Limnol. Oceanogr., 52(3), 2007, 959–965

The influence of climate variation on eastern oyster (*Crassostrea virginica*) juvenile abundance in Chesapeake Bay

David G. Kimmel[1] *and Roger I. E. Newell*
Horn Point Laboratory, University of Maryland Center for Environmental Science, PO Box 775, Cambridge, Maryland 21613

Abstract

There has been a significant downward trend in the annual abundance (= spatfall) of 0-age eastern oysters (*Crassostrea virginica*) measured in the autumn since 1940 in the Maryland portion of Chesapeake Bay. We developed a multiple linear regression model to predict spatfall from environmental conditions and the magnitude of the previous year's oyster harvest. The model explained 57% of the variance in spatfall from 1940 through 1976. We used the model to predict spatfall using data from 1977 to 2004 and found poor fit for the years after 1985. We suggest that this predictive relation was lost because an epizootic of the protistan parasite *Haplosporidium nelsoni* in 1985 and 1986 killed large numbers of oysters in the Maryland portion of Chesapeake Bay. This event disrupted the tight relation between oyster harvest and spatfall. Using the same variables as in our initial model, we constructed a second multiple linear regression model for all data after 1977. This new model explained 53% of the variance in spatfall, although there was a reduced relation between oyster harvest in the previous year and a strong relation between July salinity and spatfall. Hindcasting spatfall from 1940 to 1976, this model explained 49% of the variance. We suggest that the overall downward trend in oyster spatfall since records began in 1940 is driven by the loss of adult oysters in the spawning stock. Superimposed on this trend is large interannual variability in oyster spatfall that is strongly related to climate-driven changes in environmental conditions during the summer period of larval development and settlement.

The abundance of the eastern oyster, *Crassostrea virginica*, in Maryland waters of Chesapeake Bay has been declining exponentially since the start of major commercial exploitation in the late 19th century (Kennedy and Breisch 1981; Rothschild et al. 1994; Jordan and Coakley 2004). Since the mid-1950s, high mortalities of adult oysters in the high-salinity regions of Chesapeake Bay resulting from epizootics of two protistan parasites, *Haplosporidium nelsoni* and *Perkinsus marinus*, have contributed to the harvest-related decline in the oyster population (Ford and Tripp 1996). Recent studies (Jordan et al. 2002; Jordan and Coakley 2004) indicate that Chesapeake Bay eastern oyster populations are ~1% of the pre-exploitation levels estimated by Newell (1988). Eastern oyster spatfall, defined as the number of 0-age oysters recorded in Maryland's annual autumn survey (Krantz 1996; Tarnowski 2005), also shows a significant downward trend (Fig. 1; Kendall's trend test: $\tau = -0.29$, slope $= -0.85$, $p < 0.001$) on natural oyster reefs since monitoring was initiated in 1940. In addition, in 22 of the 40 yr since 1965, spatfall has been extremely low (<20), whereas in the 26 yr from 1940 there was only one year when such low spatfall was recorded. One plausible explanation for this overall decline in spatfall index since 1940 is that the loss of adult oysters has reduced the magnitude of larval production. Despite the downward trend, the spatfall index sporadically attained high levels, such as occurred in 1981, 1991, and 1997 (Fig. 1).

The eastern oyster has a complex reproductive cycle that begins with the storage of glycogen energy reserves during late summer and autumn (Thompson et al. 1996). This glycogen is then used to support gametogenesis during the next winter and early spring when food intake is at a minimum. The gametes start to ripen in late spring, and starting in June and proceeding through August they are spawned into the water column (Kennedy and Krantz 1982, Kennedy 1996), where fertilization occurs. The planktotrophic larvae take approximately 3 weeks to grow into eyed pediveliger larvae that are competent to metamorphose, at which time they settle on hard substrate, primarily clean oyster shell (= cultch) (Kennedy 1996). Consequently, the oyster's overall reproductive success is vulnerable to macroscale environmental changes (e.g., temperature, salinity, phytoplankton available as food) that affect different phases of the adult's reproductive cycle and that also alter conditions for the planktotrophic larvae and juvenile life stages.

Many factors, in addition to changes in larval abundance, can potentially regulate the magnitude of oyster spatfall in Maryland waters (for reviews see Abbe 1986; Kennedy 1996). Perhaps the most severe limitation to larval settlement is the diminishment of oyster reef habitat associated with high levels of harvest starting in the 1880s that have removed adult oysters and large volumes of cultch (Stevenson 1894; Kennedy and Breisch 1981; Rothschild et al. 1994). Disease-related mortalities of oysters starting in the mid-1950s in the lower and middle regions of Chesapeake Bay (Ford and Tripp 1996) further reduced the vertical relief of oyster reefs (Smith et al. 2001, 2005). These two factors have made the cultch more

[1] Corresponding author (dkimmel@hpl.umces.edu).

