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ESTIMATES OF SPAWNING STOCK SIZE OF BLUE CRAB, *CALLINECTES SAPIDUS*, IN CHESAPEAKE BAY, 1986–1987

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

ABSTRACT

We present the first estimates of female spawning stock size for the blue crab, *Callinectes sapidus* Rathbun, in Chesapeake Bay. Using trawl surveys based upon simple and stratified random sampling, we made abundance and density estimates for 1986 and 1987. The 1986 spawning stock exhibited a single abundance peak, increasing from $1.0 \cdot 10^5$ individuals in early July to $9.3 \cdot 10^6$ in late July, maintaining high levels throughout the summer, and declining in the fall to $7.4 \cdot 10^5$ individuals. The 1987 spawning stock showed two peaks of abundance. The population reached the lesser peak, $1.0 \cdot 10^6$ individuals, in late July; the greater peak, $1.5 \cdot 10^6$, in late August. By late September, the population had declined to $6.5 \cdot 10^5$ individuals. The peak abundance of the 1987 female spawning stock was only 16% as great as the peak abundance in 1986; the 1987 spawning stock size (measured in crab-days spent on the spawning grounds) was only 29% of the stock size in 1986. Variability of this magnitude calls for continued monitoring and watchful management, to prevent fishing pressure from exceeding the reproductive capacity of the stock.

The blue crab, *Callinectes sapidus*, is an important species in the commerce, recreation, and ecology of Chesapeake Bay. The blue crab stock in the Bay is experiencing increasing fishing pressure as local oyster stocks continue to decline. Ricker (1963) has shown that a fishery characterized by high recruitment can experience a "swift and drastic" decline when under heavy exploitation. For a species such as the blue crab, which is believed to have only one or two year classes spawning, effects of recruitment overfishing could be felt rapidly and have a destructive effect on the fishery.

Research on the blue crab in Chesapeake Bay dates back to Hay (1909), includes classic works of Churchill (1919) and Van Engel (1958), and also recent work by Hines et al. (1987). However, the reproductive ecology of the stock is not well known, and few components of the stock have been the subjects of abundance estimates. Chittenden (1973)¹ and Applegate (1983) made Leslie and DeLury estimates (Ricker, 1975) of the number of crabs, largely overwintering mature females, vulnerable to the winter dredge fishery in the lower Bay. However, neither of these estimates attempted to approximate the total population size, and certainly underestimated the spawning stock size, since the overwintering population is joined in the spring by mature females migrating to the lower Bay to spawn.

Tang (1985) used a modified Ricker recruitment model to search for environmentally induced variation in recruitment. Because of data limitations, Tang used the commercial catch statistics as indices of both stock and (in the following year) recruitment. Despite this effort, the relationship of recruitment to parent stock size in *C. sapidus* is still problematic. We present here the first population estimates of female spawners. Estimates were made during the 1986 and 1987 spawning seasons. We discuss differences in population size between the two years, and

¹ Chittenden, M. E., Jr. 1973. Dynamics of the winter dredge fishery for blue crabs, *Callinectes sapidus*, the Chesapeake Bay, Virginia. Virginia Inst. Mar. Sci. Gloucester Point, Virginia. Unpublished Report.

develop an estimate of the migration rate of mature females during the spring. We also present evidence of late-summer immigration of non-ovigerous females into the lower bay.

METHODS

Field Sampling. — The area sampled, which extends from the mouth of the York River to about 17 km offshore of the Virginia Capes, encompasses approximately 1,200 km² (Fig. 1). The area is heterogeneous in bottom topography, sediment type, and depth. We divided the sampling area into twenty grids of $7.4 \cdot 7.4$ km; four stations were designated randomly within each grid to serve as standing trawling locations. Before each cruise in 1986, twenty stations were chosen at random for sampling. Based on the population density information obtained in 1986, the plots were assigned to low, medium and high abundance strata, and in 1987 sampling effort was proportionally allocated to strata based on the product of the stratum's area and the standard error of the 1986 abundance (Cochran, 1977). Before each cruise, the chosen stations were arranged into a circular route to minimize travel time and maximize station coverage. The starting station and direction of travel were also chosen at random.

