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ABUNDANCE AND EXPLOITATION RATE OF THE BLUE CRAB (*CALLINECTES SAPIDUS*) IN CHESAPEAKE BAY

A. F. Sharov, J. H. Vølstad, G. R. Davis, B. K. Davis,
R. N. Lipcius and M. M. Montane

ABSTRACT

We estimated absolute abundance of the blue crab stock in Chesapeake Bay during winter from stratified random surveys conducted baywide from 1990 to 1999, using the swept-area method. We estimated catching efficiency of the survey gear from multiple depletion experiments to correct for temporal and vessel/area differences in catchability. The survey was conducted during the winter, when crabs are dormant and ''buried'' in the bottom. Analysis of crab carapace width (CW) frequency distributions revealed two size modes: CW less or equal 60 mm and CW greater than 60 mm, corresponding to age-0 (recruits) and age-1+ (one year and older), respectively. Absolute density of blue crab recruits varied from 10 to 55 crabs per 1,000 m^2 across years (95 million to 540 million baywide), with no significant trends over time. Abundance of age-1+ crabs declined significantly from 35 to 38 crabs per 1,000 m^2 in 1990–1991 (342 million to 371 million crabs baywide) to 8.3 in 1999 (82 million crabs baywide). A stronger decline in the number of males indicates that males were exploited more intensively than females. A three-year moving average of spawning stock abundance (age-1+ females) declined twofold from the early to the late 1990s. The absolute abundance of the blue crab population in Chesapeake Bay varied from 241 million to 867 million. Overwintering mortality was usually less than 2%, but substantially higher mortality occurred in 1994 (7.3%) and 1996 (11.9%). High correlation between January water temperature and the percentage of dead crabs provides strong evidence of the adverse effect of cold winter on survival of crabs. Large crabs were affected most by cold winter temperatures. We estimated exploitation rates for the commercial fishery by comparing abundance with total landings. The estimated exploitation rates varied from 40% to 52% from 1990 to 1998 and increased to a record high of 70% in 1999. Fishing mortality rates varied from 0.6 to 0.9 year^{-1} in most years and were above the level providing maximum yield per recruit ($F_{max} = 0.64$ year^{-1}) in nearly all years. The record fishing mortality in 1999 ($F_{1999} = 1.6$ year^{-1}) exceeded the overfishing threshold ($F_{10\%} = 1.0$ year^{-1}). Despite evidence of growth overfishing, the blue crab population supported large harvests throughout the 1990s. Increase of fishing mortality above the $F_{10\%}$ in 1999, indicates that the population was overfished and is at risk of recruitment overfishing if fishing mortality remains at this level.

The blue crab (*Callinectes sapidus*) is distributed from Nova Scotia throughout the East and Gulf coasts of the United States, and into the West Indies. Commercial and recreational fisheries for this species exist in many states, including New Jersey, Delaware, and the Carolinas. The largest fishery for the blue crab, both today and historically, is on Chesapeake Bay in the states of Maryland and Virginia. In 1998, the dockside value of these states commercial crab fisheries exceeded $70 million, more than the value of the harvest of any other Bay species. Blue crab provides a livelihood for many in the region and offers recreational opportunities for many more. The overall economic contribution of commercial and recreational crabbing is estimated to be in the hundreds of millions of dollars. Despite some fluctuations, blue crab commercial landings have increased substantially since the 1930s (Fig. 1). Historically, the economic importance of the blue crab commercial fishery increased as other commercially exploited species, such as oysters and striped bass, declined (Rothschild et al., 1994; Richards and Rago, 1999). Blue crab harvests remained consistently high through the 1980s and early 1990s. However, after a record harvest in 1993, commercial landings
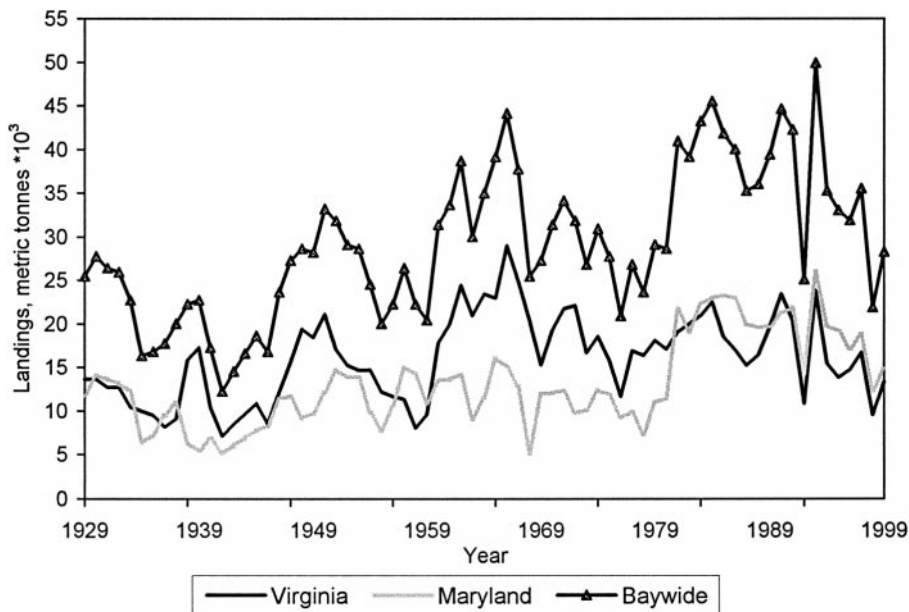
Figure 1. Hardshell blue crab landings in Chesapeake Bay in 1930–1999. Source: VA—1930–1972, National Marine Fisheries Service (NMFS); 1973–1995, Virginia Marine Resources Commission (VMRC); MD—1930–1979, NMFS; 1980–1995, Maryland DNR. Note: reporting system has been changed in 1980 in Maryland and in 1993 in Virginia. These changes are believed to have impacted (i.e., increase) estimates of landings (Miller and Houde, 1998).

and catch per unit effort decreased. The steady increase in fishing effort required to maintain large catches has raised concern that the blue crab population cannot sustain this level of exploitation and eventually may collapse.

The need for data to manage the blue crab stock effectively led to the development of a baywide winter dredge survey. Regional data on blue crab relative abundance were available from Maryland's trawl survey (Uphoff, 1998) and crab pot survey at Calvert Cliffs (Abbe and Stagg, 1996) and Virginia trawl survey (Lipcius and Van Engel, 1990; Rugolo et al., 1998). These surveys, however, had limited spatial coverage.

This paper describes the principles of the design and analyses of the winter dredge survey and presents the results of ten years of winter sampling of the blue crab population of the Chesapeake Bay. We report on trends in blue crab abundance by size/age and sex groups and present estimates of population exploitation rates and fishing mortality over time. We assess the current status of the population by comparing our estimates with several biological reference points proposed for use in the management of the blue crab population.

MATERIAL AND METHODS

THE WINTER DREDGE SURVEY.—A stratified random dredge survey for blue crab in Chesapeake Bay has been conducted between December and March each year since 1989/1990. In the following, each survey year will be referred to by the latter year of the sampling season (i.e., 1990). A crab dredge is employed in the survey to sample the crab population during winter, while crabs are dormant and buried in the sediment (Rothschild et al., 1992; Zhang and Ault, 1995). The primary objectives of the annual survey are: (1) to describe the size and sex composition of the baywide population, (2) to develop accurate estimates of baywide blue crab abundance, and (3) to estimate exploitation and fishing mortality and evaluate the status of the stock annually.

Table 1. Winter dredge survey design and total effort, 1990–1999.

Survey year	Survey design	Sampling area, km^2	Number of stations
1990	Stratified random, 25 geographic strata	7,940	904[1]
1991	Stratified random, 22 geographic strata	7,940	877[1]
1992	Stratified random, 3 geographic strata, 2 sediment sub-strata	11,057	936[1]
1993	Stratified random with proportional to strata area station allocation, 3 geographic strata	10,140	964
1994–1999	Stratified random with proportional to strata area station allocation, 3 geographic strata	9,812	1,248–1,500

[1] Two tows were made at each station.

Between 877 and 1,500 stations have been sampled each year since 1990 (Table 1) in waters deeper than 1.5 m (areas shallower than 1.5 m were not accessible to the boats used in the survey). The sampling program evolved from a pilot survey conducted during the winter of 1989 (Rothschild et al., 1992). The spatial coverage, stratification, and allocation of stations to strata varied before the design was standardized in 1994 (Table 1). In 1990 and 1991 the Bay was divided into 25 and 22 strata respectively; most of the rivers and major parts of the bay formed separate strata. Since 1992, three fixed geographic strata have been employed: (1) the Upper Bay and rivers, (2) the Middle Bay, and (3) the Lower Bay (Fig. 2). Stratum 1 represents mostly shallow waters with low salinity (0–10 ppt), where the winter population is dominated by young-of-year crabs and adult males. Stratum 3 has higher levels of salinity (25–35 ppt), deeper waters and is inhabited primarily by mature females in winter. Stratum 2 is an intermediate area.