Acknowledgments

We thank M. P. Hare, S. J. Jordan, V. S. Kennedy, G. F. Smith, M. Tarnowski, R. E. Ulanowicz, and two anonymous reviewers for helpful comments on an early draft of this manuscript. We also thank Maryland Department of Natural Resources personnel for making available their data from the annual fall oyster survey. This is UMCES Contribution No. 4044.

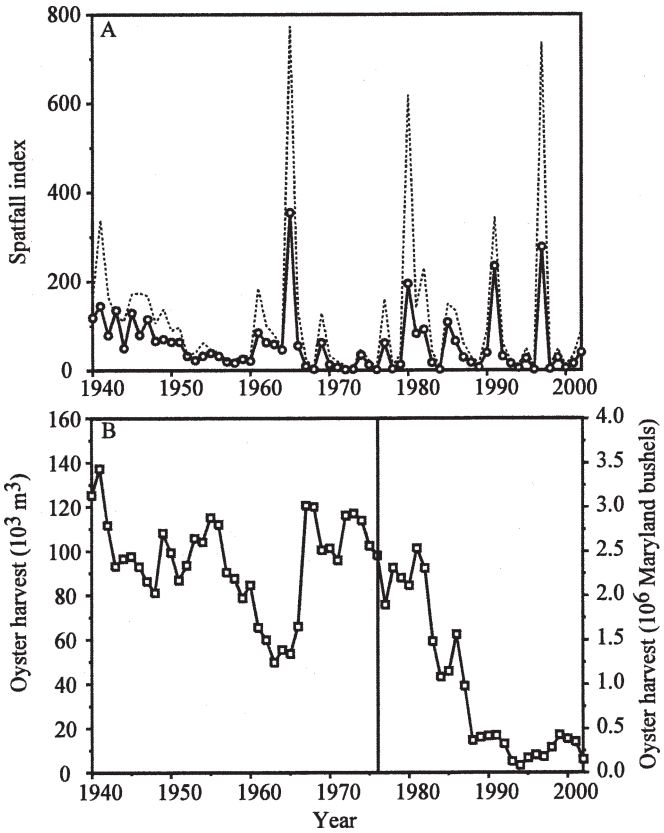

Fig. 1. (A) Spatfall index from the Maryland Department of Natural Resources November survey of the number of oyster spat present on the same volume of shell collected from oyster bars throughout Maryland waters (Krantz 1996; Tarnowski 2005). Dashed line represents +1 SD. (B) Live volume (m^3) of oysters harvested from Maryland waters (http://www.dnr.state.md.us). Solid vertical line indicates 1976.

susceptible to siltation, thereby reducing available habitat for larval settlement (Abbe 1986, Smith et al. 2005). In addition, predation by a suite of natural predators, including polyclad flatworms *Stylochus* spp., has been estimated to reduce the abundance of juvenile oysters in the estuary by over 99% during the first few months postsettlement (Newell et al. 2000).

Each autumn, the Maryland Department of Natural Resources (DNR) monitors the abundance of spat on oyster bars distributed throughout the Maryland portion of Chesapeake Bay (Krantz 1996; Tarnowski 2005) and calculates a spatfall index as an arithmetic mean of these data (Fig. 1). Ulanowicz et al. (1980) developed a mathematical model that enabled the magnitude of this spatfall index to be predicted from knowledge of environmental conditions measured on the Patuxent River, Maryland (ambient salinities, drought interval, and rainfall) and previous season fishery activity (harvest). The model is:

$$P = 63.7 + 24.9 \log(Sal) - 114 \log(RM) - 104 \log(RX) - 153 \log(H) \quad (1)$$

where P is spatfall index; Sal is the number of days salinity remained above 16.2; RM is the length in days of the maximum period without rain; RX is the maximum daily rainfall (mm) recorded during the entire year; and H is the volume of live oysters in Maryland bushels (1 Maryland bushel = 0.046 m^3 = 300 oysters of 7.6 cm shell length) harvested during the previous year. Their model was able to explain 53% of the annual variance in oyster spatfall. The most important variable was *Sal*, which explained 21% of the variability.

The focus of this paper was to revise the Ulanowicz et al. (1980) model using new environmental variables, including water temperatures, salinities, the Palmer hydrologic drought index (PHDI), precipitation, air temperature, and freshwater input. The updated model was then used to project oyster spatfall up to 2004. The model was not designed to explicitly determine what drives variability in juvenile oyster abundance; rather our goal was to determine if environmental conditions and prior harvest are still reliable indicators of oyster spatfall. Climate variables act as proxies for a host of other unknown variables that are indirectly controlled by climate, such as oyster disease, composition and abundance of the predator community, fouling of cultch, etc. If the relation described by Ulanowicz et al. (1980) no longer has explanatory power, other explanations must be sought for the significant downward trend in the oyster spatfall index (Fig. 1). If the model is unsuccessful in predicting oyster spatfall into the present time, the decline in oysters may have reached a point where an inadequate oyster stock exists to drive oyster spatfall, and other factors, influenced by climate variability, are currently driving interannual variability.