Cruises were conducted on Old Dominion University's R/V LINWOOD HOLTON, a 60-foot converted T-boat. The sampling gear comprised a 9.1-m semi-balloon otter trawl of 3.8-cm (stretched) mesh, fitted with a tickler chain. The chain increases blue crab catches significantly, and thus provides a more accurate population estimate (Chittenden and Van Engel, 1972). The footlines from the otter boards to the net were kept short (<2 m) to minimize herding of crabs from beyond the mouth of the net. At each station, the net was towed for 20 min at approximately 2 knots; the average area sampled per tow was 11,300 m². The catch was sorted on deck, and all *C. sapidus* females placed in coolers for holding. Immediately thereafter, the crabs were measured to the nearest 0.5 cm and classified by reproductive stage. Each was assigned to one of five reproductive stages: (1) no eggs nor evidence of previous spawning; (2) early stage (orange egg mass); (3) intermediate development (orange-brown egg mass); (4) late development (black egg mass); (5) no eggs but evidence of previous spawning (e.g., loose abdomen or remnants of egg capsules on the pleopods).

Laboratory observations had shown that orange eggs have only a small embryonic disc area, have not begun invagination, and consist of about 90% yolk by volume. Orange-brown eggs have completed invagination, organogenesis and eye pigmentation have begun (causing the brownish coloration), and the egg volume is about 50% yolk. Black eggs contain fully developed embryos that will hatch in less than 48 h; the egg volume is less than 10% yolk. This agrees with observations of Anderson (1982) for brachyuran development. Our classification system, while not absolute, provided a rapid and reasonable method of classifying spawners at sea.

Sampling was conducted in 1986 from 12 June through 2 October. Since the cruises of 12, 16, and 30 June were used to evaluate gears and develop an appropriate sampling scheme, data from these cruises were not used for analyses. In 1987, we sampled from 11 May through 23 September (Table 1).

Estimation of Population Size. – Estimates of the number of females occupying the spawning grounds (the female spawning stock size) during each cruise were calculated using the swept-area method (Seber, 1982). In 1986, statistics were based on simple random sampling; in 1987, on stratified random sampling (Cochran, 1977). Differences in population sizes within a year were tested using an approximate test of equality of means (Sokal and Rohlf, 1969). We used this test (a modified ANOVA) because a small fraction of the variances were heterogeneous, and the test is specific for these conditions. When the test showed significant differences in abundance, we used Tukey's multiple comparison test (Zar, 1984) to determine which cruises were significantly different. Tukey's test controls the total experimentwise Type I error.

The number of female-days, a measure of spawning stock size, was calculated by integrating the area under the yearly curves shown in Figure 2 by the trapezoidal method. The variance of female-days was derived by the delta method (Seber, 1982):

$$V(\# \text{ female-days}) = \frac{1}{4}[(t_2 - t_1)^2 V(\hat{y}_1) + \{\sum_{i=2}^{n-1} (t_{i+1} - t_{i-1})^2 V(\hat{y}_i)\} + (t_n - t_{n-1})^2 V(\hat{y}_n)]$$

where n = the number of cruises.

RESULTS

Abundance Estimates.—In 1986, estimates of the female spawning stock varied by two orders of magnitude over the season (July through September), with a low

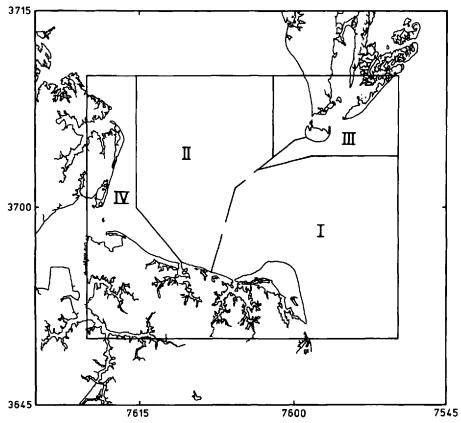


Figure 1. Area sampled (within dashed lines) to estimate blue crab female spawning stock in Chesapeake Bay.

of 10⁵ individuals on 8–9 July and a high of $9.3 \cdot 10^6$ on 30 July–1 August (Table 2, Fig. 2). The increase from the early July abundance to higher levels ($2.1 \cdot 10^6$ to $9.3 \cdot 10^6$) was rapid, and the higher levels were maintained throughout most of the summer. Analysis of variance (ANOVA) indicated significant differences among population sizes during the season (P < 0.001).

