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TEMPORAL AND SPATIAL CHANGES IN FECUNDITY OF EASTERN OYSTERS, *CRASSOSTREA VIRGINICA* (GMELIN, 1791) IN THE JAMES RIVER, VIRGINIA

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ABSTRACT Adult *Crassostrea virginica* (Gmelin) were examined during the reproductive season of 1986 to determine temporal and spatial variation in fecundity among individual female oysters from four reefs in the James River, Virginia. Sex ratio and oyster abundance were also determined to facilitate estimation of total reproductive output of oyster assemblages. Fecundity was highly variable, both within and among locations. Variation was attributed to differences in oyster size, asynchrony and variation in time since prior spawning, prevalence of parasites (especially *Haplosporidium nelsoni* (MSX) and *Perkinsus marinus*) and differing salinity regimes.

KEY WORDS: oysters, *Crassostrea*, fecundity, reproduction, James River

INTRODUCTION

The James River, third largest and southernmost tributary of the Chesapeake Bay, has traditionally been a seed oyster harvesting area (Haven & Fritz 1985). Between 1930 and 1980, an estimated 75% or more of the seed oysters planted in Virginia originated from the James River (Haven et al. 1981). Approximately 5,658 hectares of public oyster reefs extend from near the James River Bridge upriver to Deepwater Shoal Light (Fig. 1) (Andrews 1951, 1954, 1983, Haven and Whitcomb 1983).

Despite its importance, little is known about the broodstock that produces the larvae that recruit into the James River seed area. Andrews (1983) states "The importance of large broodstock populations was shown after 1960, when setting rates declined to one-tenth the 1950's level; this followed cessation of private oyster planting in the lower river." This statement suggests the importance of broodstock oysters in downstream areas of Hampton Roads from which larvae were thought to be transported upstream to the seed area by gravitational circulation. Results of dye studies in the James River Hydraulic Scale Model emphasize the importance of broodstock oysters in the low salinity seed area upstream of the James River bridge (see Fig. 1), suggesting that larvae originating here would provide maximum coverage of reefs in the seed area (Ruzecki and Hargis 1989). The downstream populations have essentially been eliminated by losses to two parasites, *Haplosporidium nelsoni* and *Perkinsus marinus*, leaving upstream oyster reefs as the only remaining broodstock source.

The contribution of oysters in the seed area to local recruitment is dependent upon their fecundity; however, quantitative information describing fecundity in James River oysters has not been examined. This study examined temporal and spatial variation in oyster fecundity within and among four oyster reefs in the James River seed area during the 1986 reproductive season. Several biotic and abiotic factors potentially affecting fecundity, including temperature, salinity, dissolved oxygen and oyster size, were examined. Estimates of the number of eggs spawned by the four oyster assemblages in 1986 were calculated from average female fecundity, sex ratio, and oyster abundances on each reef.

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MATERIALS AND METHODS

Oysters were collected from four reefs, Horsehead, Wreck Shoal, Thomas Rock, and Dog Shoal in the James River seed area (Fig. 1). The spawning season for oysters in the James usually extends from June through October (Haven and Fritz 1985). Ten collections of live oysters were made at approximate 2 week intervals from June 2 through October 16, 1986 using a 60 cm oyster dredge with teeth of 7.5 cm length. Tows were not replicated. Collections were also made by divers on June 2, August 25, and October 16. On those days, four quantitative samples, used to estimate size frequency distribution and areal density at each location, were obtained by haphazardly placing a 0.25 m^2 quadrat on the bottom and collecting all live oysters within the quadrat. These oysters were frozen for subsequent analysis.

Samples of bottom water were obtained from all stations on every collection date using a modified Van Dorn bottle. Temperature was measured in the field to the nearest 0.5°C using a stem thermometer. Water was placed in glass bottles and returned to the laboratory for salinity and dissolved oxygen analyses. Salinity was determined using a Beckman Induction Salinometer Model RS-10. Dissolved oxygen was determined using the azide modification of the Winkler titration method (APHA 1980). Percent oxygen saturation was calculated for every water sample.