The use of a small number of strata is often advantageous for marine resource surveys when the total sample size is fixed (Pennington, 1996; Pennington and Strømme, 1998). In 1992, each of the three geographic strata was divided into two substrata, with low (0–80%) and high (81–100%) gravel content, respectively (Rothschild et al., 1992). Survey results indicated that substratification by sediment type produced only marginal gains in precision (Vølstad et al., 1994). The sediment stratification was problematic because no accurate map of sediment distribution across the Chesapeake Bay exists; the size of each substratum was estimated from sediment samples. The sediment distribution may vary over time because of currents and tidal effects and can also vary along the length of a standard haul. For such reasons, the exact areas of the sediment substrata cannot be obtained from available data. The use of inaccurate substrata areas (weights) introduces a bias in estimates of mean and total abundance (see Cochran, 1977: 117); therefore substratification was discontinued in 1993. After eliminating the sediment sampling, less time was spent at each survey station, and the average number of stations sampled per day increased. Eliminating the laboratory processing of sediment samples also reduced the cost of the survey.

Since 1993, the number of sites in each geographic stratum has been proportional to the area of that stratum. Two replicate tows were conducted at each station from 1990 until 1992. For this period we used the average of the replicate tows to calculate crab density at each station. Rothschild et al. (1992) and Vølstad et al. (1994) demonstrated that catches from replicate tows within stations were correlated (r^2 varied between 0.5 and 0.7 across years), and thus the extra tow at each station only resulted in a marginal increase in precision as compared to single tows. For a fixed survey cost, it is therefore more effective to take single tows and use the time saved to increase the number of stations (Pennington and Vølstad, 1994). For a correlation of 0.6, for example, 125 independent tows yield density estimates with approximately the same precision as 200 tows from 100 random stations. Only one haul was taken at each station during and after 1994, resulting in an increase of more than 25% in the number of stations that could be sampled per day, therefore increasing the precision for fixed survey cost. Figure 3 shows location of sampling stations in winter 1997 as an example of the sampling intensity and spatial coverage of the survey.

FIELD METHODS.—At each station, a 1.83-m wide Virginia crab dredge was towed along the bottom for one minute at a speed of 5.4 km per hour (3 knots). The dredge liner was composed of either galvanized poultry wire, nylon, or polyethylene mesh. Galvanized poultry liner was used in stratum 1 (Upper Bay) and stratum 2 (Middle Bay) from 1990 to 1994, when it was replaced with nylon. The polyethylene mesh has been used in stratum 3 (Lower Bay) since 1990. The dredge, with a 1.3-cm liner, retains crabs with a carapace width (CW) larger than 15 mm (Cargo, 1954; Sulkin and Miller, 1975) and occasionally catches smaller crabs. The distance of each haul was determined by LORAN-
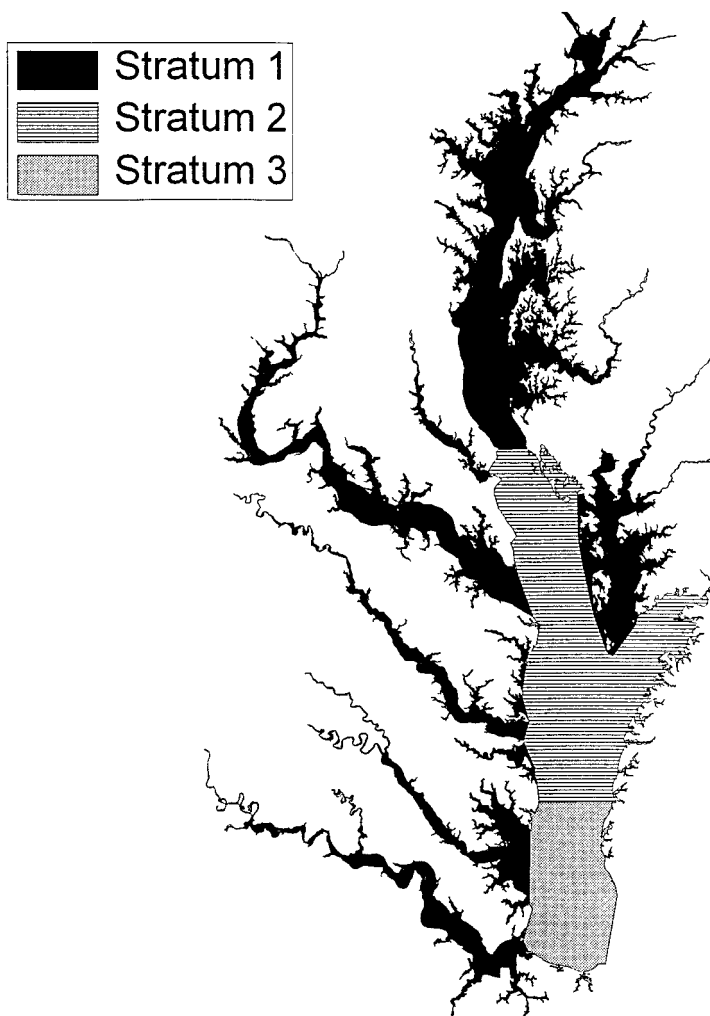
Figure 2.   Strata design, used in the winter dredge survey since 1993. Stratum 1—Upper Bay and rivers, Stratum 2—Middle Bay, Stratum 3—Lower Virginia Bay.

C (1989–1995) or Differential Global Positioning System (1996–1999) readings of latitude/longitude at the start and end of each haul; the area swept was estimated by multiplying the towing distance with the dredge width (1.83 m). Depth at the start and end of each haul, water temperature, and salinity were recorded at each station. All crabs in the catch were measured to the nearest mm from point to point, weighed to nearest 0.1 g, and their sex and maturity stage determined.

DEPLETION EXPERIMENTS.—Since 1992, each vessel participating in the winter dredge survey has conducted depletion experiments to estimate the dredge's catching efficiency (Zhang et al., 1993; Vølstad et al., 2000). The efficiency experiments generally were conducted at a random subset of survey stations with medium to high crab density. Each experiment consisted of up to ten depletions of a 100-m by 5.5-m area (three dredge widths) in Maryland or a 100-m by 9-m area (five dredge widths) in Virginia, marked by buoys. Dredge tows were made in a random order. The experiment ended if two consecutive tows did not catch crabs.

ESTIMATING CATCHING EFFICIENCY TO CALIBRATE SWEPT-AREA ESTIMATES.—An exponential model was used to estimate the gear efficiency, or catchability coefficient (q), for each experiment (Seber, 1973; Vølstad et al., 2000):

$$y_i = q(1 - q)^{i-1}P_0\epsilon \tag{1}$$

Figure 3.   Location of sampling sites in 1997 blue crab winter dredge survey in Chesapeake Bay.

where y_i is the number of crabs caught in the ith coverage, P_0 is the number of crabs present in the experimental area, and ϵ is a random error. This model is linearized by a $\log_e$ transformation:

$$\log_e(y_i) = \log_e(q) + \{\log_e(1 - q)\}(i - 1) + \log_e(P_0) + \log_e(\epsilon) \qquad (2)$$

and the parameters are estimated using linear regression. The catchability coefficient is then estimated from the slope $\{\log_e(1 - q)\}$, after re-transformation following the method of Finney (1941).

The distribution of crabs is typically patchy, and the mean density is sensitive to relatively few large catches. We estimated a weighted mean catchability coefficient for vessel j in year k as

$$\bar{q}_{jk} = \sum \frac{c_{ijk} q_{ijk}}{C_{jk}} \qquad (3)$$

where c_{ijk} = cumulative number of crabs caught in the ith experiment by vessel j in year k, q_{ijk} is the estimated catchability coefficient, and $C_{j,k}$ is the total number of crabs caught in n experiments by vessel j in year k. Because the number of experiments per vessel was small (≤ 10), mean catchability and its standard error were calculated using a jackknife estimator (Efron and Tibshirani, 1994).

TESTING FOR YEAR AND VESSEL EFFECTS IN CATCHING EFFICIENCY.—The catchability coefficients estimated from 203 depletion experiments were analyzed using a two-way unbalanced ANOVA (GLM procedure, SAS Institute, 1989) to determine temporal or vessel/area related differences in catchability. The model was specified as:

$$q_{ijkn} = m + V_j + T_k + L_n + V_j T_k + \epsilon \qquad (4)$$

where q_{ijkn} is the catchability estimate for the ith experiment involving the jth vessel with dredge liner L_n in the kth year, V_j ($j = 1, 2, 3, 4$) is a vessel/area effect, T_k ($k = 1, \ldots, 10$) is a year effect, L_n ($n = 1, 2, 3$) is a liner effect, $V_j T_k$ is an interaction between vessel/area and year, and ϵ is random error. To account for the potential effect of the number of crabs at the experimental site on the estimate of catchability coefficient, the number of crabs caught in each depletion experiment was included as a covariate in the model.

