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Estimation Of Oyster, Crassostrea Virginica, Standing Stock, Larval Production And Advective Loss In Relation To Observed Recruitment In The James River, Virginia

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ESTIMATION OF OYSTER, *CRASSOSTREA VIRGINICA*, STANDING STOCK, LARVAL PRODUCTION AND ADVECTIVE LOSS IN RELATION TO OBSERVED RECRUITMENT IN THE JAMES RIVER, VIRGINIA

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ABSTRACT Standing stock and demographic data for oysters, *Crassostrea virginica*, in the James River, Virginia are used to generate spatial estimates of egg production on a reef-specific basis. Subsequent estimates are made of losses related to density-dependent fertilization, natural mortality in the plankton, advective loss related to estuarine circulation, availability of substrate (both absolute amounts and after occlusion by fouling organisms), limited competency of pediveligers to metamorphose, and post settlement mortality to an age of 4 wk post metamorphosis. Reef-specific egg production is highly variable on a per unit basis within the James. In all reef systems fertilization losses approach two orders of magnitude, in some instances higher than estimated losses to advection over a 21-day development period. The combination of limited substrate availability compounded by substrate fouling suggests that increasing substrate availability at the time of settlement would strongly facilitate an increase in population size. Final estimates from sequential calculations of surviving juvenile densities agree within one order of magnitude with field observations.

KEY WORDS: oysters, *Crassostrea virginica*, stock assessment, larval dispersal, circulation, recruitment, modeling, James River

INTRODUCTION

The James River, Virginia has served as the focal point for the Virginia oyster (*Crassostrea virginica*) industry for over a century, being the source of the majority of seed oysters that were transplanted for growout to locations within the Virginia portion of the Chesapeake Bay and much further afield in the Middle Atlantic states. It has been the site of continuing investigations of oyster distribution in relation to bottom type (Baylor 1894, Moore 1911, Loosanoff 1931, Marshall 1954, Haven et al. 1981a, Andrews 1982, Haven and Whitcomb 1983, Mann and Wesson 1997), spawning activity (Cox and Mann 1992, Mann et al. 1994), larval biology and settlement (Loosanoff 1931, Andrews 1951, Andrews 1954, Wood and Hargis 1971, Andrews 1979, Andrews 1983, Haven and Fritz 1985, Mann 1988), larval dispersal in relation to circulation (Pritchard 1953, Ruzecki and Moncure 1968, Ruzecki and Hargis 1988, Mann 1988), disease impact (Andrews 1954, Andrews 1962, Andrews 1968, Burreson and Ragone Calvo 1996), a series of unpublished qualitative annual surveys of oyster resources by location (Virginia Institute of Marine Science Library Archive), and a development focus for three-dimensional modeling of estuarine circulation (Hamrick 1992a, Hamrick 1992b). Given the ecological importance (see Mann et al. 1991) and commercial value (see Haven et al. 1981b) of oysters originating from the James River, it is surprising that comparatively little effort has been devoted to quantitative examination of the relationships between environmental fluctuations (temperature and salinity), dominant aspects of oyster biology (gains associated with growth, spawning and recruitment versus losses to predation and disease), and the comparative impact of fishing mortality in this location.

Extensive description of the Virginia oyster resource and history of its utilization has been given by Haven et al. (1981), and more recently reviewed by Hargis and Haven (1988). These contributions, among many others, describe a state of continuing decline. Continuing losses of productive oyster reef over the past three decades to *Haplosporidium nelsoni*, commonly known as MSX, and *Perkinsus marinus* in the higher salinity regions of the James River have, ironically, provided both an impetus to understand the dynamics of the James River system to preserve the remaining oyster stock, but have also provided a unique field opportunity to examine population structure and recruitment of a dominant benthic invertebrate in a situation where the required component data sets are enviably abundant, where both circulation and the relationship of larval abundance to circulation is comparatively well studied, and where recruitment resulting from immigration, a confounding factor in most other field situations, is negligible because of the decadal time scale elimination of neighboring oyster populations by disease. This report describes a quantitative synthesis of a number of oyster related studies effected on or for the James River in the past decade, and examines the product of estimates of recruitment based on this synthesis with field observations made during the 1993 to 1994 period.

MATERIALS AND METHODS

Estimation of Oyster Standing Stock and Demographics

Data used for the current study originated in fishery independent stock assessments of the James River oyster resource effected in the Fall months of 1993 and 1994 as a cooperative effort with the Virginia Marine Resources Commission (hereafter VMRC). For the majority of effort the 1993 data set was used. The 1994 data set provided data on small size classes (young oysters originating from spawning events in 1993) that are used here to provide comparative field data for estimates of recruitment generated as a synthesis exercise from 1993 assessments and other data as described later in the text.

The oyster reefs in the James have been described in terms of spatial features and substrate several times over the past 100 y, beginning with the work of Baylor (1894), for whom the current public oyster grounds of Virginia are popularly named. The most recent comprehensive survey of "Baylor" is reported by Haven and Whitcomb (1983). Spatial variability in distribution of oysters within the oyster reef systems, and distribution of reefs at various

depths in the subtidal regions dictated using a quantitative sampling program using a stratified random grid with the documented oyster reefs or rocks in the James River forming the strata. Limits of the unknown oyster reef were mapped by the Surveying Engineering Department at VMRC and the grids for sampling set with Loran coordinates (Loran was checked daily when in the field from known markers at both the beginning and end of the day). The James River public oyster grounds are illustrated in Figure 1A as a simplification of the map of Haven and Whitcomb (1983), with presentation limited to the shoreline, extant oyster rock, and the boundary of various bottom types that can (mixed shell and mud, mixed shell and sand, and hard sand), and cannot (soft mud) support oyster populations. Figure 1A illustrates that reef systems as identified in the Baylor surveys are not uniform in substrate, and therefore are not expected to be uniform in oyster distribution within a single reef.

Since the survey of Haven and Whitcomb (1983) the spatial distribution of oyster populations in the James River has declined under both sustained disease pressure (Burreson and Ragone Calvo 1996) and commercial harvest. This decline is illustrated in the location of the 19 individual reef systems that were examined in the Fall of 1993 and 1994 (Fig. 1B) as part of a comprehensive stock assessment survey (Mann and Wesson, 1997), with notable reduction in more downstream populations. The legend of Figure 1B identifies the sampled reefs by number. These numbers are cross referenced with reef names in this report where convenience dictates. Sampling areas 1–11 in Figure 1B represent the limits of hard oyster rock strata selected, mapped, and sampled within the larger public oyster grounds in those regions. The limits of hard oyster rock strata within sampling areas 12–19 were not mapped separately, but were known to include both oyster rock strata as well as bare sandy or muddy strata. Sampling sites were picked by random numbers within the grids and oysters were sampled with a hydraulically operated patent tong with an opening of 1 square meter. In this manner a total of 825 stations were occupied in 1993, and 692 stations were occupied in 1994.

Choice of sampling gear was critical in the current application. Both tongs and dredges are commonly used to examine oyster populations; however, only the former are good quantitative tools (Chai et al. 1992). In 1993 we examined a standard patent tong of known area; however, tests proved this to be an unpredictable sampling tool in that penetration into the hard bottom on the reef surface was inconsistent, resulting in high variability in replicate samples on the same site. An hydraulically operated tong, which separates the closing actions of the tong from the retrieval action, proved to be vastly superior in providing consistent penetration of the bottom and replication sampling.

Bros and Cowell (1987) address estimation of adequate sample size within a strata in situations where minimum detectable difference cannot be specified *a priori*. Figure 2 illustrates the variability in density within a single reef system so this is of concern. Their method incorporates use of resolving power as a primary factor and sampling feasibility as a secondary factor, and suggests that the standard error of the mean (SEM) be used as a measure of appropriate sampling effort. For the current data, a plot was generated of mean number of oysters per patent tong (1 square meter) sample and SEM versus number of samples included in the calculation. This calculation was repeated 10 times for data within a strata with samples being chosen at random from those available. Random sampling eliminated any bias that resulted from sequential data entry in accordance with sampling in the field sampling
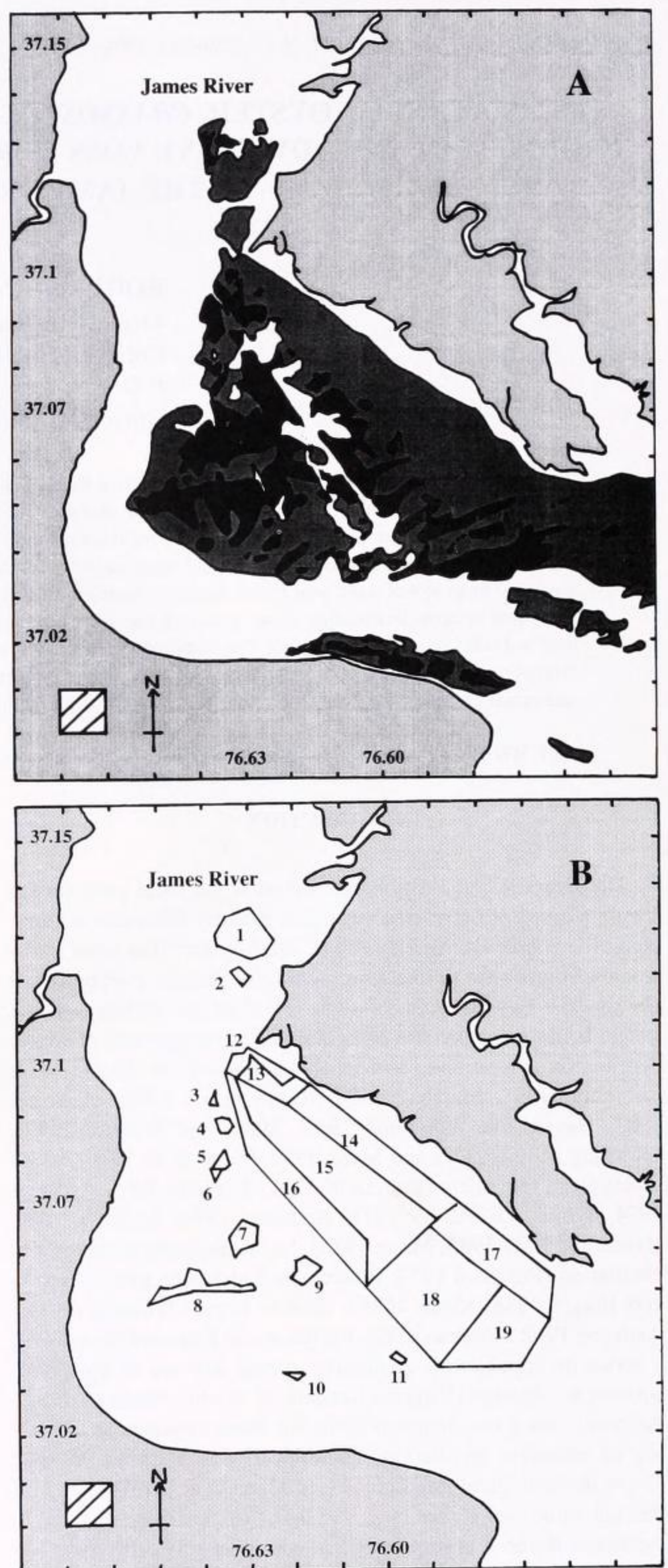

