

OYSTER REEF BROODSTOCK ENHANCEMENT IN THE GREAT WICOMICO
RIVER, VIRGINIA

A Thesis

Presented to

The Faculty of the School of Marine Science

The College of William and Mary in Virginia

In Partial Fulfillment

Of the Requirements for the Degree of

Master of Science

by

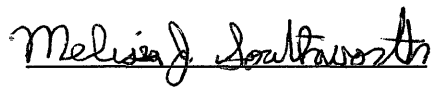
Melissa J. Southworth

1998

APPROVAL SHEET

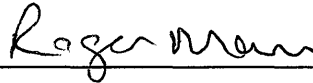
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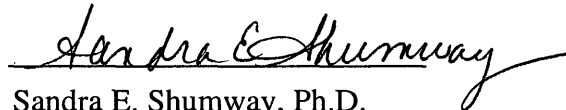
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DEDICATION

I'd like to dedicate this to my family for being so supportive in everything I do.
Especially my parents, Loren and Buzzy. They truly are my inspiration.

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I would also like to thank all of my friends, both those here at VIMS and those in other areas. They've helped me a lot over the past years and managed to keep me from losing my sanity. Most of all I wish to acknowledge my family. They have always been my biggest fans, supporting me whole-heartedly in everything I do. Thank you for all of your support!

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ABSTRACT

Natural oyster populations in the Chesapeake Bay have become severely depleted in recent years due to a combination of overfishing, declining water quality, and diseases. Replenishment programs in the form of artificial reefs are currently in effect throughout most of the Chesapeake bay region. Shell Bar reef built in the Great Wicomico River, Virginia in 1996 was supplemented with reproductively active broodstock oysters from Tangier and Pocomoke Sounds. The Great Wicomico River was historically a high spatfall and seed producing river, but production in the river has decreased in recent years. Oyster larval concentrations (in the form of plankton tows), gonad development, and circulation data were collected in the Great Wicomico River throughout the 1997 reproductive season. The broodstock oysters spawned from mid June through mid August, with a peak occurring from mid June through mid July. Larval concentrations were several orders of magnitude higher than the highest reported in the literature for extant reefs in the James River. Larvae were significantly more abundant on the flood tidal stage, suggesting some vertical migration with change in tidal cycle, thus aiding in their retention in the system. Settlement of larvae on shellstrings and on bottom substrate, was higher than in recent years. The most abundant settlement occurred near the reef and upriver of the reef. Circulation patterns observed are favorable for local retention of larvae in the system and suggest that the river is a "trap-type" estuary. Reef building, and subsequent transplants of broodstock onto these artificial reefs, can be an effective management option provided the circulation patterns of the system are similar in nature to the Great Wicomico (i.e. larvae are "trapped" in the estuary).

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INTRODUCTION

The Eastern oyster, *Crassostrea virginica* (Gmelin), plays an important ecological role in the Chesapeake Bay and its tributaries as well as being the focus of a substantial commercial fishery. Oyster reefs developed in recent geological time as the current Chesapeake Bay was inundated by rising sea level. By early Colonial times, oyster reefs had become significant geological and biological features of the Bay. Since Colonial times, overfishing of this resource has resulted in the degradation of these reefs such that only two-dimensional “footprints” of these former reefs remain. Today, these “footprints” maintain drastically reduced oyster populations. A decline in water quality due to ever increasing land use since colonial times has only intensified the degradation of the oyster reefs. The past three decades have been defined by decline in the fishery production and the oyster resource under the added insult of two protistan parasites, *Perkinsus marinus* ("Dermo") and *Haplosporidium nelsoni* ("MSX"). Since the disease organisms are active throughout most of the growing range of the oyster, there have been few sanctuaries in which to plant oysters or in which naturally occurring oysters could be found in appreciable quantities. Indeed, these parasites have effectively eliminated oysters from many sections of the Bay. Despite over 30 years of exposure to disease, the native oysters do not exhibit any recovery or resistance in disease endemic areas in Virginia. The oyster fishery is in severe decline and there is a recognized and urgent need to restore the oyster resource - not just for the commercial fishery but also to serve as both the benthic filter feeder that is so pivotal to the ecology of the Bay and the physical structure which provides habitat for a multitude of species,

including many of commercial interest.

The Commonwealth of Virginia, through the Virginia Marine Resources Commission (VMRC), supports an extensive replenishment program throughout most of their portion of the Bay. Traditional replenishment programs focused on spreading thin veneers of shell substrate for larval settlement over coastal and estuarine bottoms. The main purpose of this practice is to provide a suitable substrate for settlement at minimum cost. Ideally the end product is the retrieval of seed or market size oysters from these shell “plants”; however, these thin, two-dimensional carpets bear little resemblance to the intricate, three-dimensional reefs that once supported a large oyster population.

More recent replenishment programs have focused on the construction of three-dimensional reefs that resemble more closely what was found in Colonial times. Reefs have been constructed in the Piankatank, Great Wicomico, Coan, Yeocomico, and James Rivers, and Lynnhaven Bay. These reefs are built on the “footprint” of an old reef and consist of several mounds of shell that protrude out of the water at low tide. Essentially the reefs are built and allowed to mature naturally (i.e. no addition of broodstock to the reef). The basis of this practice was the premise that oysters would recruit to the reef from the plankton but, because there was no resident population of disease infected oysters, would develop as a predominantly disease free population. This was not the case on an artificial reef built in the Piankatank River, Virginia (Mann et al., 1996; Mann and Wesson, 1996). Endemic diseases did become established in the reef populations; however, the vertical relief of the reefs enhanced growth to such an extent that the oysters grew larger and faster than on adjacent “flat” oyster rocks. Relatively dense populations of oysters did develop, and recent surveys from fall, 1996 of the Piankatank reefs showed population densities of 50-70 oysters m^{-2} compared with 200-350 m^{-2} on the most commercially productive reefs (flat) in the James River system. While the value of 50-70 is better than many extant reefs in the James, it

illustrates that development of very dense and stable oyster communities on constructed reefs is very much a long term event. This is exemplified in the absence of initial stocking with broodstock, especially so in regions that now suffer poor natural recruitment.

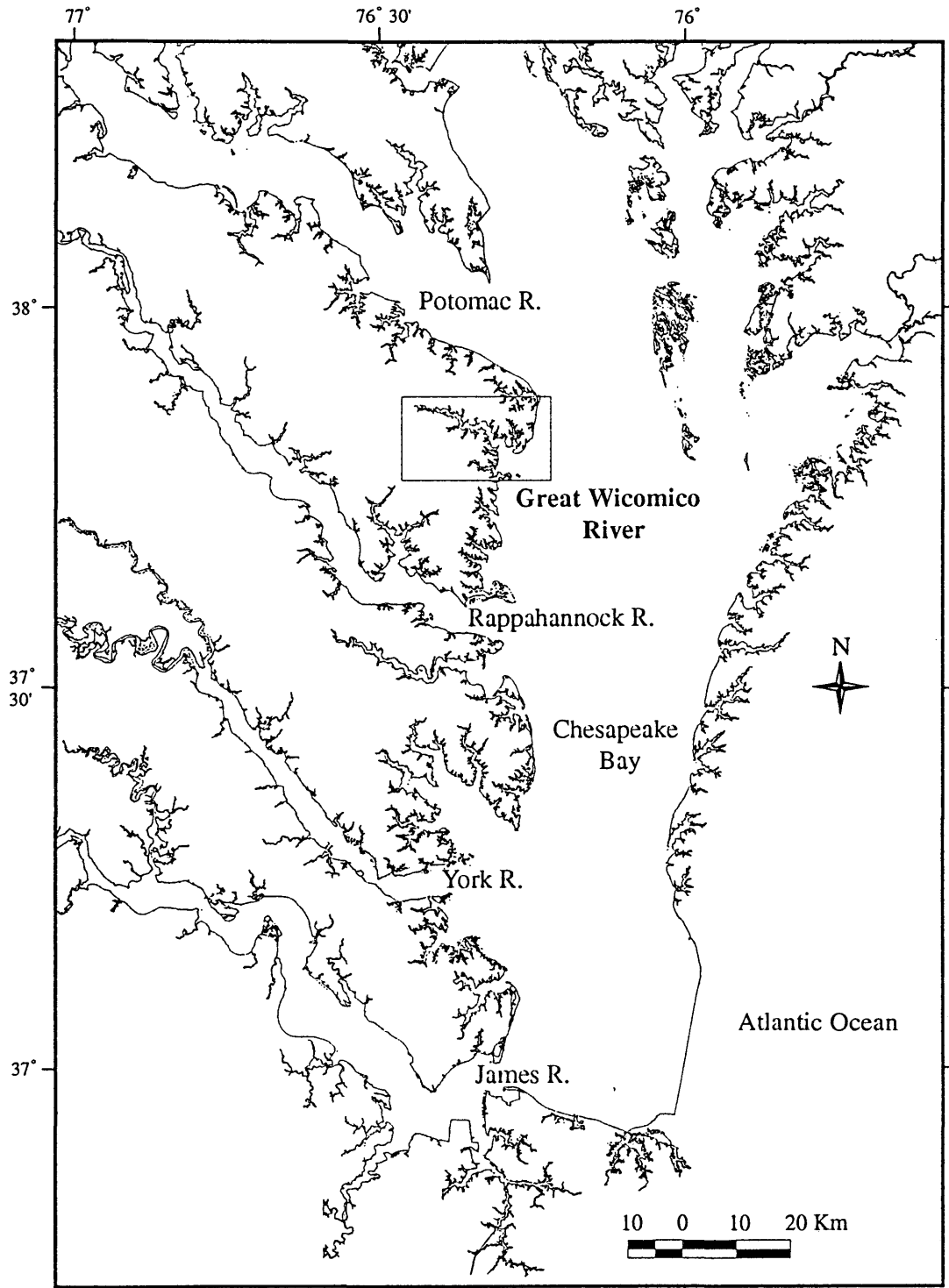
The current study was prompted by the need to examine artificial reefs that were initially “seeded” with reproductively capable oyster populations in the Great Wicomico River. To estimate the impact of adding broodstock to the reef, four distinct objectives were investigated: (1) Estimate the maximum number of eggs that would be produced in one mass spawning event on the reef; (2) Determine if and when the transplanted oysters on the reef spawn; (3) Determine when and where larvae are most abundant in the water column; (4) Determine if the circulation is favorable for some local retention of larvae in the system.

A Historical Perspective of Oyster Stocks in the Great Wicomico River

To accurately investigate the impact of adding broodstock, something must be known about what was happening in the river in terms of oyster production and abundance prior to the building of the reef. For the past 30 years the Virginia Institute of Marine Science (VIMS) has participated in two stock monitoring programs in the Great Wicomico River, Virginia (Figure 1) in the form of spatfall surveys throughout the summer months and fall dredge surveys. The spatfall survey provides an estimate of the potential of a particular area for receiving a “strike” or set of oysters on the bottom and helps define the timing of the setting events. The fall dredge survey provides information about spatfall and recruitment, summer mortality, and inter-annual changes in abundance of seed and market-size oysters.

The spatfall survey has been completed yearly from 1964 to the present. The collectors used to monitor spatfall were oyster-shellstrings. These consist of 12 oyster shells of similar size (about 76 mm, max. dimension) drilled through the center and

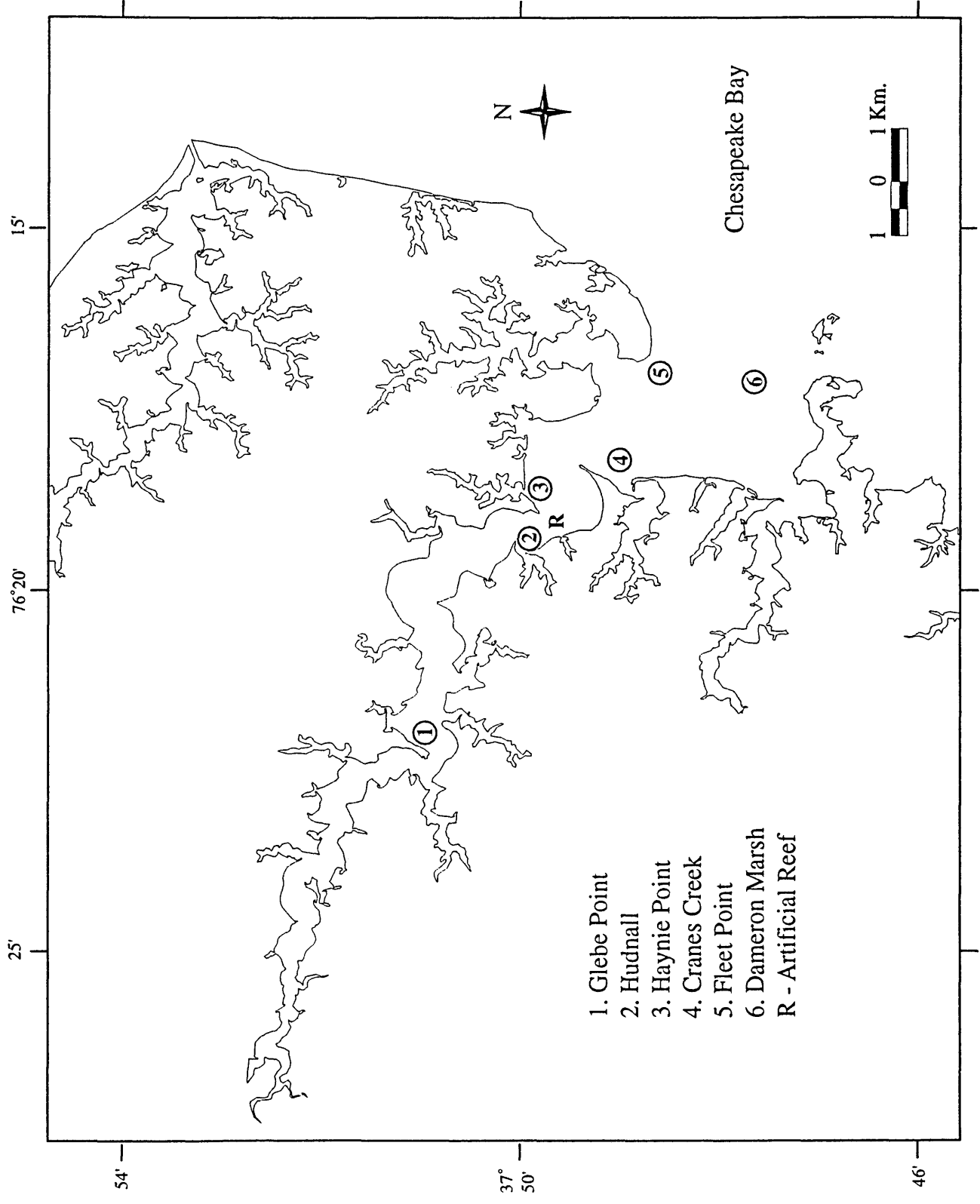
Figure 1: Map of the Chesapeake Bay outlining the location of the Great Wicomico River, Virginia.



strung (inside of shell down) on heavy gauge wire. Shellstrings were hung 0.5 m off the bottom at each station (Figure 2). Up to sixteen stations have been used at various times throughout the history of the spatfall surveys. However, for consistency between years, I will focus on the six stations (Figure 2) that have been used yearly since 1964-65. Shellstrings are replaced after a one-week exposure (with occasional deviations), and the number of spat that attach to the smooth, underside of the middle 10 shells counted with the aid of a dissecting microscope.

The following is a summary of the shellstring survey data from the VIMS database (VIMS archive). In the Great Wicomico River, spatfall from 1964 to 1971 was relatively high with average weekly sets (number of larval oysters physically adhering to the substrate) ranging from 4 to 370 spat/shellface per week. In 1970 nearly all stations received a moderate (20-50 spat/shellface) to heavy (> 50 spat/shellface) peak set and the setting period extended over most of the season. In 1971, the set occurred late in the season, with no significant set occurring until late fall. In 1972, due to Tropical Storm Agnes, spat set was nearly zero at all stations. This year marked the beginning of a major decline in spatfall in the river. The years 1973 through 1978 were characterized by a very light set, usually less than one spat/shellface per week even during “pulse” setting time. In the 1980’s it appeared that oysters were returning to the Great Wicomico River. Starting in 1979, the sets became steadier (lasting throughout most of the season) and heavier (2 to 110 spat/shellface per week). This increase in the number of spat in the late 70’s and early 80’s, coincided with a heavy private “plant” (a large number of small (seed) oysters were placed into the system) (Cowart, pers. communication). These were harvested in the late 80’s and early 90’s and once again there was a decline in the number of spat observed. The latest signal in the river occurred during the 1997 setting season, after the artificial reef was built and stocked with broodstock oysters. In 1997 spatfall was recorded between

Figure 2: Location of the historical shellstring deployment sites in the Great Wicomico River.