ESTIMATING DENSITY AND ABUNDANCE.—Let x_{hijk} denote the catch per area swept (numbers per m²) at station i in stratum h by vessel j in year k, and let $\bar{q}_{jk}$ denote the dredge catching efficiency for

vessel j in year k estimated from equation (3). For each survey, the absolute number of crabs per m^2 at station i in stratum h is estimated as

$$y_{hi} = \frac{x_{hijk}}{q_{jk}} \tag{5}$$

and the mean density of crabs in stratum h for year k is estimated by

$$\bar{y}_{h,k} = \frac{1}{n_{h,k}} \sum_{i=1}^{n_{h,k}} y_{i,h,k} \tag{6}$$

with variance

$$\text{var}(\bar{y}_{h,k}) = \frac{\sum_{i=1}^{n_{h,k}} (y_{hi,k} - \bar{y}_{h,k})^2}{n_{h,k}(n_{h,k} - 1)} \tag{7}$$

where $n_{h,k}$ is the number of hauls in stratum h in year k. The stratified mean density for the entire survey area in year k is estimated by

$$\bar{y}_{st,k} = \sum_{h=1}^{L_k} W_{h,k} \bar{y}_{h,k} \tag{8}$$

with variance

$$\text{var}(\bar{y}_{st,k}) = \sum_{h=1}^{L_k} W_h^2 \, \text{var}(\bar{y}_{h,k}) \tag{9}$$

where L_k is the number of strata in year k, and W_h is the proportion of the total survey area in stratum h. The absolute abundance (total number of crabs) in the Chesapeake Bay for year k is estimated by extrapolating the mean density for that year to the entire area A,

$$\tau_k = A \times \bar{y}_{st,k} \tag{10}$$

and the variance of the total abundance estimate is estimated by

$$\text{var}(\tau_k) = A^2 \, \text{var}(\bar{y}_{st,k}) \tag{11}$$

We assume that the estimated mean density (eqs. 5–9) in any year is representative for the entire distribution area for blue crabs in the Chesapeake Bay, although the surveys did not provide complete coverage. Shallow waters (depth < 1.5 m) that constitute about 10% of the total bay area, were sampled with a limited number of stations in 1992 and 1993 using a small modified dredge. Density estimates derived from shallow waters were not significantly different than those derived for the area deeper than 1.5 m (Rothschild et al., 1992). Absolute abundance was estimated by expanding crab density for every year to the total bay area, estimated at 9,812 km^2 by GIS.

TESTING FOR TRENDS.—We followed Hirsch et al. (1982) and used the Kendall test for trend in abundance over the n sampling occasions (10 years in this analysis). Let x_j and x_k be estimated absolute abundance in years j and k, respectively. The Kendall test statistic S is defined as

$$S = \sum_{k=1}^{n-1} \sum_{j=k+1}^{n} \text{sgn}(x_j - x_k) \tag{12}$$

where

$$\text{sgn}(\theta) = \begin{cases} 1 & \text{if } \theta > 0 \\ 0 & \text{if } \theta = 0 \\ -1 & \text{if } \theta < 0 \end{cases}$$

Under null hypothesis the mean and variance of S is

$$E[S] = 0 \qquad \text{Var}[S] = n(n - 1)(2n + 5) - \sum_t t(t - 1)(2t + 5)/18$$

where t is the number of x's involved in a given tie, and Σ_t denotes the summation of all ties. A negative value of S represents a negative trend in abundance over the ten years analyzed. Kendall's S has an approximate normal distribution for $n = 10$ (Hirsch et al., 1982); therefore, the test for trends is based on the standard normal test statistic Z, computed as

$$Z = \begin{cases} \dfrac{S - 1}{(\mathrm{Var}[S])^{1/2}} & \text{if } S > 0 \\[2mm] 0 & \text{if } S = 0 \\[2mm] \dfrac{S + 1}{(\mathrm{Var}[S])^{1/2}} & \text{if } S < 0 \end{cases} \qquad (13)$$

In a two-sided test for trend, the null hypothesis can not be rejected if $|Z| \leq z_{\alpha/2}$, with α being the significance level of the test.

ESTIMATING EXPLOITATION AND FISHING MORTALITY RATES.—An estimator of exploitation rate U of the Chesapeake Bay blue crab population is

$$U = \frac{C}{N} \qquad (14)$$

where C is the total annual catch in numbers and N is number of crabs available to the fishery, estimated as the absolute abundance of crabs in winter preceding spring through fall fishing season (Ricker, 1975). Total catch in numbers was estimated from catch in weight data assuming an average individual weight 150 g (Knotts, 1989), which corresponds to mean CW = 147 mm. We derived fishing mortality estimates iteratively by using Baranov's catch equation (Ricker, 1975):

$$U = \frac{F}{F + M}(1 - e^{-(F+M)}) \qquad (15)$$

where F is instantaneous fishing mortality, and M is natural mortality. Natural mortality was assumed to be equal to 0.375 year^{-1} following Rugolo et al. (1998).

OVERWINTERING MORTALITY.—Since 1996, a subset of sites from the random survey performed in December and January, were resampled in February and again in March to measure overwintering mortality. In 1996, 59 sites were selected for mortality sampling, and in 1997 sampling was expanded to 150 sites, all in Maryland's portion of the Bay. The same design was used in 1998 and 1999. Repetitive sampling indicated that the percentage of dead crabs increases towards the end of winter; therefore, for the period before 1996, March samples from the random survey were used to develop a time series of mortality estimates.

A regression analysis was conducted to explore a relationship between crab mortality and water temperature. Lowest bottom temperature typically occurs in February. Although bottom temperature data were not available for the entire time period, we found that mean bottom temperatures in February and mean surface temperatures in January were highly correlated ($r^2 = 0.91$, $P = 0.004$). We regressed January surface temperature with the percentage of dead crabs collected during March from 1990 through 1998 to determine if there was a significant relationship between mortality and temperature.

RESULTS

CARAPACE WIDTH FREQUENCY.—The frequency distribution of carapace width had a characteristic bimodal shape for all years of sampling (Fig. 4). The first mode (CW $\leq$ 60 mm) corresponded to young-of-year (age-0) crabs hatched during the preceding summer. The second mode (CW > 60 mm) represented crabs one year old and older. Although the population of blue crabs consist of at least three year-classes (Van Engel, 1958) and possibly six to eight (Fischler, 1965; Rugolo et al., 1998), only age-0 can be separated from older crabs based on the distribution of carapace width. Therefore, we estimated relative and absolute abundance for age-0 and age-1+ categories only, with further subdivision of age-1+ by sex.

RELATIVE DENSITY.—Relative density of the overwintering population of blue crab from 1990 to 1999 (defined as the stratified mean number of crabs per 1,000 m^2 swept by the dredge, uncorrected for gear catchability) was estimated using methods consistent with the stratification scheme applied each year. Relative density of age-0 crabs fluctuated about sevenfold from a low of 1.6 in 1992 to a high of 12.2 in 1997, with an average of 6.2 crabs per 1,000 m^2 (Fig. 5a). Two strong year classes (1995 and 1996) were observed in 1996 and 1997 sampling seasons. These cohorts appeared to be two to three times more abundant than recruitment
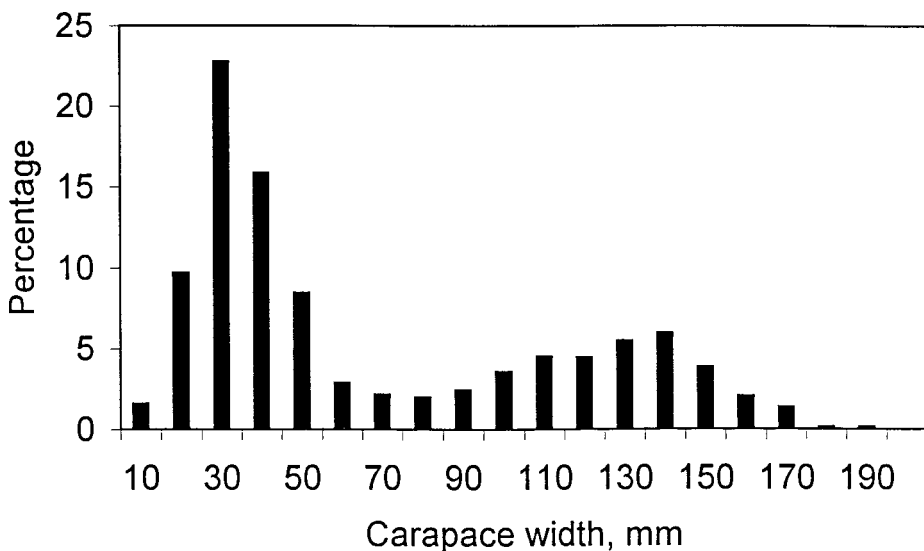
Figure 4.   Carapace-width frequency distribution of the blue crab population in Chesapeake Bay in winter 1995.

in other years. Neither of the two observations, however, was followed by an increase in density of age-1+ crabs during the following winter, as expected. Age-0 crabs were usually more abundant than age-1+ crabs. The total age-1+ index of relative density averaged 4.3 crabs per 1,000 m^2 for both sexes combined. Unlike the juveniles, the relative density of age-1+ crabs decreased substantially, more than threefold from 6.6 per 1,000 m^2 in 1990 to 1.8 per 1,000 m^2 in 1999 (Fig. 5b). The relative density of all size and sex groups combined did not show any specific long-term trend, but rather appeared to have a cyclical component (Fig. 5c). The relative density for all crabs fluctuated from 6.0 to 15.6 crabs per 1,000 m^2 with an overall mean across years of 10.5 crabs per 1,000 m^2. A comparison of relative density of all crab age/size groups combined (Fig. 5c) with the plot for age-0 crabs (Fig. 5a) indicated that recruitment variation is the principal component of the total density dynamics. When separated by sex, both males and females showed a substantial decline; however, the decline was more profound for males with highest density during earliest years (Fig. 6). The average relative density of males dropped from 3.9 per 1,000 m^2 in 1990 to 0.7 per 1,000 m^2 in 1999. Age-1+ females declined with notable interannual variability in density from 2.7 in 1990 to 1.0 in 1999. The ten-year average was 2.1 crabs per 1,000 m^2 and the decline was not monotonous.