Figure 1. A. Shoreline and bottom type in the upper James River, Virginia, modified from Haven and Whitcomb (1983). Areas in black represent oyster reef, grey represents mixed shell-mud and shell-sand, white represent primarily soft mud. Axes are longitude and latitude in decimal degrees. Cell size = 0.1 × 0.1 degrees. B. Oyster reef systems in the James River, Virginia as surveyed for stock assessment during the 1993 and 1994, and used in subsequent larval dispersal modeling exercises. Note the reduced spatial distribution compared with 1983. The numerical key identifying reefs and shoals corresponds to that used throughout the current text. 1: Upper Deep Water Shoal, 2: Lower Deep Water Shoal, 3: Upper Horsehead, 4: Middle Horsehead, 5: Lower Horsehead, 6: Moon Rock, 7: V Rock, 8: Point of Shoals, 9: Cross Rock, 10: Shanty Rock, 11: Dry Lump, 12: Mulberry Point, 13: Swash, 14: Upper Jail Island, 15: Swash Mud, 16: Offshore Swash, 17: Lower Jail Island, 18: Offshore Jail Island, 19: Wreck Shoal.
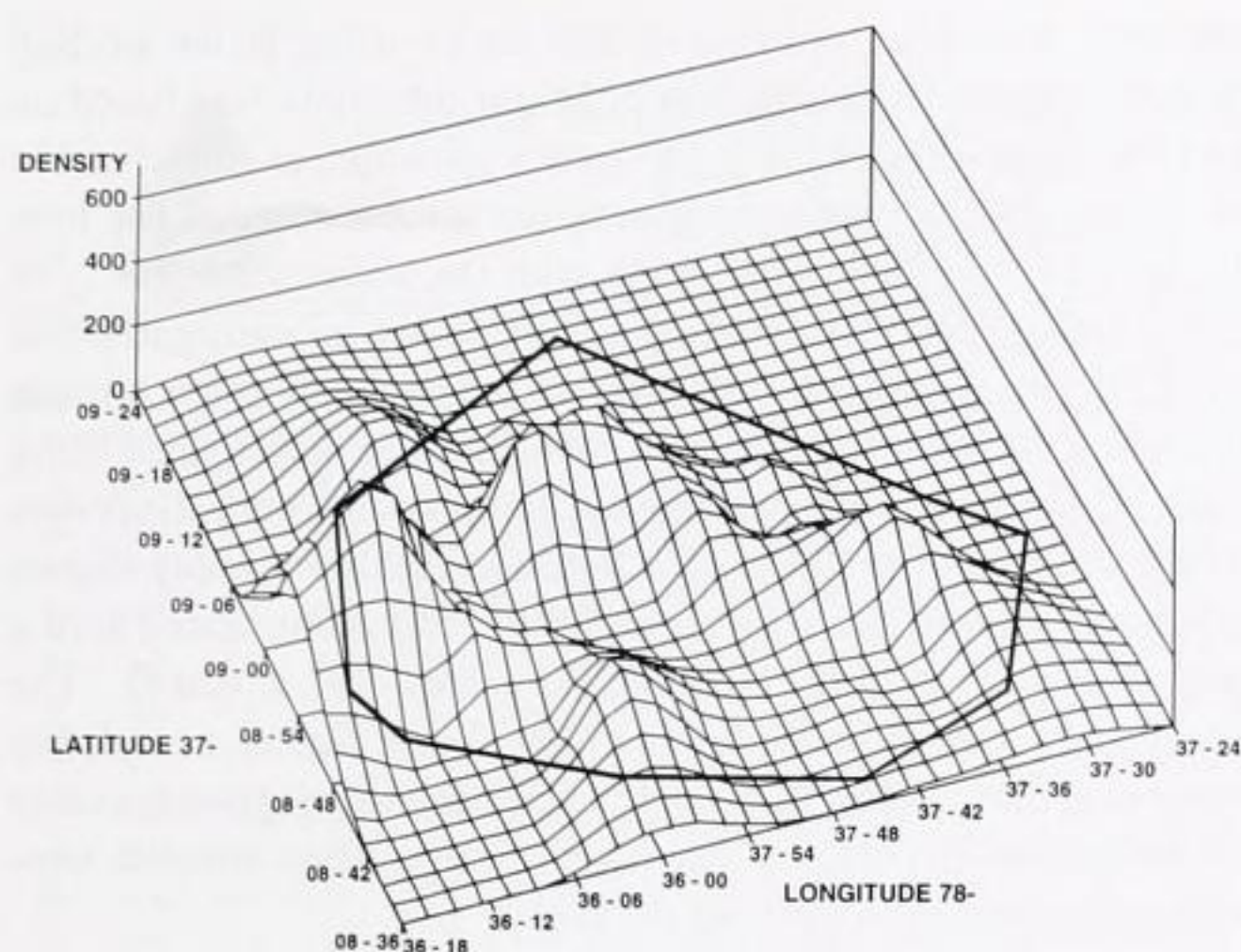
Figure 2. An illustration of spatial variability in oyster density on a single reef: a surface plot of oyster density on Deep Water Shoal from 1993 survey data. Such variability was accomodated in the sampling regime and adequacy insured using the procedures described in Bros and Cowell (1987).

(the latter may have resulted, inadvertently, in temporally focused sampling on a particular substrate type). In a regime where variability with bottom type was high and the sample size was low the mean would not stabilize, and where sampling was insufficient the SEM would not demonstrate a stable trend of decreasing value—remembering of course that the SE value will eventually continue to decrease with increasing number of samples included in the calculation because the SE is inversely proportional to the square root of the number of observations of the mean. The same criteria were applied in sampling in Fall of 1993 and 1994, and in both instances resultant plots illustrated the adequacy of the sampling used.

Upon retrieval, the sample was washed and processed for counts of live oysters per square meter, and description of size class distribution in each sample by 5 mm size class intervals. In addition, data were collected on dead oysters with paired valves (commonly termed boxes, indicating recent mortality), and the volume of shell retrieved in each tong as an index of the quantity of cultch material (settlement substrate) present at each station.

Salinity and Water Temperature in the James River

Records of salinity and temperature in the section of the James River under study come from sporadic station values associated with oyster fishery and oyster disease monitoring data, and from surveys effected by the Virginia State Water Control Board (SWCB). The former data sets are concentrated in the summer and fall months, with limited data for spring and fall and are generally limited to bottom salinity and temperature from Niskin bottle collections. The SWCB data sets are collected with greater regularity in the winter and spring months, but with greater spatial separation. In the James, two SWCB stations are of interest, one is situated upstream of Deep Water Shoal (Reef Number 1 in Figure 1B), effectively just above the upstream distribution limit of oysters, whereas the second is situated on the southwest corner of Wreck Shoal (Reef Number 19 in Figure 1B) adjacent to the main channel of the James River. SWCB data were examined for Period 4, February 1985 through 16 May 1991 for depths of 1, 3, and 5 m

at both stations. From these data, plots were generated of salinity versus river flow at Richmond, taken from US Geological Survey (USGS) records in units of cubic feet min^{-1}, for the dates of collection. Flow was used to develop a salinity predictor using the model:

$$s = s_c + b \log(f), \text{ where } f < f_c$$
$$s = s_c, \text{ where } f > f_c$$

where s is the salinity in ppt, f is the flow in cubic feet min^{-1}, and f_c is the critical flow rate above which salinity remains constant. The general appearance of the function, illustrated in Figure 3, is like a ''hockey stick'' with a linear decrease in s on a plot of s versus log (f) to a value of s_c corresponding to log (f_c). At values of f above (f_c) values of s remain constant at s_c. Fitted parameters were generated for each of the two SWCB stations. Good concordance was observed between depths at one station, therefore fits for 3 m data (nearest approximation to depths of the extant reefs) were used to generate predictive descriptors of mean monthly salinity at both stations based on mean monthly river flow data at Richmond. The downstream SWCB data, station A in Figure 3, was considered as Wreck Shoal (WS) data, with s_c, b, and $\log(f_c)$ values of 4.4 ± 0.9, -11.7 ± 0.9, and 4.2 ± 0.1, respectively (n = 111, all values mean ± SE). The upstream SWCB station, station B in Figure 3, gave s_c, b, and $\log(f_c)$ values of 0.8 ± 0.3, -11.4 ± 0.8, and 3.84 ± 0.04 (n = 104), respectively. By linear interpolation mean monthly salinities could be estimated for intermediate sites at Horsehead (HH) and Deep Water Shoal (DWS). Each of the 19 reef systems in Figure 1B is indexed by number to one of these three salinity regimes (DWS, HH, or WS) as follows: Reefs Nos. 1 and 2 (DWS), reefs Nos. 3–9 and 12–16 (HH); and 10, 11, 17, 18, and 19 (WS).

Water temperature data in the James River are also available from seasonal monitoring and SWCB surveys with the same limitations as salinity data with respect to temporal coverage. These data were compared with York River water temperature, recorded continuously at the Virginia Institute of Marine Science (VIMS) Pier for the period January 1985 to May 1991 and excellent concordance was observed. To generate a longer time frame for the current study York River data for 1985 to 1994 were used to develop a description of mean monthly water temperature that could be applied to all stations uniformly.

Estimation of Egg Production, Spawning and Fertilization

Estimation of oyster recruitment begins with estimating Julian day of spawning, followed by estimation of egg production from the density and size distribution of oysters. Estimates of egg production are subsequently used to generate estimates of recruitment to the benthos and, eventually, the juvenile through adult population. Timing of spawning is temperature dependent and simply expressed as a function of day-degrees, D' where:

$$D' = d (t - t_o)$$

where:

d = number of days to attain a ripe state

t = temperature to which oysters are exposed (ambient field temperatures)

t_o = temperature below which no evidence of gonad development is found.