25'

76°20'

15'

54'

37°
50'

46'

- 1. Glebe Point
- 2. Hudnall
- 3. Haynie Point
- 4. Cranes Creek
- 5. Fleet Point
- 6. Dameron Marsh
- R - Artificial Reef

Chesapeake Bay

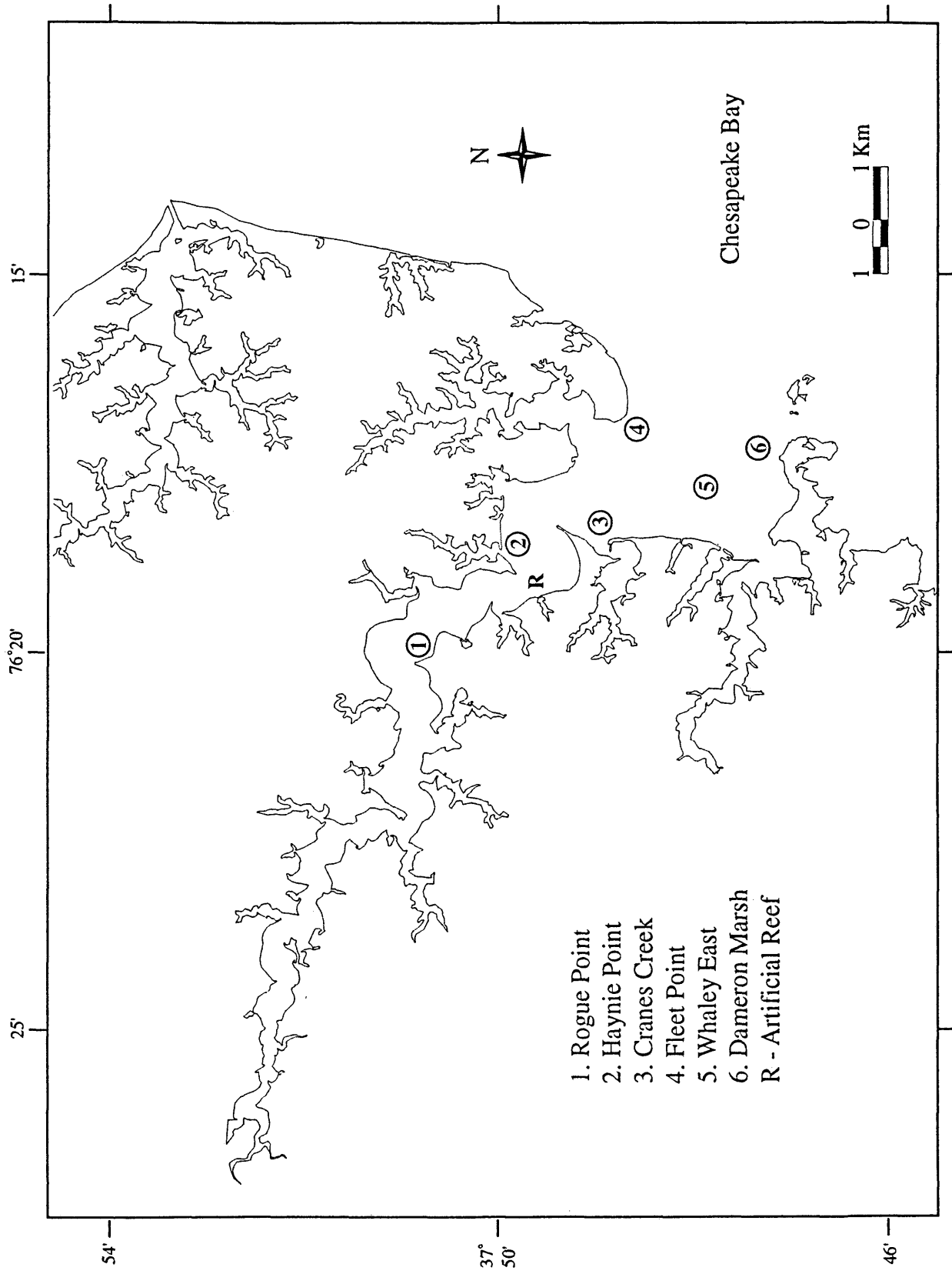


the end of June and the beginning of September, with a peak set occurring in mid to late July. During this peak set, spatfall ranged from 0 to 29.3 spat/shellface per week, with the most intense sets occurring up river or immediately adjacent to the reef (Glebe Point, Hudnall, Haynie Point, and on the reef; Figure 2).

The fall dredge survey has been completed yearly from 1971 to the present excluding 1974-1976. Figure 3 shows the geographical locations of the bars sampled in the Great Wicomico River during this time. As with the shellstring data, only the most consistently sampled stations were used in the analysis. Only three stations (Fleet Point, Whaley's East and Haynie Point) have been sampled since 1986. Three to four 0.5 bushel samples of bottom material were taken at each bar using a 24-inch dredge having 4-inch teeth. For each sample the following were determined: number of market-size oysters (> 76 mm, max. dimension), number of small oysters (submarket size and yearlings), and the number of spat. From these samples either 0.5 or one bushel increments were used. In the case where only 0.5 bushels were counted, they were standardized to one bushel by doubling the counts.

The fall dredge data taken from the VIMS database (VIMS archive) can be summarized as follows: Between the years 1971 to 1987, the number of small oysters ranged from 90 to over 600 per bushel for all six stations (Figure 3). During this time the number of spat per bushel ranged from a low of 0 in 1973 (the year of Hurricane Agnes) to a high of 2,000 per bushel in 1987. For the three stations where data were available beyond 1987, this year marked the beginning of a slow decrease in the number of oysters in the system. For the past three years, numbers of small oysters have ranged from 30 to 150 per bushel. 1987 also marked the beginning of essentially the absence of market-size oysters in the system. Before 1987 there were comparatively more market oysters (0-128) per bushel than after (0-14 oysters per bushel). The number of spat recorded per bushel also started to decrease in the late

Figure 3: Location of the historical fall dredge survey stations in the Great Wicomico River.

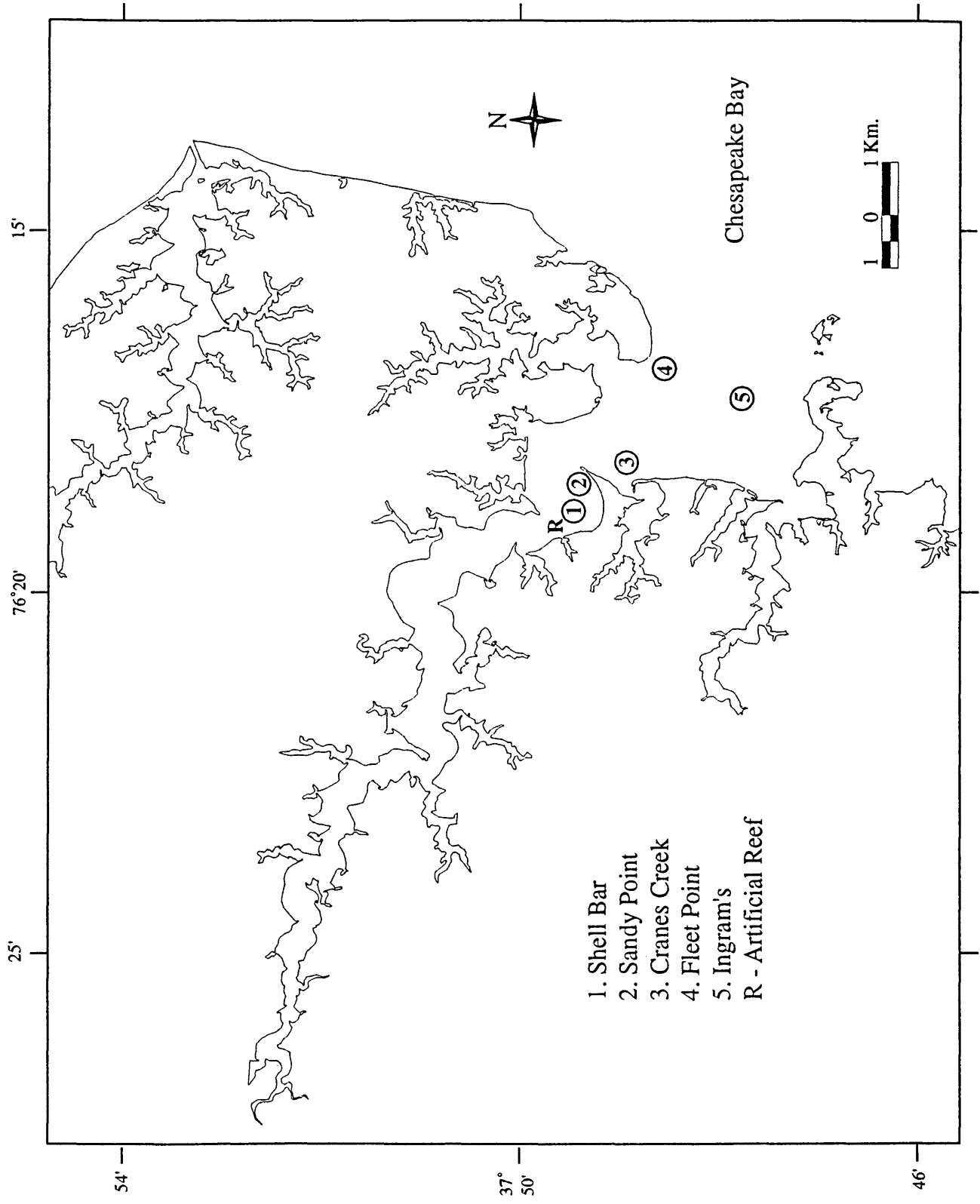


80's. For the five years prior to the building of the reef, spatfall averaged about 55 spat per bushel, whereas an average of 155 spat per bushel was recorded for the 1997 fall survey (almost a 3 fold increase in spatfall).

In the fall of 1995 and 1997, a collaborative survey effort between the Virginia Marine Resources Commission (VMRC) and the Virginia Institute of Marine Science (VIMS), resulted in a formal stock assessment on the oysters in the Great Wicomico River using patent tongs. Previously, Chai et al. (1992) evaluated the oyster sampling efficiency of patent tongs versus an oyster dredge and found patent tongs to be a much better sampling tool. Densities obtained from using patent tongs were not significantly different from diver-harvested quadrat surveys, whereas the dredge surveys were only 2-32% of the diver estimates. Based on these findings patent tongs are the preferable sampling gear for conducting oyster stock assessment surveys. The five oyster reefs that were sampled in the Great Wicomico River in 1995 and 1997 are shown in Figure 4. For each reef a uniform grid was generated over a current reef boundary map. Each grid location had a reference which could be located electronically by LORAN from the research vessel. Grid references were assigned a sampling order from a random number table to generate a randomized sampling grid. Samples were collected using hydraulic patent tongs with an opening of one m^2 . All of the retained material was washed and counts of live oysters as spat (young of the year), small oysters (<76 mm, max. dimension), and market oysters (> 76 mm, max. dimension) were taken. The volume of shell retrieved in each tong was also recorded as an index of the quantity of cultch material present at each station.

In 1995 the number of market oysters ranged from 0.3 m^{-2} at Fleet Point to 1.6 m^{-2} at Sandy Point. The number of small oysters ranged from 4 to 22 oysters m^{-2} with the lowest densities at Shell Bar and Fleet Point and the highest at Sandy Point. The number of spat m^{-2} , ranged from 6.5 at Cranes Creek to 13.4 at Fleet Point. The overall average m^{-2} for the five rocks combined, was 0.7 market oysters, 10.2 small

Figure 4: Location of patent tong stock assessment stations in the Great Wicomico River.



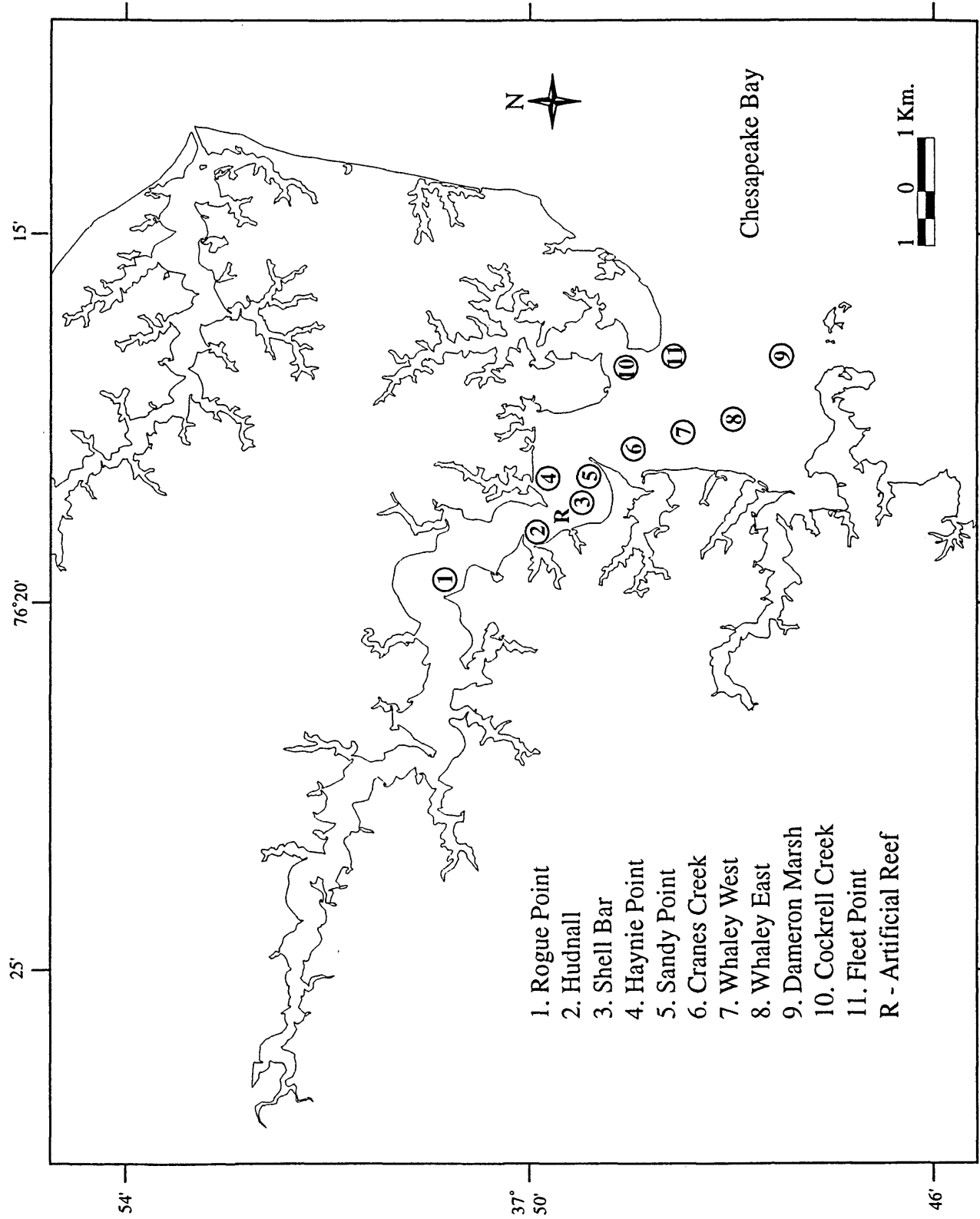
oysters, and 9.7 spat. While the average number of market (1 to 5 m⁻²) and small (9 to 36 m⁻²) oysters recorded in 1997 were similar to those recorded in 1995, the number of spat were considerably higher in 1997. Spat numbers ranged from 5 m⁻² at Ingrams and Fleet Point to 102 m⁻² at Shell Bar. On average this represented a three-fold increase in density of spat from 1995 to 1997.

Collectively, these survey data can be summarized as follows: Oysters were present in relatively great abundance in the Great Wicomico River until about 1971. The combined effects of Hurricane Agnes in 1971, and disease decimated the natural broodstock population in the system. This in turn led to a decrease in larval production and spat recruitment. For a brief time during the 1980's, oysters appeared to be returning to the Great Wicomico, but this was found to be due to a large private plant that served as broodstock for the system. Once these oysters were harvested, recruitment once again plummeted. With the building of the three dimensional reef and the addition of broodstock on the reef, recruitment once again showed an increase from previous years.

Estimation of Egg Production, and Fertilization

To estimate the impact of adding broodstock, it is also necessary to have estimates of historical egg production (i.e. when adult oysters were still abundant in the river) to use as a comparison to egg production observed on the reef. There are no good historical stock assessment data for the Great Wicomico, but there are data for extant reefs in the James that are similar to historical conditions (comparison of dredge survey data and stock assessment data; Morales, unpublished data). I have therefore taken data from reefs in the James, where recent stock assessment data exists, and extrapolated to the historical conditions in the Great Wicomico using Baylor survey data (Haven et al., 1981) on reef area (see Figure 5 for reefs used from the Great Wicomico River). Since salinity plays a role in reproductive success, it is also necessary for the

Figure 5: Location of the oyster reefs used to calculate per square meter and total egg production in the Great Wicomico River, during historical conditions.



- 1. Rogue Point
- 2. Hudnall
- 3. Shell Bar
- 4. Haynie Point
- 5. Sandy Point
- 6. Cranes Creek
- 7. Whaley West
- 8. Whaley East
- 9. Dameron Marsh
- 10. Cockrell Creek
- 11. Fleet Point
- R - Artificial Reef

Chesapeake Bay



15'

76° 20'

25°

54'

37° 50'

46'

reefs being compared to have similar salinity regimes. Figure 6 shows the location and the salinity regimes (8.5, 10.5, and 13.5 ppt) of the reefs in the James River used in the comparison. Egg production was then estimated using the following protocol from Mann and Evans (in press).

Egg production or Fecundity (F, in millions) is sum of individual (F_{ind}) fecundity in size class intervals, here 5 mm length intervals. Length is considered as the maximum dimension measured from the hinge. Within each interval L = mid point of length (for convenience 3, 8, 13 mm and so on for 0-5, 5-10, and 10-15 mm size intervals is used). Size specific fecundity is estimated using the relationship:

$$\text{Fecundity } (F_{ind}) = 39.06 \times \text{Weight}^{2.36}$$

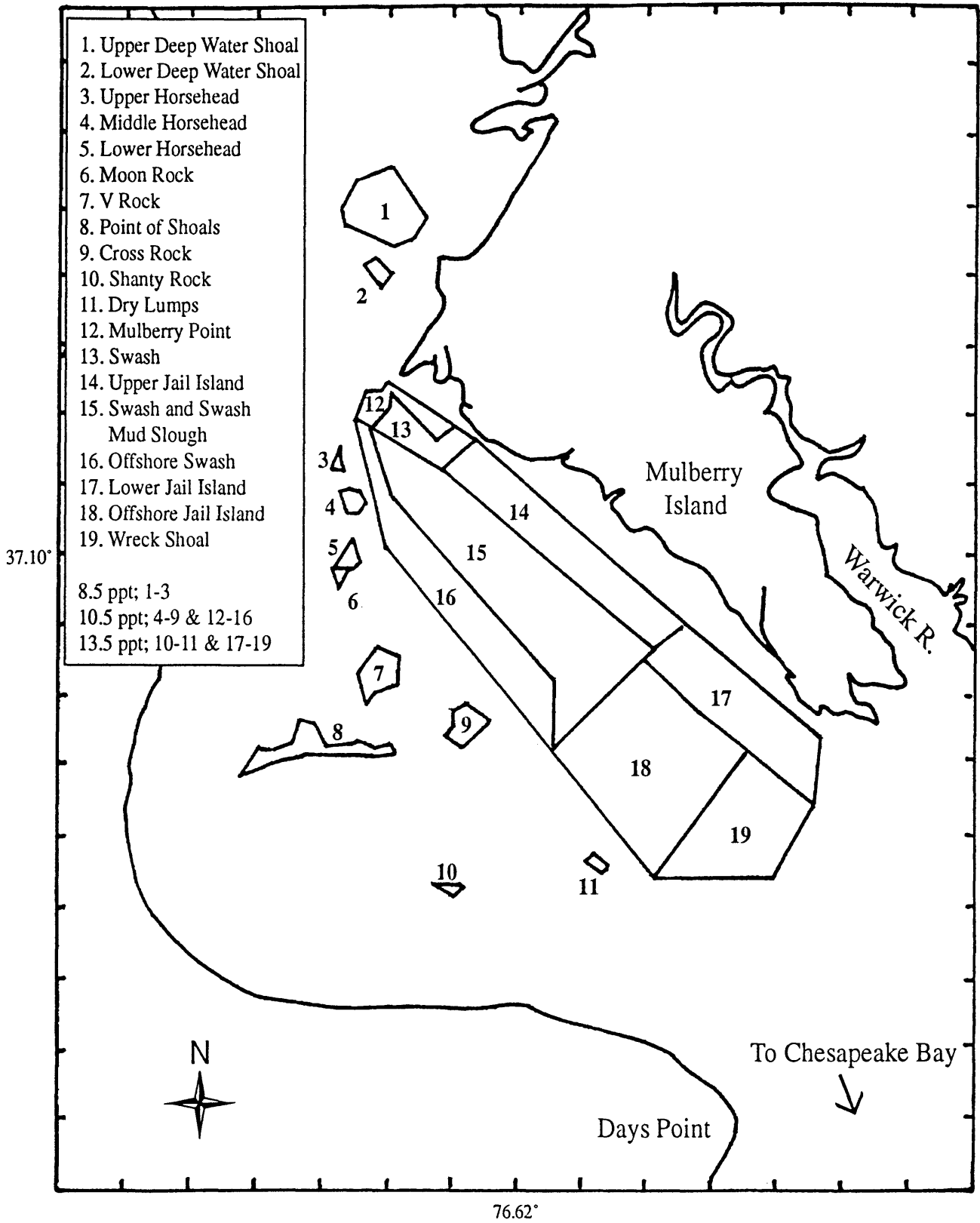
where F is in millions, and W is dry tissue weight in mg. This relationship is taken from Thompson et al. (1996) and based on a re-analysis of earlier data from Cox and Mann (1992) which eliminated all individuals in partially spawned or completely spawned condition.