Methods

We examined multiple environmental variables for inclusion in a regression model for predicting eastern oyster recruitment. Spatfall, for the purpose of this discussion, is defined as the number of 0-age oysters (spat) found by Maryland DNR in their survey of oyster bars conducted each November since 1940 throughout Maryland waters. Spatfall index data for the surveys from 1940 through 1984 were obtained from Krantz (1996) and for later surveys from Tarnowski (2005). Annual Maryland oyster harvest data in customary units of Maryland bushels were also from Maryland DNR (http://www.dnr.state.md.us). Water temperature and salinity data from the mesohaline region of mainstem Chesapeake Bay were from the Environmental Protection Agency's Chesapeake Bay Program (http://www.chesapeakebay.net; region CB4MH). These water temperature and salinity data were collected sporadically by the Chesapeake Bay Institute from 1949 to 1984 (18 yr of data are available during this period [Table 1], with these data collected on specific cruises in each year, mostly during the summer months; for more information see http://www.chesapeakebay.net) and biweekly from 1984 to present. Despite these data gaps, there was sufficient data coverage to construct statistically valid and representative models. We used annual freshwa-

Table 1. Regression models shown in text as Eq. 2 and Eq. 3 fitted using different months of salinity and water temperature values. N is the number of years for which environmental data were available for that particular month and r^2 is goodness of fit. * indicates model was significant at $p < 0.01$. All other models were not significant at this level. Note that some large r^2 values are not significant because of smaller N values compared to other months.

	Equation 2 1940–1976		Equation 3 1977–2004	
Month	N	r^2	N	r^2
January	9	0.78	17	0.32
February	9	0.32	16	0.42
March	11	0.65	21	0.29
April	13	0.40	18	0.13
May	15	0.51	22	0.29
June	10	0.48	21	0.39
July	18*	0.57*	21*	0.53*
August	17*	0.67*	19*	0.70*
September	15	0.35	22*	0.49*
October	13	0.41	20	0.39
November	13	0.55	19	0.31
December	10	0.61	21	0.05

ter flow into Chesapeake Bay measured at Harrisburg, Pennsylvania, at the United States Geological Survey gauging station (http://waterdata.usgs.gov/nwis). Air temperature and precipitation data were obtained for Maryland climate regions 1 to 6 from the National Climate Data Center (NCDC; http://cdo.ncdc.noaa.gov); we used monthly mean air temperature and precipitation values for the analysis. The PHDI data were also obtained from the NCDC (http://www1.ncdc.noaa.gov/pub/data/cirs/).

We constructed the regression model using SPLUS statistical analysis software (Insightful). We initially restricted the range of data from 1940 to 1976 to match the time period previously used by Ulanowicz et al. (1980) to construct their multiple linear regression. This approach allowed us to compare the accuracy of our model to that of Ulanowicz et al. (1980) and also to compare the accuracy of our model predictions to post-1976 values for oyster spatfall index. The aforementioned variables for inclusion in the model were tested for independence and normality and transformed where necessary. Salinity was correlated with PHDI, precipitation, and freshwater input ($R = -0.65$, -0.64, and -0.72 respectively); therefore we retained salinity alone in the analysis, and the other three variables were removed. Stepwise multiple regression was used to select variables for the regression model, and only variables that were significant at $\alpha = 0.05$ were included. Linear regression between the observed spatfall and the predicted spatfall was used to assess the fit using the coefficient of determination (r^2).

Results and Discussion

The regression equation that best fit the 1940 to 1976 data with the fewest variables was:

$$\log_{10}SI = 6.18 - 1.33 \log_{10}H + 0.10\ WT + 0.09\ Sal \quad (2)$$

where SI is spatfall index, H is previous-year oyster harvest (in Maryland bushels), WT is July water temperature (°C), and Sal is July salinity. We fitted models for a number of months, and although August had the best fit, explaining 67% of the variance, we chose to report the July model since it had environmental data available for more years (Table 1). Equation 2 explained 57% of the variance in spatfall index ($F_{3,14} = 6.13$, $p < 0.01$). This was a slight improvement upon the Ulanowicz et al. (1980) equation that explained 53% of the variance in spatfall. Spatfall was positively related to increases in salinity and temperature and negatively related to the previous year's oyster harvest. The semipartial coefficients of determination revealed that the magnitude of the oyster harvest in the previous season explained 34% of the variance in spatfall, with July salinity and temperature explaining 18% and 5%, respectively. There was no significant agreement ($r^2 = 0.04$) between predicted and observed spatfall when this equation was applied to predict oyster spatfall from 1976 to 2004 (Fig. 2). The spatfall index declined even though the model predicted heavy spatfall for recent years.