Quantitative quadrat samples were treated as follows. All oysters with the exclusion of young-of-the-year, which were considered to be the only reproductively inactive size class, were counted and measured. Natural log transformed mean oyster abundance was calculated and abundance was compared among stations and over time.

Sex ratio (male:female) was calculated for oysters from the 4 reefs using 40 randomly chosen individuals from every dredge collection. Shell height (defined here as the maximum distance between the umbo and the ventral shell margin) was measured to the nearest millimeter using dial calipers. Gonadal material was collected with a Pasteur pipette and examined microscopically. Sex was determined by the presence of eggs or sperm. Calculated ratios were compared to the expected 1:1 ratio using chi-square analysis for both individual collections and pooled data for the entire study period. Gonadal smears were also examined for the presence of cercaria of the digenean trematode *Bucephalus cuculus*

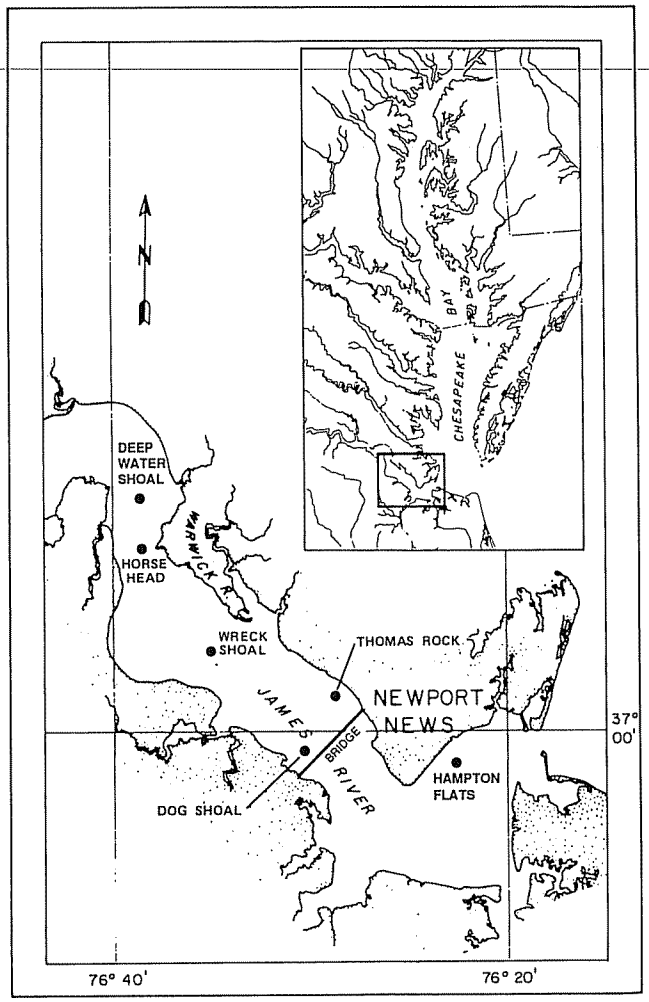

Figure 1. Locations of sample collection sites in the James River, Virginia. The seed bed area is generally considered to be upstream of the James River Bridge and below Deepwater Shoal. Significant oyster beds were located on Hampton Flats prior to disease losses after 1960.

(McCrady), which occurs in the gonads and digestive gland (Tennent 1906, Menzel and Hopkins 1955). No examinations were made for prevalence and intensity of either *H. nelsoni* or *P. marinus*.