Weight to Length (in mm) conversions were effected using data from James River collections (raw data from Rainer and Mann, 1992):

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

with the resultant size specific function relating fecundity to size class, egg production m^{-2} (F_{tot}), can be estimated as the sum of the individual fecundities. Within a single 5 mm size class the sum of the individual fecundities is ($n_i \times F_{ind}$) where n_i is the number in the size class with mid point l in mm. The given formulation does not address the proportion of the population that is female. For convenience, Cox and Mann (1992)

Figure 6: Location and salinity regimes of the extant oyster reefs in the James River, that were used to estimate total egg production in the Great Wicomico River, during historical conditions.



suggest parity in sex ratio, and given the lack of other data a single sex ratio modifier is adopted, F_q , with the value arbitrarily set at 0.5 (50% female in all size classes).

Fecundity can be modified based on salinity effects. A modifier, F_s , can be employed to decrease F by a proportion, effected by multiplying by a value from 1.0 (no effect) to 0.0 (total effect). The size specific fecundity relationship previously described was developed for material collected in 1988 at a mean salinity of 13.5. For the purpose of this study an estimate of the magnitude of F_s was made from the data of Mann et al. (1994). The lowest salinity at which viable eggs were found was 8.5 ppt. At values of salinity less than 8.0 ppt assume $F_s = 0.0$ (total compromise of eggs). 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. A tentative linear relationship is proposed from 8 to 13.5 ppt with the following estimators for F_s :

$$\text{If Salinity (S) > 13.5, } F_s = 1.0$$

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

$$\text{If Salinity (S) < 8.0, } F_s = 0$$

Fecundity can also be modified by disease that can be incorporated with a further modifier, F_d . This decreases fecundity in the same manner as F_s , ranging from 1.0 to 0.0. Disease is described by a weighted prevalence value. No adequate data are available to provide a meaningful relationship between weighted disease prevalence and F_d . Therefore this value was fixed at 1.0 (no effect).

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's work on sea urchins (1991):

$$\% \text{ fertilization} = 0.49 \times \text{OD}^{0.72}$$

where OD is oyster density in oysters 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), is therefore estimated by ($F_{tot} \times F_q \times F_s \times F_d \times F_f$) in units of larvae m^{-2} .

Using these formulae for fecundity, I estimated the total and per area egg production in the Great Wicomico (Table 1) in the following manor. I first obtained the number of eggs per unit area produced on each reef in the James River, based on the appropriate size frequency distribution. I then averaged these values across all of the reefs that pertained to each of the three salinity regimes (Figure 6 and Table 1; column 3). These values were then applied to the area of the analogous reefs (i.e. the same salinity (Table 1; column 5) in the Great Wicomico to obtain a total egg estimate for the Great Wicomico reefs. Given that information, as well as the corrections for disease, salinity, and fertilization efficiency, the total number of fertilized eggs (strictly speaking embryos) in the Great Wicomico River is estimated at 7.1×10^{12} . I then estimated the total egg production seen on Shell Bar reef (see next section for description of reef), after being enhanced with reproductively active oysters. Salinity used to calculate F_s was set at 10.8, giving a modifier value of 0.509. Reef area and oyster density used in the calculations were $3900 m^2$ and 300 oysters m^{-2} respectively (Olsen and Wesson, 1997). Using these numbers, the fertilization modifier, F_f , was estimated to be 0.298. Taking size frequency distribution data, attained from measuring 150 oysters from the reef (Figure 7), I obtained an estimate of 5.4×10^{12} embryos (larvae) produced on the reef. These calculations suggest that by aggregating the broodstock oysters into very dense populations, such that fertilization efficiency is greatly improved, the production

of larvae on the reef is similar to that of the entire Great Wicomico system in pre disease conditions (i.e. the order of magnitudes are the same).

Table 1: Estimates of historical egg production in the Great Wicomico River using demographics obtained from analogous reefs (Figure 6) in the James River in 1993. See below for the origin of the data. See text for explanation of calculations.

Reef #	Reef area m ²	Egg production 10 ⁶ m ⁻²	Total # of eggs 10 ¹²	Salinity to estimate F _s	F _s	F _r	Corrected production 10 ⁶ m ⁻²	Corrected total # eggs 10 ¹²
1	29355	1160	34	8.5	0.091	0.159	16.8	0.49
2	23475	565	13	10.8	0.509	0.134	38.5	0.90
3	3636	565	2	10.8	0.509	0.134	38.5	0.14
4	29462	565	17	10.8	0.509	0.134	38.5	1.1
5	33261	565	19	10.8	0.509	0.134	38.5	1.3
6	83452	136.2	11	13.5	1.0	0.036	4.9	0.41
7	137735	136.2	19	13.5	1.0	0.036	4.9	0.68
8	251573	136.2	34	13.5	1.0	0.036	4.9	1.2
9	82723	136.2	11	13.5	1.0	0.036	4.9	0.41
10	22047	136.2	3	13.5	1.0	0.036	4.9	0.11
11	71929	136.2	10	13.5	1.0	0.036	4.9	0.35
TOTAL			173					7.1

Reef area - taken from Great Wicomico Baylor survey data (Haven et al., 1978).

Egg production - calculated from size specific fecundity of oysters in the James (average of all reefs in James with the same salinity).

Total # of eggs - reef area (in the Great Wicomico) multiplied by egg production (based on James River demographics).

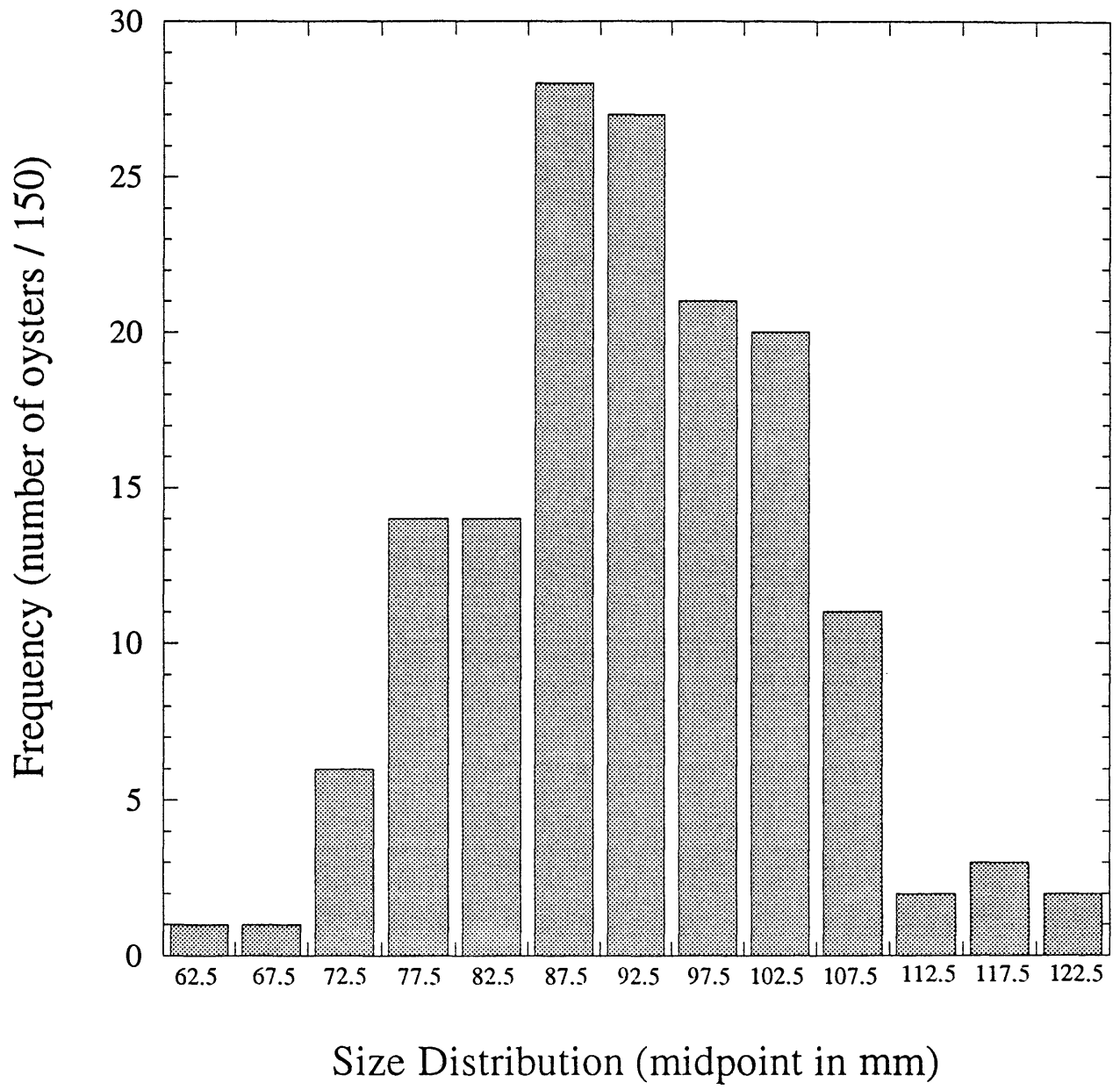
F_s - Correction for salinity, based on reefs sharing similar salinities in both rivers.

F_r - Correction for fertilization efficiency, based on densities found in the James River (also used for egg production calculations).

Corrected production - Egg production / m² corrected for salinity, fertilization efficiency, and disease (Production * F_d * F_s * F_r).

Corrected total # of eggs - Corrected egg production multiplied by reef area (in the Great Wicomico).

Figure 7: Size frequency distribution of broodstock oysters on Shell Bar reef
(n=150).



1997 FIELD STUDIES

Study Site

The location selected for the study was Shell Bar Reef in the Great Wicomico River, Virginia. The Great Wicomico River, although small, was regularly identified as a region of high oyster spatfall prior to the decimation of resident oyster populations by the combined ravages of MSX and *Perkinsus*. The circulation of the river, like that of the Piankatank, served to retain planktonic oyster larvae originating within the river (Andrews, unpublished data). The lack of resident oysters in the river has resulted in siltation and partial burial of good oyster bottom in the river in recent years. As described earlier, VIMS has maintained oyster settlement monitoring (by shellstrings) and reef survey (by dredge) programs in the river for nearly three decades, and the data show a collapse of the local oyster resources in recent years. These data have recently been supplemented by quantitative patent tong surveys supported in part by federal funds from the NOAA Chesapeake Bay Stock Assessment Program. The low population density of oysters has been confirmed by such surveys. Given that very few oysters remain in the Great Wicomico, it was chosen as a site for reef placement in 1995.

The reef was constructed in June of 1996, by deploying old oyster shells from a barge with a crane into a series of intertidal structures approximately 215 meters long and 18 meters wide. Broodstock oysters from the Tangier and Pocomoke Sound regions were planted on the reef in December of 1996. Oysters surviving as sparsely distributed individuals in many regions of the Bay are continually exposed to intense disease challenge and selection pressure. Consequently, they would be expected to

have higher resistance to disease than low salinity populations where intermittent disease pressure fails to eradicate genetically susceptible individuals, which then continue to breed with more resistant individuals and thus fail to promote the process of developing uniformly high resistance. Tangier and Pocomoke Sounds, are such a location where higher salinities (25-30 ppt) occur, but densities are low ($< 1 \text{ m}^{-2}$), thus failing to maximize the fertilization efficiency. If the intent of sanctuaries is to develop actively breeding populations with higher than typical resistance, there is good argument for aggregating the few remaining oysters from disease endemic areas where they are so sparse that fertilization efficiency of freely released eggs is minimal or absent.

Target Organism

The native Eastern oyster *Crassostrea virginica*, reproduce by releasing their eggs into the water column where they are externally fertilized. Individual females release anywhere from 100,000 (in poorly developed females) to 50 million eggs per spawning event, with 2-3 spawnings occurring per summer in a temperate bay such as the Chesapeake. Larvae are planktivorous for 2 to 3 weeks, during which time they are essentially passive drifters (Kennedy, 1996), at the mercy of the currents. Local retention of larvae in a system is brought about by a combination of water movement and larval behavior (Mann, 1988). Depending on the strength of the water movement in the system, this behavior can play an important role in aiding the retention of larvae by moving them further upstream each tidal cycle.

METHODS

Field studies

Field studies were conducted bi-weekly from the 23rd of June through the 22nd of September 1997 (total of 8 field days). This time frame was chosen based on the historical timing of spat set in the system (i.e. to ensure that I caught any or all pulses of setting) and the estimated larval period of 2 to 3 weeks in the water column. To characterize tidal patterns of circulation and larval abundance in the system, all sampling was effected over one complete tidal cycle (approximately 12 hours).

Egg production

Estimates of egg/embryo production on the reef, using this information were calculated earlier in this document (see estimation of egg production and fertilization section). To briefly reiterate, oyster standing stock and density was obtained from VMRC records (Olsen and Wesson, 1997). According to these records, 2281 bushels of oysters were planted on the 3900 m² reef in December of 1996. Estimating 500 oysters per bushel (Wesson, personal communication), density of broodstock oysters on the reef was approximately 300 m⁻². Broodstock oyster size was obtained by measuring 150 random oysters collected with the aid of hand tongs, from the reef.

Reproductive Development

To follow reproductive development of the broodstock oysters on the reef, 200 oysters were collected with hand tongs (25/sampling day). Sections of the gonad and visceral mass were cut and fixed in Bouin's solution. Following fixation specimens

were dehydrated in alcohol, cleared in xylene, and embedded in paraffin wax. Specimens were sectioned at 7-10 μm , subsequently stained in Delafield's Hematoxylin, and counterstained in Eosin Y following the methodology of Humason (1962). Developmental stages were identified based on those originally described for *C. virginica* by Kennedy and Battle (1964) and for *C. gigas* by Mann (1979). In the present study, the stages of gonadal development were defined as follows:

Inactive.

No evidence of the presence of follicles peripheral to the digestive gland. Sex is essentially indeterminable.

Early active.

Male. Many follicles filled primarily with spermatogonia and spermatocytes. No spermatozoa.

Female. Eggs not well developed. A few nuclei in oocytes, but no nucleoli. Oocytes are still attached to the follicle wall.

Late active.

Male. Follicles predominately filled with spermatids. Characteristic swirling pattern of spermatozoa with tails oriented toward the center beginning to be evident, but follicle is not completely filled.

Female. Some free oocytes. Most have distinct nuclei, with fewer than 50% having distinct nucleoli.

Ripe.

Male. Classic swirling of tails in the middle of the follicle (similar to a pile of iron filings in a magnetic field).

Female. Primarily free oocytes. Greater than 50% have a distinct nuclei and nucleoli. All of the oocytes are about the same size.

Spawning or spent.

Male. Most follicles are empty or partially so. Some phagocytes present.

Female. Granular looking eggs (ameobocyte activity). Eggs of varying sizes that appear to be breaking down. Follicles are empty or partially so.

Disease assays

Monthly assays to determine *Perkinsus marinus* and *Haplosporidium nelsoni* (MSX) infections were effected using oysters collected for the reproductive development portion of the study. *Perkinsus* infection and prevalence were measured by Fluid Thioglycollate assay (Ray, 1963). MSX infections were detected using paraffin histology as in Burreson et al. (1988).

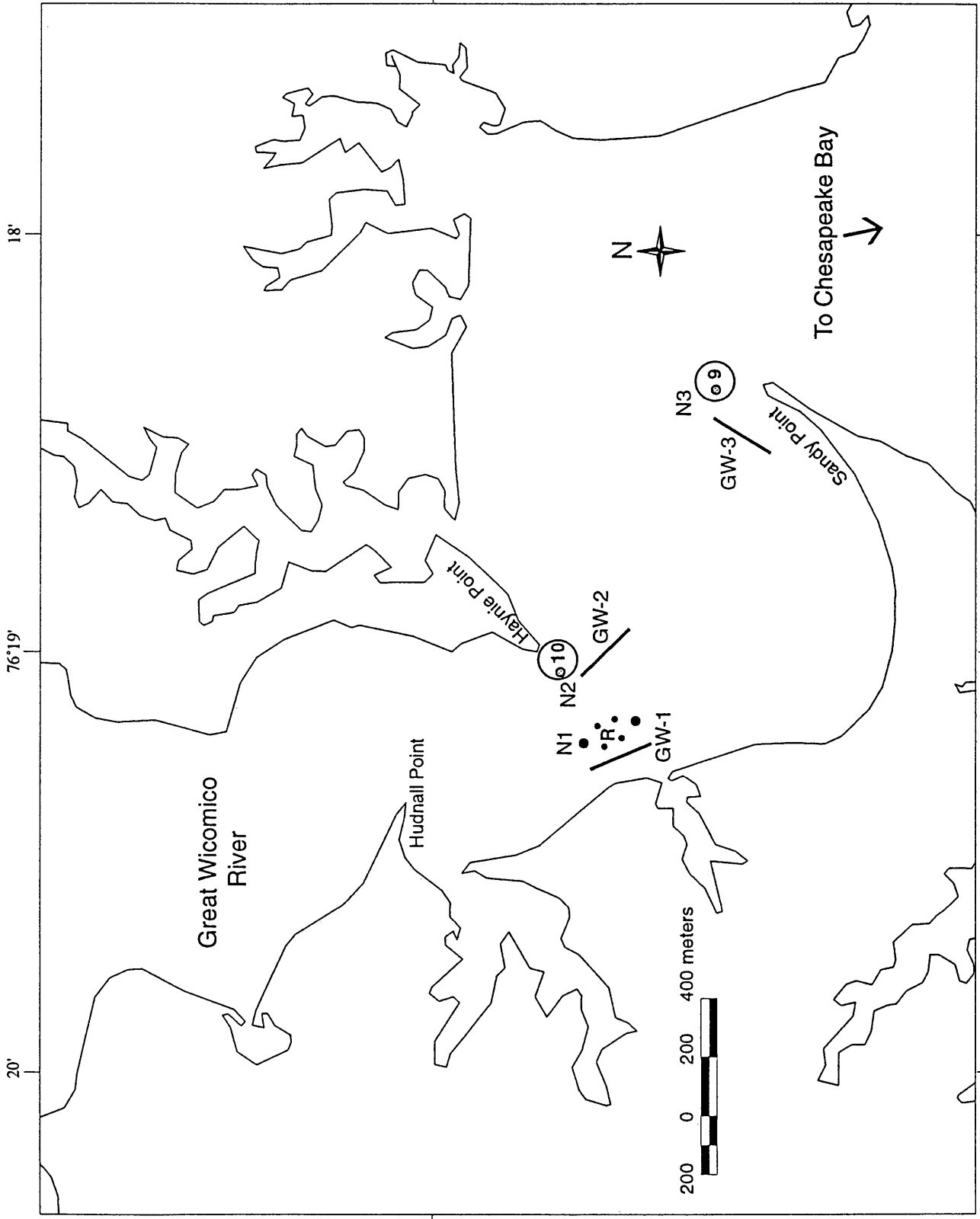
Larval Production

Field protocols

A series of 36 zooplankton samples were taken on each sampling day (3 replicates per site, per tidal stage). Samples were collected at three stations in the river (Figure 8). Plankton samples at GW-1 describe larval abundance near the reef, GW-2 describes abundance in the main of the river, and GW-3 describes abundance near the sand spit. This sand spit is thought to be a barrier that affects and effects some local retention in the system.