Such an abrupt change in the predictive capacity of the regression model suggests that a major change in the oyster stock and spatfall relation occurred circa 1985 (Fig. 2). The most obvious explanation is the mortality of large numbers of mature oysters due to the *Haplosporidium nelsoni* epizootic that occurred in 1985 and 1986 (Ford and Tripp 1996). This parasitic disease, which had previously been largely confined to the high-salinity waters of lower Chesapeake Bay, moved into the upper regions of the bay when higher-than-usual salinities occurred as a consequence of a 2-yr drought in the mid-Atlantic region at this time. This *H. nelsoni* epizootic not only devastated the commercially exploited oyster bars (Ford and Trip 1996), but also likely killed isolated oysters that lived throughout the bay and those in waters too deep to be harvested. Such large and fecund "residual" oysters may have been contributing a large proportion of the larvae to the upper Chesapeake Bay. An important component of the regression model used by Ulanowicz et al. (1980), and in Eq. 2, is the magnitude of the oyster harvest in the previous season. The basis for this relation is that the more adult oysters removed by harvest, the fewer the oysters available to reproduce and contribute to larval production and hence spatfall. However, the *H. nelsoni* epizootics of the mid-1980s caused a precipitous decline in eastern oyster stocks and hence harvests, which, on the basis of our initial parameterization of the model without this source of mortality, should potentially have generated higher spatfall.

To explore the changes in the relation between oyster stock and spatfall in the period subsequent to this *H. nelsoni* epizootic, we constructed a similar regression model for all data for 1977 to 2004 using the same variables in Eq. 2. The regression equation was:

$$\log_{10}SI = -5.29 + 0.41 \log_{10}H + 0.10\ WT + 0.15\ Sal \quad (3)$$

where the variables are as in Eq. 2. Equation 3 explained 53% of the variance in spatfall index ($F_{3,17} = 6.36$, $p < 0.01$)

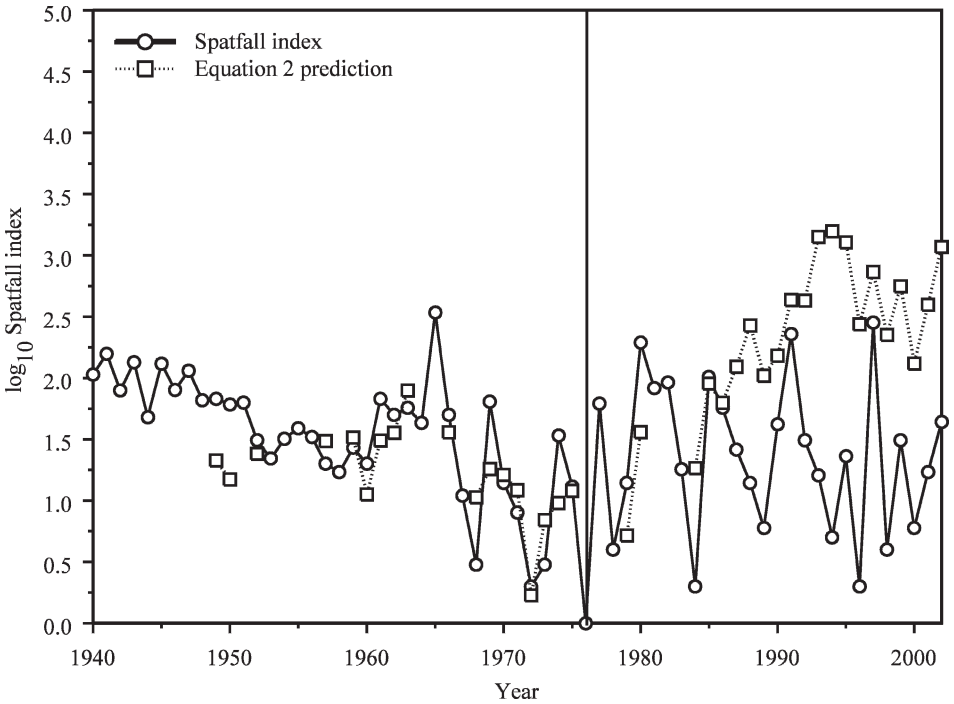

Fig. 2. Spatfall index data and predicted spatfall index calculated from Eq. 2. Solid vertical line indicates 1976. Note that there are no predicted spatfall values for some years before 1984 because no water temperature and salinity data were available.