Fecundity values were obtained as direct estimates of the number of eggs in the gonad, not the number of eggs released at spawning. The two values will only be equal in instances where the gonad is completely evacuated on spawning. The present method differs from previously reported approaches using histological or direct spawning methods. The practical limitation of processing the number of animals collected in this study by either of the latter methods precluded their use. Ten females were randomly selected from each collection for fecundity determination. Individual oyster meats were placed in a commercial kitchen blender containing 150 ml of filtered York River water adjusted to 20‰ with distilled water, and blended on medium setting for 30 seconds. The resultant homogenate was sequentially filtered through 90 um and 53 um mesh Nitex nylon sieves; the liquid containing the eggs was retained in a 1 l graduated cylinder. Blender, sieves and funnel were rinsed with 750 ml of estuarine water; additional water was added to bring the volume in the cylinder to 1 l. Total number of eggs was estimated following mixing of the cylinder contents, removing a 10 to 1000 ul aliquot (depending upon egg concentration) to a Sedgwick-Rafter Cell, counting on a compound microscope, and correcting for proportional volume of aliquot and cylinder contents. The mean of three aliquots counted for each oyster was used as the estimated fecundity.

Boundaries of Dog Shoal, Thomas Rock, and Horsehead were estimated and area was obtained by digitizing NOAA Chart 12248. Boundaries of Wreck Shoal were unclear, so area was estimated as that reported by Moore (1910). The product of reef area, number of females per m^2, and mean fecundity was used to estimate spawning potential of the four broodstock assemblages.

Statistical analyses were performed using SPSS-X (Release 2.1) on a PRIME 9955 computer. Unless otherwise indicated, data were analyzed using one-way or multivariate Analysis of Variance (ANOVA) and subsequent Student-Neuman-Keuls (SNK) multiple range tests when appropriate. When nonparametric statistics were necessary, the Kruskal-Wallis (KW) nonparametric one-way ANOVA was employed; multiple comparisons were made using Dunn's Approximation (Dunn 1964). In all statistical tests, significance was tested at an alpha level of 0.05.

RESULTS

Bottom water temperature and salinity values recorded at the study sites are depicted in Figure 2. Horsehead had the largest range of temperature and salinity, 19–31°C and 6.6–18.4‰, respectively. Thomas Rock experienced the smallest temperature and salinity ranges, 22–29°C and 14.9–20.8‰. Temperature varied significantly over the study period (ANOVA: $F = 63.98$, $df = 9$, $P < 0.00005$), but there was no temperature difference among the stations (ANOVA: $F = 1.36$, $df = 3$, $P = 0.277$). Salinity generally increased over the course of the summer (ANOVA: $F = 13.68$, $df = 9$, $P < 0.00005$) at all sites. Variation in salinity among stations was significant (ANOVA: $F = 65.51$, $df = 3$, $P < 0.00005$) with that at Horsehead significantly lower than at the other locations (SNK: $P < 0.05$). Oxygen saturation did not vary significantly among stations (ANOVA: $F = 2.96$, $df = 3$, $P = 0.052$) and was never below 75% saturation.

Oyster distribution was irregular on all reefs, ranging from 0–107 oysters per 0.25 m^2. Oysters were more abundant at Horse-

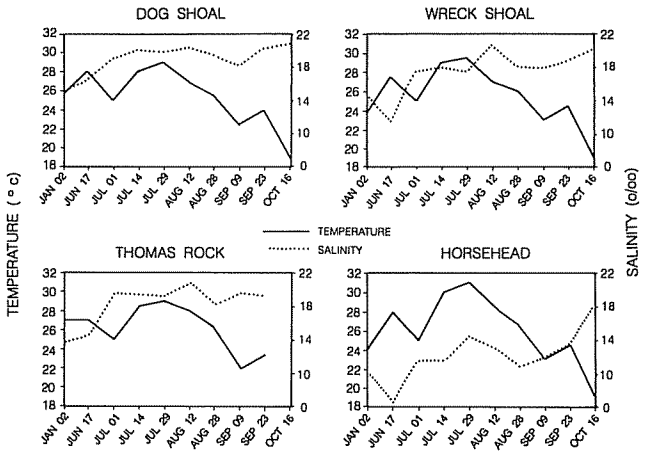

Figure 2. Temperature and salinity records for sample locations during the summer of 1986.

head than at other stations (SNK: $P < 0.05$). Thomas Rock and Wreck Shoal had significantly more oysters than Dog Shoal (SNK: $P < 0.05$), but abundance was not different between the two (SNK: $P > 0.05$). Mean abundance of oysters remained fairly constant at Dog Shoal and Wreck Shoal through the study (Table 1). Abundance decreased at Thomas Rock and Horsehead; the decline at Thomas Rock from June 2 to October 16 was significant (SNK: $P < 0.05$).