CATCHABILITY ESTIMATES.—Because the dredge used in the survey does not catch all crabs in the area swept, an estimate of the catchability coefficient is needed to obtain the "true" density of crabs in the area. There was substantial variation in catchability estimates between years and boats (Table 2). This variation can be explained potentially by the effect of different factors, such as boat characteristics, captain's skills, dredge liner, bottom sediment, depth, and others. Unfortunately, the detection of the boat and year effect in our study was complicated by the fact that different boats and dredge liners were used at different time intervals (Table 2). To alleviate this problem, we attempted to confine the data to the shorter time period (1993–1996) when each of the three principal vessels was used. A balanced ANOVA indicated a statistically significant vessel effect ($P \ll$
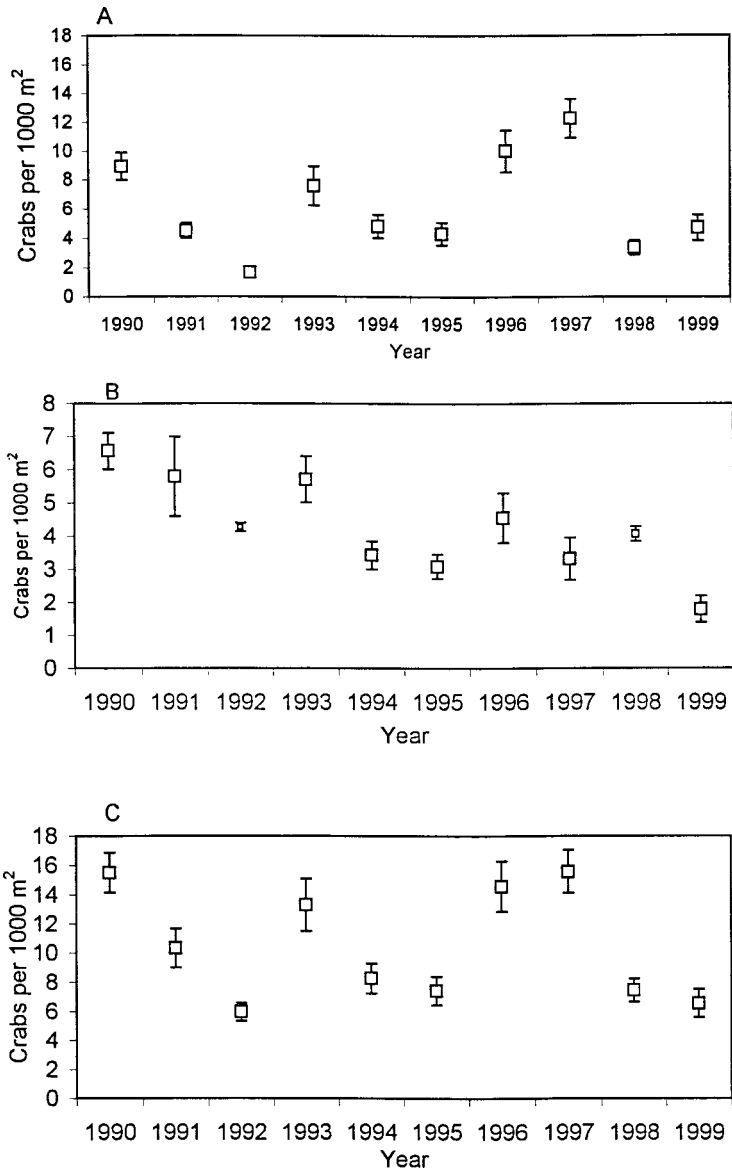
Figure 5.   Relative density of blue crabs (unadjusted for catchability) in 1990–1999. A—age-0, B—age-1+, C—total. Error bars represent 95% confidence intervals.

0.01), but the year effect was not statistically significant ($P = 0.233$). An unbalanced ANOVA using all data (SAS; proc GLM) showed significant effects of year ($P \ll 0.01$), boat ($P \ll 0.01$), and liner ($P < 0.05$), but no effect of crab abundance at the experimental sites on estimates of catchability ($P = 0.358$) or boat–year interaction ($P = 0.156$). Because of the conflicting results of the two analyses regarding the year effect, it remains unclear whether year is indeed a significant factor. Because we were unable to separate year and liner effects, we used vessel-specific estimates of the catchability coefficient calculated as a mean for each period when a certain liner was in use (Table 3).
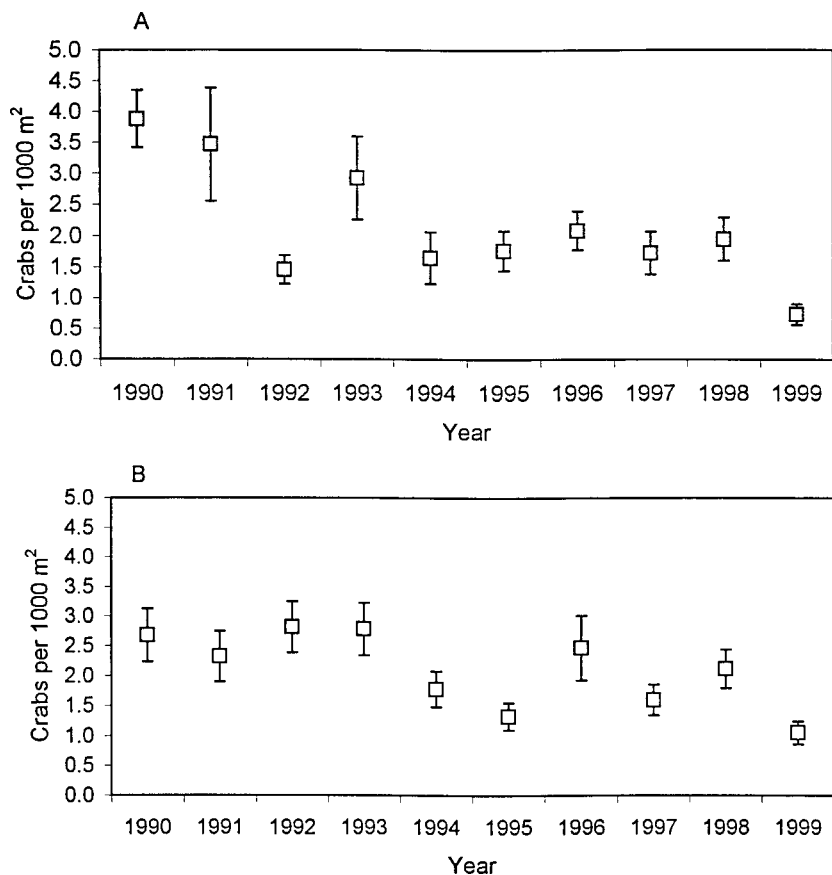
Figure 6.   Relative density of age-1+ blue crabs in 1990–1999 (unadjusted for catchability) separated by sex. A—males, B—females. Error bars represent 95% confidence intervals.

ABSOLUTE DENSITY AND ABUNDANCE.—Absolute density of age-0 crabs, estimated as mean relative abundance corrected for catchability (eq. 8), varied from 9.7 to 55 crabs per 1,000 m². Corresponding absolute abundance, estimated by extrapolating the absolute density to the entire baywide distribution area (eq. 10), varied from 95 million to 540 million with a periodic pattern (Fig. 7a). No significant trend was detected for age-0 crabs ($Z = -0.18$). The density of age-1+

Table 2. Jackknifed yearly estimates of catchability coefficients by year and vessel (standard errors presented in parentheses).

Vessel	1992	1993	1994	1995	1996	1997	1998	1999	2000
F/V ERIN KAY	0.17	0.18	0.16	0.06	0.08	0.15	—	—	—
	(0.02)	(0.01)	(0.04)	(0.03)	(0.06)	(0.04)			
F/V BRI-STEFF	0.18	0.15	0.14	0.23	0.19	—	—	—	—
	(0.05)	(0.03)	(0.03)	(0.04)	(0.16)				
F/V LONI	0.20	0.15	0.28	0.17	0.31	0.42	0.42	0.15	0.24
CAROL II	(0.09)	(0.03)	(0.04)	(0.03)	(0.09)	(0.03)	(0.03)	(0.03)	(0.03)
R/V BAY EAGLE	—	—	—	—	—	—	0.22	0.06	0.29
							(0.08)	(0.03)	(0.03)

Table 3. Vessel specific catchability coefficients calculated as mean for the time period when the same dredge liner was in use. Superscripts indicate the type of the liner: c—chicken wire, n—nylon, p—polyethylene.

