STATISTICS

The mean carapace width of all crabs collected was 14.7 cm; the estimated standard deviation of width was 1.8 cm. The distribution of carapace width appears approximately normal (Fig. 1). The mean fecundity of all crabs was $3.2 \cdot 10^6$ eggs; the estimated standard deviation of fecundity is $1.6 \cdot 10^6$ eggs. The frequency distribution of fecundity is skewed to the right (Fig. 2), and is not approximately normal under log transformation. Detailed univariate statistics are given in Table 2. As shown in Figure 3, fecundity is correlated with carapace width (1986, $r = 0.47$; 1987, $r = 0.50$; pooled, $r = 0.46$; all, $P < 0.001$). Although fecundity was higher in 1987, its variance was higher in 1986 (Table 2).

MODELS OF FECUNDITY

Initial Multiplicative Model.—Our first working hypothesis was that fecundity was proportional to the volume of the body cavity (Hines, 1982). Thus we developed

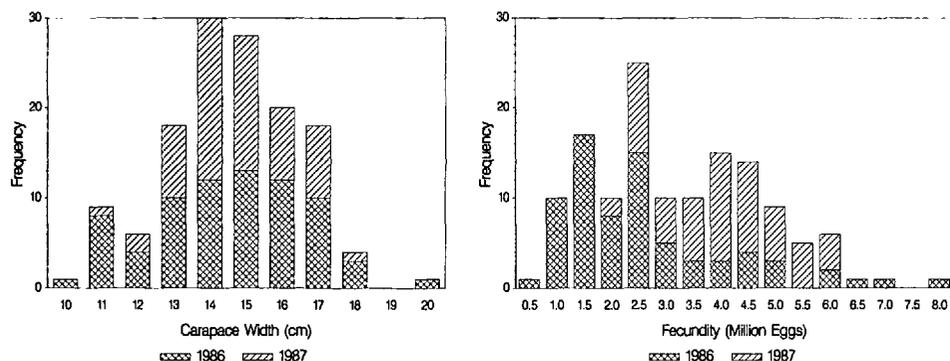


Figure 1 (left). Frequency distribution of carapace width of 135 ovigerous specimens of *Callinectes sapidus* taken from Chesapeake Bay in 1986 and 1987.

Figure 2 (right). Frequency distribution of fecundity (number of eggs per individual) of 135 mature female specimens of *Callinectes sapidus* from Chesapeake Bay.