In 1987, the estimated abundances differed by an order of magnitude over the spawning season, with a low of $1.4 \cdot 10^5$ in late July and a high of $1.5 \cdot 10^6$ in late August. The series of estimates showed two peaks: one in late May to early June, and a larger peak in late August (Table 2, Fig. 2). The first peak was statistically significant when compared to abundances in early May and late June at P < 0.01; the second was significant at P < 0.001.

Stratification of the 1987 sampling design was successful in reducing variance. The mean coefficient of variation (C.V.) of the estimates in 1986 was 51.7%, compared to 37.1% in 1987 (Table 1).

We estimated that $3.29 \cdot 10^8$ female-days were spent on the spawning grounds in 1986 (Standard error = $8.74 \cdot 10^7$) and $9.69 \cdot 10^7$ female-days in 1987 (Standard error = $1.18 \cdot 10^7$); this represents a 71% reduction in 1987. Since the sampling period in 1987 was longer than in 1986, the true difference may have been even greater. This difference, however, was not statistically significant due to the large variability in 1986, which was due, in part, to the lack of stratified sampling.

Cruise (no.)	Dates	Tows made	Crabs caught	
Preliminary	12, 16, 30 Jun 1986	20		
86-1	8–9 Jul 1986	20	20	
86-2	16–18 Jul 1986	20	258	
86-3	30 Jul-1 Aug 1986	18	1,668	
86-4	15-16 Aug 1986	10	841	
86-5	21, 28 Aug 1986	6	125	
86-6	5 Sep 1986	7	181	
86-7	10-12 Sep 1986	19	312	
86-8	30 Sep-2 Oct 1986	20	148	
87-1	11–12 May 1987	15	29	
87-2	26-27 May 1987	19	182	
87-3	8–9 Jun 1987	16	212	
87-4	21, 22, 26 Jun 1987	20	31	
87-5	8-9 Jul 1987	20	97	
87-6	23–24 Jul 1987	19	253	
87-7	5-7 Aug 1987	20	264	
87-8	19–21 Aug 1987	19	379	
87-9	8–10 Sep 1987	18	207	
87-10	21-23 Sep 1987	17	145	
1986 Totals		120	3,553	
1987 Totals		183	1,779	
Grand totals		303	5,332	

Table 1. Sampling dates, tows, and catches in 1986 and 1987

Density Estimates. — The mean observed density of female crabs over the 1986 survey period was $2.9 \cdot 10^{-3} \text{m}^{-2}$, and ranged from $8.9 \cdot 10^{-5} \text{m}^{-2}$ in early July to $8.2 \cdot 10^{-3} \text{m}^{-2}$ in late July (Table 2). The mean density in 1987 was $2.0 \cdot 10^{-4} \text{m}^{-2}$; estimated densities ranged from $6.9 \cdot 10^{-5} \text{m}^{-2}$ in late June to $3.9 \cdot 10^{-4} \text{m}^{-2}$ in mid-September.