Individual oysters varied in height from 22 to 122 mm, with the majority between 30 and 105 mm. Mean size of Horsehead oysters was significantly smaller than that of oysters from all other locations (Dunn's Approx: $P < 0.05$).

In most collections male oysters were more abundant than females, the male to female ratio ranging from approximately 1 to 4 (Table 2). Since sex ratio was not found to differ significantly over time (ANOVA: $F = 0.76$, $df = 1$, $P = 0.607$), a seasonal mean sex ratio, pooling data from all dates was calculated for every station. Seasonal mean sex ratio of oysters was significantly greater than the expected 1.0 for each reef.

Fecundity differed significantly among the stations (KW: $X^2 = 11.97$, $n = 330$, $P = 0.0075$). Oysters from Thomas Rock were the most fecund, followed by those from Wreck Shoal, Dog Shoal, and finally Horsehead (Table 3). The most fecund Thomas Rock individual contained approximately 45.95×10^6 eggs, while the most fecund Horsehead individual contained approximately 22.03×10^6 eggs. Unequal sample size and large variation among individual females limited statistical comparisons; however, oysters from Thomas Rock were more fecund than oysters from Dog Shoal (Dunn's Approx: $P < 0.05$). A regression between fecundity and oyster shell height was not attempted because values of the former were not normally distributed at each value of the latter. The prerequisite of homogeneity of variance was not fulfilled.

Synchronous mass spawning was marked by a statistically significant decrease in mean fecundity between two dates with small variation about the mean values. Large variation about the means suggests that spawning was not synchronous at any station except Horsehead (Table 3). Asynchronous spawning events may be characterized by a reduction in mean fecundity but an associated high variability about the mean. Unlike the synchronous events, the high variability generally precludes identification of asynchronous spawnings by statistically significant decreases in mean values. Four asynchronous periods of spawning are apparent at Dog Shoal: these being represented by high mean fecundity and large variation about the mean on June 17, July 14, August 12, and September 9, with subsequent samples characterized by low mean fecundity. Characterizing the decrease in mean egg number from June 17 to July 1 as a spawning was potentially compromised by the lack of demonstrably ripe gametes at this site (unpublished observations made during sex ratio studies); however, gametes may have ripened subsequent to the June 17 sampling and been released before the July 1 sampling.

Large scale spawning at Thomas Rock appears to have begun between July 14 and July 29. Mean fecundity on July 14 differed significantly from other dates (Dunn's Approx: $P < 0.05$). Large variation in fecundity within the June 17 and July 1 samples can probably be attributed to asynchronous gonad maturation of the oysters. As in the case of Dog Shoal, Thomas Rock oysters did not contain fully mature eggs in June. There was no indication of a second spawning event at Thomas Rock.

Wreck Shoal and Horsehead oysters began producing mature eggs before oysters at Thomas Rock and Dog Shoal. Although there was no significant date effect on fecundity at Wreck Shoal, the increase in mean fecundity and variation around the mean indicated that spawning began between July 1 and July 29. Further comment is limited by the omission of a July 14 sample, damaged in processing. Fecundity data suggest a second spawning event in Wreck Shoal oysters at the beginning of September; however, the increase is not statistically significant (Dunn's Approx: $P > 0.05$).

Spawning patterns at Horsehead were different than those seen at Dog Shoal and Thomas Rock. There was a mass spawning at Horsehead at the beginning of July. A second, significant (Dunn's Approx: $P < 0.05$) increase in fecundity in late July was followed by spawning which persisted into September. Horsehead oysters ceased spawning activity before those at other stations; no oysters contained eggs in the October collection.