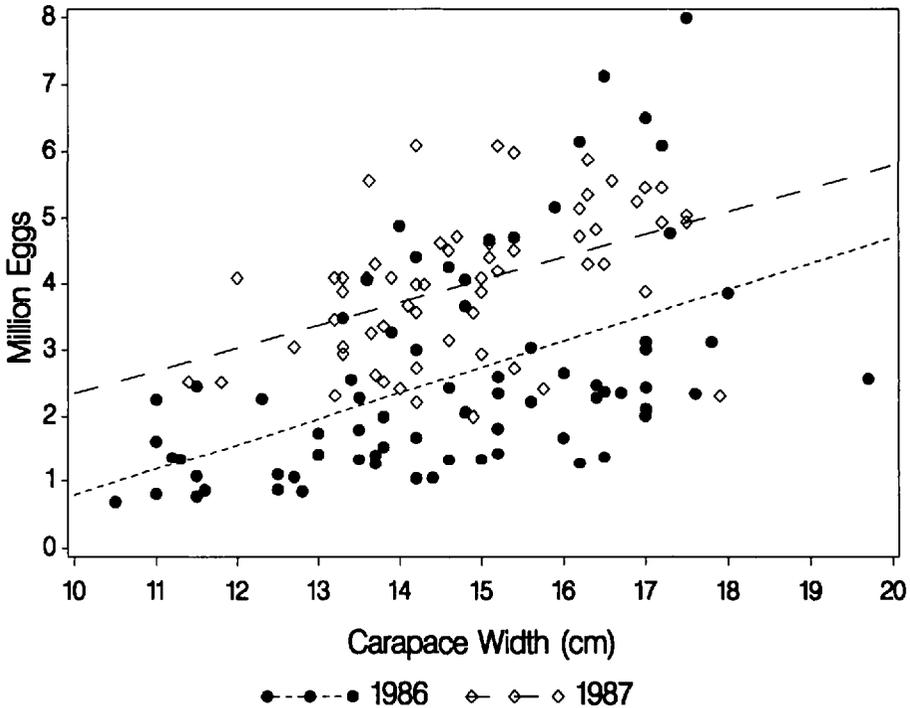


Figure 3. Relationship of carapace width to fecundity in 135 ovigerous specimens of *Callinectes sapidus* from Chesapeake Bay. Distinct regression lines for each year are for illustration and do not reflect models discussed in the text. Overall and single-year correlations are all significant at $P < 0.001$.

an initial model of fecundity as proportional to a power of the carapace width; we expected the power to be between 2 and 3. This model also allowed for different observed fecundities at size in the 2 years, whether arising from differences in the population or as an artifact of the two different measurement methods. The proposed model was:

$$E_{ij} = \beta W_i^\lambda \cdot \alpha_j \cdot \epsilon_{ij} \quad (1)$$

where E_{ij} is expected fecundity (10^6 eggs) of crab i in year j , W_i is carapace width (cm), β and λ are scale and shape parameters, α_j is a parameter modifying the basic relationship in year j , and ϵ_{ij} , with mean 0, is the usual error term.

The model can be fit directly by nonlinear least squares, or after log transformation by ordinary (linear) least squares (OLS). Although log transform yields biased parameter estimates, the correction is well known (Baskerville, 1972; Sprugel, 1983). More important, the method with residuals closest to homogeneity will have lower variance and be more robust (Kennedy, 1979; Neter and Wasserman, 1974). Examination of Figure 3 suggests that the variance of fecundity increases with increasing carapace width; this was confirmed ($P < 0.001$) by Levene's test for homogeneity of variance.

We log-transformed the widths and fecundities, and fit the resulting model (including an intercept) by analysis of covariance. Both width and year effects were significant ($P < 0.001$ and $P = 0.031$); the residuals appeared random and homoskedastic. When an additional parameter representing the eggs' four developmental stages (as defined by Jones et al., 1989) was added, it was not statistically

Table 2. Summary statistics on carapace width (cm) and fecundity (millions of eggs) of 135 blue crabs from Chesapeake Bay

Collection number	Carapace width		Fecundity	
	\bar{x}	SD	\bar{x}	SD
All (1986)	14.61	2.05	2.59	1.60
All (1987)	14.80	1.50	4.00	1.10
1	12.93	0.87	1.23	0.35
2	14.28	1.81	3.93	1.62
3	15.95	2.10	4.27	2.07
4	14.37	2.25	2.02	1.07
5	15.03	2.21	1.91	1.00
6	14.03	2.56	1.73	0.78
7	15.42	0.92	2.16	0.60
8	13.77	1.67	3.28	0.99
9	14.60	1.25	3.70	1.01
10	15.61	1.46	4.26	1.15
11	14.20	0.83	3.80	1.23
12	15.30	1.46	4.50	0.49
13	15.11	1.49	4.26	1.24

significant ($P = 0.32$), indicating no major loss (or gain) of eggs during development.

Assuming the validity of equation 1, the year effect can be eliminated by rescaling one year's data to give a simple width-fecundity model. To examine this possibility, we fit a log-transformed model similar to equation 1, but also containing an interaction effect between year and width. This term was significant at $P = 0.06$. While $P = 0.06$ might not be considered sufficient for rejection of a null hypothesis, we felt the interaction effect was strong enough to hinder development of a simple model applicable to both years, and indeed interpretation of the results in general. This situation is not often discussed in the biological literature, but in general the transformation that stabilizes variances may not provide a parsimonious and easily interpreted model.