Abundance Estimates by Reproductive Stage. – Abundance estimates by reproductive stage are shown in Table 3 and Figures 3 and 4. Changes in abundance

Table 2. Estimates of density and abundance (and related statistics) of female *Callinectes sapidus* in the survey area, 1986–1987 (CV stands for coefficient of variation)

Cruise (no.)	Mean density, crabs per 10 ³ m ²	SE of density	Estimated population size, 10 ⁶ crabs	SE of pop. size	CV of pop. size
86-1	0.089	0.049	0.100	0.056	55.7%
86-2	1.142	0.657	1.290	0.741	57.4%
86-3	8.200	4.140	9.250	4.670	50.5%
86-4	7.443	3.560	8.396	4.016	47.8%
86-5	1.844	0.706	2.080	0.796	38.3%
86-6	2.288	1.348	2.581	1.521	58.9%
86-7	1.453	0.532	1.639	0.601	36.6%
86-8	0.655	0.448	0.739	0.505	68.4%
87-1	0.219	0.092	0.247	0.104	42.1%
87-2	0.381	0.222	0.430	0.251	58.4%
87-3	0.413	0.224	0.467	0.253	54.2%
87-4	0.122	0.060	0.138	0.068	49.3%
87-5	0.390	0.069	0.440	0.078	17.7%
87-6	0.926	0.382	1.045	0.431	41.2%
87-7	0.766	0.194	0.864	0.219	25.3%
87-8	1.281	0.164	1.445	0.184	12.7%
87-9	0.979	0.395	1.104	0.446	40.4%
87-10	0.577	0.172	0.650	0.194	29.8%

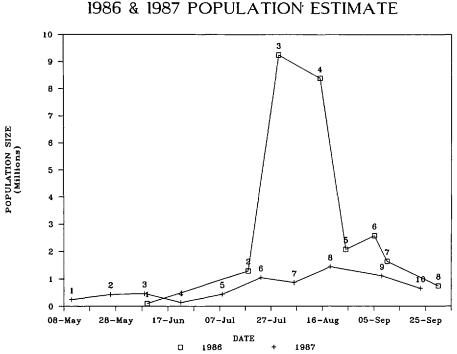


Figure 2. Estimated abundances of female *Callinectes sapidus*. 1986 and 1987 sampling seasons are overlaid to show respective abundances ($\Box - \Box$ 1986, +---+ 1987).

of stage 1 females through the 1986 season were not statistically significant, probably due to the large variability of catches within each cruise. The trend was for increasing abundance early in the summer, followed by relatively constant abundance for the rest of the season. The abundance of stage 2 females peaked in late July and early August, when they were significantly higher than at other times (P < 0.001). Stage 3 females reached their peak abundances in mid-August (cruise 4), and maintained a moderate abundance in the 10⁵ order of magnitude throughout the summer. Their mid-summer peak in abundance is statistically significant (P < 0.01). Stage 4 females reached a statistically significant peak of abundance in mid-August (P < 0.01), concurrent with the peak abundance of stage 5 individuals. Stage 5 abundance increased quickly from levels of $4.3 \cdot 10^4$ in mid-July to the 10⁶ order of magnitude, remained there until late September and early October, when it declined to approximately $3.0 \cdot 10^4$. No stage 5 females were taken before mid-July. These differences in abundance were significant (P < 0.05).

In 1987, changes in abundance throughout the summer were significant (P < 0.001) for all stages (Table 3, Fig. 2). There was a significant decrease in abundance of stage 1 crabs from mid-May ($2.5 \cdot 10^5$) through June ($4.2 \cdot 10^3$), and a significant increase in abundance from July through the end of sampling in late September ($1.3 \cdot 10^5$ to $4.4 \cdot 10^5$). Stage 2 females were first captured in late May (estimated abundance $2.7 \cdot 10^5$), then declined in number through June ($7.6 \cdot 10^4$). A second and larger peak of abundance occurred in late July through early September, at levels of abundance ranging from $1.4 \cdot 10^5$ to $3.8 \cdot 10^5$ individuals. Stage 3 females reached peak abundance in July ($2.4 \cdot 10^5$ individuals), and August ($3.3 \cdot 10^5$ to $3.8 \cdot 10^5$). Stage 4 females had a single broad significant (P < 0.001) peak in