The mean fecundity per female was calculated for each location from the mean values obtained in biweekly sampling to avoid weighting against limited samples of less than 10 individuals (see Table 3). Estimated spawning potential, as calculated from mean fecundity, density of female oysters and area of oyster reef (see Table 4) indicate there were more eggs produced at Thomas Rock than at the other three sites; however, large variations in individual fecundity measurements around mean values for any chosen date (see Table 3) suggest a large range estimate for spawning potential at all sites. The estimate of spawning potential for Dog Shoal was an order of magnitude lower than at Wreck Shoal and Horsehead.

Bucephalus cuculus cercaria were present in oysters from all collection locations; however, no difference in prevalence was evident between locations. Oysters of both sexes, as well as those of indeterminate sex, were observed to contain cercaria. No evidence of hermaphroditism or "sexual aberration" as described for *Bucephalus*-infected oysters by Tripp (1973), was observed. Percentage of oysters parasitized could not be reliably estimated since examination was focussed on presence of cercaria in a single gonad smear, and certain cercaria may reside in the digestive gland and/or gonad of oysters.

TABLE 1.

Oyster abundance at four stations in the James River, Virginia.

	Dog Shoal		Thomas Rock		Wreck Shoal		Horsehead	
Date	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.
6/2	10.3	11.0	45.5	38.0	18.0	7.8	71.7	40.7
8/25	6.3	5.0	21.5	5.6	20.8	6.1	65.0	17.4
10/16	9.8	7.4	9.8	7.4	16.3	9.6	44.5	22.2

Abundance is mean ± standard deviation (s.d.) of four quadrat collections of 0.25 m^2 each.

DISCUSSION

Fecundity of female oysters from four major reefs in the James River was highly variable, both within and among locations, during the 1986 spawning season. The large variation may be influenced by several biotic and abiotic factors. Major abiotic factors potentially influencing fecundity include water temperature (which affects gonad maturation rate), and salinity regime. Biotic influences include time since last spawning, food supply and resultant nutritional status of the individuals, size of females, and prevalence of parasites.

TABLE 2.

Sex ratio of oysters collected from four stations in the James River, Virginia between June 17 and September 19, 1986.

	Dog Shoal		Thomas Rock		Wreck Shoal		Horsehead	
Date	Ratio	P	Ratio	P	Ratio	P	Ratio	P
6/17	3.0	0.002*	3.0	0.002*	1.9	0.058	0.7	0.206
7/1	4.0	0.000*	1.7	0.114	3.4	0.001*	0.9	0.752
7/14	2.1	0.027*	1.7	0.114	2.1	0.027*	2.1	0.027*
7/29	1.7	0.114	1.2	0.527	0.9	0.752	1.2	0.631
8/12	3.4	0.001*	1.2	0.527	1.5	0.206	3.0	0.002*
8/26	1.7	0.144	2.1	0.027*	2.5	0.009*	1.6	0.170
9/9	1.3	0.637	3.4	0.011*	2.0	0.046*	0.8	0.655
All	2.4	<0.001*	1.8	<0.001*	1.9	<0.001*	1.3	<0.05*

* Denotes a ratio significantly different from 1.0 (Chi-square analysis).

Variation in fecundity among females on the same reef occurred in part because of asynchrony in gonadal development and spawning activity (see also Nelson 1928, Loosanoff and Davis 1952, Kennedy and Krantz 1983). An oyster which spawned immediately prior to collection presumably contained fewer eggs than a similar oyster in which spawning was imminent. Methods used in this study do not distinguish between oysters which recently spawned and those which had not but were truly less fecund. Fecundity estimations were also influenced by the time of sampling relative to spawning events. Seasonal mean values which include a preponderance of immediate post-spawning animals will not reflect the high fecundities of immediate pre-spawning animals. Large oysters usually produce more eggs than do small oysters (Davis and Chanley 1956). Consequently, it would appear reasonable to attribute some of the recorded variation in fecundity within and among reefs to body size. The observed lack of normal distribution of fecundity values at each shell height in the present study was probably related to asynchrony in spawning activity at each location, and limited the use of regression analysis to examine size versus fecundity relationships.