Vessel	1990–1991	1992–1994	1995–1996	1997	1998–1999
F/V ERIN KAY	0.13[p]	0.13[p]	0.13[p]	0.13[p]	—
F/V BRI-STEFF	0.16[c]	0.16[c]	0.21[n]	—	—
F/V LONI CAROL II	—	0.20[c]	0.29[n]	0.29[n]	0.29[n]
R/V BAY EAGLE	—	—	—	—	0.19[p]

declined between 1990–1991 (35 to 38 crabs per 1,000 m^2) and 1999 (8.3 crabs per 1,000 m^2) (Fig. 7b). Absolute abundance declined from a range of 342 to 371 million crabs in 1990 and 1991 to 82 million crabs in 1999. The dynamics of total crab density (age-0 and age-1+ combined) was clearly driven by recruitment (Fig. 7c), with no significant trend in abundance over time ($Z = 1.61$, 95% confidence level). Estimated absolute abundance of the Chesapeake Bay blue crab population for 1990 through 1999 fluctuated extensively from 241 million to 867 million. The 95% confidence intervals accounting for variance of the estimator of average density were relatively small. Within the age-1+ class, males declined about fivefold between 1990 and 1999; females declined only two-fold (Fig. 8). The absolute abundance of males declined substantially more (from 213 million to 31 million crabs) than that of females (from 145–185 million between 1990 and 1993 to 51 million in 1999). The negative trends were significant for both males ($Z = -2.33$) and females ($Z = -1.97$) at 95% significance level. At the beginning of the time series, age-1+ males were more abundant than females, but that ratio was reversed in later years, when the densities and absolute abundance of females was greater (Fig. 8). Average density of age-1+ females may serve as a proxy of spawning stock index because age-1+ includes mostly mature females. Those that are immature at the time of the winter dredge survey are likely to mature during the next summer. The absolute density of spawning stock varied by four-fold with a maximum of 19 crabs per 1,000 m^2 in 1992 and a minimum of 5 crabs per 1,000 m^2 in 1999. A three-year moving average declined twofold from 15.8 in 1990–1992 to 8.2 crabs per 1,000 m^2 in 1995–1999. Corresponding absolute abundance of the spawning stock fluctuated between 51 million and 185 million crabs. The amplitude of variation in crab abundance was about threefold for total number of crabs and fivefold for recruitment.

EXPLOITATION AND FISHING MORTALITY RATES.—Age-1+ abundance typically was near the estimated number of crabs landed and was less than the landings during three years out of ten (Fig. 9). If the number of crabs available to the fishery (N) is estimated based on age-1+, the corresponding exploitation rates (eq. 14) are close to or exceed 100%. When N is based on total abundance (age-0 and age-1+), the estimated exploitation rates range from a low of 0.39 in 1990 and 1993 to a high of 0.70 in 1999 (Fig. 10). With the exception of 1999, however, the annual commercial exploitation rates varied in a narrow range between 0.4 and 0.5 (the overall mean 0.47). There was a significant increase in exploitation rate in 1999. These estimates are conservative because they account for commercial landings only. The number of crabs in the recreational harvest might contribute significantly to the total removals, but the effect of recreational harvest could not be quantified because of lack of information. Corresponding fishing mortality of the blue crab population fluctuated from 0.7 to 1.15 year^{-1} between
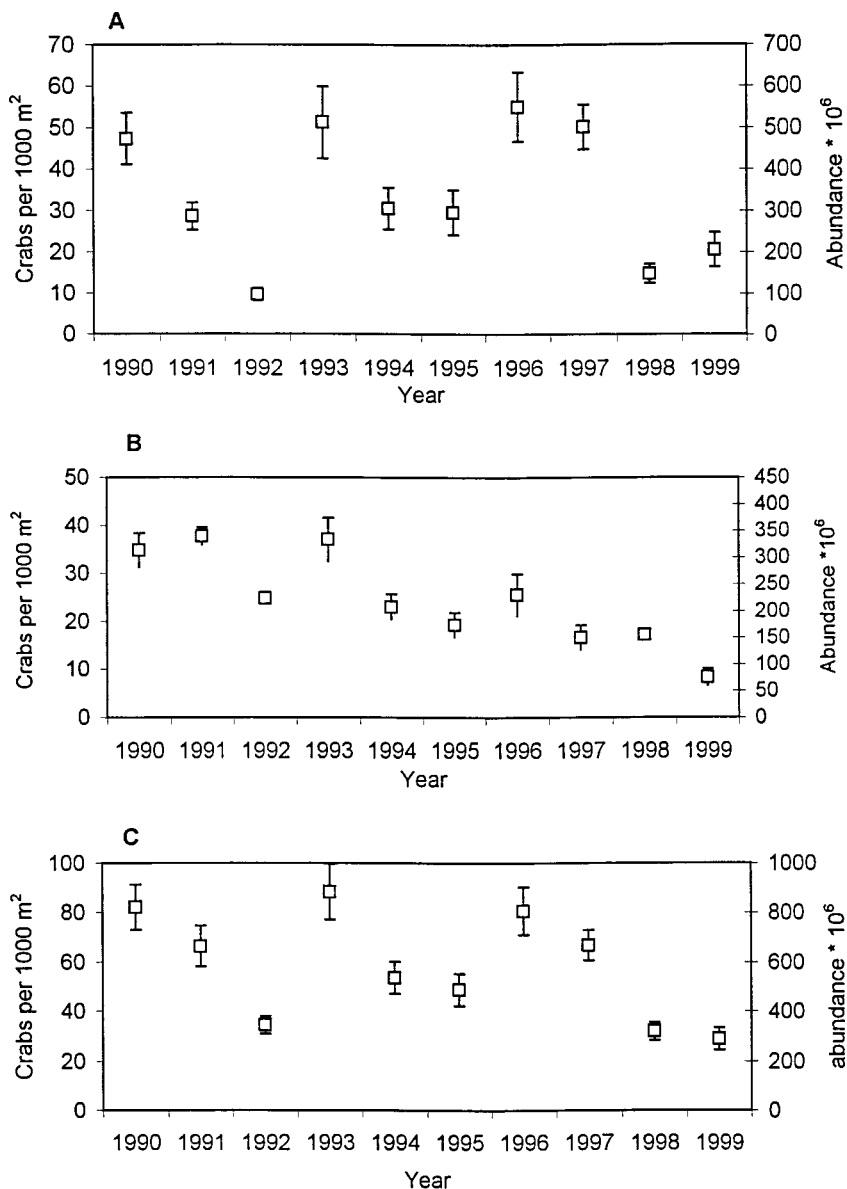
Figure 7.   Absolute density of blue crabs (adjusted for catchability) in 1990–1999. A—age-0, B—age-1+, C—total. Error bars represent 95% confidence intervals.

1990 and 1998 with an average of 0.94, but increased significantly to 1.6 year^{-1} in 1999 (Fig. 11).

OVER-WINTERING MORTALITY.—The percent of dead crabs in repetitive sampling increased with every round of sampling from January to March (Table 4), indicating that sampling in March allows us estimate cumulative over-wintering mortality for interannual comparisons. In seven out of ten years less than two percent of crabs were dead in March sample (Table 5). More significant mortality of crabs occurred in 1994 (7.3%), the record high occurred in 1996 (11.9%). Large crabs
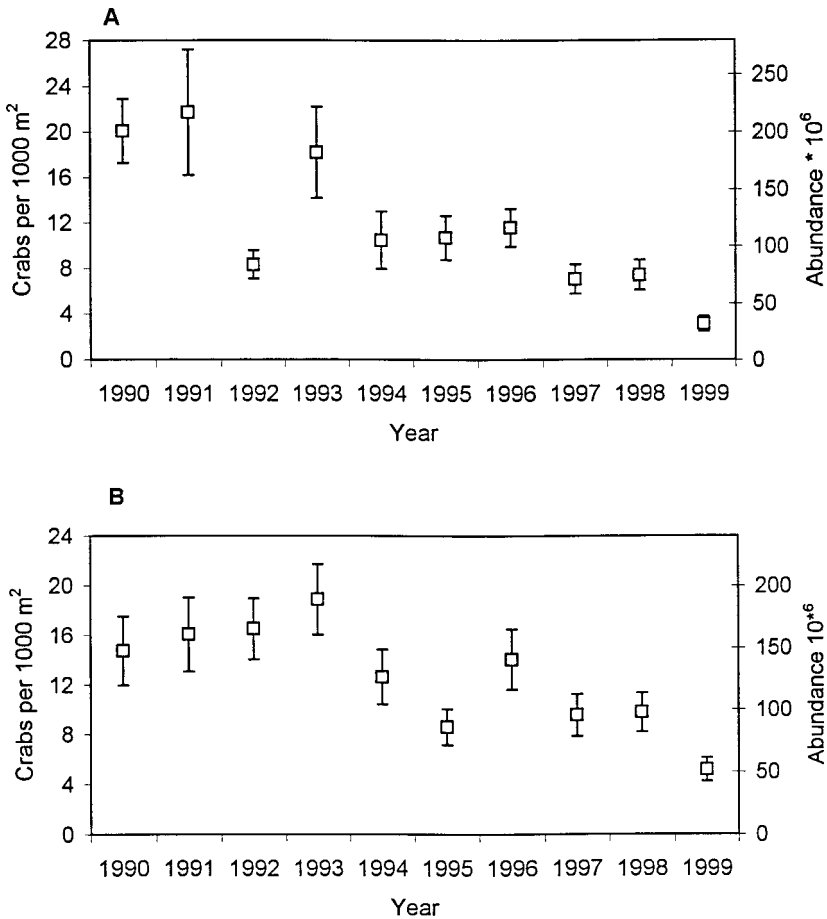
Figure 8.   Absolute density of age-1+ blue crabs (adjusted for catchability) separated by sex. A—males, B—females. Error bars represent 95% confidence intervals.