Cruise _ (no.)	Estimated abundance and SE of the estimate, in 10 ⁵ individuals						
	Stage 1	Stage 2	Stage 3	Stage 4	Stage 5		
86-1	0.598 (0.266)	0.200 (0.156)	0.099 (0.098)	0.099 (0.069)	0.000 (0.000)		
86-2	2.445 (0.986)	2.246 (1.646)	2.594 (2.131)	4.742 (2.835)	0.848 (0.436)		
86-3	12.260 (3.846)	15.030 (4.910)	4.603 (1.765)	7.209 (1.890)	5.600 (2.081)		
86-4	6.589 (1.812)	29.950 (9.763)	13.180 (7.464)	12.970 (4.867)	2.096 (0.934)		
86-5	4.326 (2.151)	6.988 (2.499)	0.666 (0.211)	7.320 (3.089)	1.497 (0.763)		
86-6	7.986 (3.696)	8.414 (5.028)	3.137 (2.645)	4.991 (3.684)	1.284 (0.836)		
86-7	7.617 (4.173)	2.732 (0.909)	1.366 (0.631)	2.259 (1.297)	2.416 (0.773)		
86-8	6.888 (4.759)	0.150 (0.109)	0.000 (0.000)	0.050 (0.050)	0.299 (0.206)		
87-1	2.470 (0.394)	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)		
87-2	0.904 (0.423)	2.710 (2.170)	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)		
87-3	0.042 (0.043)	1.120 (0.264)	0.423 (0.321)	0.344 (0.204)	1.220 (0.706)		
87-4	0.042 (0.043)	0.763 (0.610)	0.409 (0.140)	0.303 (0.179)	0.296 (0.168)		
87-5	1.730 (0.216)	1.530 (0.499)	0.523 (0.121)	0.523 (0.135)	0.078 (0.053)		
87-6	1.300 (0.441)	2.400 (1.020)	2.410 (1.640)	3.010 (1.370)	0.646 (0.310)		
87-7	2.560 (0.744)	1.360 (0.186)	1.070 (0.299)	2.600 (0.545)	1.460 (0.434)		
87-8	2.880 (0.628)	3.830 (1.290)	3.270 (0.650)	2.060 (0.652)	2.120 (0.655)		
87-9	2.860 (0.653)	3.300 (1.460)	3.800 (1.940)	1.040 (0.510)	0.446 (0.244)		
87-10	4.370 (1.890)	0.483 (0.257)	0.315 (0.171)	0.602 (0.389)	0.588 (0.164)		

Table 3. Estimates of abundance of female Blue Crabs in each reproductive stage during 1986 (See text for definition of reproductive stages)

abundance in late July and August $(2.1 \cdot 10^5$ to $3.0 \cdot 10^5$ individuals). Stage 5 females had two peaks of abundance, a smaller peak noted in early June $(1.2 \cdot 10^5$ individuals), and a larger broader peak in August $(1.5 \cdot 10^5$ to $2.1 \cdot 10^5)$, both statistically significant.

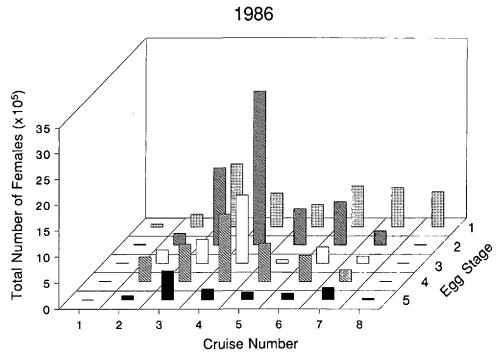


Figure 3. Estimated abundances of female *Callinectes sapidus*, by reproductive stage, during the 1986 spawning season.

1987

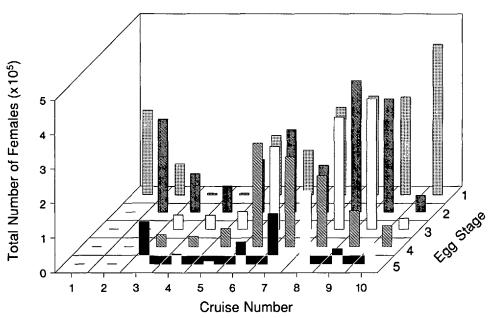


Figure 4. Abundance of females classified by egg stage for the 1987 sampling season.