for 1977–2004 compared with 57% explained for 1940–1976 (Eq. 2). The semipartial coefficients of determination for our regression model revealed that the magnitude of the oyster harvest in the previous season explained 5% of the variability, a large drop from 34% in Eq. 2. July salinity and water temperature explained 29% and 2%, respectively. Equation 3 was used to hindcast oyster spatfall from 1940 to 1976 (Fig. 3). Good agreement (r^2 = 0.49) was found between predicted and observed spatfall, indicating that a strong relation between oyster spatfall and climate was still present. It also showed the reduced importance of oyster harvest in determining interannual variability in spatfall in recent decades. The model also underestimated spatfall during the early period of the record, further indicating the important role oyster harvests played in the past (Fig. 3). To explore these relations further, we also constructed an alternate model using time periods specifically selected to be before the major decline in oyster harvests in 1982 and after the harvest had stabilized in 1988 at the low postdisease epizootic levels (Fig. 1). Models using data before 1982 found oyster harvests to be an important predictor of spatfall intensity. Models using data post-1987 were not statistically significant and did not find oyster harvests to be an important predictor of spatfall. This analysis supports our conclusion that the ~85% reduction in oyster harvests after the mid-1980s was the major factor in causing the loss of a relation between spatfall index and the number of oyster harvested in the previous season.

Although we tested for inclusion in this regression model all months for which salinity and temperature data were available, we found that only data from summer months explained a significant proportion of the variation in the spatfall index the following autumn (Table 1). Histological analysis of the gonads of oysters collected from Maryland's portion of Chesapeake Bay indicates that they start to spawn in early June and that spawning is largely complete by the end of August (Kennedy and Krantz 1982; Kennedy et al. 1995). This timing is confirmed by weekly measurements in the same region of rates of oyster larval metamorphosis on off-bottom collector plates (Kennedy 1980; Newell et al. 2000). These field studies indicate that larval metamorphosis starts in June, peaks in mid July, and is complete by early September (Kennedy 1996). These data on time of spawning and larval settlement period indicate that the processes of gametogenesis and vitellogenesis that are associated with the adult's contribution to larval production are largely completed by July. These temporal patterns suggest that the positive relation we found between spatfall and salinity in summer is due to the effect of the environment on the planktotropic larval stages or on the immediate postsettlement life stages (Table 1) rather than on the reproductive processes of adult oysters.

Salinity was the most important climatological variable that explained spatfall in our models and in the model presented by Ulanowicz et al. (1980). Salinity is a major determinant of the physiology of all life stages of estuarine animals because of its direct effect on many processes, including osmotic balance and feeding rates (Newell and Langdon 1996; Shumway 1996). Salinity may also represent the influence of other related variables that exert indirect effects. Survival to settlement of meroplanktonic

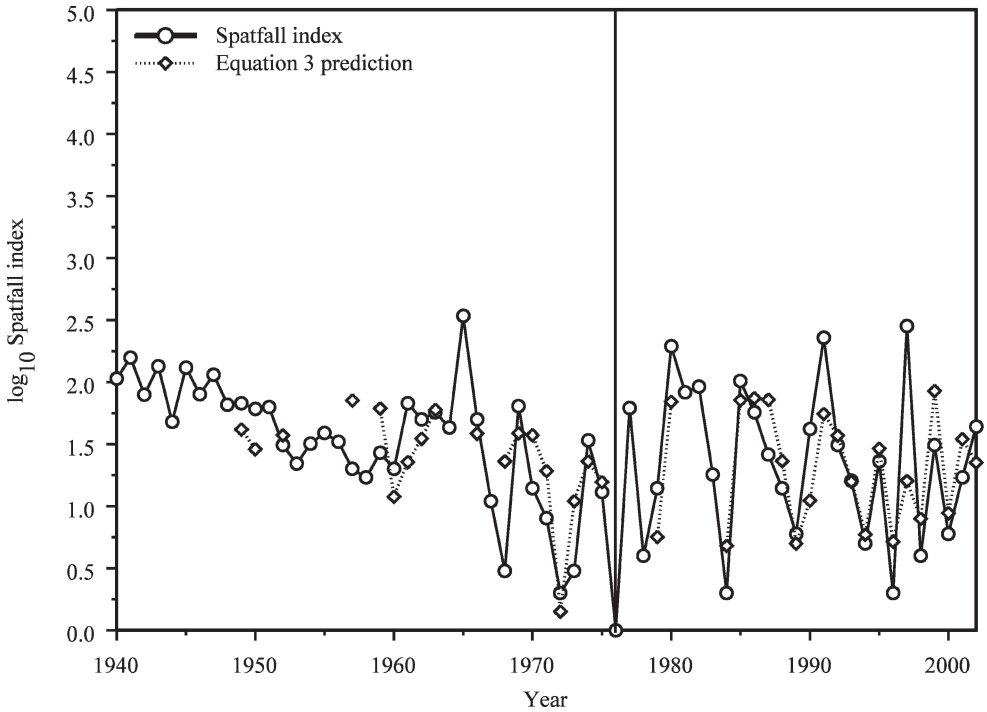

Fig. 3. Spatfall index data and predicted spatfall index calculated from Eq. 3. Solid vertical line indicates 1976. Note that there are no predicted spatfall values for some years before 1984 because no water temperature and salinity data were available.

larvae is affected by a myriad of factors, with larval mortality rates perhaps in excess of 99% (Pechenik 1987; Rumrill 1990; Roegner 1991; Kennedy 1996). Rumrill (1990) suggested that the four factors of most importance in regulating meroplanktonic larval settlement success are low fertilization success from broadcast spawning, adverse hydrographic conditions, failure to locate adequate substrate, and predation. Whatever the mechanism responsible for the positive relation we found between summer salinity and oyster spatfall, it suggests that the larvae and spat in the first few weeks postmetamorphosis are the most sensitive life stage of the eastern oyster.