Additive Model.—We next examined the additive model,

$$E_{ij} = \beta_0 + \beta_1 W_i + \alpha_j + \epsilon_{ij}, \quad (2)$$

where E_{ij} is expected fecundity of crab i in year j ; W_i is carapace width in cm; β_0 and β_1 are intercept and slope parameters; and the α_j parameter represents year effects in year j . We added a year-width interaction term to detect any nonadditivity (change in slope between years).

The interaction parameter was not statistically significant ($P = 0.71$), and was dropped from the model. Width and year effects were both significant ($P < 0.001$). Using the additive model gave several advantages: nonadditivity was minimized; the bias of log transformation was eliminated; the model was easier to interpret. Snedecor and Cochran (1980, p. 295) suggest: "In view of the simplicity and efficiency of an additive model, much can be said for giving primary attention to removal of nonadditivity while keeping an eye on heterogeneity of variance" Treatment of heterogeneity of variance is described later in the paper.

We compared the fit of the two models by examining estimated coefficients of variation. The coefficient of variation (CV) of the multiplicative model was estimated by the formula

$$CV = \exp(s) - 1, \quad (3)$$

Table 3. Analysis of variance for additive model, including year and width effects, of blue crab fecundity

Source	df	Sum of squares	Mean square	F value	P > F
Model	2	128.89	64.45	43.0	0.0001
Error	132	197.80	1.50		
Corr. total	134	326.70			

where CV is the estimated coefficient of variation, and s is the square root of the mean squared error from the analysis of variance (Snedecor and Cochran, 1980). In the linear model, the CV at the mean value of fecundity is estimated by

$$CV = s/\bar{E}, \quad (4)$$

where s is as above and \bar{E} is the mean fecundity. The respective CV's were 0.49 and 0.38, indicating that the linear model fit the data better near the mean.

The width-fecundity relationship estimated from equation 2 was

$$\hat{E} = -2.915 + 0.377W + 1.33Y, \quad (5)$$

where \hat{E} is estimated fecundity (10^6 eggs); W is carapace width (cm); $Y = 0$ in 1986, 1 in 1987. The standard errors of the regression parameters are 0.058 and 0.212; $R^2 = 0.39$. The ANOVA table is shown in Table 3.

Other Fitting Approaches.—The residuals from model (5) tended to be larger at larger carapace widths. Under such heteroskedasticity, OLS is unbiased, but inefficient. To examine the sensitivity of the estimates to heteroskedasticity, we used two forms of weighted least squares (WLS) and one additional "robust" method to refit equation 2. The first method was the iteratively reweighted bi-weight least-squares procedure of Beaton and Tukey (1974). The procedure uses two ad hoc parameters: σ , a measure of the scale of the data, and B , which sets the sharpness of the cutoff for outliers. After examining weights from several pairs of values, we chose $\sigma = 1.2$ and $B = 4.6$ as conservative (no zero weights and few weights lower than 0.5), yet reducing the effects of outliers. The resulting estimate was:

$$\hat{E} = -2.333 + 0.321W + 1.59Y, \quad (6)$$

where symbols are as defined for equation 5. The asymptotic standard error of the width parameter is 0.049; of the year parameter, 0.177; unweighted $R^2 = 0.38$. The ANOVA table is given in Table 4.

In the second weighted analysis, we arranged the data into three groups of 45 observations with low, medium, and high values of carapace width. We assigned as weights the reciprocal of the variance of the within-group year-adjusted fecundity. (Year effects were removed by adding half the effect estimated by equation 5 to the 1986 fecundity values and subtracting the same amount from the 1987 values.) This WLS model is:

$$\hat{E} = -3.057 + 0.383W + 1.40Y, \quad (7)$$

where symbols are as defined for equation 5. The asymptotic standard error of the width parameter is 0.054; of the year parameter, 0.187; the unweighted R^2 is 0.39. The ANOVA table forms Table 5.