DISCUSSION

Migration. — The increase in population size during early summer of 1986 suggests migration into the spawning area early in the season, a phenomenon that has not been documented before. The evidence for immigration is best demonstrated by the abundance of females in different reproductive stages (Table 3). The period of development from stage 1 to stage 5 is believed to be about two weeks (W. Van Engel, Virginia Institute of Marine Science, Gloucester Point, VA, pers. comm.). The estimated $2.5 \cdot 10^5$ stage 1 females on the spawning grounds in mid-July (cruise 86-2) would not be sufficient to result in the estimated $5.6 \cdot 10^5$ stage 5 females present two weeks later (cruise 86-3). The difference, approximately 310,000 females, forms a minimum estimate of the amount of migration onto the spawning grounds during this period; any mortality that occurred in the survey area during this time would tend to make this a more conservative estimate. Although admittedly imprecise, this is a first attempt to assess a previously unknown quantity.

Immigration would account, at least in part, for the slow modal progression of female reproductive stages through the summer (Figs. 3 and 4). Sixty percent of the females captured on cruise 86-1 were in reproductive stage 1. By the second cruise, over half of the females were in later stages (i.e., stages 3 to 5). Slightly more than 20% of the females were in stage 3, and 37% in stage 4; these proportions would be expected in the absence of multiple spawning. The results of Wenner (1988) suggest that secondary spawns would not occur this early in the season. Over the next four cruises over half of the females in substantial numbers during these cruises is likely to be from several causes. For stage 1 females immigration into the sampling area is likely. The continued substantial abundance of stage 2 females

observed through the summer of 1986 indicates either repeat spawning or maturation of females previously in stage 1. The sustained abundance of stage 1 females late into the season seems to indicate an influx of maturing females from the 1985 year class.

In the absence of immigration and multiple spawning, a quick progression from stage 1 to stage 5 egg development would be expected, as is seen in the first two weeks of the spawning season. Females would be expected to follow a normal distribution of maturation, and this "population" egg maturation would be seen to progress throughout the summer. In a situation where new stage 1 and 2 females continually enter the population (e.g., through immigration and production of new egg batches) the distribution of egg stage development is broadened by the constant influx.

In early 1987 the modal progression of egg stage development is clear in the early part of the season (Table 3). Only stage 1 females were present on cruise 1, 75% were in stage 2 by cruise 2, and 39% were in stage 3 by cruise 3. These data tend to support the hypothesis that females complete one egg development cycle in approximately 2 weeks. After cruise 3, however, no clear progression of modes is seen in the data. This is not surprising. New females are entering the spawning grounds and are spawning for the first time and females which previously spawned are initiating new broods. Hence, the overlap in developmental stages would be expected to broaden.

The 1987 population, analyzed by egg stage, often showed the pattern of a smaller peak in abundance, followed by second larger peak (Stages 1, 2, and 5). The major peak, however, is consistent in timing from year to year.

Evidence of immigration in 1987 differs from that in 1986. Unlike 1986, in 1987 there are consistently enough stage 1 females to account for the abundance of stage 5 females through egg maturation alone (Table 3). However, from late June through the end of sampling in September (cruises 4–10), a significant increase is noted for stage 1 abundance (P < 0.001). The increase from cruise 4, $4.2 \cdot 10^3$, to cruise 10, $4.4 \cdot 10^5$, is approximately 433,000 stage 1 females over a 14 week period, or about 62,000 per two-week period. This is an approximate measure of immigration onto the spawning grounds of females newly recruited to the spawning stock.

Since there is evidence of extensive immigration to the spawning grounds during the reproductive season, estimating stock size from the winter dredge fishery measures abundance of only one component of the spawning stock, the overwintering females. If the migration rate varies from year to year as indicated by our data, estimates based on the winter dredge fishery will not provide a consistent measure of relative abundance of mature females.