Egg maturation and peak spawning occurred earlier at the upriver stations Horsehead and Wreck Shoal, than it did downriver at Thomas Rock and Dog Shoal. Even though bottom water temperature did not vary significantly among sites during the study period, earlier differences in temperature may account for the timing of spawning in that gametogenic development is time and temperature dependent (Price and Maurer 1970). Whitcomb (1986) recorded a bottom water temperature of 19.5°C on May 1 at Horsehead. On May 6, temperature at Wreck Shoal was 19.0°C, while downriver at two shoals close to Thomas Rock and Dog Shoal, temperatures were 17.1°C and 17.0°C, respectively. Egg maturation and subsequent spawning were probably delayed in 1986 at the downriver locations by the extended period of cooler temperatures (see Loosanoff and Davis 1952). The consistently high observed values for percentage dissolved oxygen suggest that this was not a source of stress to oysters examined in this study.

Egg production is dependent upon the nutritional health of the oyster since accumulation of egg reserves takes place at the expense of stored glycogen (Gunter 1941, Medcof and Needler 1941, Engle 1950, Galtsoff 1964, Gabbott 1975, Mann 1979). Horsehead oysters are notably slower growing than from higher salinity locations in the James River (unpublished personal observations) and their occurrence in dense assemblages on the reef suggests possible intraspecific competition and food limitation, with subsequent reduction in physiological status and energy that may have influenced the amount of energy available for reproduction. Quantitative data to support this hypothesis are, however, lacking.

TABLE 3.

Fecundity of oysters (in millions of eggs) collected from four stations in the James River, Virginia between June 2 and October 16, 1986.

	Dog Shoal			Thomas Rock			Wreck Shoal			Horsehead		
Date	Mean	SD	N	Mean	SD	N	Mean	SD	N	Mean	SD	N
6/02	8.58	—	1	3.29	3.39	9	2.70	—	1	1.34	1.48	10
6/17	8.34	6.85	10	14.52	9.30	10	5.04	3.22	10	5.47	2.08	10
7/01	2.78	3.69	10	15.55	13.42	10	13.86	13.18	10	**11.86***	6.16	10
7/14	8.81	11.85	6	**26.93***	15.41	10	sample damaged			3.15	3.34	10
7/29	1.90	2.06	10	14.11	12.19	10	6.13	7.22	10	**6.09***	3.30	10
8/12	6.06	4.01	10	4.22	4.97	10	5.62	3.28	10	4.66	3.27	10
8/26	1.11	1.38	10	3.52	2.47	10	2.01	1.55	10	2.34	1.51	10
9/09	8.48	14.23	9	3.75	5.66	10	4.61	5.38	10	1.59	1.75	10
9/23	1.96	3.30	10	2.50	3.15	10	1.88	3.43	7	0.39	0.80	7
10/16	1.09	0.53	4	0.91	—	1	0.68	0.71	5	—	—	—

Values given are mean, standard deviation (SD), and number of individual oysters (N).

* Denotes a significant difference ($P < 0.05$, Dunn's Approximation) from preceding and following collections at the same station.

TABLE 4.

Oyster spawning potential at four stations in the James River, Virginia.

	Dog Shoal	Thomas Rock	Wreck Shoal	Horsehead
Reef area (m^2)	449,912	1,559,700	2,047,709	603,062
Female oysters m^{-2}	10.4	33.8	27.7	105.5
Mean fecundity	4.91×10^6	8.93×10^6	4.73×10^6	4.10×10^6
Spawning potential	2.30×10^{13}	4.71×10^{14}	2.68×10^{14}	2.61×10^{14}

Reef area is estimated from NOAA chart 12248 or data of Moore (1910), see text.
Abundance (Table 1) and mean sex ratio (Table 2) data for all dates are used to estimate mean number of female oysters m^{-2}.
Mean fecundity is estimated from biweekly fecundity data (Table 3) as mean of biweekly mean values to avoid weighting against samples containing <10 individuals.
Spawning potential = (reef area × female oysters m^{-2} × mean fecundity).