A value of 12.0°C is adopted for t_o from Price and Maurer (1971)

Station A — depth: 3m
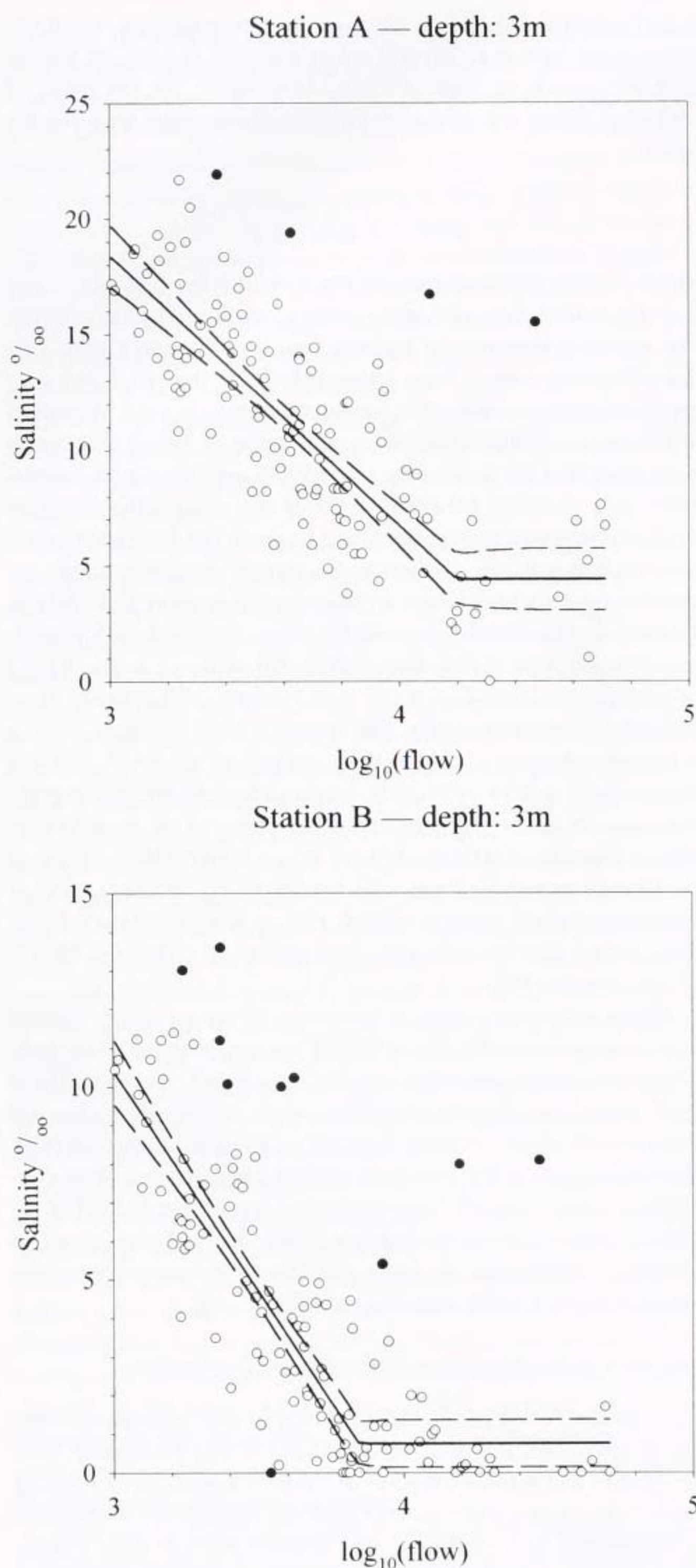

Station B — depth: 3m

Figure 3. Predicted relationship of salinity versus river flow at Richmond (USGS data in cubic ft. min^{-1}, for the period 4 February 1985 to 16 May 1991, SWCB salinity data) for 3 m depth. The model is s = s_c + b log(f), where f < f_c and s = s_c where f ≥ f_c, where s is the salinity in ppt, f is the flow in cubic ft. min^{-1}, and f_c is the critical flow rate above which salinity remains constant. Fits illustrate mean ± 95% confidence interval. Filled circles illustrate points greater than 2.5 standard deviations from the mean, which are excluded from the mean fit calculation. A. Downstream SWCB data, considered as Wreck Shoal (WS), with s_c, b, and log(f_c) values of 4.4 ± 0.9, −11.7 ± 0.9, and 4.2 ± 0.1 respectively (n = 111, 4 points excluded, all values mean ± s.e.). B. Upstream SWCB station, with s_c, b, and log(f_c) values of 0.8 ± 0.3, −11.4 ± 0.8, and 3.84 ± 0.04 (n = 104, 10 points excluded). See text for further details.

who also provide an estimate of 450 for D' using Delaware Bay oysters. Independent estimation of D' for this study was based on data from Mann et al. (1994) for oysters spawning at Horsehead in the James River in 1988. Spawning dates are estimated for June 22, July 27, and August 17, 1988 with the above value for t_o of 12°C. Using York River water temperatures as surrogates this gives D' values of 420, 449, and 443, respectively, with a mean value for D' of 434. Frequency of spawning was investigated using a mean annual water temperature cycle from daily York River data for the years 1985 to 1994 by the following analysis. A day-degree counter is initiated when t reaches 12.0°C and accumulated until a spawning event is triggered based on values of d, t, and D'. The day-degree counter is then reset to 0 and a further cumulative count begun. A second spawning is subsequently triggered, and so on. Sequential day-degree calculations cease when ambient temperature decreases to 12°C in the Fall.

Egg production or fecundity (F) is the sum of individual (F_{ind}) fecundity in each size class interval, here 5 mm length intervals. Length is considered as the maximum dimension measured from the hinge (strictly this is height but length is used to conform to common use). Within each interval L = mid point of length (for convenience, we used 3, 8, 13, 18 mm and so on for 0–5, 5–10, 10–15, and 15–20 mm size intervals). Weight to length (in mm) conversions were effected using data from James River field collections (raw data from Rainer and Mann 1992, and unpublished data, Mann, collected in 1994):

$$W = 0.000423 \times L^{1.7475}$$

Size-specific fecundity is estimated using the relationship:

$$F_{ind} = 39.06 \times W^{2.36} \ (r^2 = 0.887, 24 \ d.f.)$$

where F is in millions, and W is dry tissue weight in mg. This relationship is taken from Thompson et al. (1996) and based on a re-analysis of earlier raw data from Cox and Mann (1992), which eliminated all individuals in partially spawned or completely spawned condition. Note that fecundity increases very quickly with increasing size. Thus, even small changes in the demographics of the population in the upper size classes has disproportionate effects on egg production. Using the size-specific function relating fecundity to size class, egg production m^{-2} can be estimated (F_{tot}) as the sum of the individual fecundities. Within a single 5 mm size class the sum of the individual fecundities is ($n_1 \times F_{ind}$), where n_1 is the number in the size class with midpoint 1 in mm. The given formulation does not address the proportion of the population that is female or the size distribution of female oyster relative to males. For size-specificity this requires a modifier for each size class. For example, the size class with mid point at 28 mm and with 35% female would modify the value ($n_1 \times F_{ind}$) to (0.35 × n_{28} × 0.40). Cox and Mann (1992) suggest parity in sex ratio, and given the lack of other relevant data a single sex ratio modifier is adopted, F_q, and the value arbitrarily set at 0.5 (50% female in all size classes).

F_{ind} and hence F_{tot} can be modified based on salinity effects. A modifier, F_s, can be used to decrease F by a proportion, effected by multiplying by a value from 1.0 (no effect) to 0.0 (total effect). The described size-specific fecundity relationship was developed for material collected in 1988 at a mean salinity of 13.5. For current application an estimate of the magnitude of F_s can be made from the data of Mann et al. (1994, Tables 1 and 2). The lowest salinity at which viable eggs were found was 8.5 ppt. At values of salinity

TABLE 1.

Oyster size class distribution by 5mm interval and reef number based on Fall 1993 survey data.
All values are individual oysters per sq. m.
Reef numbers correspond to reef names and locations on Figure 1B.

	Mid point of size class (mm for 5 mm interval)																								
Reef	12.5	17.5	22.5	27.5	32.5	37.5	42.5	47.5	52.5	57.5	62.5	67.5	72.5	77.5	82.5	87.5	92.5	97.5	102.5	107.5	112.5	117.5	122.5	127.5	Total
1	0.0	0.0	0.1	0.7	1.5	3.8	5.3	7.8	7.6	10.9	9.0	8.4	6.3	4.0	1.8	1.2	0.3	0.1	0.1	0.0	0.0	0.0	0.0	0.0	68.9
2	0.0	0.0	0.0	0.0	0.2	0.2	0.6	1.2	1.7	2.4	2.9	3.2	1.9	1.8	1.1	0.8	0.3	0.1	0.0	0.1	0.0	0.0	0.0	0.0	18.4
3	0.0	0.0	0.0	0.0	3.1	0.0	6.1	27.6	27.6	52.2	55.3	70.6	36.8	30.7	21.5	9.2	3.1	3.1	0.0	3.1	0.0	0.0	0.0	0.0	350.0
4	0.5	0.5	0.6	5.3	9.7	19.0	22.5	39.9	31.4	36.7	23.4	16.5	7.6	3.0	2.4	1.9	0.4	0.2	0.0	0.0	0.0	0.0	0.0	0.0	221.6
5	1.3	1.3	2.3	2.6	10.7	12.2	25.4	37.8	41.0	40.9	39.5	29.6	15.7	7.5	1.9	1.3	0.4	0.8	0.0	0.0	0.0	0.0	0.0	0.0	272.2
6	0.0	0.0	4.2	6.4	0.0	10.6	10.6	31.9	53.1	38.2	36.1	21.2	21.2	14.9	8.5	4.2	2.1	6.4	2.1	0.0	0.0	0.0	0.0	0.0	271.8
7	0.2	0.0	0.2	1.2	2.8	6.7	10.7	19.7	24.8	30.5	28.5	22.3	11.6	6.1	4.0	2.8	1.3	0.0	0.0	0.2	0.0	0.0	0.0	0.0	173.4
8	0.0	0.0	0.0	1.1	4.2	9.1	12.7	24.0	15.2	19.2	13.7	14.6	5.8	4.9	1.7	1.0	0.3	0.3	0.3	0.2	0.2	0.0	0.0	0.1	128.6
9	0.0	0.0	0.0	0.2	1.3	4.6	8.9	11.9	12.2	16.1	9.7	7.3	4.3	3.2	0.8	0.8	0.5	0.5	0.2	0.2	0.0	0.0	0.0	0.0	82.9
10	0.0	0.0	0.3	0.8	2.2	3.0	7.3	5.7	5.2	4.6	2.2	0.8	0.5	1.4	0.0	0.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	34.8
11	0.0	0.0	0.9	0.9	3.1	2.3	2.2	2.0	1.4	0.2	1.6	0.4	0.5	0.2	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	15.8
12	0.0	0.0	0.1	0.1	0.8	2.6	2.7	3.2	2.9	3.2	2.9	2.6	1.5	0.8	0.2	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	23.9
13	0.0	0.0	0.0	0.0	0.1	0.5	0.3	0.8	0.6	0.9	0.5	0.5	0.4	0.2	0.1	0.1	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	4.8
14	0.0	0.0	0.0	0.0	0.2	0.4	0.6	1.3	1.2	1.3	1.5	1.2	1.1	0.6	0.6	0.3	0.3	0.1	0.0	0.1	0.1	0.0	0.0	0.0	11.0
15	0.0	0.0	0.1	0.2	0.9	1.8	3.1	3.9	4.0	4.0	2.7	2.0	1.5	0.9	0.4	0.3	0.2	0.1	0.1	0.1	0.1	0.0	0.0	0.0	26.4
16	0.0	0.1	0.7	2.1	4.0	4.7	5.0	4.7	3.3	2.4	1.3	1.0	0.4	0.2	0.1	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	30.2
17	0.0	0.0	0.0	0.1	0.4	0.6	1.0	1.1	1.2	1.5	1.9	1.9	1.3	1.2	0.5	0.6	0.3	0.2	0.0	0.0	0.1	0.0	0.1	0.0	14.2
18	0.0	0.0	0.0	0.1	0.4	0.7	1.3	1.5	1.3	1.3	1.1	0.9	0.6	0.4	0.2	0.2	0.1	0.1	0.0	0.0	0.0	0.0	0.0	0.0	10.2
19	0.0	0.0	0.1	0.1	0.3	0.9	0.9	1.5	1.3	1.4	0.9	0.5	0.3	0.3	0.1	0.1	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	8.7