Density Estimates. – Dintaman (1984) found mean densities of mature crabs of both sexes in Maryland waters of $1.1 \cdot 10^{-3} \text{m}^{-2}$ during June through September, 1980–1984. Densities were quite variable within and among years. We estimated only female densities in areas of spawning aggregation; however, our findings (2.9 $\cdot 10^{-3} \text{ m}^{-2}$) for 1986 are close to Dintaman's. Our density estimates for 1987 (0.2 10^{-3} m^{-2}) are less than the seasonal average densities found by Dintaman and most similar to 1980, the poorest year in his study. Since the abundance of female crabs was considerably less than in 1986 over the same survey area, the decrease in density follows.

Interannual Variability. -- Van Engel (1958) described the normal spawning curve for blue crabs as having two peaks, the first in late spring and the second in mid

summer. The 1987 abundance curve reflects this pattern. However, the 1986 curve shows only a single peak. Cruises in early and late June, 1986 (Table 1) are not shown on Figure 2, but trawls from these cruises showed only an occasional crab, and support the absence of the late spring peak. The lack of a spring peak in abundance in 1987 is corroborated by several authors (Provenzano et al., 1983; McConaugha et al., 1983; Varnell and McConaugha, in prep.). Using abundance of stage one C. sapidus larvae as an indicator of spawning activity, they suggest that spawning can be either unimodal or bimodal for the Bay population. Data from 1980 and 1982 suggest a single peak of spawning in late July and early August (McConaugha et al., 1983) similar to the one we observed in 1986. Data from 1983 indicate bimodal spawning with a small peak in early to mid June and a larger peak in early August (Varnell and McConaugha, in prep.). We know of no published evidence whether the lack of a spring peak in abundance is fairly common or an unusual event. In either case, the observed changes in abundance and timing of spawning, potential changes in residence time on the grounds, as well as observed shifts in fecundity (Prager et al., 1990), suggest that patterns related to spawning in C. sapidus are highly variable.

The C. sapidus female spawning stock size appears quite variable. Our survey encompassed only two years, but from 1986 to 1987, we estimated a 71% reduction in spawning stock size, a remarkable change by any measure. Even though this difference was not statistically significant due to large variances in 1986, we believe that the reduction in abundance is real. That the reduction is not a statistical artifact is supported by the observation of several successive estimates of high abundance in 1986 and no estimates of high abundance in 1987. Five of the highest abundances for both years occurred within the eight cruises of 1986. Blue crab recruitment is also quite variable, possibly because of the dynamics of pelagic larval stages, which develop offshore (Provenzano et al., 1983; Epifanio et al., 1984; McConaugha, 1988). Since the blue crab is a short-lived species, without only one or two year classes forming the spawning stock, variable recruitment would be expected to cause variable spawning population size. On the other hand, the variability in recruitment implies that the smaller spawning stock in 1987 will not necessarily bring forth smaller recruitment in 1988. However, for many short lived stocks, smaller spawning stock sizes result on average in smaller recruitments, and decreased chances of large recruitments. Thus from a management perspective, continued data collection and watchful management of the stock would seem appropriate. Yearly monitoring of the spawning stock would provide a valuable data series, especially when combined with the existing series of recruitment and harvest estimates and proposed improved estimates of fishing effort. One cannot hope to investigate the dynamic relationship of stock to recruitment without collecting a sufficiently long time series of data on the spawning stock.

The change in abundance patterns from 1986 to 1987 underscores the limitations of using the number of female crab-days on the spawning grounds as an index of spawning stock size. By using this simple index, we have obtained valuable order-of-magnitude estimates, and demonstrated patterns unknown previously. However, a major objective of an index of spawning stock is to estimate year-toyear changes in the number of eggs released. To make these estimates from abundance surveys, one additional piece of information is needed: the mean residence time of a female on the spawning grounds. If we could assume that this is constant from year to year, its absolute magnitude would not be critical, although still of interest. However, the substantial changes in timing and magnitude of the spawning aggregation from 1986 to 1987 raise the possibility that residence time may also vary significantly. Thus estimates of residence time (preferably made by tagging) would greatly enhance our observations on abundance. Combined, these data would help us to understand the reproductive ecology, and ultimately the recruitment dynamics of *C. sapidus*.

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