(CW > 120 mm) suffered significantly higher mortality than smaller crabs. For example, 56.5% of large crabs were dead in March 1996 compared to 6.1% for age-0. When March mortality was regressed against January surface water temperature for the time series, temperature was significantly associated with mortality of both age-0 ($r^2 = 0.50$, $P = 0.05$) and large crabs ($r^2 = 0.59$, $P = 0.026$).

DISCUSSION

The baywide winter dredge survey, conducted from 1990 to 1999, allowed us to identify trends in absolute abundance and characterize size and sex composition of the Chesapeake Bay blue crab population. Estimates of the catchability coefficient from depletion experiments combined with the data on relative abundance collected using a stratified random survey permitted an assessment of the absolute population abundance of the blue crab in Chesapeake Bay. The procedures developed set the stage for interannual comparisons of crab abundance and enabled us to assess the effects of fishing.

Analysis of the survey data revealed that the total abundance of the blue crab population (CW > 15 mm) fluctuated between 240 million and 870 million crabs
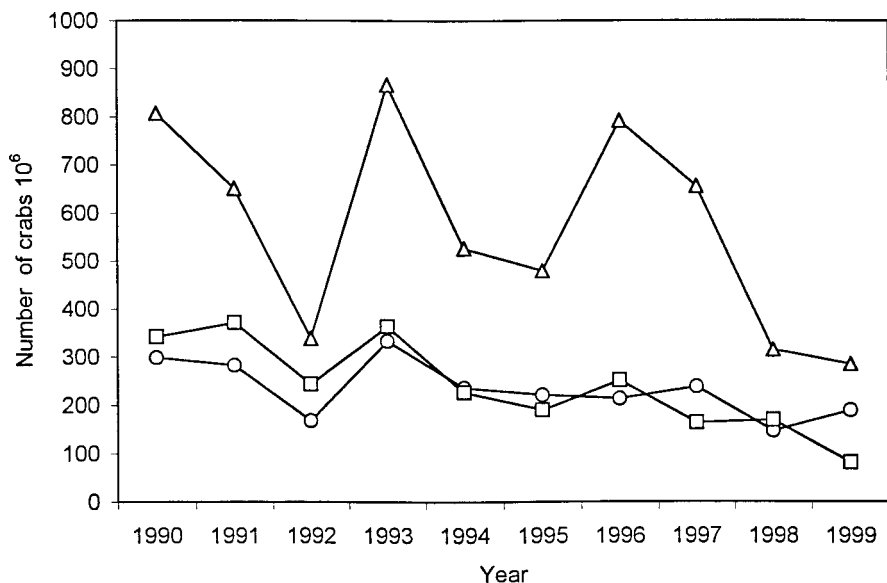
Figure 9. Commercial catch in numbers (closed circles), absolute abundance of 1+ age group (squares) and total population of blue crabs with carapace width >15 mm (triangles).

in a pattern best described as periodic. Comparing the dynamics of total population abundance with the dynamics of age-0 crabs indicated that the former was mostly driven by recruits, which constituted more than 50% of the population. Visual inspection of age-0 abundance dynamics also suggested a periodic component (Fig. 7). Such periodicity in recruitment abundance can be caused either by environmental forcing or by the presence of a strong compensatory stock-recruitment relationship (Ricker, 1954). For example, Kriksunov et al. (1992)
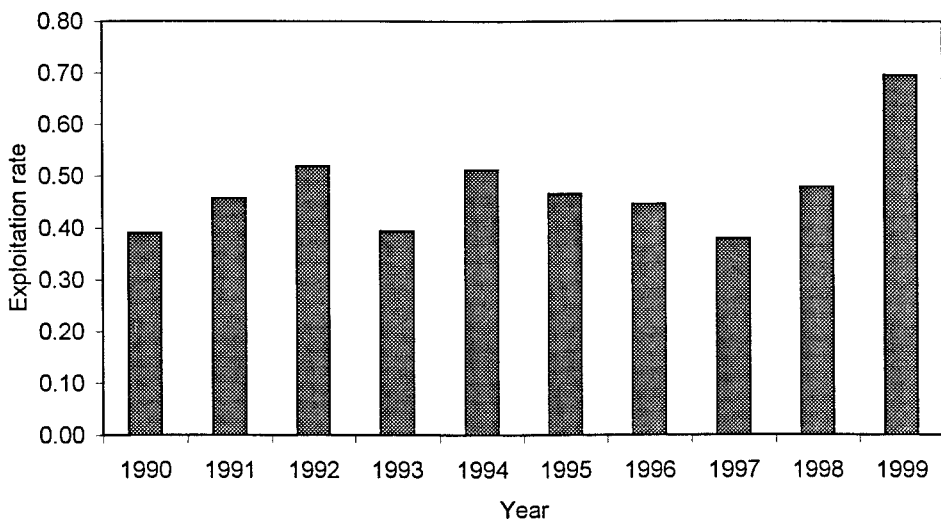

Figure 10. Commercial fishery exploitation rate of blue crab population in Chesapeake Bay estimated by comparing winter dredge survey absolute abundance estimates with commercial landings in numbers.
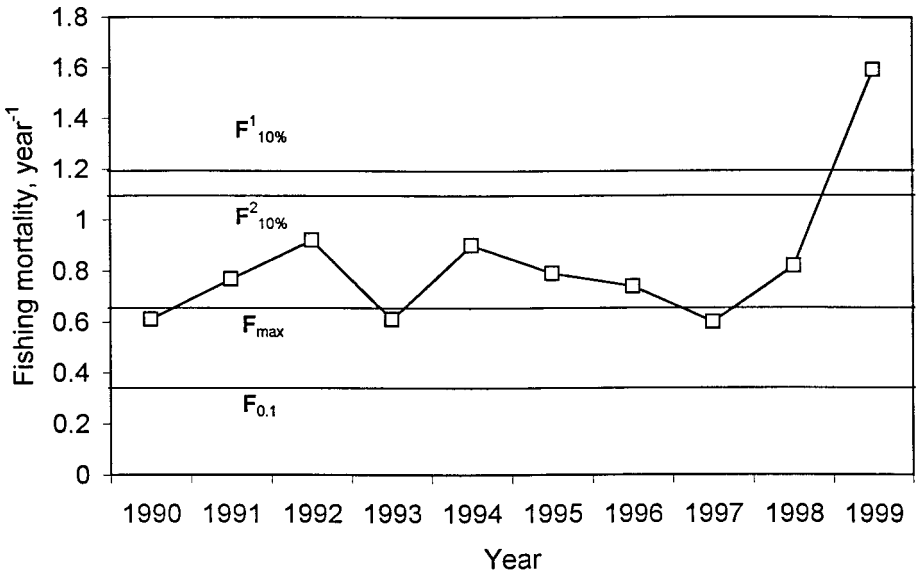
Figure 11.   Blue crab population fishing mortality rate in Chesapeake Bay in 1990–1999 in relation to biological reference points $F_{0.1}$, F_{med}, $F_{10\%}$. ($F^1_{10\%}$ is estimated by Rugolo et al. (1998), $F^2_{10\%}$ estimated by Miller and Houde (1998).

showed that fish populations can exhibit periodic auto-oscillations predetermined by life history parameters. At present we cannot identify a single environmental factor of cyclical nature that would affect blue crab recruitment. On the other hand, the idea of a density-dependent stock-recruitment relationship has been explored in several studies. Tang (1985) fitted Ricker's stock recruitment model to the Chesapeake Bay blue crab data, incorporating several abiotic factors into the model. Attempts to fit Ricker's stock-recruitment model and arguments in favor of the model were also reported for the blue crab in the Virgina's portion of the Chesapeake Bay (Lipcius and Van Engel, 1990) and Maryland's portion of the Chesapeake Bay (Uphoff, 1998). The fits of the model, however, were generally poor, probably because of low precision of the spawning stock and recruitment estimates. Although the winter dredge survey produces relatively precise estimates because of the baywide coverage and intensive sampling, we could not detect any significant relationship between spawning biomass and recruitment based on the current time series. Accumulating additional data in the future will be critical to verify the existence of the periodic component and determine its nature.