The third heuristic analysis used least absolute values (LAV) regression, which

Table 4. Analysis of variance for additive model, incorporating year and width effects, of blue crab fecundity. Model was fit by Beaton-Tukey iteratively reweighted least-squares procedure, as described in text

Source	df	Weighted SS	Weighted MS
Model	3	1,315.0	438.3
Error	132	126.0	0.95
Uncorrected total	135	1,441.0	
(Corrected total)	134	254.8	

minimizes the sum of absolute values of the residuals, and is thus less sensitive than OLS to extreme values. The LAV estimates were:

$$\hat{E} = -2.788 + 0.356W + 1.31Y, \quad (8)$$

where symbols are as defined for equation 5. Standard errors of the parameters were not computed.

Seasonal Effects.—Our final analysis examined within-year variations in fecundity. After determining by ANOVA that no significant variation in mean carapace width existed across collections ($P = 0.123$), we computed the mean fecundity of each collection (Fig. 4). In 1986 fecundity reached a sharp peak, and then declined; in 1987 mean fecundity was relatively constant, although it may have increased slightly throughout the season. We also compared the width-fecundity relationship at the peak (cruises 2 and 3) to the other pooled 1986 observations. The intercepts were not significantly different ($P = 0.84$), but the slopes were ($P < 0.001$); the slope during the peak being 0.47, for the other cruises, 0.30. The slope during the peak has a relatively high standard error (0.15), largely because of one outlying datum (which we believe is correct). Without this datum, the contrast between these cruises and the values observed in rest of 1986 is even stronger.

DISCUSSION

Comparison of Fitting Methods.—The results of fitting the additive model with the four methods described are summarized in Table 6. The importance of the robust methods and choice among them is subjective (Draper and Smith, 1981). Compared to OLS, the Beaton-Tukey procedure estimated a larger difference in fecundity between years, and a lower slope to the width-fecundity relationship. This is because the Beaton-Tukey method gave lower weights to outlying observations, such as those during the spawning peak of 1986. These large crabs with high fecundity did not fit the general pattern of lower fecundity in 1986. The Beaton-Tukey model would be appropriate if one believed that the observed peak

Table 5. Analysis of variance for additive model, incorporating year and width effects, of blue crab fecundity. Model was fit by weighted least-squares with weights based on variance of nominal fecundity within carapace width grouping (See text for details)

Source	df	Sum of squares	Mean square	F value	$P > F$
Model	2	115.68	57.84	61.2	0.0001
Error	132	124.75	0.95		
Corr. total	134	240.43			