Parasitism probably contributed to the observed variation in fecundity. Barber et al. (1988) demonstrated the deleterious effects of increasing infection intensity of *H. nelsoni* on *C. virginica:* a progression from uninfected to epithelial to systemic infection was accompanied by 31 and 81% decreases in fecundity. Record high salinities, caused by consecutive droughts in 1985 and 1986, allowed oyster diseases to invade areas of the James River where they normally would not occur (Burreson 1986). Oysters from Wreck Shoal, Dog Shoal, and Horsehead were infected by *H. nelsoni* with Wreck Shoal showing the highest infection rate in August, 1986 (Burreson, personal communication). Although Thomas Rock oysters were not heavily infected by *H. nelsoni,* at least 20% and perhaps as many as 96% were infected by the protozoan parasite *P. marinus* (Burreson 1986). Finally, one to several pea crabs (*Pinnotheres ostreum*) were found in a large percentage of oysters from all sites, potentially reducing energy available for egg production (see Haven 1959).

Male oysters generally were present in greater numbers than females at all sites. This contrasts with findings of Morales-Alamo and Mann (1989) who found a sex ratio of approximately 1.0 for Wreck Shoal oysters of greater than 60 mm height. Two scenarios may be invoked to explain these differences. The observations of Burkenroad (1931) and Needler (1932) suggest that a greater proportion of small (<60 mm) oysters are males. Therefore, the inclusion of small oysters in the present study may account for the observed preponderance of males. Alternatively, Kennedy (1983) suggests that an increased proportion of males in an oyster population is indicative of environmental stress such as the occurrence of pea crabs (from Awati and Rai 1931, in Coe 1938). If stress related to infection by *H. nelsoni* and *P. marinus* is similarly reflected in sex ratio data then the current observations may be indicative of increased infections since the collections of Morales-Alamo and Mann (1989). Unfortunately, estimates of the prevalence and intensity of these parasites were not made in either Morales-Alamo and Mann (1989) or the present study. Although the contributions of the parasite *Bucephalus cuculus* to stress on the host organism also remains unquantified, all other cumulative effects of parasitism, acting either directly on individual fecundity or indirectly sex ratio change, are consistent in reducing population egg production.

Spawning events were more predominant in periods of increasing temperature and stable salinity; however, exceptions were observed. Of the four projected spawnings at Dog Shoal two, in late June and mid August, coincided with decreasing temperature whereas the July and September events coincided with increasing temperature. All occurred in periods of increasing or relatively stable salinity conditions. The July spawnings at Thomas Rock, Wreck Shoal and Horsehead occurred during or after a period of considerable rise in temperature accompanied by stable salinity. The projected minor spawning at Wreck Shoal coincided with a brief temperature and salinity increase after a consistent decrease in both. The late July spawning at Horsehead occurred directly after summer maxima for both temperature and salinity, as both began a period of consistent decline. With the exception of Horsehead, all spawnings occurred at or above 17‰ salinity. Only the September spawnings at Dog Shoal and Wreck Shoal occurred at less than 25°C.

Although no data are available to allow comparison of the relative contributions of oysters in the Hampton Roads and seed bed regions of the James River to the spawning potential and maintenance of the James River oyster stocks prior to losses to *H. nelsoni* (see Haven and Fritz 1985), the present data allow some statements concerning relative contributions from spatially distinct reef populations within the seed bed area in 1986. Warmer temperatures in the early summer in the Horsehead and Wreck Shoal area suggest that spawning commenced earlier in these upriver locations but the contribution of the higher salinity population at Thomas Rock was comparable over the spawning season. This relationship underscores the vulnerability of the James River population to both *H. nelsoni* and *P. marinus* in that the distribution of both disease organisms is strongly determined by salinity. Continuing losses of oysters in the higher salinity sections of the seed bed area (Barber, unpublished data), where salinities may be more conducive to larval development and metamorphosis, may have disproportionately large impacts on spawning potential and subsequent recruitment events, with detrimental effects on both the ecology of the James and the commercial fishery supported by the oyster resource.

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