The pattern of high interannual variation in eastern oyster spatfall in central Chesapeake Bay is also typical of many other species with meroplanktonic larvae (Rumrill 1990). There has been a long-term effort to understand the mechanisms responsible for such annual variation in the abundance of juvenile bivalves, with many studies focusing on processes that affect the reproductive output of adult bivalves (Bayne 1976). The number of eggs spawned and quantity of nutrients sequestered in the egg yolk of bivalves is dependent on the nutritional status of the female parent (Sastry 1979; Gabbott 1983). If the adults are subject to nutritive stress after the initiation of gametogenesis, the eggs spawned may be smaller in size than normal because of reduced yolk content, and such eggs have a lower rate of fertilization and produce less viable larvae than those spawned by unstressed females (Helm et al. 1973; Bayne et al. 1978; Gallager and Mann 1986; Kennedy et al. 1995). The results of our study suggest that these environmental effects on adult bivalves may not have as much influence on the magnitude of spatfall as the environmental conditions to which the larvae and the immediate postsettlement life stages are exposed. To ascertain if the pattern we have observed here applies to other bivalve species it is important that similar analyses of long-term records of spatfall be undertaken.

Maryland DNR measures oyster spat abundance each autumn on oyster bars widely distributed throughout the Maryland portion of the bay (Krantz 1996; Tarnowski 2005). The number of bars sampled has been fixed at 53 since 1986, and in the preceding 40 yr a variable number of bars, generally between 20 and 50, was sampled; these data have been presented as an annual mean spatfall index by Ulanowicz et al. (1980) and Krantz (1996). This mean provides a useful estimate of juvenile oyster abundance but masks any spatial variability inherent in oyster spatfall throughout this large geographic region. We examined the dispersion of these data over the entire time period by calculating the standard deviation and coefficient of variation (CV; Zar 1974) of the spatfall index (Fig. 1). We compared the variance between spatfall in earlier years (1940–1976) with more recent spatfall (1977–2002) and found no significant difference in variance between the two time periods (F test; $p > 0.05$). However, the CV of the spatfall index for each year had a significant, upward trend in variability over time (Kendall trend test; $\tau = 0.26$, slope $= 1.22$; $p < 0.01$). It appears that recent oyster spatfall patterns are more variable than those in the past. It is also apparent that years of high spatfall have very large standard deviations, indicating that relatively few of the oyster bars sampled are experiencing high oyster spatfall

(Fig 1). The exact cause of this increasing variability is unknown, but may be related to a host of environmental changes in Chesapeake Bay that have occurred over the last 50 yr associated with increasing human population in the watershed and resulting cultural eutrophication (see Kemp et al. 2005). Tarnowski (2005) drew attention to the fact that in 1997 over 75% of the spatfall index was accounted for by only 5 of the 53 sentinel bars sampled, whereas 10 contributed nearly 95%. Spatfall in 1991 was slightly more widespread, with 15 of the 53 sentinel bars totaling 75% of the index. Years with a high spatfall index represent locally favorable conditions for exceptionally high larval survival/settlement, rather than moderate levels of oyster recruitment across all oyster bars surveyed.

A drawback of the Maryland DNR oyster spatfall survey is that the methods were designed to provide only an index of spatfall and not a statistically valid estimate of the magnitude of total spatfall. The total magnitude of spatfall cannot be estimated because the survey is based on counting the numbers of spat per unit volume of cultch collected by dredge, with no quantification of effort required to collect that volume of shell. The drawback of this approach is that it does not take into account changes over time in the total available cultch required as settlement substrate. To convert these spatfall data into a quantitative assessment of larval settlement, the numbers of spat per unit volume of cultch must be multiplied by the total amount of cultch present on their oyster bars. Unfortunately, there is little quantitative information available on the amount of cultch available as habitat in Chesapeake Bay, which precludes us from making such a calculation. Before Chesapeake Bay eastern oyster stocks were heavily fished starting in the 1880s, oyster reefs were large structures that extended into the water column (Stevenson 1894, Kennedy and Breisch 1981). Removal of large numbers of oysters meant that oyster reefs became eroded and vulnerable to siltation associated with excessive sediment runoff (Seliger and Boggs 1988; DeAlteris 1989; Smith et al. 2001). Recent surveys of selected oyster bars in Maryland waters by Smith et al. (2005) indicate that oyster cultch is reduced to ~10% of the area present historically (Yates 1913). Because of this steady reduction in cultch quantity, the magnitude of total oyster spatfall represented by recent sporadic peaks in spatfall index is substantially lower than in earlier decades, when the overall amount of cultch available for larval settlement was much larger. We caution that these recent peaks in spatfall index should not be interpreted as indicating that sufficient large and fecund oysters are still present to ensure adequate juvenile abundance.