< 8.0 assume $F_s = 0.0$ (total compromise of eggs—no viability). There is no clear salinity-fecundity relationship in this limited data set. Nor is there a good data set from the literature for this salinity range. For the current application, a tentative linear relationship is proposed from 8 to 13.5 ppt with the following estimators for F_s:

$$\text{If Salinity } (S) > 13.5, F_s = 1.0$$
$$\text{If Salinity } (S) < 13.5, \text{ then } F_s = [(S - 80.0)/(13.5 - 8.0)] \times 1.0$$
$$= (S - 8.0)/5.5$$

Fecundity can be modified by disease. This can be incorporated with a further modifier, F_d. This decreases fecundity as a modifier in the same manner as F_s, ranging from 1.0 to 0.0. Disease is described by a weighted prevalence value. Given that the size-specific fecundity estimator was developed with oysters that probably had low prevalence of disease, but at low intensity (therefore, low-weighted prevalence, see Cox and Mann 1992) the estimator already incorporates the disease effects for this site, that is F_{ind} is effectively ($F_{ind} \times F_d$). This value was therefore fixed at 1.0.

TABLE 2.

James River Stock Assessment: Fall 1993. Estimates of small (<62.5 mm) and market (>62.5 mm) oyster standing stock for defined reefs.
Values given as mean number of bushels with 95% CI for whole reef

Reef #	Reef name	Area acres	Small oysters			Market oysters			Total		
			mean	mean + CI	mean – CI	mean	mean + CI	mean – CI	mean	mean + CI	mean – CI
	Upper Deep Water										
1	Shoal	234	46472	61252	31692	37579	49240	25918	84051	110492	57610
	Lower Deep Water										
2	Shoal	20	798	1089	508	1371	1773	969	2169	2862	1477
3	Upper Horsehead	3	3588	6747	429	1348	2594	101	4936	9341	530
4	Middle Horsehead	19	16877	22083	11671	1158	1795	521	18035	23878	12192
5	Lower Horsehead	19	19963	24487	15439	2954	4729	1179	22917	29216	16618
6	Moon Rock	4	3948	6152	1744	791	1360	223	4739	7512	1967
7	V-Rock	72	45950	52120	39780	11842	13906	9777	57792	66026	49557
8	Point of Shoals	132	55906	68893	42919	25463	31617	19309	81369	100510	62228
9	Cross Rock	37	11151	15252	7050	2329	2972	1685	13480	18224	8735
10	Shanty Rock	4	471	909	32	65	160	0	536	1069	32
11	Dry Lump	6	360	578	142	40	90	0	400	668	142
12	Mulberry Point	87	6436	9899	2973	3937	5633	2240	10373	15532	5213
13	Swash	165	2356	4052	657	1687	2989	385	4043	7041	1042
14	Upper Jail Island	612	13560	19624	7497	27578	43337	11818	41138	62961	19315
15	Swash Mud	1245	104703	125738	83669	56092	66346	45838	160795	192084	129507
16	Offshore Swash	627	62175	89705	34644	28911	60710	0	91086	150415	34644
17	Lower Jail Island	629	23571	37856	9286	24936	33768	16104	48507	71624	25390
18	Offshore Jail Island	1017	31884	42626	21141	20117	26343	13890	52001	68969	35031
19	Wreck Shoal	585	15188	23107	7269	10671	15716	5625	25859	38823	12894
	Reefs 1-19 inclusive	5517	465357	612169	318542	258869	365078	155582	724226	977247	474124

Where size-specific weighted prevalence data exist within a population (they did not for this study) the contributions of Barber et al. (1988), Choi et al. (1989, 1993), and Kennedy et al. (1995) provide the basis for further development of appropriate F_d values.

Fertilization efficiency is density dependent, and described as a multiplier, F_f. Values range from 1.0 (100% fertilization) to 0.0 (no fertilization). The following is rewritten from Levitan (1991):

$$\log \% \text{ fertilization} = 0.72 \, (\log OD) + 0.49 \text{ or}$$
$$\% \text{ fertilization} = 0.49 \times OD^{0.72}$$

where OD is total oyster density in oyster m^{-2}. To provide a correction factor for the present application the values must be expressed on a 0–1 range, rather than a percentage.

$$F_f = 0.0049 \times OD^{0.72}$$

Production of larvae (strictly speaking embryos or fertilized eggs) m^{-2} is therefore estimated by $(F_{tot} \times F_q \times F_s \times F_d \times F_t)$ in units of larvae m^{-2}.

Estimation of Retention of the Larvae Within the James River During Planktonic Development

Retention of larvae in the James River during their planktonic stage is estimated by use of a 3-D flow model with a 12 × 15 second grid size, approximately square at this latitude and longitude with 160 × 160 m dimension (Hamrick 1992a, Hamrick 1992b), and a time step of 90 sec. Duration of the larval development (= planktonic) period is set at 21 days, a conservative estimate of planktonic existence. Given the exponential nature of larval mortality curves and the nature of retention in the James River, both described later in the text, the effect of reduction in this estimate is relatively minor until estimated larval duration becomes unreasonably short for prevailing salinities and temperature. The 3-D model provides estimates of loss to advection only, and gives the cumulative number of competent to metamorphose larvae in each of the cells of a grid overlaying the area of origin and the adjacent region. To develop estimates of retention and advective losses river wide, egg production estimates were developed using data from Table 1 (see Results) as further described in Table 5 (see Results). To estimate losses to advective processes only the simulation was run with an assumption of 100% fertilization, that is the following values were assumed: $F_q = 0.5$, $F_s = 1.0$, $F_d = 1.0$, and $F_t = 1.0$. In the simulation eggs were released into the water column for the entire oyster population over a 12-h period in one tidal cycle with the initial concentration in each cell being dictated by oyster density and demographics within the strata underlying that cell. Larvae were assumed to be slightly negatively buoyant passive particles, the model did not incorporate complex larval behavior responses to oriented environmental stimuli. Advective loss estimates were subsequently incorporated into fertilization, growth, and recruitment estimates that incorporate density dependence as will be illustrated later.

To examine settlement after advective loss was accounted for, a 21-day simulation (the assumed duration of larval development) was run. At hourly intervals after the 21-day pelagic component the cumulative counts of larvae in the bottom of three layers of the water column were estimated and "deposited" on the bottom. This process was repeated for the following 11 "model hours" to give a 12-h cumulative total. Although larvae may settle over a period of greater than 12 h in the field the simulation effectively removed the vast majority of the larvae in the water column in this period. Development of spatial settlement estimates does not discriminate with respect to source of larvae, only the eventual size of settlement and metamorphosis, that is the output procedure does not discriminate between larvae that originate on each of the 19 reef sources. The "larval pool" is considered homogenous once it is constructed with respect to source. Thus, estimating return of larvae to the source reef within the confines of the total area was not attempted, only numbers of larvae retained from a simulation of a single simultaneous spawning of all reefs. This is an acknowledged deficiency of the simulation, but was dictated by computational limitations.

Estimation of Larval, Metamorphic and Post Settlement Mortality

While in the water, column larvae are subjected to daily mortality associated with biological and physical stress. This is accommodated by a larval mortality estimator, where L_{mort} is the daily larval mortality rate [a proportional value between 1.0 (all died) and 0.0 (no mortality)]. Survival is $(1-L_{mort})$ for a period of 1 day or $(1-L_{mort})^n$ for a n-day planktonic development period. For the current application L_{mort} values are adopted from typical data obtained in the VIMS Oyster Hatchery at Gloucester Point, which operates in salinity ranges comparable to those of the appropriate section of the James River covered by the 3-D model. Typical L_{mort} values for the hatchery are in the range 0.1–0.07 with extreme values of 0.25 only occurring with red tide (Cochlodinium helicoides) incidence. For the immediate application the range of L_{mort} is set at 0.1–0.07. This modifier can be applied as a single computation to estimate competent to metamorphose larval supply at the end of the 21-day larval development period. Thus, when L_{mort} is set in the range 0.1–0.07 the terminal modifier is $(1-L_{mort})^{21}$. The decreasing exponential nature of this curve is such that the terminal value is gradually but increasingly insensitive to change in number of days of larval development above 21, but becomes increasingly sensitive if the duration of the larval phase is significantly decreased.

A modifier was developed to describe the probability of finding suitable substrate, P_{sub}, a modifier with a value between 1.0 and 0.0, that can be estimated from field surveys of substrate abundance. Relevant data is taken from Table 5.2 (see Results), is specific to the reef location in the James River, and based on 1994 survey data. A shell layer 1 cm thick covering 1 sq. m of bottom has a volume of 10 L. For the current purpose a premise is adopted that a shell layer a minimum of one cm thick is required to offer a suitable substrate (respecting the fact that above data include buried shell retrieved in the collection process that could not be consistently distinguished from surface shell, and thus the estimates are probably generous with respect to available area). Therefore, the values in Table 5.2 (see Results), when divided by 10 give an estimate of P_{sub} as a dimensionless factor. Thus:

$$\text{If shell volume} > 10 \text{ L } m^{-2}, P_{sub} = 1.0$$
$$\text{If shell volume} < 10 \text{ L } m^{-2}, P_{sub} = 0.1 \times \text{Shell Vol (no units)}$$

A modifier was developed to describe the probability of finding substrate free of fouling organisms that precluded settlement. This was termed P_{foul} and can vary between 1.0 (no fouling) and 0.0 (complete preclusion of settlement). A value of $P_{foul} = 0.33$ was adopted based on the findings of Rheinhardt and Mann (1990) for the James River. A further modifier was developed to describe the

TABLE 3.