A trend in the amplitude of variation in abundance may serve as an indicator of negative changes in population status. The fivefold range of variation in the

Table 4.   Percent of dead crabs by size and month found in repeatedly sampled stations in 1996.

Month	Crab size in carapace width (CW)			
	CW ≤ 60	60 < CW ≤ 120	CW > 120 mm	Total
January	0.3	0	9.47	1.04
February	3.76	13.89	20.21	6.09
March	6.08	30.16	56.45	11.89

Table 5. Annual mortality of blue crabs by size category and mean January surface water temperature.

Year	Temperature °C	Crab size in carapace width (CW)			
		CW ≤ 60	60 < CW ≤ 120	CW > 120 mm	Total
1990	1.88	0.1	1.0	11.1	1.9
1991	4.16	0.3	1.3	4.5	1.4
1992	4.05	0	0	14.3	2.0
1993	4.32	0	1.6	3.4	1.7
1994	2.06	2.8	5.2	26.1	7.3
1995	4.61	0.7	1.1	4.9	1.7
1996	0.92	6.1	30.2	56.5	11.9
1997	2.69	0	3.8	4.96	0.74
1998	3.5	0	2.6	2.07	1.31
1999	3.12	0	2.1	7.1	1.8

abundance of age-0 blue crab observed in the winter dredge survey is consistent with the recruitment variation reported for trawl data collected during spring through fall from 1954 through 1989 in Virginia's (Lipcius and Van Engel, 1990) and Maryland's (1978 to 1996) portions of the bay (Uphoff, 1998; Rugolo et al., 1998). Both Maryland's and Virginia's trawl surveys covered periods of high and low catches and presumably a wide range of population abundance; therefore, they provided an estimate of the typical range of variation in blue crab recruitment. There has been no apparent increase in the range of recruitment variation of the blue crab during the 1990s as compared to the period from 1954 through 1996. Absence of a declining trend in recruitment abundance and stability of the range of its variation suggests that there were no signs of recruitment overfishing during the 1990s.

   At the same time, there are some warning trends in the dynamics of the adult component of the population. Survey results indicated a significant decline of age-1+ crabs from 1990 to 1999. This age group is considered to be the principal component of the exploitable stock. The decline is probably the result of an increase in natural mortality, fishery exploitation or both, because there was no apparent diminishing trend in recruitment. A more pronounced decline in male abundance (about threefold for three-year moving average) than for females (about twofold for three-year moving average) most likely indicates higher exploitation rates for males than females. Male blue crabs are traditionally more valued, and landings of male crabs usually exceed those for females. In some years the male/female ratio in Maryland harvest was 1.8 to 2.5 (Speir et al., 1994). Our observations corroborate the decline in abundance of male crabs in a longterm crab pot study at Calvert Cliffs reported by Abbe and Stagg (1996). The observed decline of the adult component of the stock and increase in fishing effort (Rugolo et al., 1998) supports concern about potential overfishing of the blue crab population.

   Spawning stock abundance (age-1+ females) also declined substantially; the average value for the second half of the 1990s was twice as low as in the first half of the 1990s. This decline may pose a significant risk of reduction in the reproductive potential of the population which could result in recruitment overfishing and subsequent collapse of the population. However, reduction in spawning stock abundance does not seem to have adversely affected recruitment during the 1990s. In fact, the two strongest year classes were produced by moderate spawning stocks in 1995 and 1996. Despite the decline in abundance, the spawning stock seemed to be able to produce sufficient recruits during the 1990s. This

suggests that the spawning stock biomass did not fall below the critical value associated with recruitment failure.

Traditionally, the absolute abundance and biomass of mature females is a major concern when evaluating the reproductive potential of a population. Recent studies by Hines et al. (2003) demonstrated that a decline in the abundance of male blue crabs, especially large males, may result in a deficit of sperm transferred to females during copulation. Significant reduction of sperm stored by females in spermatheca can cause a substantial reduction in egg production that would be followed by a decline in recruitment. In view of these findings, a significant decline of mature male abundance during the 1990s may cause a decline in egg production by the population. This seems to be a unique example of male deficiency as a limiting factor in reproductive success and sustainability of the exploited population.

Although fishing is considered to be one of the principal factors affecting blue crab abundance (Rugolo et al., 1998), some abiotic factors significantly affect blue crab population dynamics. For example, Pearson (1948) and Tagatz (1969) indicated that unusually hot summers or cold winters could be a threat to blue crabs. The possibility of significant over-wintering mortality was suggested for blue crabs in Delaware Bay (Kahn et al., 1998) and Chesapeake Bay (Uphoff, 1998). For the first time in the Chesapeake Bay area we were able to quantify the over-wintering mortality rate and demonstrate its cumulative nature. Estimates of over-wintering mortality during the 1990s indicated that the percentage of dead crabs was usually low (less than 2% in most years), but relatively high percentages of large dead crabs in 1994 (26%) and 1996 (56%) indicated substantial over-wintering mortality of blue crabs. High correlation of water temperature with the percentage of dead crabs provides strong evidence of the adverse effect of a cold winter on survival of crabs in general and large crabs in particular. Apparently in years with significant over-wintering mortality, an adjustment of the total abundance estimate for the loss due to over-wintering mortality could improve estimates of the exploitable stock size before the beginning of the new fishing season and forecasted landings.

Absolute population abundance is one of the most desirable pieces of information for fisheries management. The most accurate and precise estimates of mean number of crabs per area swept will provide only a relative abundance index unless they are corrected for gear efficiency (Zhang and Ault, 1995; Vølstad et al., 2000). We cannot overstate the importance of obtaining precise estimates of the catchability coefficient for estimating absolute abundance from a random survey. Not only a reliable catchability coefficient needed to estimate absolute abundance, but also to provide unbiased estimates of trends in population dynamics. For example, catchability-corrected absolute density of age $1+$ crabs (Fig. 7b) showed a steeper declining trend than uncorrected values (Fig. 5b). Further direct evidence of the importance of correcting for gear efficiency is the significantly higher correlation between landings and the absolute density ($r^2 = 0.68$, Fig. 12a) compared to the correlation between landings and relative density ($r^2 = 0.41$, Fig. 12b). High correlation between landings and catchability-corrected absolute density of crabs leads us to conclude that both characteristics are good measures of the stock size and this relationship can be used as a predictive model. Estimates of relative abundance can be used to describe trends only if the catchability coefficient of the sampling gear remains constant through time. Because the dredge used in our survey is relatively inefficient (catchability coefficient varied from 0.1 to 0.3), even small changes in the catchability coefficient will have a very large effect on the absolute abundance estimate. For example, a change of catchability
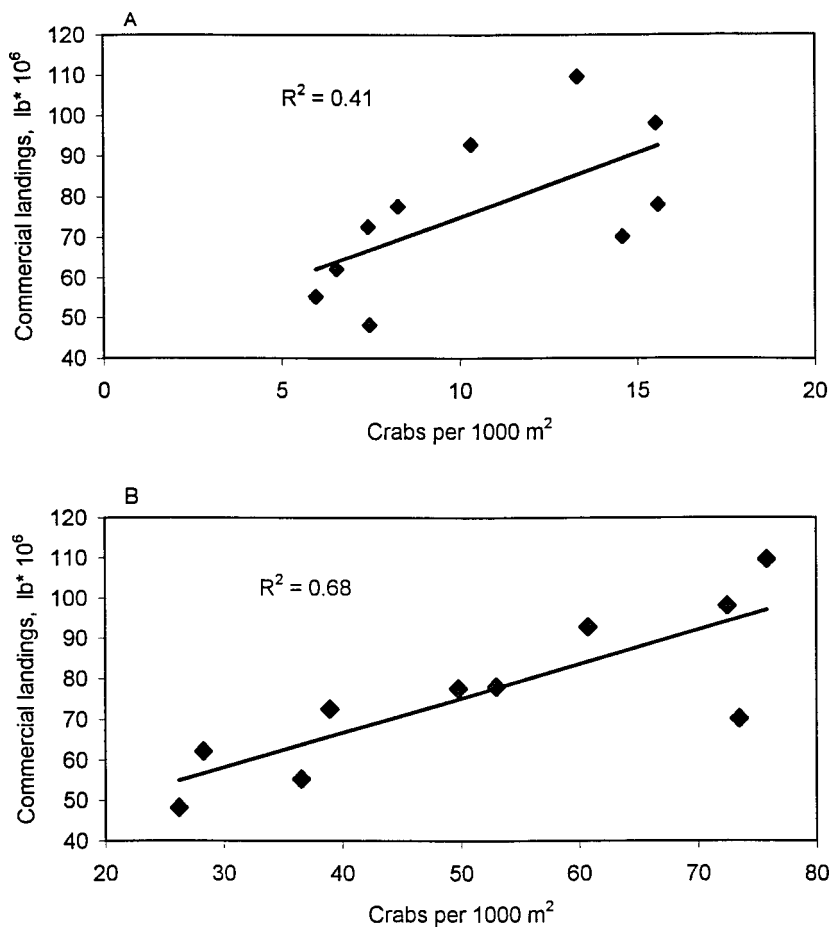
Figure 12.   Relationship between blue crab commercial harvest and baywide population density un-corrected for gear catchability (A) and corrected for catchability (B).

from 0.2 to 0.1 will double an absolute abundance estimate. When the catchability coefficient depends on a sampling year, vessel, or dredge liner, as in our study, it is strongly recommended to conduct depletion experiments annually to calibrate survey results. Although we cannot eliminate a ''year effect'' in catchability, we can reduce variation in catchability estimates by maintaining consistency in the survey procedure (i.e. use the same boat and dredge liner throughout the time series). When a sufficient number of depletion experiments are conducted each year at randomly selected sites that are representative of the sampled area by each vessel participating in the survey, unbiased and precise estimates of catchability can be obtained (Vølstad et al., 2000).