All samples were collected using a 0.3 m diameter, 3:1 aspect ratio zooplankton net (Sea Gear Corporation, Melbourne, FL). The filtering surface consisted of an 80 μm Nytex mesh cone attached to a PVC collection bucket lined with 80 μm mesh. The net was attached to a metal ring and towed by a three point bridal system attached to the ring. The net was towed 0.05 to 0.10 m below the water surface at approximately 1.5

Figure 8: Location of zooplankton (GW 1-3) samples and water samples (N 1-3) taken in the Great Wicomico River. R denotes the location of the reef. 9 & 10 mark the main channel in the river.



18'

76°19'

20'

37°
50'

Great Wicomico
River

Hudnall Point

Haynie Point

To Chesapeake Bay

200 0 200 400 meters



N3
GW-3

N1 N2 R
GW-1

N2
GW-2

9

10

m sec⁻¹ for 3.25 min. The nets used were calibrated in a separate study following the same protocol (Harding and Mann, in review). Samples were taken over a full tidal cycle (see Appendix I for details of the sampling days), to characterize the tidal cycle phases of larval movement. All samples were immediately preserved in 95% ethanol.

Laboratory protocols

Samples were split using a 0.5 L Folsom plankton splitter (Wilco Supply Company, Cass, MI). Final splits were filtered through a 400 µm Nytex mesh filter to remove large zooplankton (such as copepods), that interfered with the counting. To ensure no oyster larvae were lost in this process, samples were randomly chosen and counts were made before and after filtering. The difference between these counts was less than 1%. Non-enumerated splits as well as the filtrate from the final splits were archived.

Counts of umbo stage oyster veligers (larvae) in each sub-sample were made with the aid of a dissecting scope. To verify adequate mixing (i.e. a homogenous mixture of larvae within the sample), both halves of the final split were counted, and coefficients of variation (CV) were calculated following Van Guelpin et al. (1982). Acceptable CV's for invertebrate samples range from 5 to 20 %. Counting error of the total abundance of organisms within a sample was kept to 10% or less by ensuring (when possible) that at least 100 veligers were counted from each sub-sample. Total number of larvae per sample were obtained by multiplying the number of veligers in the split by the split number. The number of larvae per m³ was then obtained by dividing the total number per sample by the volume of water filtered. The average volume of water filtered, was determined to be 1.054 m³ in a separate net calibration study (Harding and Mann, in review).

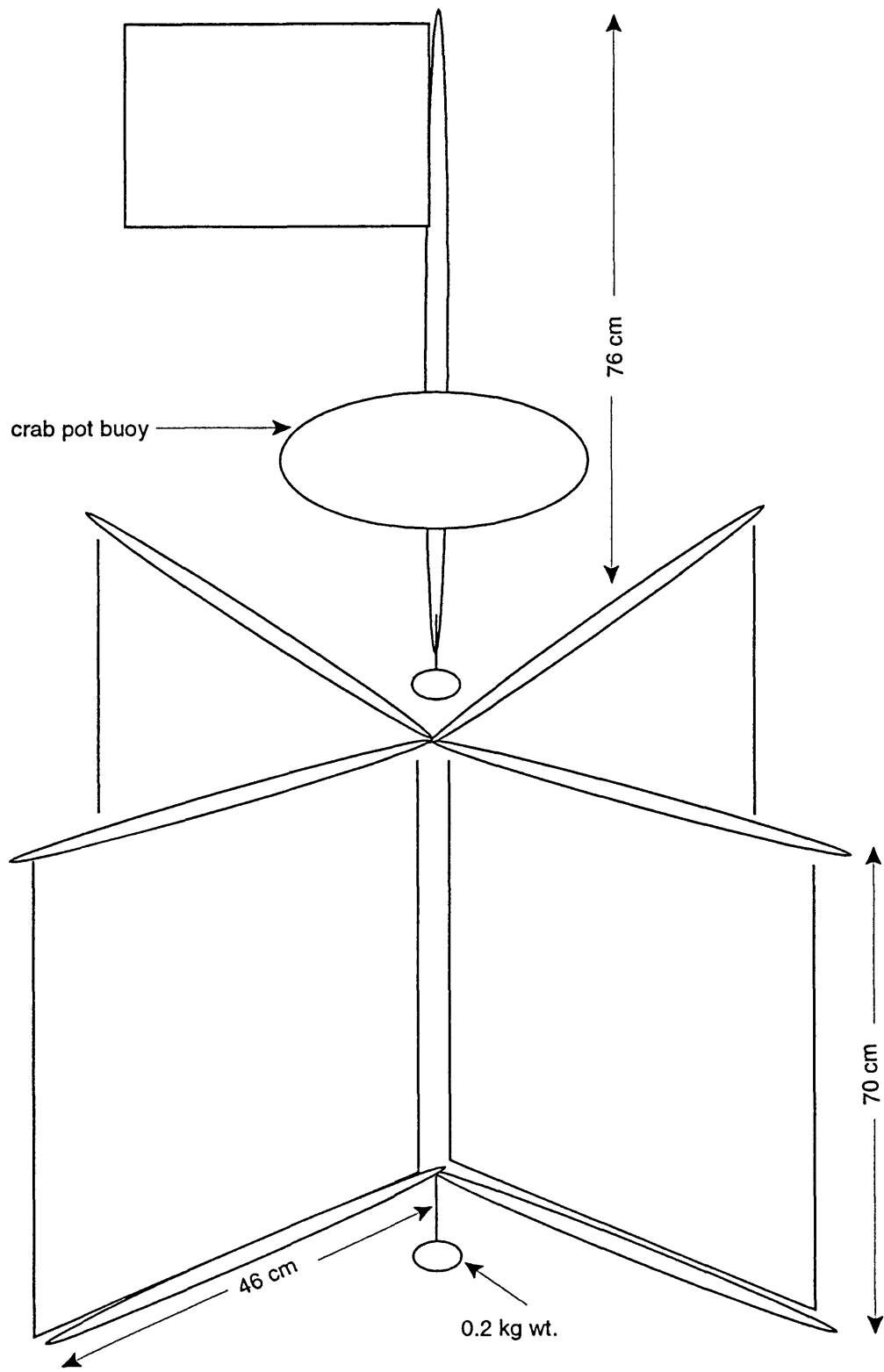
Temperature and Salinity

Surface temperature near the reef was measured (Station N1; in Figure 8) throughout the duration of the study. Temperature and salinity at the surface and bottom of the water column were obtained at three sites in the River (Figure 8) starting on July 28th (dates of collection coincided with the circulation study). Two samples per sampling day were taken, one at each end of the tidal cycle. Bottom water was collected using a Niskin bottle. Temperature was measured with an alcohol thermometer and salinity was measured with a refractometer.

Circulation

Simple surface drogues (drifters) were constructed after Davis et al. (1982) (Figure 9). This design was used to ensure the drifter was moved by the currents in the system with little input from the wind. The drifters were released at various sites around the reef and in the channel. The drifter locations were recorded approximately every hour using a hand held GPS system. The paths traveled were followed over one full tidal cycle. In the case that a drifter ran aground, it was repositioned to another location, with exact location depending on the stage of the tide. Throughout the course of the sampling season, a total of twenty-three drifter paths were obtained on five separate days. Drifter time and location information was loaded into the Geographical Information System / ArcView computer program in the Coastal Inventory Program at VIMS. The drifter paths were then plotted in Arcview and average current speeds were measured for each series of drifter recordings. These were then compared with predicted tidal flow for Sandy Point (the sand spit area) in the Great Wicomico River system (Tides and Currents for Windows, version 2.2, Nautical Software Inc).

Figure 9: Design of surface drogue (drifter) used in the circulation studies (after Davis et al., 1982).



RESULTS

Reproductive Development

By the beginning of the study, both males and females were either in the late active or ripe stage of development (Figure 10). Evidence of spawning (i.e. spent specimens) were first seen in the July 14th samples (Figure 10). Most of the specimen sampled were completely spawned out by early September, with a large majority of them returning to the inactive stage by the end of September.

Disease Assays

MSX was absent in all of the oysters examined. *Perkinsus* prevalence increased from 32% in June to 100% in July and continued at that level for the remainder of the study (Figure 11). Intensity of *Perkinsus* infection increased from June to September, with the highest percentage of highly infected oyster occurring toward the end of the study.

Larval Production

The number of observed oyster larvae in plankton samples ranged from a high of $37,362 \pm 4,380 \text{ m}^{-3}$ on June 23rd at station GW-2 to a low of 0 at all stations on several different sampling days. Larvae were most abundant at all stations on the 23rd and 30th of June, and on the 14th of July (Figure 12). From the 14th of July onward, there was a continuous decrease in the number of larvae seen in the water column. Coefficient of variation for most samples were within the accepted limits between 5 and 20% (Van Guelpin et al., 1982). Higher CV's were observed when larval abundances

Figure 10: Seasonal changes in gonadal development by sex in *Crassostrea virginica* oysters collected on the reef from June 23 - September 22, 1997. Number of male and female oysters sampled on each day are represented by the numbers above and below each bar.

| 6/23 | 6/30 | 7/14 | 7/28 | 8/11 | 8/25 | 9/8 | 9/22 |

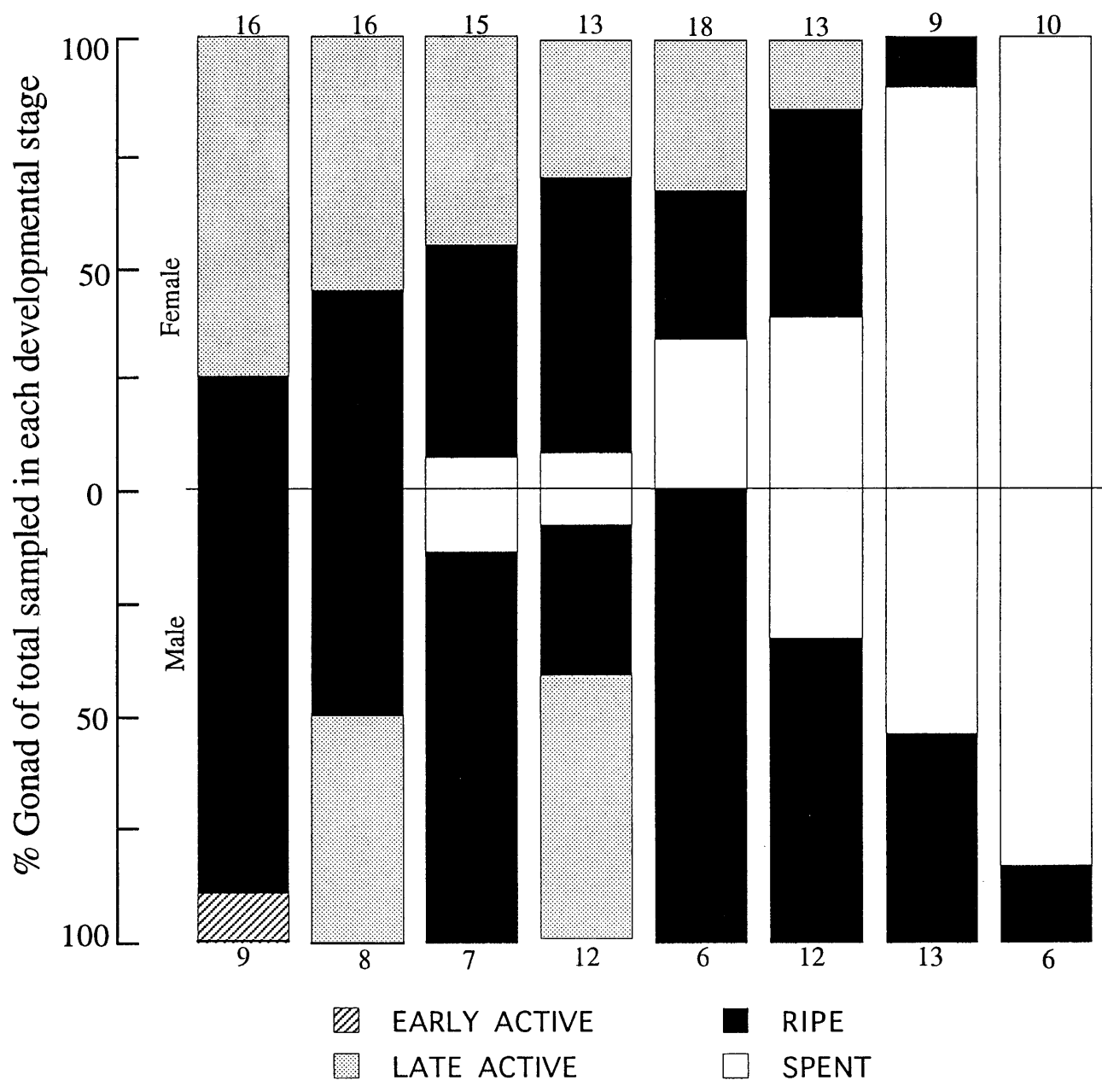
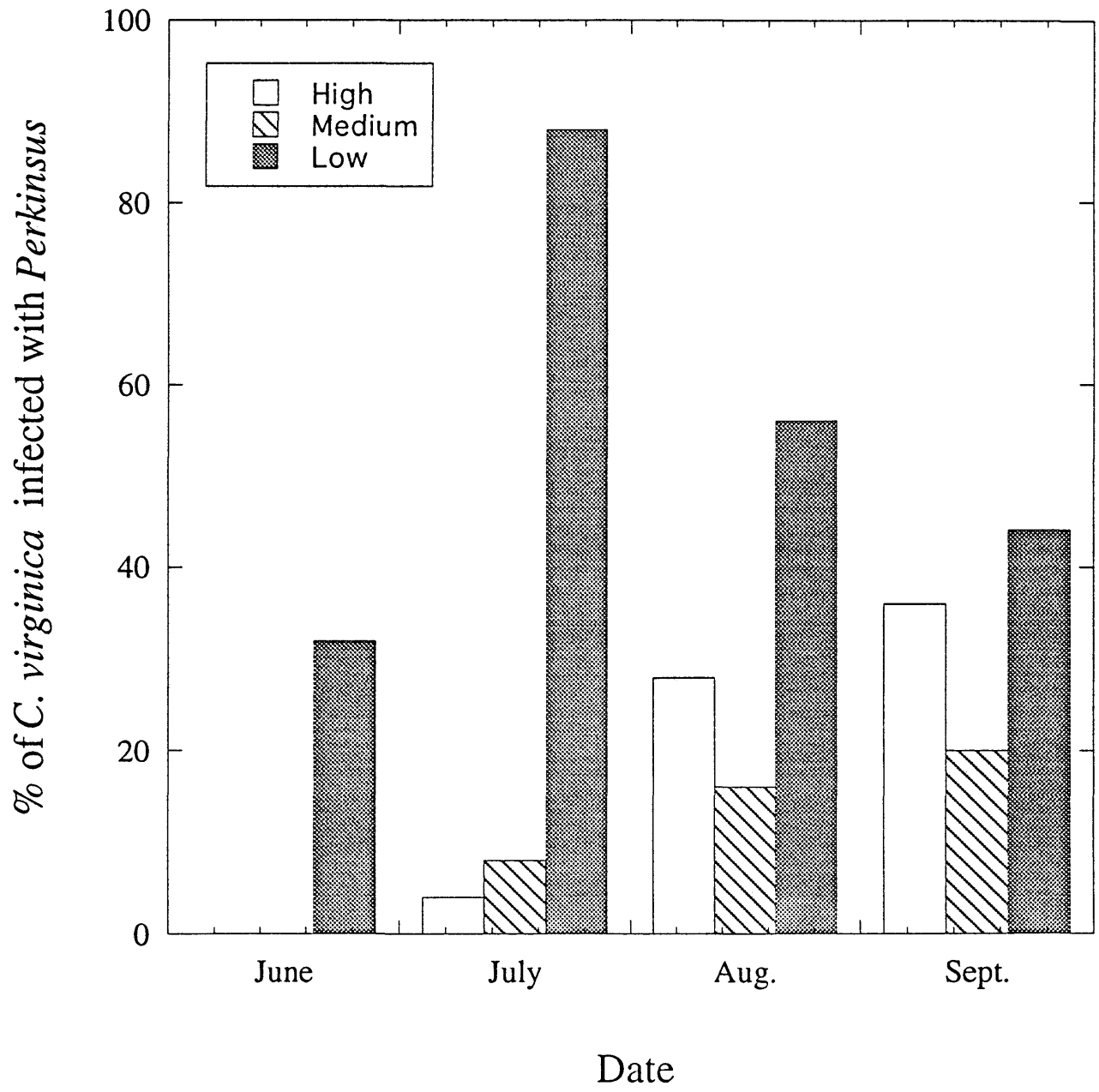


Figure 11: Progression of *Perkinsus* infections in broodstock oysters over the 1997 reproductive season (n=25).