Mean monthly salinity and temperature for reef sites in the James River based on river flow data (salinity) and York River continuous data (temperature).

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Salinity (ppt)												
DWS (Deep Water Shoal)	4.25	3.94	3.63	4.02	4.18	6.42	7.87	8.86	8.76	8.51	6.30	4.77
HH (Horsehead)	5.95	5.63	5.09	5.56	5.91	8.35	9.84	10.80	10.58	10.32	8.15	6.64
WS (Wreck Shoal)	8.35	8.03	7.16	7.75	8.37	11.09	12.63	13.55	13.17	12.88	10.78	9.28
Temperature (°C)	4.83	5.14	7.93	13.72	19.00	24.07	27.01	27.19	24.61	19.18	13.73	8.26

probability of successful completion of metamorphosis to the attached form, P_{met}. This can again vary between 1.0 (all survive) and 0.0 (no survival). For the present application the value is set to that typical of VIMS Oyster Hatchery operation at 0.25. Thus, $P_{met} = 0.25$.

Recruitment to the benthos is therefore estimated from larval supply values in Table 5.2 (see Results) by modifying the correction function to incorporate $(1-L_{mort})^{21}$, P_{sub}, P_{foul} and P_{met} thus:

$$\left\{ \sum_{reef19}^{reef1} [(F_{tot} \times F_q \times F_s \times F_d \times F_f) \times (1-L_{mort})^{21} \times P_{sub} \times P_{foul} \right.$$

$$\left. \times P_{met} \times A] \right\} / 3068 \times 10^{12}$$

where 3068×10^{12} is the sum of larval production for all reefs (Table 5.1, see Results).

Post settlement mortality rate for the time period required to attain the mid point of the 5 mm size class is described by J_{mort} (anywhere between 1.0 and 0.0), the daily juvenile mortality rate. Survival is $(1-J_{mort})^{dp}$ where dp is the number of days to the mid point of the 5 mm size class. Values of J_{mort} are given in Roegner and Mann (1995, Table 2, Summer data at −75 cm exposure) and vary weekly, from 13.3 for Week 1 post settlement, to 0.4 for Week 2, to 0.2 for Week 3, and 0.1 for Week 4. The value of dp is estimated from growth rate of post settlement juveniles. In a number of trials with oysters from the VIMS Oyster Hatchery at Gloucester Point growth rate varies in the range 0.9–2.5 mm week^{-1}, with typical values of 1.5–2.0 mm week^{-1}. This gives typical daily values of 0.215–0.29 mm day^{-1}. Data from Roegner and Mann (1995, Figure 3B, −25 and −74 cm exposure level oysters) estimates growth to the equivalent area of a 6 mm diameter circle (considered representative of a 8 mm height oyster) to require 20 days. This is equivalent to a daily growth rate of 0.4 mm day^{-1}, slightly higher than that of hatchery oysters. These animals were, however, hung in a vertical array above the bottom and probably enjoyed marginally increased growth relative to bottom dwelling individuals. Adopting a time to 8 mm of dp = 28 days requires a linear growth rate of 0.29 mm day^{-1}, in agreement with hatchery experiments and only marginally slower than Roegner and Mann (1995). Cumulative mortality to 8 mm is taken as 93% (from Roegner and Mann 1995). Thus:

$$(1-J_{mort})^{dp} = 0.07.$$

Recruitment to the mid point of 5 mm size class is estimated by further by modifying the correction function to the larval supply values in Table 5.2 to incorporate $(1-J_{mort})^{dp}$ thus:

$$\left\{ \sum_{reef19}^{reef1} [(F_{tot} \times F_q \times F_s \times F_d \times F_f) \times (1-L_{mort})^{21} \times P_{sub} \times P_{foul} \right.$$

$$\left. \times P_{met} \times (1-J_{mort})^{dp} \times A] \right\} / 3068 \times 10^{12}$$

Values per unit area for individual reefs are obtained by not incorporating the reef area descriptor A.

RESULTS

Estimation of Oyster Standing Stock and Demographics.

Data are presented in two formats. Table 1 gives demographic information by reef number on a per sq. meter (hereafter m^{-2}) basis. This table is also an input matrix to the 3-D larval retention simulation model. Note that percentage distribution within each size class is fairly constant throughout the various reefs. Note also that these values probably represent the end of growth in that calendar year. There is a lack of representation in the very small size classes in Table 1 because the oysters grew since the preceding summer. Table 2 provides further information on total standing stock by incorporating individual reef area, which is highly vari-

TABLE 4.

Estimated spawning dates of oysters in James River using D′ values from 420 to 460 and mean daily temperature by Julian day from Table 3.

		D′: day-degree minimum requirements			
Date	Julian day	420	434	450	460
14-Jun	165	430			
15-Jun	166		443		
16-Jun	167			455	
17-Jun	168				467
15-Jul	196	423			
17-Jul	198		440		
19-Jul	200			458	
20-Jul	201				461
12-Aug	224	423			
15-Aug	227		438		
18-Aug	230			453	
20-Aug	232				467
12-Sep	255	431			
16-Sep	259		434		
22-Sep	265			457	
26-Sep	269				469
9-Nov	313	421			

TABLE 5.1.

Estimates of larval supply to individual reefs based on egg production data as described in text.

Reef	Area acres	Area m^2*10^3	Total eggs *10^12	Egg production 10^6 m-2	Ff %fert.eggs	Salinity to estimate Fs	Egg production corrected for Fs and Ff *10^6 m-2	Egg production corrected for Fs and Ff *10^12	Survival to pediveliger at Lmort=0.1 10^6	Survival to pediveliger at Lmort=0.07 10^6
1	233.92	947	377	398	1.81	8.5	0.66	0.62	67993	135366
2	19.93	81	12	155	1.40	8.5	0.20	0.02	1737	3457
3	3.01	12	36	2927	2.32	10.8	34.60	0.42	46096	91773
4	19.47	79	65	828	2.18	10.8	9.19	0.72	79208	157696
5	19.47	79	95	1203	2.24	10.8	13.74	1.08	118405	235732
6	3.95	16	28	1780	2.24	10.8	20.32	0.32	35546	70768
7	72.05	292	279	958	2.10	10.8	10.25	2.99	326986	650997
8	131.71	533	329	617	2.01	10.8	6.31	3.36	368024	732698
9	36.89	149	62	414	1.87	10.8	3.95	0.59	64472	128356
10	3.58	14	6	414	1.60	13.5	6.63	0.10	10508	20920
11	5.93	24	1	37	1.35	13.5	0.50	0.01	1309	2606
12	86.85	351	37	104	1.48	10.8	0.79	0.28	30248	60220
13	165.00	668	17	25	0.98	10.8	0.12	0.08	9089	18096
14	611.80	2476	223	90	1.24	10.8	0.57	1.41	154140	306877
15	1244.90	5038	656	130	1.51	10.8	1.00	5.05	553054	1101075
16	626.51	2535	179	71	1.56	10.8	0.56	1.42	155508	309600
17	628.93	2545	341	134	1.32	13.5	1.77	4.50	492847	981209
18	1017.20	4117	231	56	1.22	13.5	0.68	2.81	307261	611725
19	584.76	2366	94	40	1.17	13.5	0.46	1.09	119694	238299
Total			3068					26.89	2942124	5857471

Total egg production based on oyster demographics as described in Table 1 using the following relationships:
(i) Weight = 0.000423 *Length ^1.7475 from Mann and Rainer (1992) and unpublished field data by Mann collected in 1994.
(ii) Fecundity = 39.06 *Weight ^2.36 from Thompson et al. (1996) using data of Cox and Mann (1992)
(iii) Egg production estimates assume 50% female in all size classes
Ff, % fertilization = $0.49*OD^{0.72}$ (from Levitan 1991) where OD is oyster density in oysters m-2
Salinity to estimate Fs is based on salinity index of reef: reefs 1-3 incl. = DWS; reefs 4-9 incl. and 12-16 incl. = HH; reefs 10, 11, 17, 18 and 19 = WS (see text).
Fs = [(S − 8.0)/(13.5 − 8.0)] *1.0 = (S − 8.0)/5.5 from Mann, Rainer and Morales (1994, JSR, 13(1): 157-164)
Survival to pediveliger is estimated as = $(1-Lmort)^{21}$
L mort = 0.1 is 10% survival per day for a 21-day development period
L mort = 0.07 is 7% survival per day for a 21-day development period
L mort values estimated from VIMS hatchery experiments
Larval supply from 3D model, see Figures 4 and 5.
Shell substrate availability from Fall 1994 survey, see text

able as illustrated by Figure 1B. A brief summary of 1993 population sizes is appropriate. Absolute densities of oysters by reef are highly variable, from high values of 350, 272, 271, 222, 173, and 129 per sq. meter at Upper Horsehead, Lower Horsehead, Moon Rock, Middle Horsehead, V Rock and Point of Shoals respectively, to low values of 14, 11, 10, 9, and 5 at Lower Jail Island, Upper Jail Island, Offshore Jail Island, Wreck Shoal, and Swash respectively. Mean estimates of standing stocks of seed (small) and market oysters (<62.5 and >62.5 mm maximum dimension respectively[1]) are 465,356 and 258,869 bushels respectively, for a total of approximately 724,225 bushels in the surveyed section of James River. The confidence interval around these values gives upper and lower values of 318,542 and 612,169 bushels for seed (small), and 155,582 and 365,078 bushels for market oysters respectively. A limited number of individual rocks had lower estimates of zero for market oysters—these reflect analysis of data that include a large number of samples with zero market size oysters present. Substantial seed (small) oyster resources are present in a number of locations: Upper Deep Water Shoal, the components of Horsehead Rock, V Rock, Point of Shoals, Cross Rock, and the large areas of Swash and Jail Island. The bulk of market oysters are located on the same rocks.

Salinity and Temperature

Table 3 gives monthly mean data for salinity at three locations, Deep Water Shoal, Horse Head, and Wreck Shoal estimated from river flow as described earlier. At Deep Water Shoal the annual range is from <4.0 to 8.86 ppt. At Horse Head the annual range increases to 5.09–10.8 ppt, whereas at Deep Water Shoal the annual range is from 7.16 to 13.55 ppt. Lowest values are observed in March and maximum values observed in August. The annual temperature range, based on York River continuous data, varies from 4.83°C in January to >27°C in July and August.

[1]The adoption of a 62.5 mm distinction is in accordance with harvest regulation at the time of the study. Before the study period the minimum size for market oysters was 76 mm. The larger size limit was again adopted by regulation in 1995.

TABLE 5.2.