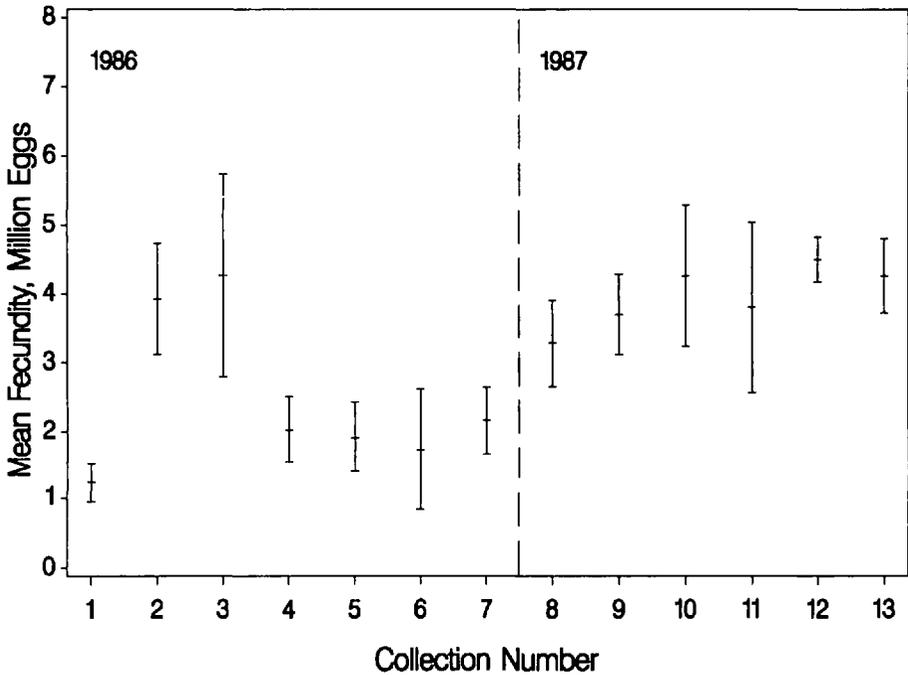


Figure 4. Mean fecundity (millions of eggs) of *Callinectes sapidus* from 13 collections during the spawning seasons of 1986 and 1987. Collections are numbered chronologically. Error bars are ± 2 SE of each mean, and thus approximate 95% confidence intervals. Mean carapace width of crabs from each collection did not differ significantly.

in 1986 was not representative of typical fecundities at width. We have no reason to believe this, and thus discount the implication that year effects are stronger and width effects less strong than those estimated by OLS. The Beaton-Tukey estimates differ from the OLS estimates by only about one standard error; this fitting method was a useful heuristic that demonstrated the robustness of OLS in this case.

The parameter estimates of the model weighted by the variance of width-group fecundity were close to those of the OLS model. The change in the width parameter was about 0.007 (approximately 12% of one standard error of the OLS estimate). This small difference indicates that the regression results were not particularly sensitive to the weighting used; i.e., that heteroskedasticity in the data did not influence the parameter estimates strongly.

The least-absolute-values procedure also produced estimates close to those of the OLS model. As this procedure also gives less emphasis than OLS to extreme observations, its estimates were in the direction of those produced by the Beaton-Tukey procedure. We discount these results for the reasons given in the discussion of that procedure; at the same time, we find it encouraging that least-absolute-values regression gave results very near to those of ordinary least squares.

In summary, we believe that the ordinary least squares estimator (equation 5) is the best model of fecundity derivable from these data. Since we do not believe that our observations with larger residuals are outliers in the sense of being un-

Table 6. Summary of parameter estimates from four fitting methods (See text for description of methods)

Fitting method	Estimated parameters		
	Intercept	Width	Year
Ordinary least squares	-2.915	0.377	1.33
Beaton-Tukey weighting	-2.333	0.321	1.59
Weighting by width group	-3.057	0.384	1.40
Least absolute values	-2.788	0.356	1.31

reliable, the Beaton-Tukey and LAV estimators are not preferred, although they were good heuristics to examine the robustness of the OLS results. Weighting the regression by width group was probably the best of the three robust methods, as making inferences is easiest from weighted least squares models. The results of the WLS analysis suggest a slightly higher slope to the width-fecundity relationship; however, this is of little importance at this stage of our knowledge of the species.

Temporal Patterns.—The results reveal two striking temporal patterns. The first is that the expected fecundity for a given width is 1.33 million eggs higher in 1987 than in 1986 (equation 5). We do not know whether this difference is real or was introduced by bias in one or both of the laboratory methods for estimating fecundity. No crabs were subjected to both methods of fecundity estimation, so it is impossible to compare the results of the two methods statistically. Further studies of variation in fecundity from year to year would shed more light on this phenomenon.

Despite these differences, a general width-fecundity relationship is of interest. The year effect can be removed from the model by adding 0.667 (half the year coefficient from equation 5) to fecundity from 1986, and subtracting an equal amount from the 1987 values. The resulting width-fecundity relationship becomes

$$\hat{E} = -2.248 + 0.377W, \quad (9)$$

where symbols are as described for equation 5. The standard error of the width parameter in this model is 0.058 (as in equation 5); $R^2 = 0.24$. The ANOVA table is given in Table 7. This is the width-fecundity model we would use for management modeling at present.