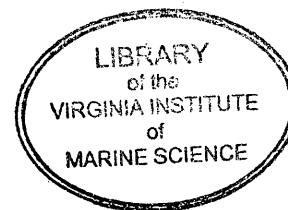
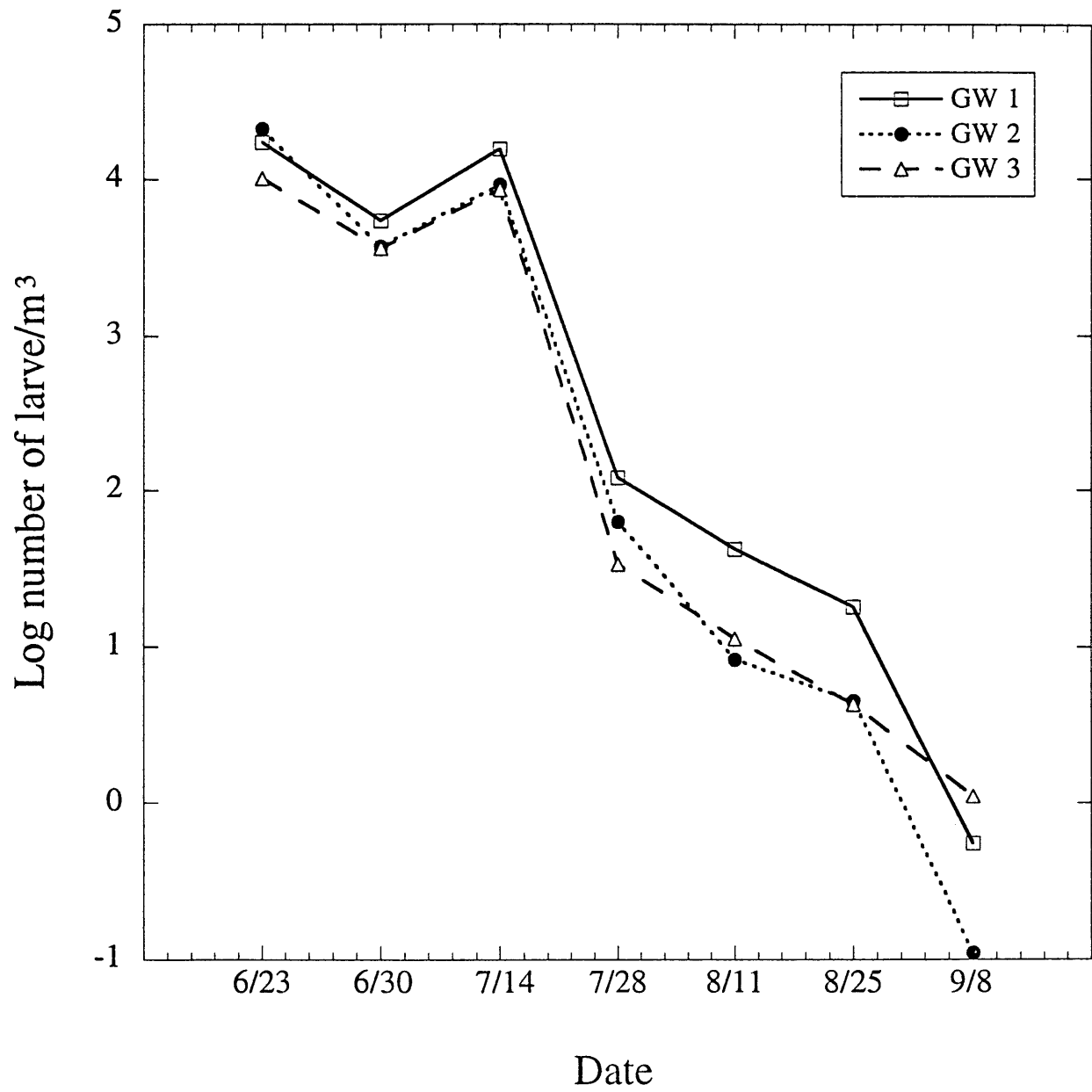


Figure 12: Log number of larvae m^{-3} averaged over each sampling day (averaged over all 4 stages of the tide).



were below 10 m^{-3} .

The total number of larvae m^{-3} was transformed to meet the assumptions of normality and homogeneity of variance. Differences in larval abundance between tidal stage and station were then compared with ANCOVA using day of the year as the covariate. The power transformation ($X' = X^{0.20}$), recommended by Downing et al. (1987) for use in estimating zooplankton populations was used. The use of this transformation met the assumptions of homogeneity of variance, but did not meet the assumptions of normality. Given that ANCOVA's are generally robust to non-normality (Underwood, 1997), this transformation was still used and the resulting data was utilized in performing the ANCOVA.

There was a significant difference in larval concentration between tidal stages ($p < 0.01$) and stations ($p < 0.05$), with no interaction between the two factors ($p = 0.55$). Student Newman Keuls (SNK) multiple comparison test for station effect, showed there were significantly more larvae at GW-1 than at the other two stations (Table 2a). There was no difference in larval abundance between GW-2 and GW-3. The SNK for tidal stage, showed there were significantly more larvae during the flood tidal stage than during the ebb or slack onto flood stages. (Table 2b). No differences were found between any of the other tidal stages.

Temperature and Salinity

Surface temperature at the reef (station N1; Figure 8), reached a maximum of $29.5 \text{ }^\circ \text{C}$ on July 28th (Figure 13). The difference between the surface and bottom temperature increased in a down river direction (station N1 to N3) away from the reef (Figure 14). The maximum temperature difference occurred on July 28th for all 3 stations. As with the temperature, the difference in salinity between the surface and bottom water increased down river (from N1 to N3; Figure 15). Salinity at the 3

Table 2a: SNK test for station rank mean. Asterisks indicate $P < 0.05$. Calculation of D based on an $SE = 0.130$.

1 (GW-3)	2 (GW-2)	3 (GW-1)	Q	D
3.066	3.112	3.543		
³⁻¹ 0.477*			3.35	0.44
²⁻¹ 0.046	³⁻² 0.431*		2.79	0.37

Table 2b: SNK test for tidal stage rank mean. Asterisks indicate $P < 0.05$. Calculation of D based on an $SE = 0.15$.

1 (Slack-flood)	2 (Ebb)	3 (Slack-ebb)	4 (Flood)	Q	D
2.872	3.113	3.289	3.687		
⁴⁻¹ 0.815*				3.68	0.55
³⁻¹ 0.417	⁴⁻² 0.574*			3.35	0.51
	³⁻² 0.175	⁴⁻³ 0.398		2.79	0.42

Figure 13: Surface temperature measured at station N1 (the reef) from June 23 - September 22, 1997.

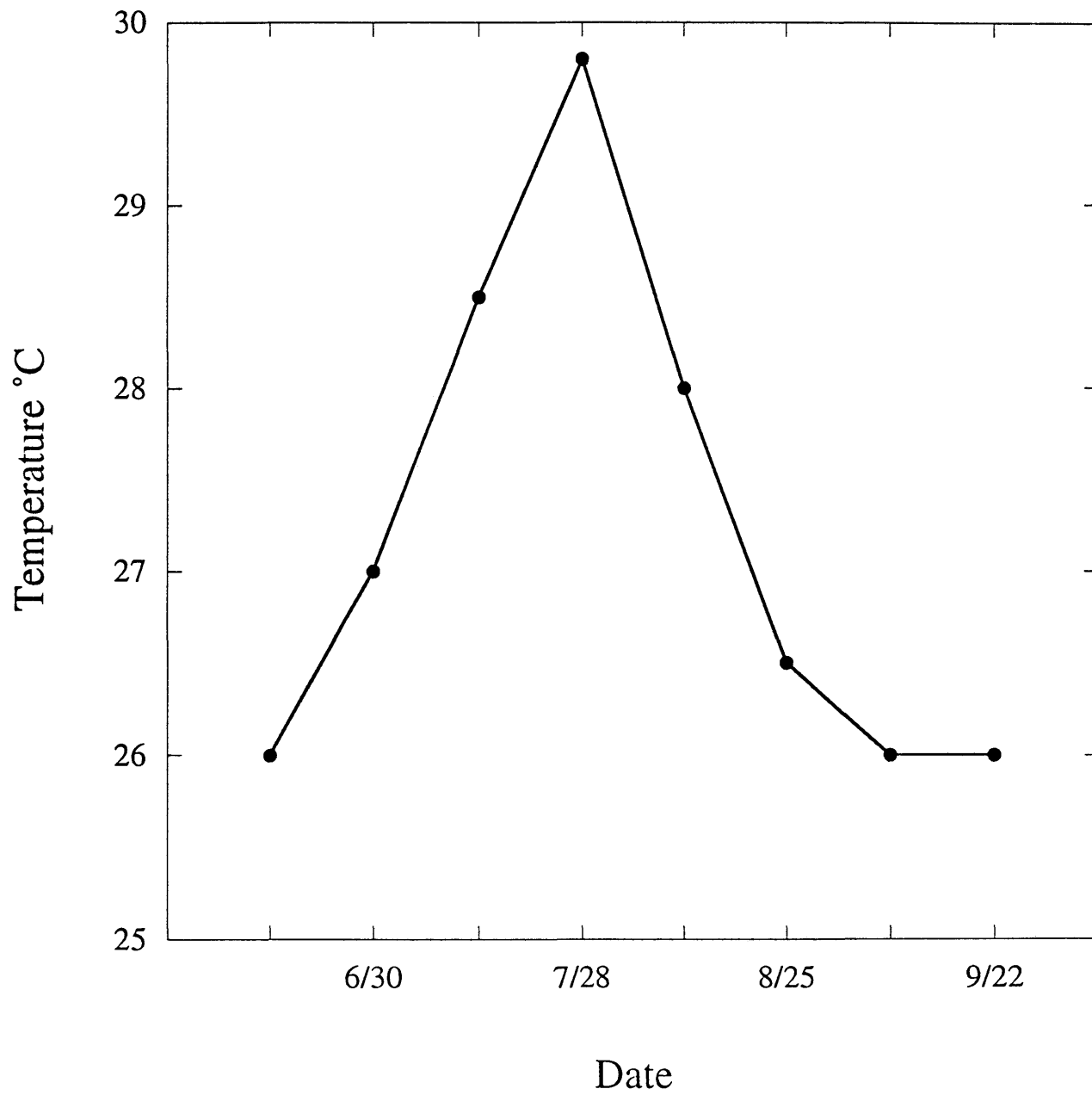


Figure 14: Surface and bottom temperature for all three stations (N1 - N3) measured from July 28 - September 22, 1997.

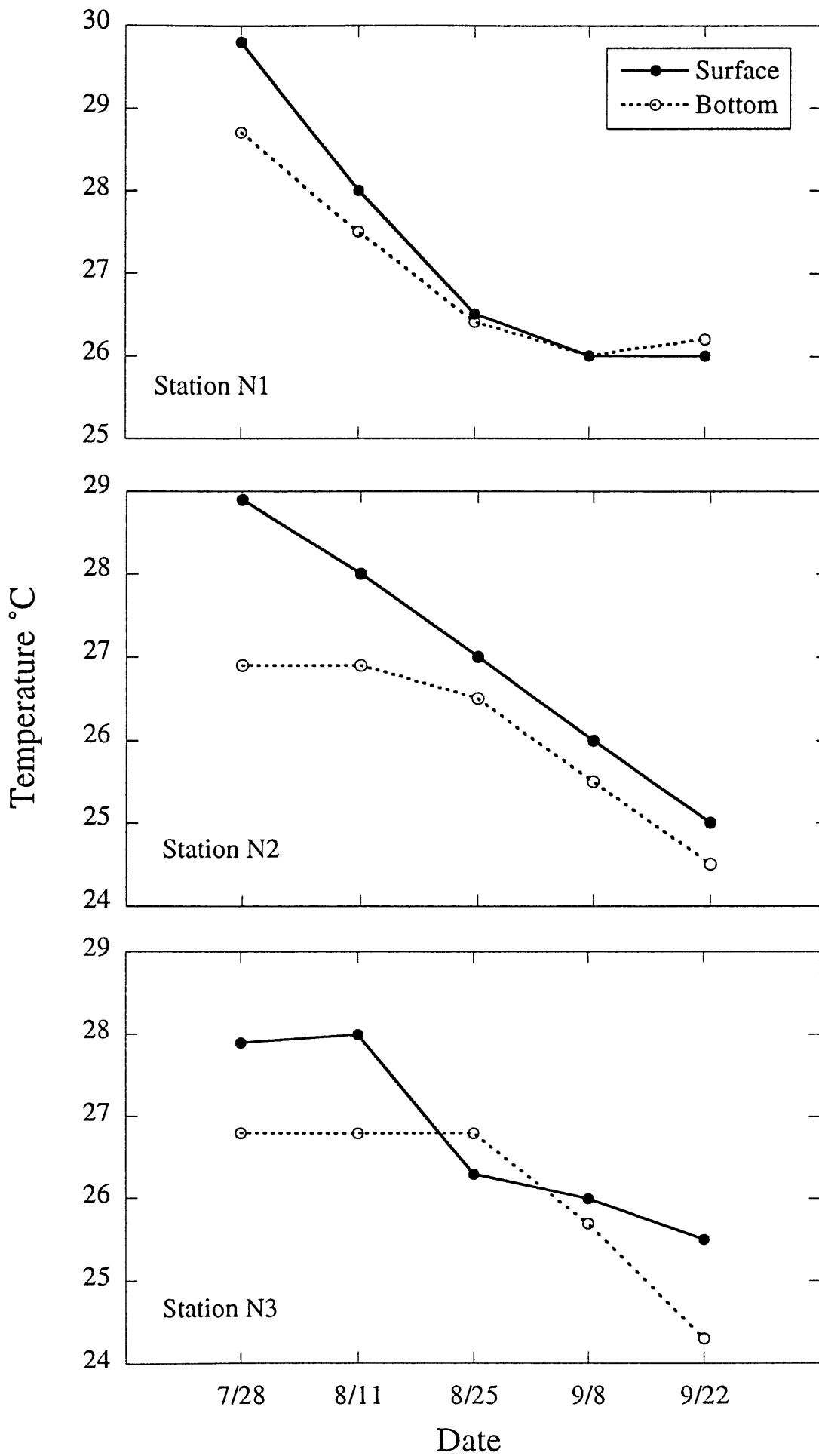
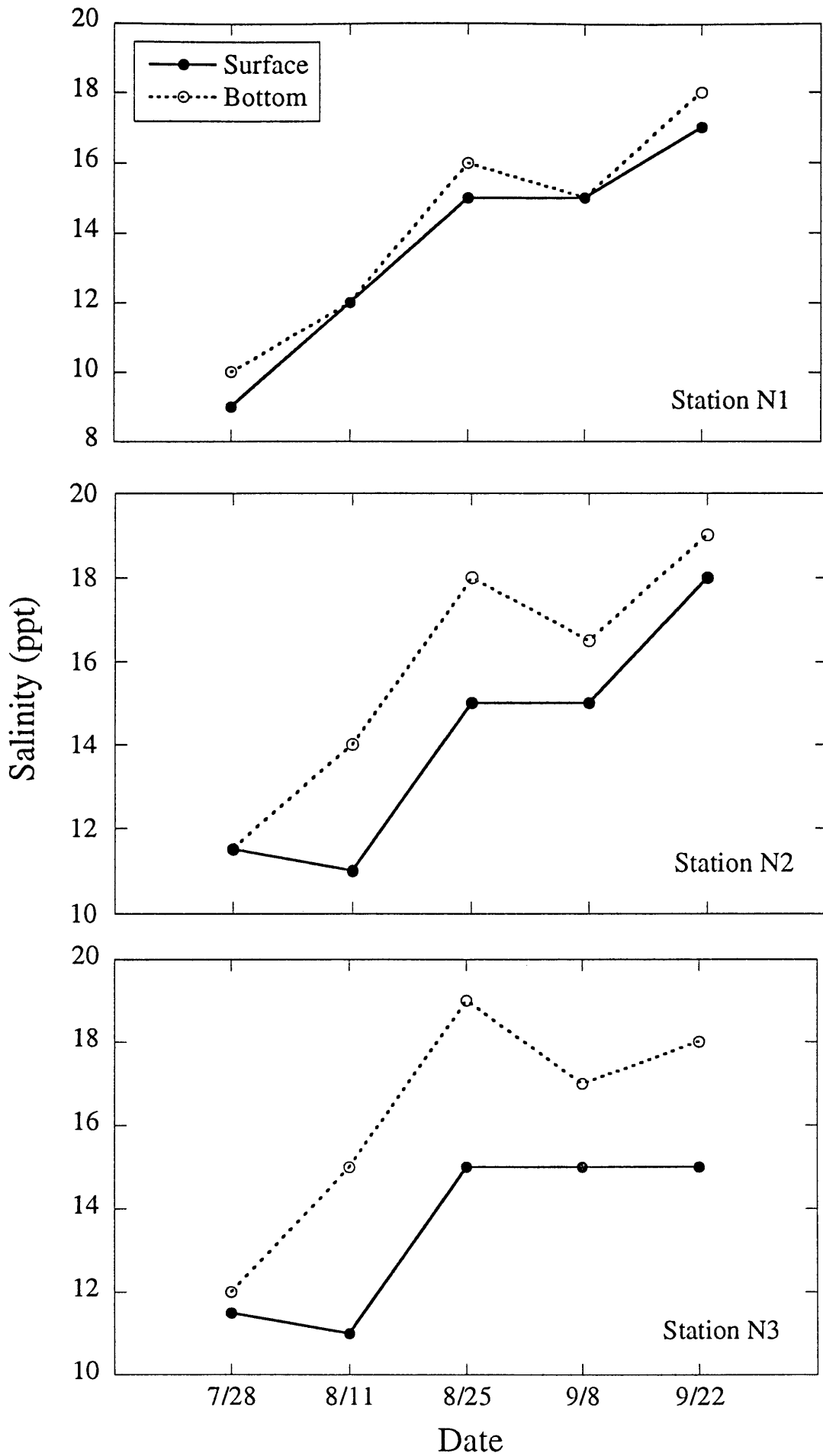


Figure 15: Surface and bottom salinity for all three stations (N1 - N3) measured from July 28 - September 22, 1997.



stations ranged from 12 to 18 ppt. The maximum difference encountered was 3 ppt at station N2 and N3.

Circulation

The direction and average speeds traveled by the drifters on each sampling day, for each fix during the day, was recorded and calculated (see Appendix II for details). Tidal cycle was recorded as the stage/s of the tide occurring between a particular fix and the previous fix. For example, if the tide was ebbing for the first half, then changed to slack water for the second half, it was recorded as E-S. If the tide was flooding for the entire time, then tidal stage was recorded as F. Average speeds recorded by the drifters ranged between 0 and 15.9 cm/sec. Maximum predicted tidal current was between 10 and 20 cm/sec on all sampling days.

Figure 16 A-D show the drifter tracks recorded on July 28. All of the drifters were released near the reef at the beginning of ebb tide. Due to lost data (GPS malfunction), several hours are missing from mid-day on tracks 1 and 4 (Figure 16 A & D). Both tracks follow the predicted tide down river on ebb and up river on flood. Drifter 3 (Figure 16 C), followed the ebb down river, until about 1100, then started back up river, despite the fact that the predicted tide was still ebbing. Drifter 2 (Figure 16 B), ran aground several times and no pattern in movement was evident.