In summary, we suggest that the overall significant downward trend in the oyster spatfall index recorded since 1940 is driven primarily by a reduction in the number of adult oysters, associated with harvesting and disease epizootics. Our model suggests that the removal of oysters through harvesting currently does not exert as large an effect on spatfall as it once did. At the present time, climatic conditions are largely responsible for the annual variability in oyster spatfall index. The model does highlight the important role that the size of the oyster stock once played in governing the magnitude of spatfall. We suggest that this reduction in the significance of the loss of adult oysters through prior seasons' harvest on the spatfall index is largely because those harvests have greatly diminished since the mid-1980s to <2,300 m^3 (50,000 Maryland bushels) today (Fig. 1). In earlier years, harvests were 2 to 3 million bushels and hence the removal of the larval production from that many large oysters caused this statistically significant relation. The loss of statistical significance should not be construed as a rationale for the continuing unbridled oyster harvests in Maryland. Rather, if oyster stocks could be conserved and rebuilt, then a situation where the abundance of oysters was once again an important component in determining the magnitude of spatfall might be reestablished. In such circumstances, climate would still be an important overall determinant of spatfall, but would not be the only driving factor.

References

Abbe, G. 1986. A review of some factors that limit oyster recruitment in Chesapeake Bay. Amer. Malacol. Bull. Special Edition. **3:** 59–70.

Bayne, B. L. 1976. Aspects of reproduction in bivalve molluscs, p. 432–448. *In* M. L. Wiley [ed.], Estuarine processes, V. 1. Academic.

———, D. L. Holland, M. N. Moore, D. M. Lowe, and J. Widdows. 1978. Further studies on the effect of stress in the adult on eggs of *Mytilus edulis*. J. Mar. Biol. Ass. U.K. **58:** 825–841.

DeAlteris, J. T. 1989. The role of bottom current and estuarine geomorphology on the sedimentation processes and productivity of Wreck Shoal, an oyster reef of the James River, Virginia, p. 279–307. *In* B. J. Neilson, A. Kuo and J. Brubaker [eds.], Estuarine circulation. Humana.

Ford, S. E., and M. R. Tripp. 1996. Diseases and defense mechanisms, p. 581–660. *In* V. S. Kennedy, R. I. E. Newell and A. F. Eble [eds.], The eastern oyster: *Crassostrea virginica*. Maryland Sea Grant, College Park, Maryland.

Gabbott, P. A. 1983. Developmental and seasonal metabolic activities in marine molluscs, p. 165–217. *In* P. W. Hochachka [ed.], The mollusca, V. 2. Academic.

Gallager, S. M., and R. Mann. 1986. Growth and survival of larvae of *Mercenaria* (L.) and *Crassostrea virginica* (Gmelin) relative to broodstock conditioning and lipid content of eggs. Aquaculture **56:** 105–121.

Helm, M. M., D. L. Holland, and R. R. Stephenson. 1973. The effect of supplementary algal feeding of a hatchery breeding stock of *Ostrea edulis* L. on larval vigour. J. Mar. Biol. Assoc. U.K. **53:** 673–684.

Jordan, S. J., and J. M. Coakley. 2004. Long-term projections of eastern oyster populations under various management scenarios. J. Shellfish Res. **23:** 63–72.

———, K. N. Greenhawk, C. B. McCollough, J. Vanisko, and M. L. Homer. 2002. Oyster biomass, abundance, and harvest in northern Chesapeake Bay: Trends and forecasts. J. Shellfish Res. **21:** 733–741.

Kemp, W. M., and others. 2005. Eutrophication of Chesapeake Bay: Historical trends and ecological interactions. Mar. Ecol. Prog. Ser. **303:** 1–29.

Kennedy, V. S. 1980. Comparison of recent and past patterns of oyster settlement and seasonal fouling in Broad Creek and Tred Avon River, Maryland. Proc. Natl. Shellfish. Assoc. **70:** 36–46.

———. 1996. Biology of larvae and spat, p. 371–421. *In* V. S. Kennedy, R. I. E. Newell and A. F. Eble [eds.], The eastern oyster: *Crassostrea virginica*. Maryland Sea Grant College, College Park, Maryland.

———, and L. L. Breisch. 1981. Maryland's oysters: Research and management.Maryland Sea Grant Publication UM-SG-TS-81-04, 286 p.

———, and L. B. Krantz. 1982. Comparative gametogenic and spawning patterns of the oyster *Crassostrea virginica* Gmelin in central Chesapeake Bay. J. Shellfish Res. **2:** 133–140.