Working example of recruit estimate: Surviving pediveliger numbers corrected for advection loss, after further correction for substrate limitation (Psub), fouling (Pfoul) and competency (Pmet)

Reef	Larval supply *10^6 m-2	After loss to advection only *10^12	Advection corrected Lmort = 0.1 total pediv *10^6	Lmort = 0.07 total pediv *10^6	Psub	#pediveliger*Psub *Pfoul*Pmet Pfoul = 0.33, Lmort = 0.1 *10^6	Pmet = 0.25 Lmort = 0.07 *10^6	Corrected *0.07 for survival to 4 weeks Lmort = 0.1 *10^6	Lmort = 0.07 *10^6	4 weeks post set: 5–7 mm Lmort = 0.1 spat m-2	Lmort = 0.07 spat m-2	15–20 mm* spat per sq. m
1	5	4.73	6232	12407	0.43	221	439	15	31	16	32	5.32
2	8	0.65	159	317	0.29	4	8	0	1	3	7	2.8
3	15	0.18	4225	8412	0.93	325	647	23	45	1870	3722	30
4	15	1.18	7260	14454	0.52	311	620	22	43	277	551	53.8
5	16	1.26	10853	21607	1.00	895	1783	63	125	796	1584	104.5
6	16	0.26	3258	6486	0.70	188	375	13	26	824	1640	187.3
7	16	4.67	29971	59669	0.76	1867	3717	131	260	448	892	79.17
8	14	7.46	33732	67158	0.66	1826	3635	128	254	240	477	61.05
9	16	2.39	5909	11765	0.74	361	718	25	50	169	337	77
10	15	0.22	963	1918	0.73	58	115	4	8	280	558	44
11	13	0.31	120	239	1.50	15	30	1	2	43	86	35.7
12	12	4.22	2772	5520	0.21	48	96	3	7	10	19	8
13	12	8.01	833	1659	0.04	3	5	0	0	0	1	2
14	11	27.23	14128	28128	0.19	224	446	16	31	6	13	1.17
15	14	70.53	50692	100923	0.24	1020	2032	71	142	14	28	5.85
16	16	40.57	14254	28377	0.31	366	728	26	51	10	20	12.92
17	10	25.45	45174	89936	0.16	585	1165	41	82	16	32	1.05
18	13	53.51	28163	56070	0.41	957	1906	67	133	16	32	7.12
19	12	28.40	10971	21842	0.71	638	1270	45	89	19	38	8.43
total		281.23	269671	536887		9912	19733					

Psub: substrate dependency based on shell volume m-2. If shell volume > 10 L m-2, Psub = 1.0; if < 10 L m-2 Psub = 0.1 * shell vol
Pfoul = % of substrate available for settlement (not fouled). Pfoul = 0.33 taken from Rheinhardt and Mann (1990, Biofouling, 2:13–25)
Pmet: % completing metamorphosis from apparent competency (VIMS hatchery)
Survival rate to 4 wk post settlement (approx. 5–7 mm length) taken from Roegner and Mann (1995, MEPS, 117:91–101)
*spat data from stock assessment: Mann. unpublished data

Egg Production, Spawning and Fertilization

Estimates of spawning dates are given in Table 4 for values of D', the day degree estimator, of 420, 434 (the mean value calculated for James River oysters in 1988), 450 (estimated by Price and Maurer 1971), and 460 using mean daily temperatures estimated from Table 3. Mean water temperature exceeds 12°C on April 7 and stimulates first spawning in the Julian day period 165–168 (June 14 to 17). A second spawning is estimated in the Julian day period 196–201 (July 15 to 20). By the estimated third spawning (Julian day 224–232, August 12 to 20) a slight lag is observed for the higher D' values. By the fourth estimated spawning (Julian day 255–269, September 12 to 26) the time lag between D' values of 420 and 460 is 14 days, with the cumulative effects of three prior spawnings being exacerbated by decreasing Fall water temperatures. A D' value of 420 suggests a fifth possible spawning in November; however, this is at a period of decreasing water temperature when absolute temperature is too low to stimulate spawning and larval forms would not survive. There is support for the above estimates in that long term records of oyster spat settlement in the James (VIMS archives) indicate settlement from as early as June and ending as late as October. Although the employed D' value of 434 is based on direct observations from the study site, any error incurred will probably be toward a low value for D' if weight is given to the observations of Barber et al. (1991) on spawning patterns of oysters from east coast origins when maintained in the Delaware Bay environment—namely, that oysters from more northerly origins spawned at lower temperatures, sug-

gesting an increasing D' in the current context with more southerly origin. Exceptionally late spat settlements associated with a fourth spawning only occur in years when unusually high water temperatures are observed in September and October.

Using size distribution data for spawning oysters of the form given in Table 1 allows estimates of egg production m^{-2} for the chosen reef system. To make river-wide estimates of egg production the required calculation is the sum of (F_{tot} × reef area) for all 19 reefs. An example of this calculation is given in Tables 5.1 and 5.2 using the data presented in Table 1 as a base for calcuation.

Retention of the Larvae Within the James River During Planktonic Development

Figures 4A through 4F illustrate predicted distributions of larvae in the bottom water layer after release over one tidal cycle (4A at time step 1), and then after 5, 10, 15, 20, and 25 tidal cycles (4B through 4F respectively). The simulated release is driven by June 1985 river flow data and describes only advective loss in that no mortality function is incorporated at this stage. The data on larval concentration are given in $\log_{10}$ larvae m^{-3}. As expected there is an initial concentration on the spawning ground and a subsequent dispersal event. Field studies by Mann (1988) reinforced earlier suggestions by Ruzecki and Hargis (1988) that a tidal related frontal system off Newport News Point, marked by the letter N in Figure 4 A–F, was important in retaining larvae that were swept downstream of the reefs described in Figure 1. Figure 4 A–F
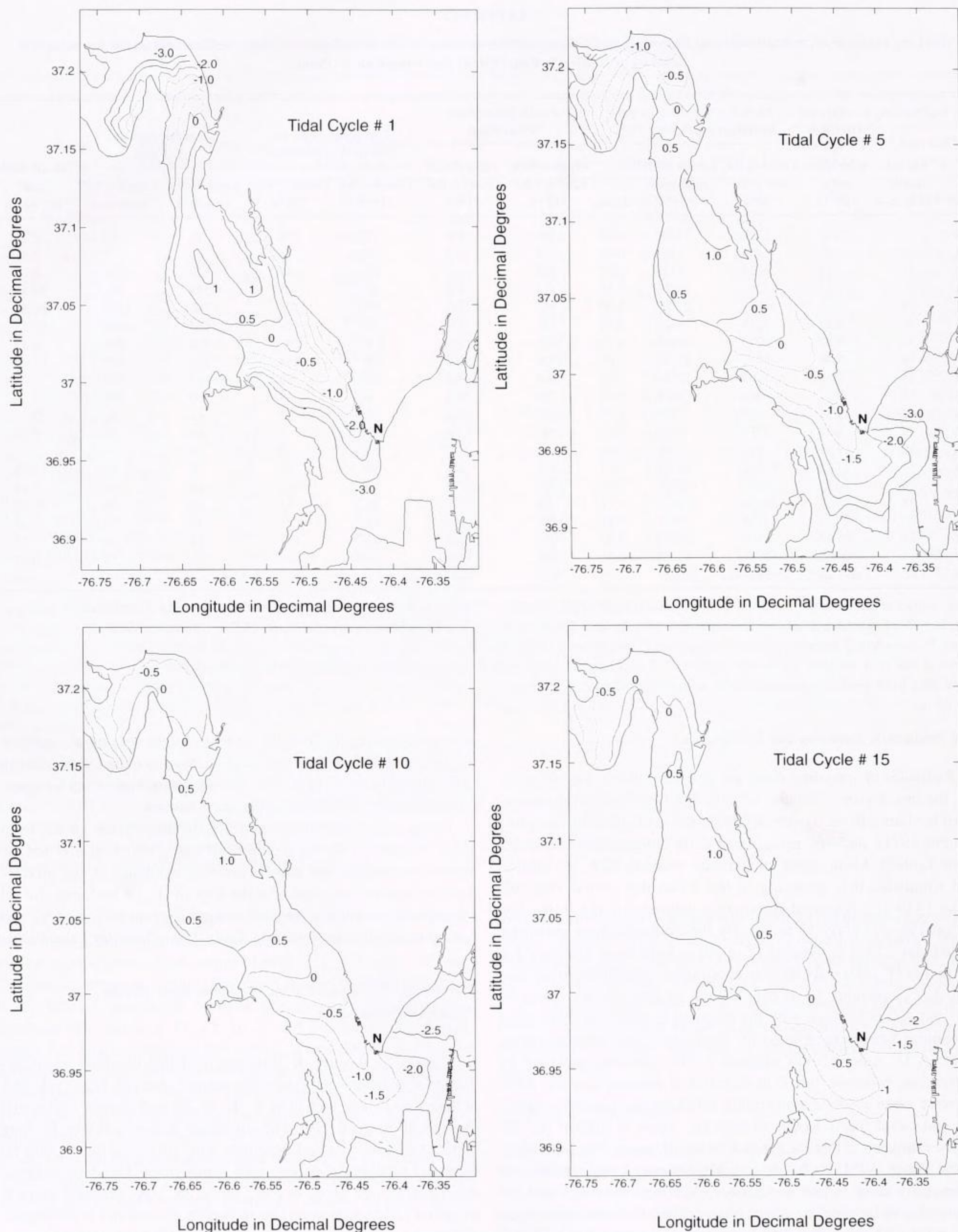
Figure 4. Predicted distribution of oyster larvae in the bottom water layer at time step = 0 after release over one preceding tidal cycle (4A), and then after 5, 10, 15, 20, and 25 tidal cycles (4B through 4F respectively). Units are $\log_{10}$ oyster larvae m^{-3}. Data were generated from fecundity estimates as given in Table 4. F_q was set at 0.5. F_s, F_d, and F_f were all set at 1.0. 100% fertilization was assumed with no mortality. Water flow was set at July 1985 values. N marks the location of Newport News Point. See text for further details.
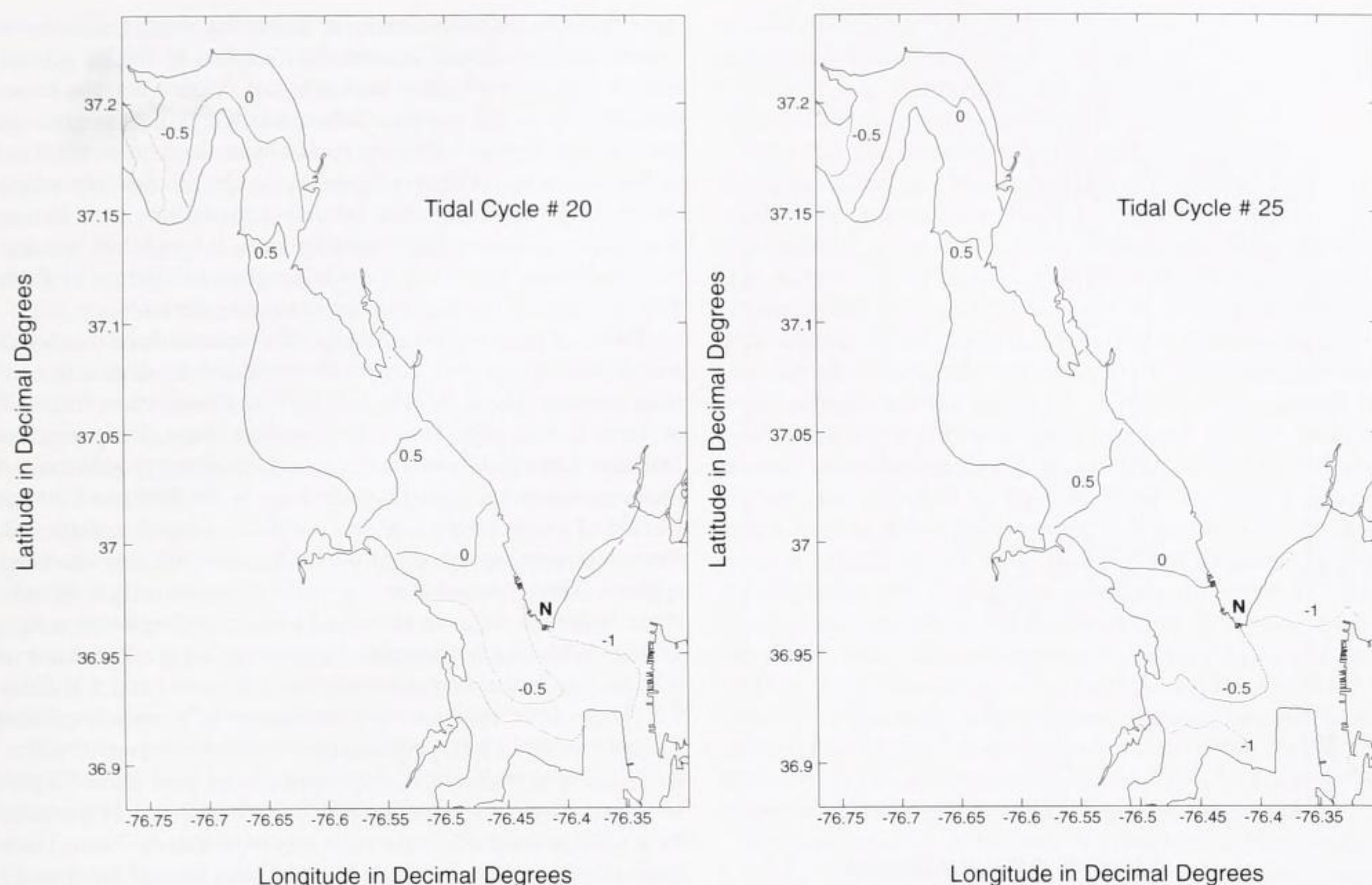
Figure 4. Continued.