The low R^2 of equation 9 is partly due to a second striking temporal pattern in the data: the differences between shapes of the fecundity time-plots for each year (Fig. 4). The remarkable fecundity peak in 1986 coincided with a similar peak in density of organisms on the spawning grounds (Jones et al., 1989). Density of crabs on the spawning grounds was less variable in 1987 than in 1986 (Jones et al., 1989); our data (Fig. 4) show that fecundity was less variable in that year, as well.

What might have caused such patterns? We speculate as follows: Perhaps some conditions, possibly climate, caused favorable growth early in the 1986 season. Many mature female crabs increased weight rapidly and directed much of this biomass to reproduction. These crabs then spawned at the peak spawning time. Because of their higher weight, they had higher fecundity than normal for their size, and thus caused the observed fecundity peak. Since many or most of the mature females had spawned at the spawning peak, those spawning later were not

Table 7. Analysis of variance for linear model of blue crab fecundity as a function of width only. Year effects have been adjusted out by standardizing fecundity values to the mean of expected fecundity at width for 1986 and 1987 (See text for details)

Source	df	Sum of squares	Mean square	F value	P > F
Model	1	69.64	69.64	36.0	0.0001
Error	133	257.06	1.93		
Corr. total	134	326.70			

subject to the favorable conditions, or were second spawners, and thus had lower fecundity. In 1987, no period of exceptionally favorable conditions existed, so no group of crabs experienced rapid growth in weight. Instead of a large group of very fecund crabs spawning at once, individual crabs spawned as they reached some particular state of maturity. Under these conditions, no peak of spawning density nor of fecundity would be expected. We repeat that this scenario is purely speculative. We have made no attempt to examine the climatic data in search of an explanatory factor, as fitting a model to two points would not be particularly revealing. Further bioenergetics work, together with a long-term study of fecundity in situ, would seem to be the prescription for answering this question.

Management Considerations.—Sharply varying fecundity, either within or between seasons, makes fishery management more difficult. The success of a policy that aims at a constant escapement, for example, will be hard to judge if the constant escapement represents a highly variable contribution to the larval population. If such a policy were to be implemented for blue crab, allowances for variable fecundity would appear necessary.

The blue crab commercial fishery in 1987 (a typical recent year) was valued at \$10.6 million ex-vessel in Virginia alone (Anon., 1988). At present commercial landings are recorded, but the effort statistics are somewhat crude. Regulatory agencies in Virginia and Maryland are moving toward a more unified catch and effort data collection system (Austin et al., 1988), presumably to be used for a catch-effort model of abundance. While a catch-effort model will represent a large step forward, it is less than optimal for this fishery. Such models assume constant (or known) catchability; however, catchability is known to change because of technological and behavioral changes by the fishermen and behavioral characteristics of the target species (Gulland, 1983; Paloheimo and Dickie, 1963). Clark (1974) and Gulland (1975) have discussed the difficulties of using catch-effort models in short-lived, aggregated fish species. In addition, Peterman and Steer (1981) have demonstrated density-dependent catchability coefficients in salmon. Although *Callinectes* is certainly not a fish, it shares life history patterns with fish species that have undergone sharp declines in abundance after heavy exploitation.

Fishery-independent monitoring of the abundance of *Callinectes sapidus* is needed in the near future. As the species is migratory and patchy, an ideal place for monitoring is on or near the spawning grounds. Jones et al. (1989) have demonstrated that one way to monitor the stock there is through a trawl survey. Another way might be through plankton surveys, using a variation of the egg production method of Lasker (1985). The egg production method uses knowledge about reproductive biology and the abundance of eggs to estimate the biomass of the reproductive population. Further clarification of the observed patterns in fecundity would be useful to apply this method, and the method would require

modification (for example, the use of early-stage larvae instead of eggs); however, its applicability to *C. sapidus* in Chesapeake Bay should be investigated.

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