Figure 17 A-D show the drifter tracks recorded on August 11. The drifters were released near the reef at approximately the same time. Drifters 1, 2, and 4 show similar patterns of movement. Slack water occurred around 1400. Drifters 1, 2, and 4 (Figure 17 A,B,&D), all started to turn in, away from the channel, 2-3 hours earlier around 1130. Drifter 3 ran aground several times (Figure 17 C), so no pattern of movement was discernible.

The 5 drifter tracks recorded on August 25, are shown in Figure 18 A-E. The drifters were released up river from the reef. Four of the 5 tracks show similar

patterns. These 4 drifters traveled down river with the tidal current until about 1030, when they started to turn South / West away from the channel (Figure 18 B-E). As on the 11th of August, this “turning” occurred several hours prior to slack water. Drifter 1 (Figure 18 A) had a dissimilar pattern from the other 4 tracks. It remained in the channel, and followed the tidal current, turning around 1300, when the predicted tidal flow changed from ebb to flood.

On September 8, 3 of the 5 drifters showed similar patterns (Figure 19 A-E). All drifters were released up river from the reef, around maximum ebb flow. Drifters 2-4 traveled down river, remaining South / West of the channel and remained there for the rest of the time, despite the turning of the tide from ebb onto flood (Figure 19 B-D). Drifter 1 ran aground several times, so no definitive pattern was evident (Figure 19 A). Drifter 5 (Figure 19 E) followed the ebb tide down river, then started back up river when the tide started flooding around 1200. It followed this pattern until about 1500 (max. flood), when it completed a loop around the reef and started traveling back down river.

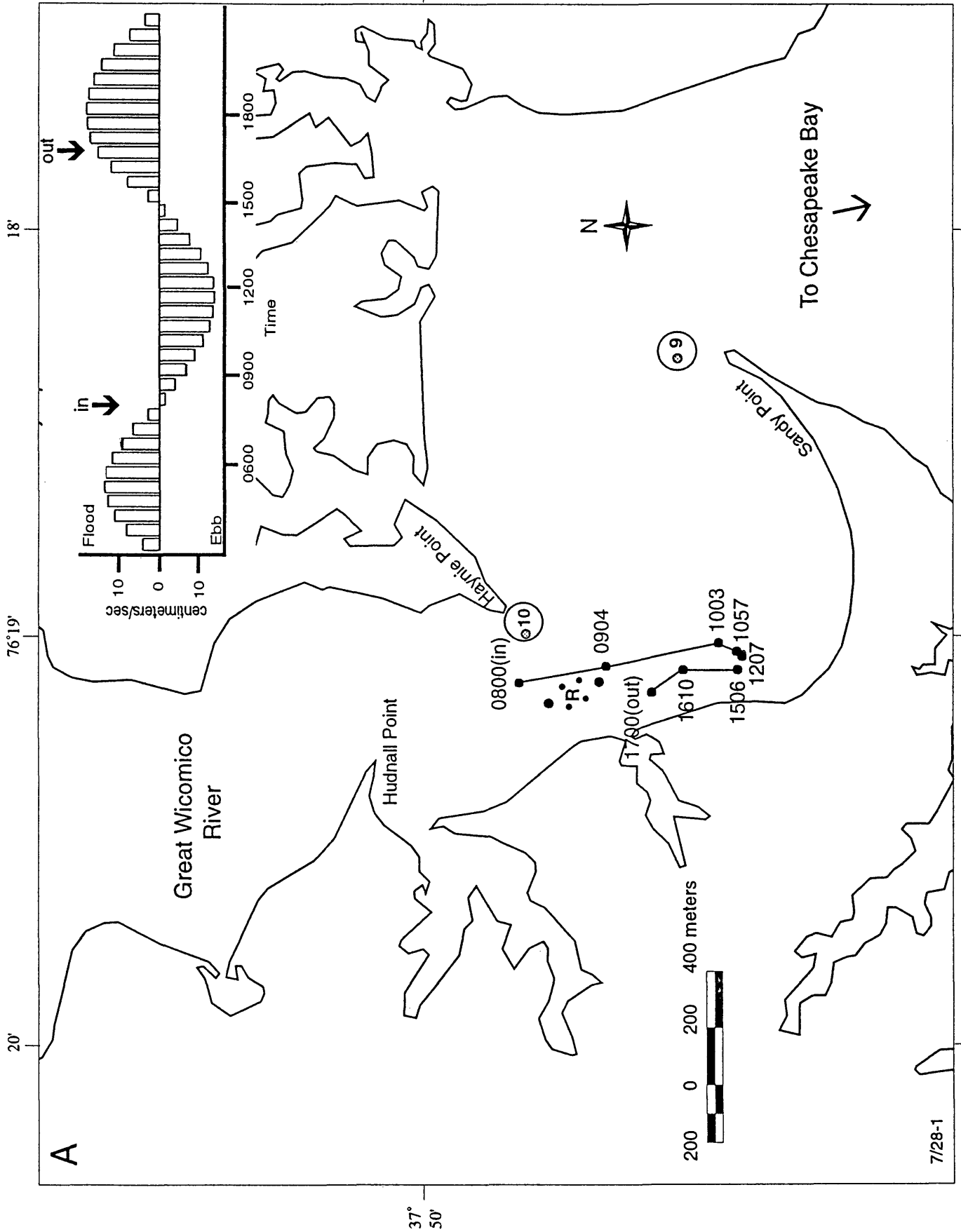
The drifter tracks obtained on September 22 only covered half of a tidal cycle (just after maximum ebb to just after maximum flood). All of the drifters were released up river or adjacent to the reef (Figure 20 A-E). There was a large 2 hour gap in GPS recordings during slack water, therefore the estimated distance traveled is not accurate for this sampling day. All 5 drifters tracks agreed with predicted tidal flow, but due to the scarcity of the GPS recordings, no definite pattern of movement is evident.

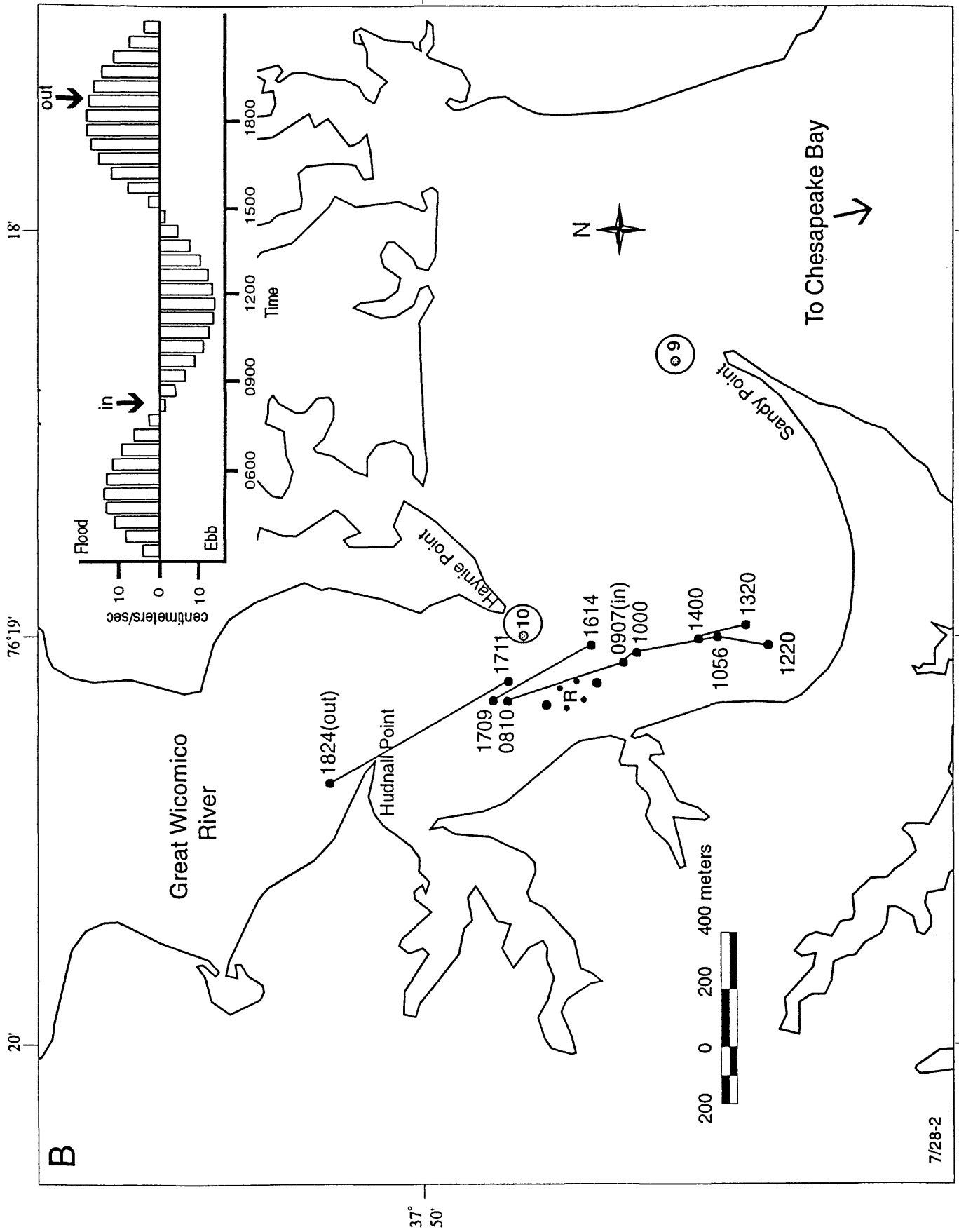
Settlement

As previously mentioned, VIMS maintains an oyster stock monitoring program in the Great Wicomico River. Spatfall estimates from shellstring data ranged from 1.42 to 43.39 spat per week (Figure 21). Setting was first recorded at Hudnall’s dock in late June and continued until the end of August. The most intense setting period occurred

throughout the month of July. Setting was most intense on, upriver, and adjacent to the reef. This pattern of setting was also evident in the patent tong survey data (Figure 22). Spatfall estimates from patent tong surveys ranged from a high of 102.6 m⁻² on Shell Bar to a low of 4.6 m⁻² on Ingram reef. The most intense set occurred up river of the sand spit, near or adjacent to the artificial oyster reef. The general trend was a decrease in set as one moves downstream from the reef.

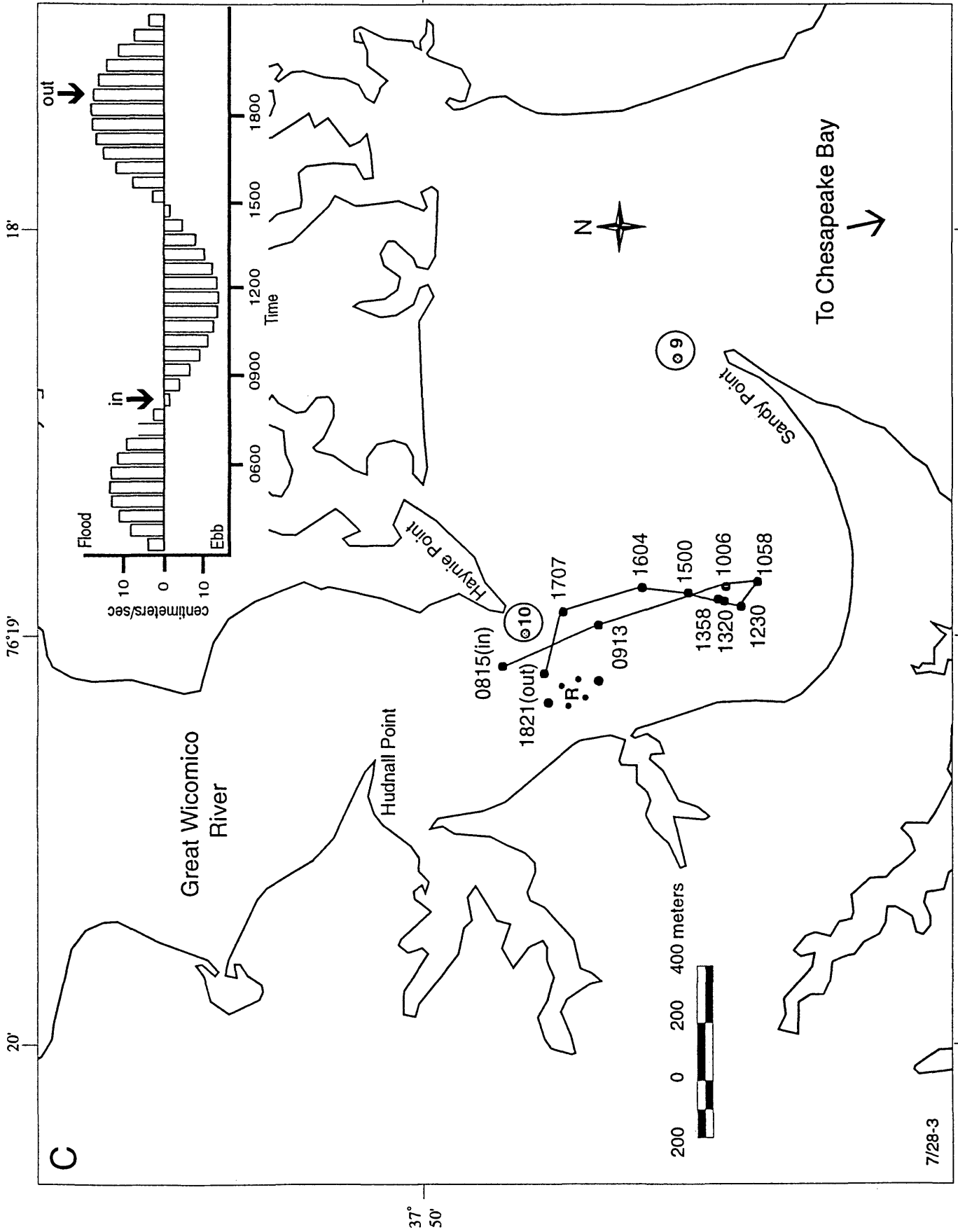
Figure 16: Drifter tracks for July 28, 1997. (A-D) represent drifters 1-4 respectively. Inset shows predicted tidal currents for Sandy Point, with arrows representing approximate times of deployment (in) and retrieval (out) of the drifters. Time is reported as Eastern Standard (E.S.) Military time. R denotes the location of the reef and 9 and 10 mark the main channel in the river.





B

7/28-2



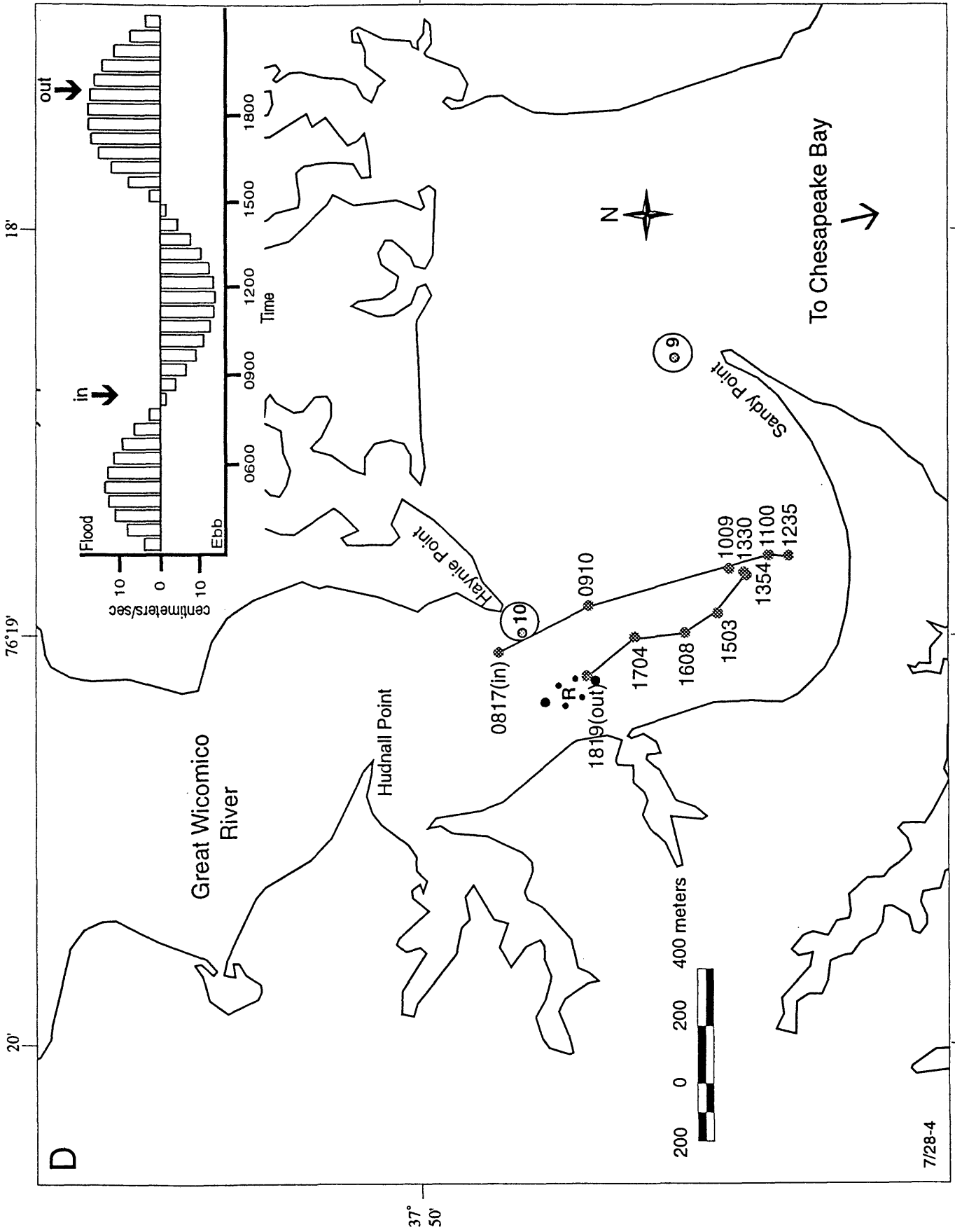
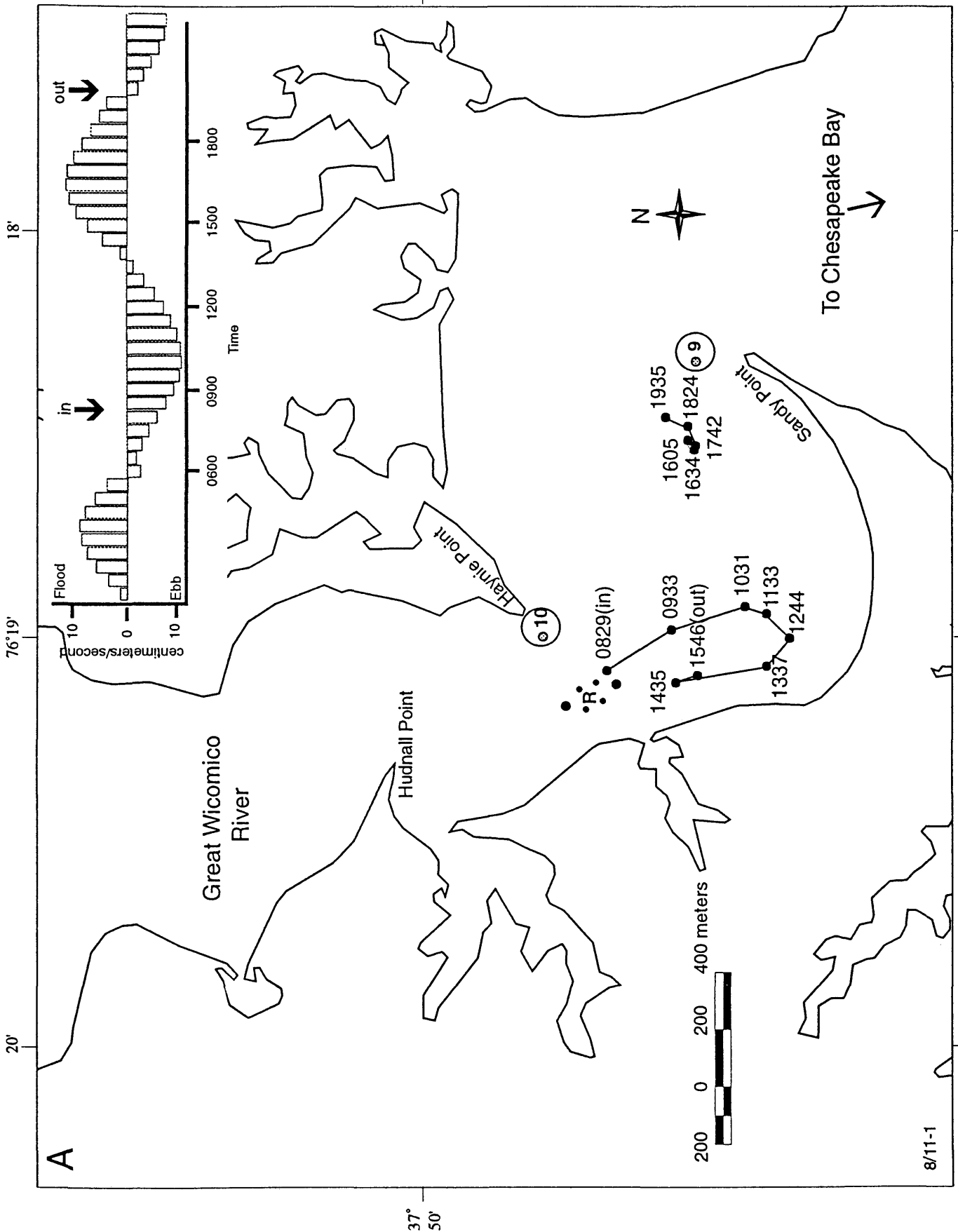