———, R. I. E. Newell, G. E. Krantz, and S. Otto. 1995. Reproductive capacity of the eastern oyster *Crassostrea virginica* (Gmelin) infested with the parasite *Perkinsus marinus*. Dis. Aquat. Org. **23:** 135–144.

Krantz, G. E. 1996. Oyster recruitment to the Chesapeake Bay, 1939 to 1993.MDDNR Fish. Serv. Spec. Publ. Oxford, Maryland.

Newell, R. I. E. 1988. Ecological changes in Chesapeake Bay: Are they the result of overharvesting the American oyster, *Crassostrea virginica*?, p. 536–546. *In* M. P. Lynch and E. C. Krome [eds.], Understanding the estuary: Advances in Chesapeake Bay research. Chesapeake Research Consortium, Gloucester Point, Virginia.

———, G. S. Alspach, V. S. Kennedy, and D. Jacobs. 2000. Mortality of newly metamorphosed eastern oysters (*Crassostrea virginica* Gmelin) in mesohaline Chesapeake Bay. Mar. Biol. **136:** 665–676.

———, and C. J. Langdon. 1996. Mechanisms and physiology of larval and adult feeding, p. 185–230. *In* V. S. Kennedy, R. I. E. Newell and A. F. Eble [eds.], The eastern oyster: *Crassostrea virginica*. Maryland Sea Grant College, College Park, Maryland.

Pechenik, J. A. 1987. Environmental influences on larval survival and growth, p. 551–608. *In* A. C. Giese and J. S. Pearse [eds.], Reproduction of marine invertebrates, V. 9. Blackwell Scientific.

Roegner, G. C. 1991. Temporal analysis of the relationship between settlers and early recruits of the oyster *Crassostrea virginica* (Gmelin). J. Exp. Mar. Biol. Ecol. **151:** 57–69.

Rothschild, B. J., J. S. Ault, P. Goulletquer, and M. Heral. 1994. Decline in the Chesapeake Bay oyster population: A century of habitat destruction and overfishing. Mar. Ecol. Prog. Ser. **111:** 29–39.

Rumrill, S. S. 1990. Natural mortality of marine invertebrate larvae. Ophelia **32:** 163–198.

Sastry, A. N. 1979. Pelecypoda (excluding Ostreidae), p. 113–292. *In* A. C. Giese and N. J. Blake [eds.], Reproduction in marine invertebrates, V. 5. Academic.

Seliger, H. H., and J. A. Boggs. 1988. Evidence for loss of suitable habitats for oysters in tributaries of the Chesapeake Bay, p. 111–127. *In* M. P. Lynch and E. C.. Krome [eds.], Understanding the estuary, advances in Chesapeake Bay research. Publication No. 120. Chesapeake Research Consortium, Solomons, Maryland.

Shumway, S. E. 1996. Natural environmental factors, p. 467–513. *In* V. S. Kennedy, R. I. E. Newell and A. F. Eble [eds.], The eastern oyster: *Crassostrea virginica*. Maryland Sea Grant, College Park, Maryland.

Smith, G. F., D. G. Bruce, and E. B. Roach. 2001. Remote acoustic habitat assessment techniques used to characterize the quality and extent of oyster bottom in the Chesapeake Bay. Mar. Geod. **24:** 171–189.

———, D. G. Bruce, ———, A. Hansen, R. I. E. Newell, and A. M. McManus. 2005. Habitat conditions of mesohaline oyster bars in the Maryland Chesapeake Bay: An assessment of 40 years of oyster management. N. Am. J. Fish. Man. **25:** 1569–1590.

Stevenson, C. H. 1894. The oyster industry of Maryland. U.S. Fish. Comm. Bull. **12:** 203–298.

Tarnowski, M. 2005. Maryland Oyster Population Status Report 2003 and 2004 Fall Surveys.MDDNR Publ. No. 17-1072005-62. Maryland Department of Natural Resources Fisheries Service, Annapolis, Maryland. 33 p.

Thompson, R. J., R. I. E. Newell, V. S. Kennedy, and R. Mann. 1996. Reproduction and larval development, p. 335–370. *In* V. S. Kennedy, R. I. E. Newell and A. F. Eble [eds.], The eastern oyster: *Crassostrea virginica*. Maryland Sea Grant, College Park, Maryland.

Ulanowicz, R. E., W. C. Caplins, and E. A. Dunnington. 1980. The forecasting of oyster harvest in central Chesapeake Bay. Estuar. Coastal Mar. Sci. **11:** 101–106.

Yates, C. C. 1913. Summary of survey of oyster bars of Maryland, 1906–1912., Department of Commerce, U.S. Government Printing Office, Washington DC (USA). 81 p.

Zar, J. H. 1974. Biostatistical analysis. Prentice-Hall.

Received: 12 July 2006
Accepted: 19 December 2006
Amended: 12 January 2007