suggest that most of the larvae from extant reefs in the upper James River do not extend in significant numbers that far downstream in typical summer flow conditions, but spread out in both up and downstream directions and remain in the approximate region of their production in the simulation. This pattern becomes quite stable at 20–25 tidal cycles, as demonstrated by the similarity in Figures 4E and F. The simulated retention of larvae in their region of origin is in agreement with monitoring data shellstrings in the field surveys (Virginia Institute of Marine Science Library Archive), and previous dye simulations reported in Ruzecki and Hargis (1988). The important observation serves to offset a limitation of the current simulation, namely the lack of a larval behavior component. The water column in the region of retention is relatively shallow, generally <5 m with the exception of the major channel, and demonstrates weak vertical density structure in comparison to the frontal system region further downstream (see Mann 1988). The lack of density structure in the majority of the water column probably serves to minimize larval redistribution by oriented swimming with the exception of upstream movement of larvae entrained in bottom water in the channel (see Figure 1 in Mann 1988). The simulation is further aided in that minor wind driven mixing serves to maintain homogeneity of the upper water column containing early larval stages; however, the simulation remains limited with respect to behavior of pediveliger forms.

Figure 5 shows contour plots of cumulative estimated settlement over a twelve hour period after a 21-day larval development period. Input data for egg production in the computer code that generated Figure 4 A–F is in units of millions m^{-2} (the range of values for input of eggs in the model was between 2.4×10^7 and 3×10^9 m^{-2}). Consequently, the contour values depicting larval

concentrations in Figure 5 are also in millions m^{-2} with values in the range $4–16 \times 10^6$ m^{-2}. The immediate visual comparison of Figure 5 is with Figure 1, A and B, the distribution of oyster habitat and surveyed reefs in the river. The sweep of high values on Figure 5 corresponds to Reef Numbers 3 through 8, 12, 13, and parts of 15 and 16 in Figure 1B. These are major productive reef systems. The high concentrations on the western shore of the river in Figure 5 coincide to the deep channel with a muddy bottom in Figure 1A, where little settlement occurs. From Figure 5 the intensity of larval supply to the individual reef systems was estimated by overlay of Figure 5 on Figure 1B of this report, estimates are given in Table 5.2. Of note are the modest losses to advection when all other losses are not considred, a decrease from 3068×10^{12} to 281×10^{12} in total number (compare column 4 in Table 5.1 versus column 3 in Table 5.2). These vary from <1 to approximately two orders of magnitude. Sequential re-examination of Figures 4A through 4F support these estimates of modest losses.

Thus advective losses from a pool fertilized eggs that number:

$$\sum [(F_{tot} \times F_q \times F_s \times F_d \times F_f) \times A]$$

where $F_q = 0.5$, F_s, F_d, and $F_f = 1.0$, and A is reef area, for each of the 19 reefs are reflected in the relative values of egg production, with a cumulative value of 3068×10^{12} for the entire system as simulated, and competent to metamorphose larval supply in units of both millions m^{-2} and total values for the reef, as given in Tables 5.1 and 5.2. Although fixed values were employed for F_q, F_s, F_d, and F_f in this simulation the formulation can be modified to accommodate variation in these functions between different source reefs. Supply of competent to metamorphose larvae to individual
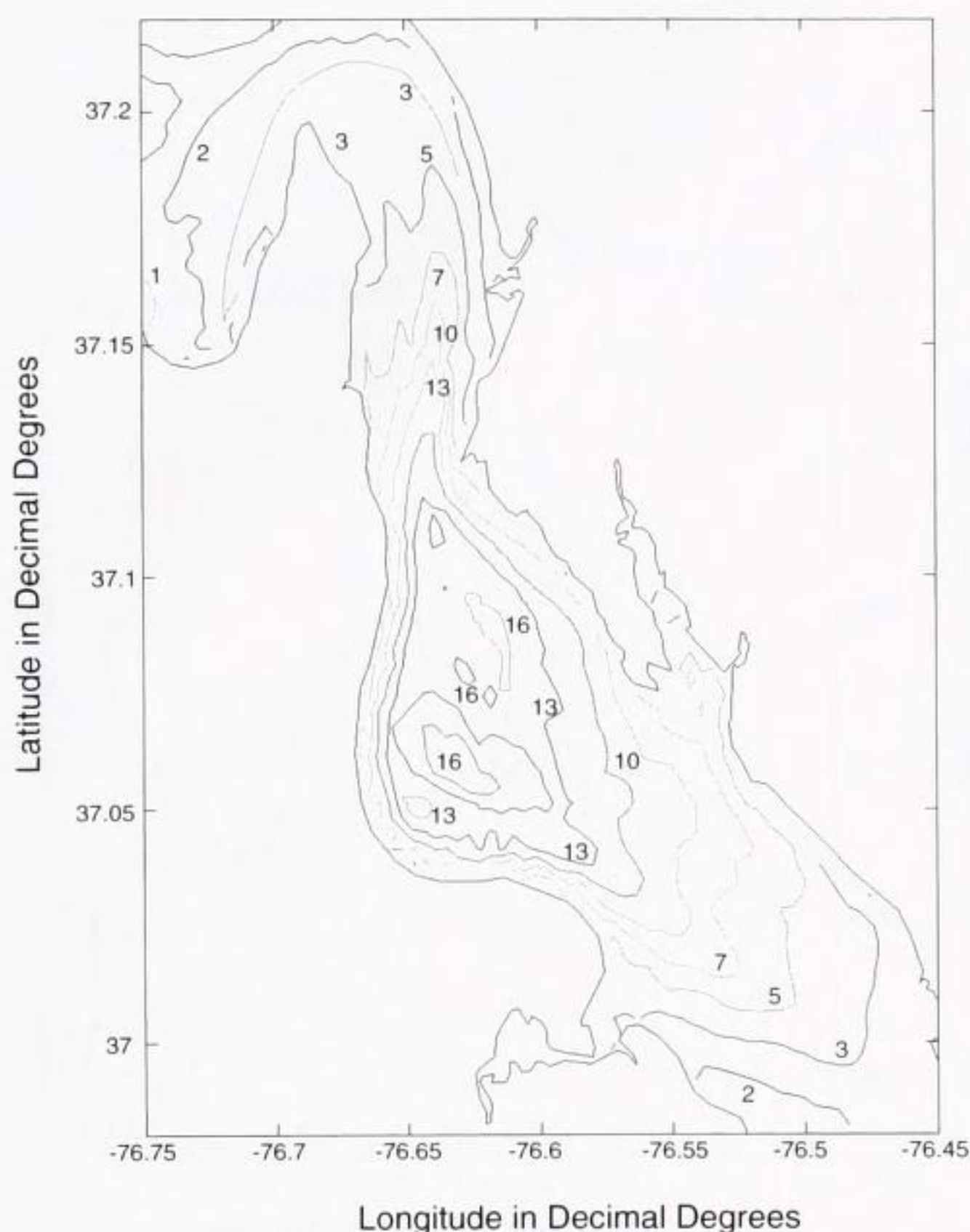
Figure 5. Contour map estimating cumulative numbers of oyster larvae, in millions m^{-2} accumulated over a twelve hour period, available for settlement in the James River, VA from a single simultaneous spawning of all oysters in the region as described in Table 4 and with constraints as for Figures 4, A–F. The simulation is terminal status after a 21 day developmental period. Spatial distribution patterns can be compared with Figures 1, A–B. See text for further details.

reefs in these instances is estimated by inflating or reducing the values in Table 5.2 by the ratio of total egg production for the chosen simulation to that employed for the development of data in Figure 5 and Tables 5.1 and 5.2. That is larval supply values, in units of millions of larvae m^{-2}, in Table 5.2 are corrected by the factor:

$$\left\{ \sum_{reef19}^{reef1} [(F_{tot} \times F_q \times F_s \times F_d \times F_f) \times A] \right\} / 3068 \times 10^{12}$$

where the value 3068×10^{12} reflects estimates of total egg production in the 3-D model run as described, and the incorporation of A, reef area, gives total larvae per reef in the sum estimation.