A series of estimates of absolute abundance combined with the landings data provided an opportunity to determine both exploitation and fishing mortality rates for the blue crab population. Exploitation and fishing mortality rates strongly depend on the age or size at which crabs enter the fishery. Until recently it was assumed that blue crabs reach minimum legal size (CW = 127 mm) by their third summer (Van Engel, 1958), or approximately at age two (Rothschild et al., 1992). In previous analyses of blue crab population dynamics three age classes were

assumed to be present in the overwintering population: age-0 or recruits of CW less than 60 mm, age 1 of CW between 60 and 120 mm, and age 2 (or 2+) with CW greater than 120 mm (Rothschild et al., 1992; Rugolo et al., 1998). It was assumed that only crabs that are age 1 and older at the time of the survey would contribute to the fishery during the following fishing season. Our comparison of absolute abundance of crabs age 1 and older with total catch showed that the number of crabs removed by the fishery was close to or exceeded the estimated absolute abundance of age-1+ crabs in the Chesapeake Bay (Fig. 9), which seems to be unreasonable. To explain this inconsistency, one should assume either that we underestimated the number of age-1+ crabs, or that small crabs grow faster than assumed, and that crabs classified as age-0 class during winter survey are recruited to the summer/fall fishery. We believe that it is unlikely that we substantially under-estimated the number of age-1+ crabs in the survey area because a stratified random survey produces unbiased estimates, and the high sampling intensity of our survey resulted in highly precise abundance estimates. A possible source of underestimation is the extension of the average catch-per-unit area to the shallow waters (<1.5 m) that were not sampled consistently. If the actual density of age-1+ crabs in waters shallower than 1.5 m was greater than the baywide average, we underestimated age-1+ abundance in shallow waters; however, this area is only about ten percent of the Chesapeake Bay. A limited number of stations sampled in shallow waters in 1991–1992 using a small modified dredge produced estimates of the average density of age-1+ crabs that were not significantly different than those for the area deeper than 1.5 m (Rothschild et al., 1992); consequently, if we underestimated age-1+ absolute abundance, the underestimation probably was small. Recreational landings of blue crab were not considered in this comparison because accurate estimates of historic recreational catches were not available. Stagg et al. (1992) indicated, however, that the recreational fishery could contribute substantially to the total removals. Recreational surveys conducted by National Marine Fisheries Service (NMFS) and Maryland Department of Natural Resources (MDNR) in 1983, 1988, and 1990 estimated yearly recreational catches in Maryland only as 18.7, 9.6, and 5.0 thousand tons respectively, which corresponds to 79%, 50% and 26% of commercial harvest (Stagg et al., 1992). If recreational landings were added to the total removals, estimates of the total catch would certainly exceed the exploitable population of blue crab. More reasonable estimates of exploitation rate were obtained when we compared landings with total abundance composed of both age-0 and age-1+ crabs. This suggests that crabs identified as age-0 in winter can reach minimum legal size of 127 mm CW during the following summer and recruit to the fishery within the same season. Past and recent studies of blue crab growth in both the natural environment and the laboratory provide growing evidence that blue crabs can grow to harvestable size by their second summer. Van Engel (1958, 1987) noted that crabs hatched during late May and June (prior to the peak of spawning season) become legal adults (127 mm CW) or larger by August of the following year in Chesapeake Bay. Eldridge and Waltz (1977) showed that on southern sounds of South Carolina males recruited to the fishery in September or October. Archambault et al. (1990) observed a similar growth rate at Charleston Harbor. Rothschild and Sharov (1997) simulated blue crab growth, using information on growth per molt and intermolt period reported by Churchill (1919), Gray and Newcombe (1938), Newcombe et al. (1949), Tagatz (1968), and Leffler (1972), Fitz and Weighert (1991), Rothschild et al. (1992) and found that crabs of 30 to 60 mm CW in winter can reach minimal legal size by August of the same year. A recent study of blue crab growth in experimental ponds also indicated that

small crabs that are classified as age-0 in winter can grow to minimum legal size and more by the end of the following summer (Se-Jong et al., 1999; D. Secor, Chesapeake Biological Laboratory, unpubl. data). In addition, our analysis indicated that the correlation between landings and the total crab abundance ($r^2 = 0.68$) during winter was better than the correlation between landings and age-1+ abundance ($r^2 = 0.58$). This lends additional support to the suggestion that age-0 crabs recruit to the fishery the following summer. Given the structure of the blue crab fishery (i.e., large number of participants and wide coverage of the Bay area by fishing gears), we expect a strong relationship between crab abundance and catch. This suggests that winter estimates of blue crab absolute abundance can be used successfully to forecast summer catch, provided that fishing effort remains stable or that changes in effort can be predicted.

When the total abundance of the blue crab population was used to calculate the exploitation rate, we found that the commercial fishery removed about half of the population with exploitation rates fluctuating between 45% and 55% between 1990 and 1998 and a corresponding range of fishing mortality of 0.6–0.9 year^{-1}. Our estimates of exploitation rates for 1990 through 1998 were similar to those reported by Rugolo et al. (1998) for blue crab in Chesapeake Bay for 1960 through 1995. Rugolo et al. (1998) used Hoenig's (1987) method, which estimates total mortality based on mean carapace width of crabs in the population. It appears that exploitation rates for the blue crab population from 1990 through 1998 were relatively stable and similar to the rates experienced by the population during the past 30 years, when the stock proved to be sustainable. Estimated exploitation rates probably are robust because two independent studies employing different techniques reached similar conclusions. The exploitation rate increased substantially to 70% in 1999 with a very high corresponding fishing mortality of 1.6 year^{-1}. To determine whether these increases will lead to overfishing, current fishing mortality rates must be compared with a reference point that defines the limit beyond which overfishing occurs. Several reference points have been considered for use in managing blue crab fishery, such as the fishing mortality level that produces the maximum yield per recruit (F_{max}), the fishing mortality that corresponds to the point on the yield-per-recruit curve that has a slope of 10% of the slope of the curve at the point of origin ($F_{0.1}$), and the fishing mortality rate that reduces the spawning stock biomass to a certain percent of the virgin stock (e.g., $F_{10\%}$; Rugolo et al., 1998; Miller and Houde, 1998). Rugolo et al. (1998) estimated $F_{0.1} = 0.36$ and $F_{max} = 0.64$, whereas $F_{10\%}$ was estimated as 1.21 year^{-1}. Miller and Houde (1998) found $F_{10\%}$ to range from 0.88 to 1.22 with a mean of 1.08 year^{-1}, depending on the maturity schedule. The Bi-state Blue Crab Advisory Committee recently selected the $F_{10\%}$ value as a threshold fishing mortality rate for the Chesapeake Bay blue crab stock (Anonymous, 2001). The fishing mortality rate estimated from the winter dredge survey data exceeded F_{max} in most years from 1990 through 1999, indicating growth overfishing (Fig. 11). Rugolo et al. (1998) determined that fishing mortality rates have varied principally between 0.8 and 1.0 year^{-1} since1956. These rates of fishing mortality exceeded F_{max}, but were below $F_{10\%}$. The history of the fishery, therefore, has demonstrated that the blue crab population can sustain long-term exploitation with a fishing mortality rate in the range of 0.8–1.0 year^{-1}. Fishing mortality exceeded the $F_{10\%}$ estimates of both Rugolo et al. (1998) and Miller and Houde (1998) in 1999, indicating that population overfishing occurred in that year. If our estimates of fishing mortality are accurate, and if fishing pressure remains high, the blue crab population's ability to replace itself may be undermined. This is especially critical, given the compensatory nature of the blue crab fishery, when the exploitation rate and fishing

mortality are inversely related to the population abundance (Lipcius and Montane, 2001). Rugolo et al. (1998) noted that the blue crab fishery is severely overcapitalized in terms of fishing effort; therefore, there is growing risk of collapse if the fishing effort remains very high, while the population size is declining. For conservative management, the fishing mortality rate has to be maintained below the overfishing threshold. A long-term goal should be set to reduce the effort to the level corresponding to a target fishing mortality (e.g., F_{max}) that is sufficiently lower than the overfishing threshold. Continuing the winter dredge survey is critically important because it will assure effective monitoring of trends in population abundance and size/sex structure and allow managers act appropriately in a timely matter to maintain the blue crab population at a sustainable level.

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