Figure 17: Drifter tracks for August 11, 1997. (A-D) represent drifters 1-4 respectively. Inset shows predicted tidal currents for Sandy Point, with arrows representing approximate times of deployment (in) and retrieval (out) of the drifters. Time is reported as Eastern Standard (E.S.) Military time. R denotes the location of the reef and 9 and 10 mark the main channel in the river.



18'

76°19'

20'

A

Great Wicomico River

Hudnall Point

Haynie Point

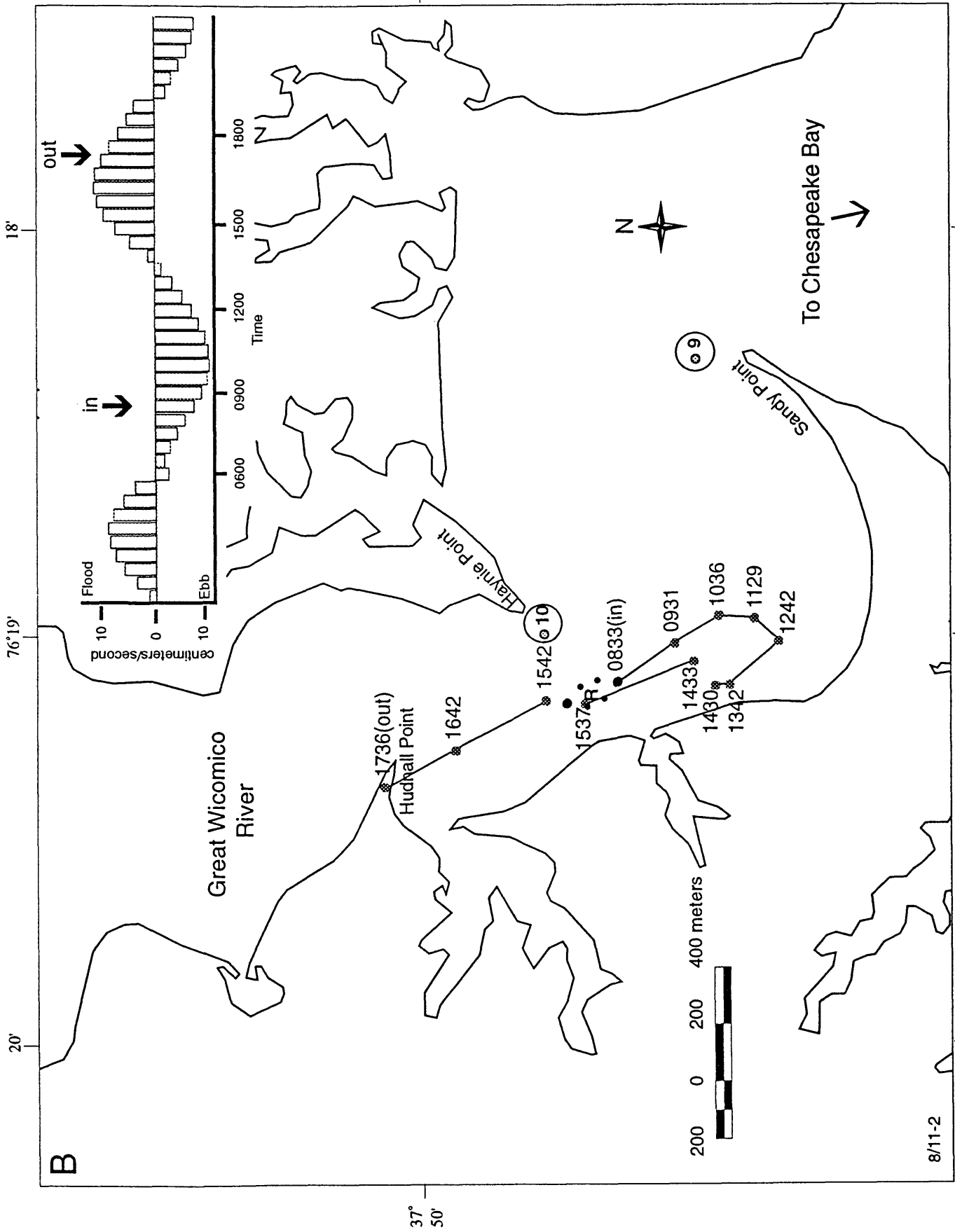
Sandy Point

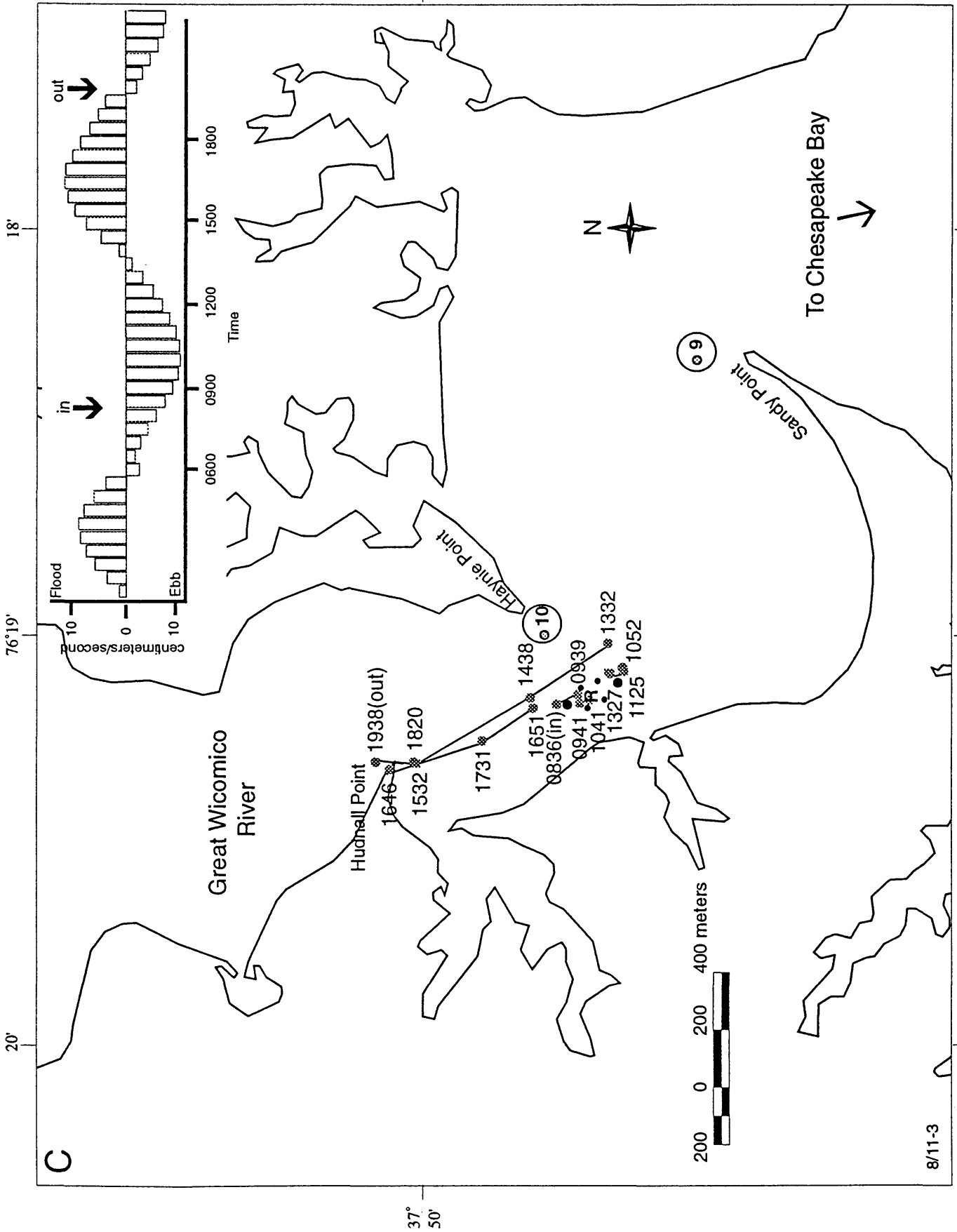
To Chesapeake Bay

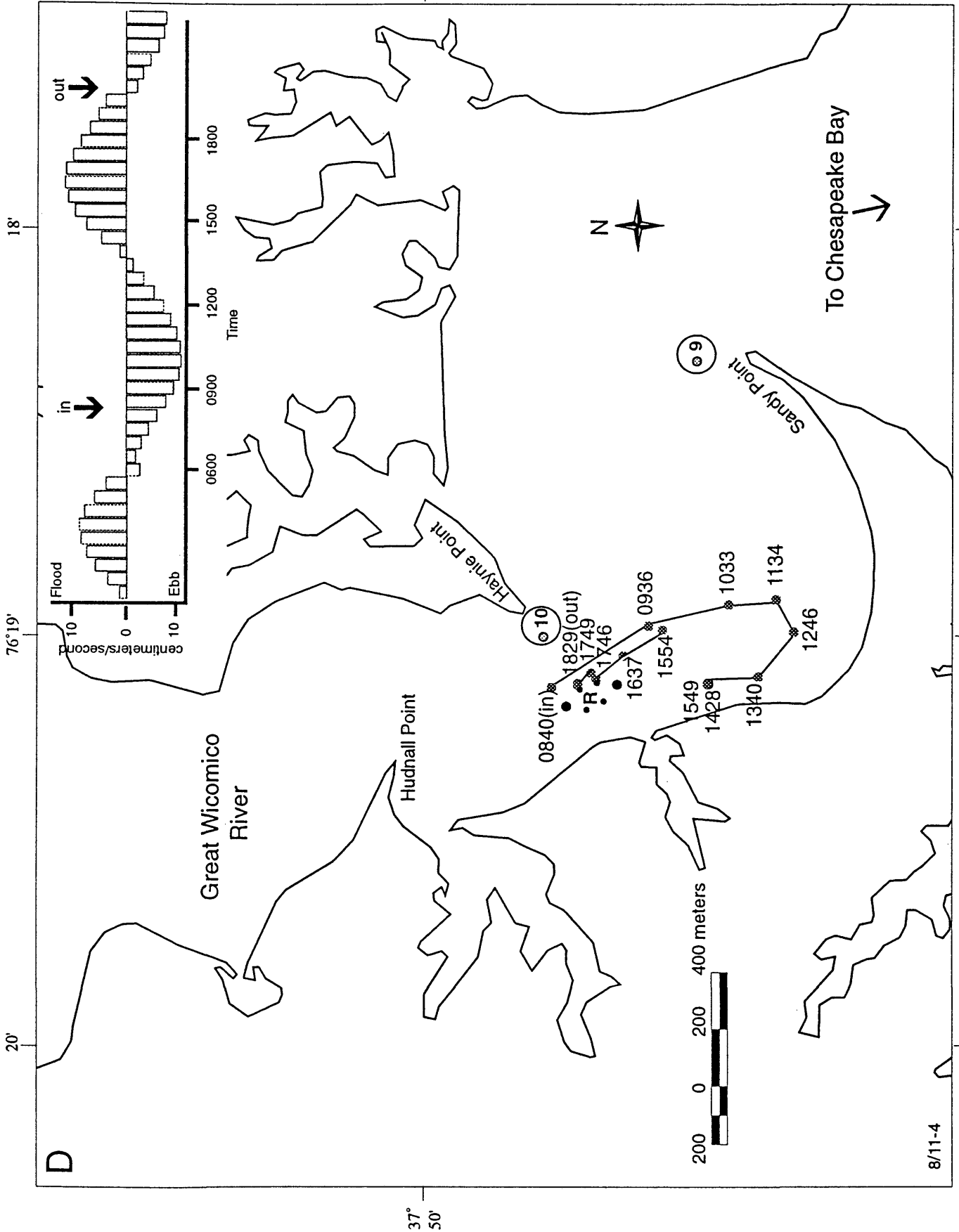


37° 50'