Estimation of Larval, Metamorphic and Post Settlement Mortality

Estimation of larval, metamorphic and post settlement mortality, including incorporation of advective loss to give final estimates of recruitment, are given in a sequential manner in Tables 5.1 and 5.2. All data is given on a reef specific basis. Table 5.1 gives reef area and unit area egg production. The correction function F_f generated from Levitan (1991) is given, together with the ambient salinity at spawning data (Table 3), and, with the reef specific association, used to estimate F_s. Note the very substantial losses associated with density effects at fertilization. In undisturbed oyster reefs where aggregate settlement occurs the use of

mean densities might over estimate loss at this stage; however, the current situation of reefs continually disturbed by fishing activity and the lack of contiguous hard substrate suggest that the losses described by F_f are realistic. Subsequently, egg data is given as absolute and density values by reef at spawning and as fertilized embryos after correction for F_s and F_f. Table 5.1 continues with a list of results of a correction for larval mortality over a 21-day period at two chosen daily mortality rates, 0.1 and 0.07 per day. Note the changing order of magnitude values in columns of Table 5 as the sequential calculation moves across the table.

Table 5.2 presents larval supply data obtained from overlay of reef distribution (Figure 1B) on the results of the dispersal modeling exercise (Figure 5). The reef specific data given in column 2 of Table 5.2 describe losses to advection alone. The correction functions generated from comparison of initial egg production and final egg supply are applied to the values in the final two columns of Table 5.1 to give the values of Columns 4 and 5 in Table 5.2. These represent supply of pediveliger larvae to the individual reef systems. These two columns are subjected to correction for substrate limitation, P_{sub}, as described earlier, fouling using a P_{foul} value of 0.33, and metamorphic competency using a P_{met} value of 0.25, to give further corrected values in Columns 7 and 8 of Table 5.2. These latter columns represent successfully metamorphosed junvenile oysters (spat) resulting from larval developments suffering differing mortality rates. In Columns 9 and 10 of Table 5.2 post settlement survivors are subjected to field estimates of mortality for a 4-wk period while growing to approximately 5–7 mm. These same values are then corrected to a unit area basis in columns 11 and 12 of Table 5.2. Finally, Column 13 provides, for comparison, field data for 15–20 mm juveniles (spat) from 1994 surveys. Given that mortality will continue in the growth period from 5 to 15 mm, the concordance between estimated and observed recruitment is reasonable—generally within or approaching one order of magnitude. The notable extreme is Reef Number 3, which exhibits a two order of magnitude discrepancy in values. No obvious explanation is forthcoming for this one data point.

DISCUSSION

Although the advancement of theoretical considerations remains important, elucidation of the quantitative basis of the relationships between cyclical environmental change, population growth, and natural and fishing mortality has clear utility as both disease and commercial exploitation maintain significant pressures on this limited resource. In developing the Paulik diagram as a conceptual tool for quantitative descriptions of the stock-recruit relationships in marine organisms, especially those with multistage life histories, Paulik (1973) underscored the importance of a sound quantitative basis to studies employing physical models of water flow in effecting larval dispersal. Such an approach allows estimation of sequential mortality and other losses on a quantitative basis during a progression from egg to recruit. Complete accounting in life history studies is rare, a situation that underscores the poor understanding of losses or gains associated with emigration and immigration respectively in species with planktonic larval forms. The role of dispersal rates and habitat patches as a governing factor in population fluctuations has not been limited to commercially exploited species like oysters, indeed it has been extensively discussed in context of aquatic organisms (Pulliam 1988, Gilpin and Hanski 1991, Pulliam and Danielson 1991, Pulliam et al. 1992, Doherty and Fowler 1994, Hanski 1994) with the general

conclusion that highly dispersive, planktonic life stages may dictate population abundance and allow colonization of new areas (see Strathmann 1974, Roughgarden et al. 1988, Doherty 1991, Alexander and Roughgarden 1996). While metapopulation dynamics theory continues to develop, comprehensive examples in the marine invertebrate literature remain limited. The current example contributes to the discussion and is unusual, as stated earlier, because of the ability to quantify both emigration by modeling, and assumes negligible immigration.

Estimation of standing stock through classic fishery independent stock assessment procedures has rarely been effected for oysters. This is surprising given their economic value and the suitability of random stratified sampling with hydraulic tongs for generating population estimates in support of management policies. In a continuing program, Mann and Wesson (1997) have expanded the 1993 to 1994 effort, briefly reported here, to a 4-y survey, and have demonstrated an ability to localize freshet impacts in marginal salinity zones, the effects of substrate enhancement in historically high settlement zones, and spatial demographic changes associated with regulatory limitations for "seed" and market oyster harvesting. The data strongly encourage the adoption of such assessments in other exploited oyster (and other bivalve) populations in shallow water locations.

Within given limitations oyster demographics (standing stock estimates) can be used to estimate individual and population level fecundity. Of considerable concern, however, is the inability to offer good values for disease and salinity related modifiers of fecundity. Although salinity and disease are widely acknowledged as major influences on bioenergetics of oysters they are poorly described in a quantitative sense in the literature, especially so for prevailing salinities in the upstream extant reefs in the James. Continuing efforts to develop coordinated bioenergetic and disease impact models (Powell et al. 1992, 1994, Powell et al. 1996, Hoffmann et al. 1995, Ford et al. 1997) do, however, offer some prospects for progress in this subject in the near future.

Development of larval production estimates from fecundity values involves a series of assumptions concerning synchrony and completeness of spawning, half life of gametes in the water column, dispersal (effective dilution) of those gametes during that half life period, and probability of fertilization given absolute concentrations of sperm and eggs. Choice of an appropriate model for the current application reflects a continuing and diverse debate in the literature. Good models for sessile bivalves are absent, but surrogates can be garnered from the echinoderm and annelid literature where prevailing small scale hydrodynamic conditions are similar to that encountered on an estuarine oyster reef. In addition to the model used here, that of Levitan (1991), other options are discussed by Levitan et al. (1991, 1992), Oliver and Babcock (1992a, 1992b), Babcock et al. (1994), Benzie et al. (1994), Benzie and Dixon (1994), and Thomas (1994). Contrasting models of fertilization are, however, offered for high-energy environments like the surf zone (Denny and Shibata 1989) but are considered inappropriate here. Note that the current data are for a model assuming a single, simultaneous spawning of the entire population. This is an unlikely event, and historical data from both direct examination of adult oysters (Mann et al. 1994) and temporal variation in settlement (Haven and Fritz 1985) indicate more than one spawning per year in the extant populations. Localized synchrony in spawning is highly probable, so the cumulative effect of these events approximates in magnitude that of a single synchronized spawning in the entire populations. Multiple spawnings (estimated at three to four events per oyster depending on annual temperature and salinity patterns) suggest variability in cumulative production over a spawning season within an order of magnitude interval of the single synchronized event estimate.

The importance of the James River oyster resource has been discussed earlier, and was the stimulus for earlier studies of larval dispersal by Ruzecki and Hargis (1989). Using the James River Hydraulic Model at the Vicksburg, Mississippi laboratory of the U.S. Army Corps of Engineers, Ruzecki and Hargis effected dye releases to simulate oyster spawning at six locations between Point of Shoals and Wreck Shoal (see Figure 1B) in the upstream direction and below Newport News Point in the downstream direction. After periods approximating larval development (20–40 tidal cycles were employed) all releases suggested greatest larval concentrations (settlement) at a point upstream from the point of origin with the exception of Point of Shoals and Wreck Shoal releases, both of which show general consistency with the current study in suggesting that while dispersion of the larvae occurs in both upstream and downstream directions, the region of greatest concentration remains in the upriver portion of the river over extant oyster beds. This consistency is further emphasized in the detail of the contours Figure 3 of Ruzecki and Hargis (1989) and Figure 5 of this study, where highest predicted concentrations of settlement occur over a swath of extant reefs from Lower Deep Water Shoal through Horsehead, Moon Rock, V Rock, Point of Shoals and Cross Rock (Numbers 2–9, Figure 1 B).

Spatial agreement of observed and predicted settlement regions is comforting, but there remains a discrepancy in the magnitude of variation observed between sites in the field, where two orders of magnitude might be expected between the highest and lowest sites, and that suggested by modeling where site differences are considerably lower. The model is not without limitations. Computational limitations resulting in treatment of the larval releases as a single pool have been mentioned earlier. In addition, the cell size used in modeling is 12 sec × 15 sec, approximating to a 160 × 160 m cell size at the latitude and longitude of the study site. Even though this scale incorporates approximately 3,000 cells in the models illustrated in Figures 4 and 5, the absolute cell size remains considerably larger than many features, notably local shell aggregation, that determine spatial elements of settlement in the field. Also, to reiterate an earlier comment, the effects of larval behavior within the water column have not been incorporated extensively into the model, even though they may be important (Mann 1988). Finally, the effects of absolute values and variation in water velocity, which is intimately related to bottom friction in the shallow regions and influenced by bottom microtopography associated with exposed substrate in an otherwise uniform bottom of sand and mud, on the settlement process are poorly understood.

The role of metamorphic inducers (Turner et al. 1994) has recently been emphasized for oysters, but in a practical sense the availability of substrate remains a very critical issue in the James River. The once formidable three dimensional reef structures in the upper James River have been reduced to disparate, two dimensional patches with presence or absence of exposed shell substrate varying on a scale of meters, mostly in the shallower regions of the river. The serial impact of limited substrate availability, in both an absolute sense as shell per unit area and especially after correction for fouling occlusion, underscore the long term impact of shell removal on a decadal scale as part of oyster harvest and as a direct mining operation for commercial use. The calculations of Table 5.1 and 5.2 argue strongly that the most cost effective restorative

practice for oyster populations in the James remains the timely application of oyster substrate to extant reefs immediately before the season of documented settlement.

A complete accounting of the fate of progeny from a single spawning to subsequent maturity is not complete without a consideration of predation losses. Relatively little is known of predation losses during the larval phase, and in the present study this loss is subsumed in the L_{mort} calculation. This is worthy of further examination. Post settlement losses are subsumed in the J_{mort} value. Roegner and Mann (1995) address underlying problems of substrate limitation and overgrowth of adjacent individuals in such situations, but a more comprehensive examination of predation (e.g., Eggleston 1990) related losses, not examined as a field component of this study, is required to complete the synthesis from one generation of spawning individuals to the next.

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