8/11-1



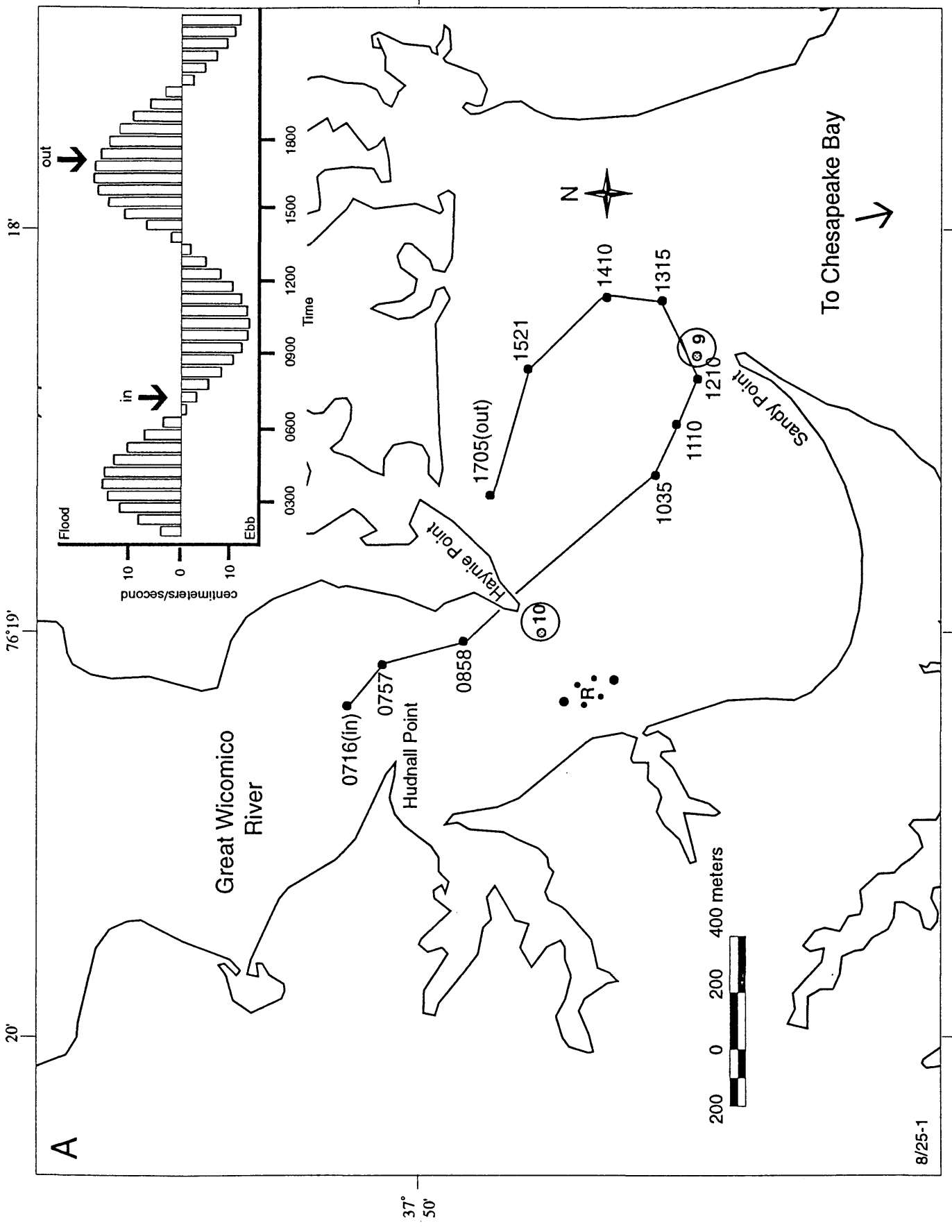




D

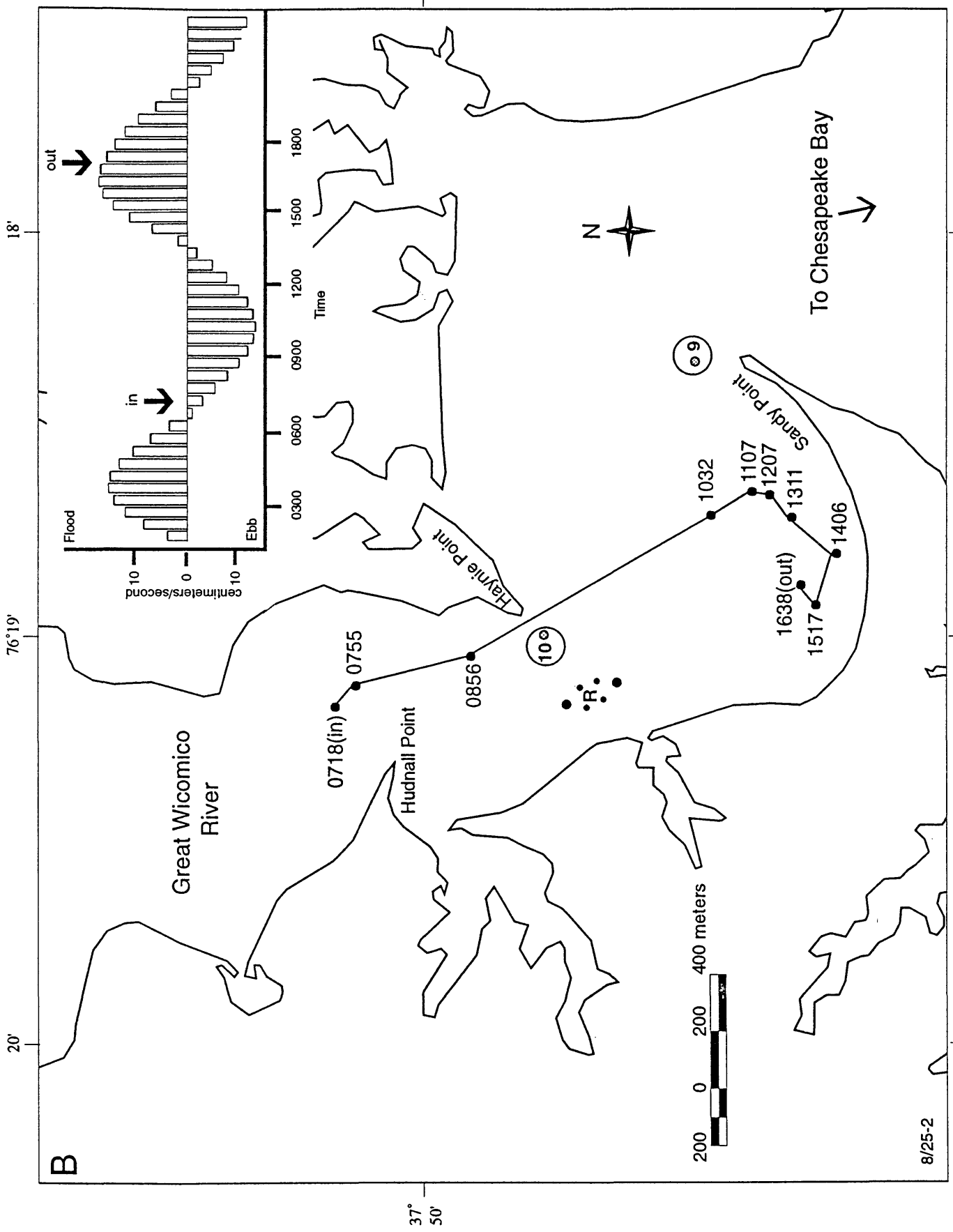
8/11-4

Figure 18: Drifter tracks for August 25, 1997. (A-E) represent drifters 1-5 respectively. Inset shows predicted tidal currents for Sandy Point, with arrows representing approximate times of deployment (in) and retrieval (out) of the drifters. Time is reported as Eastern Standard (E.S.) Military time. R denotes the location of the reef and 9 and 10 mark the main channel in the river.



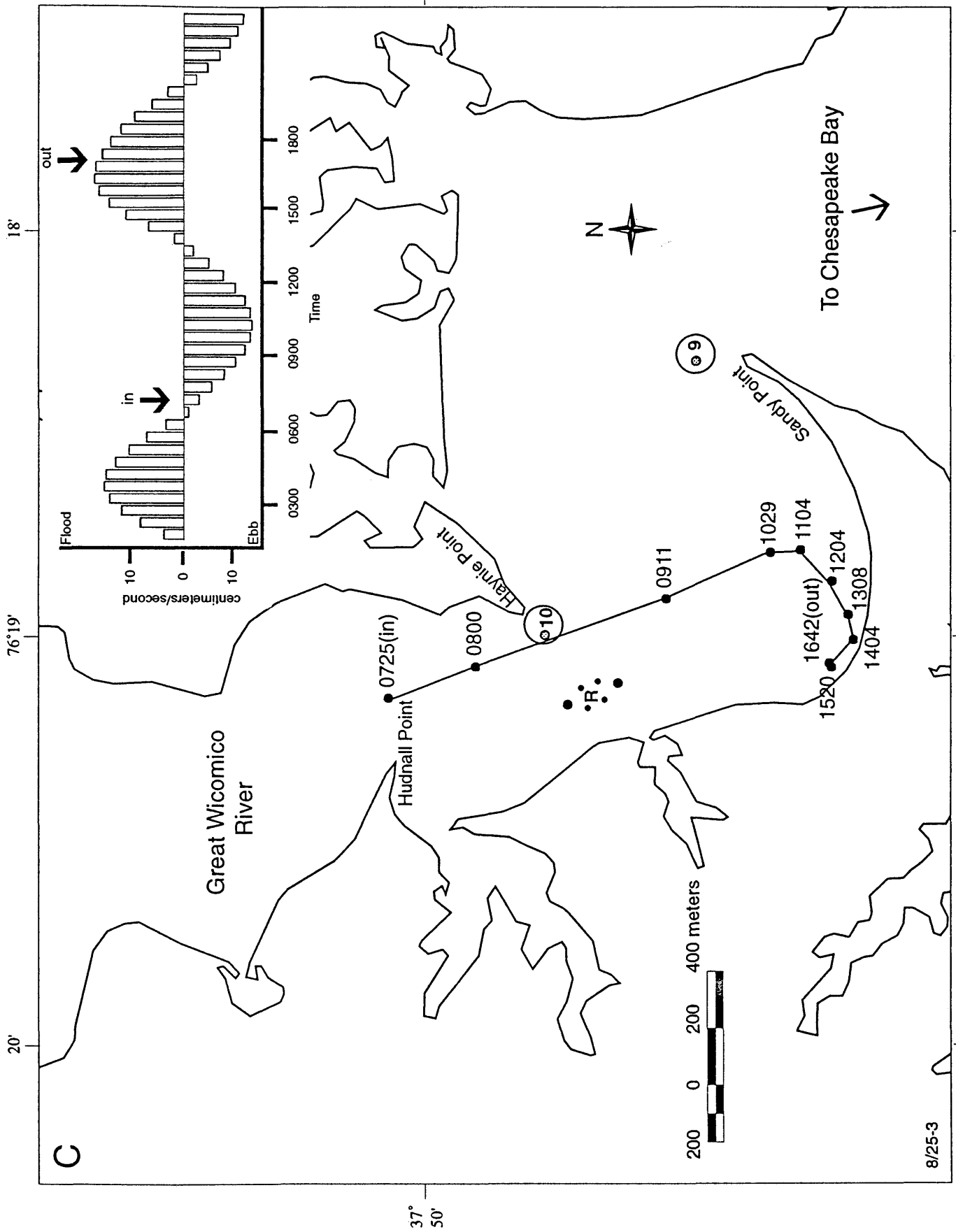
A

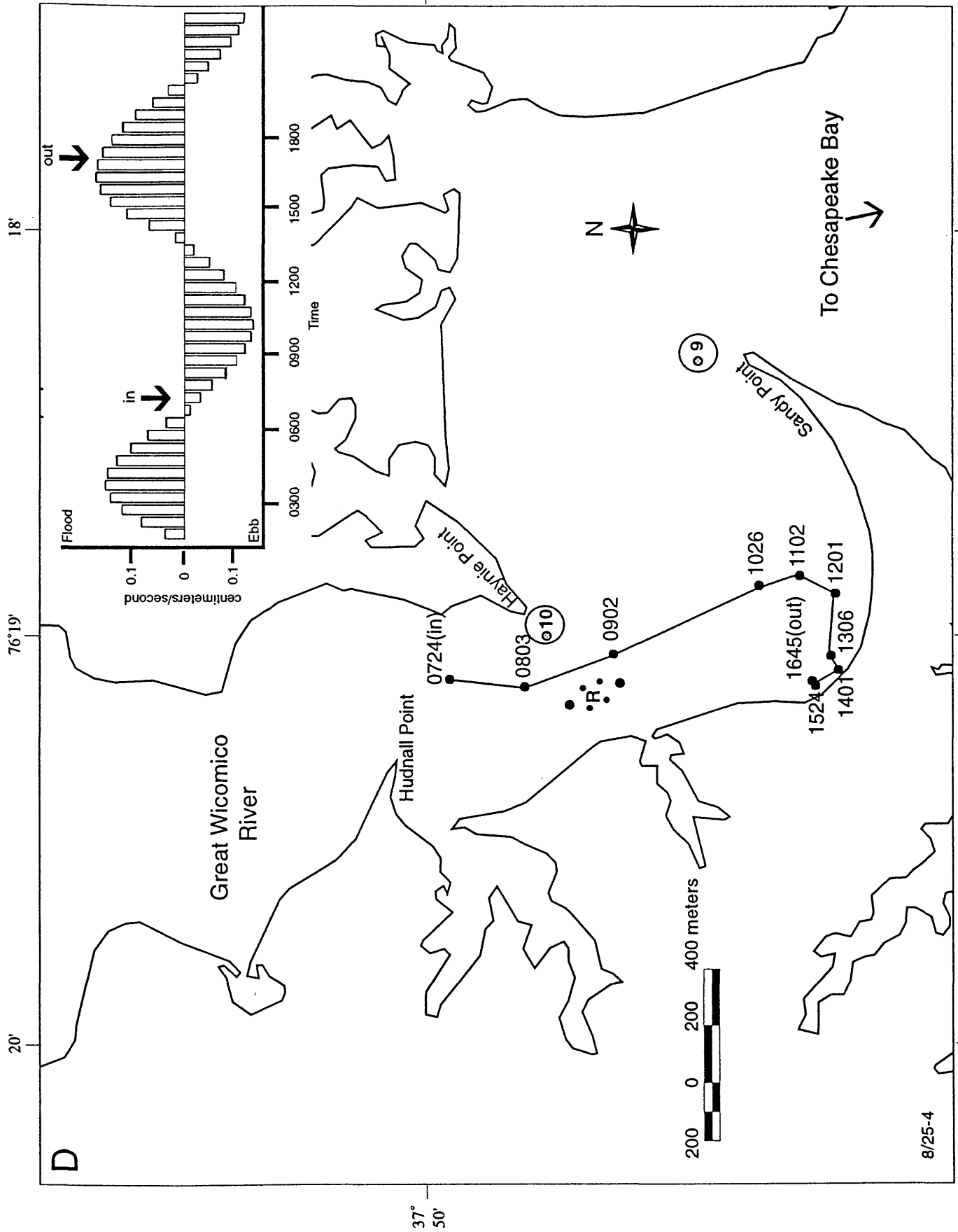
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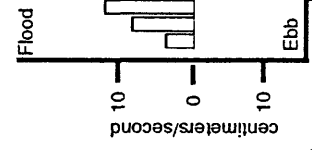
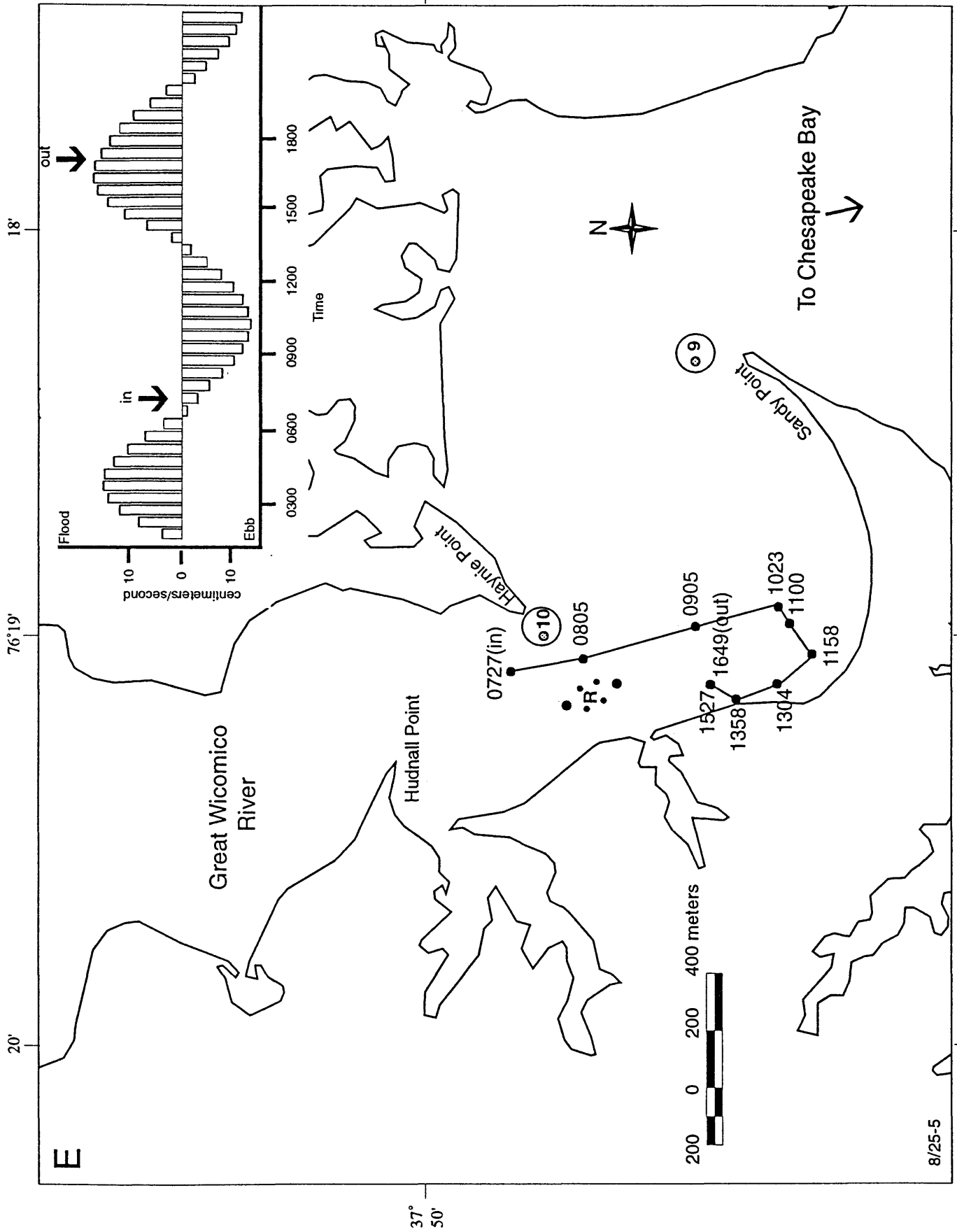


B

8/25-2



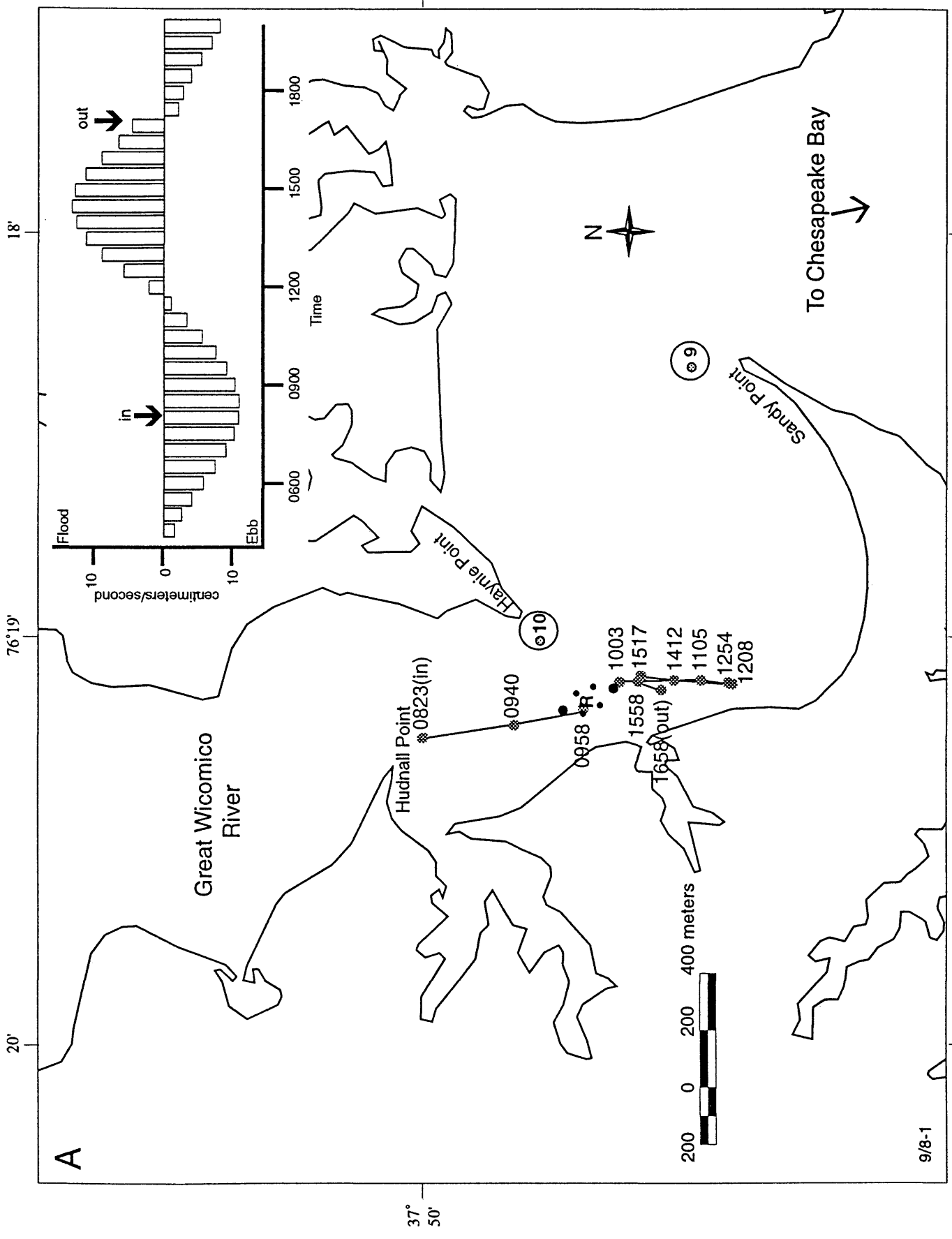




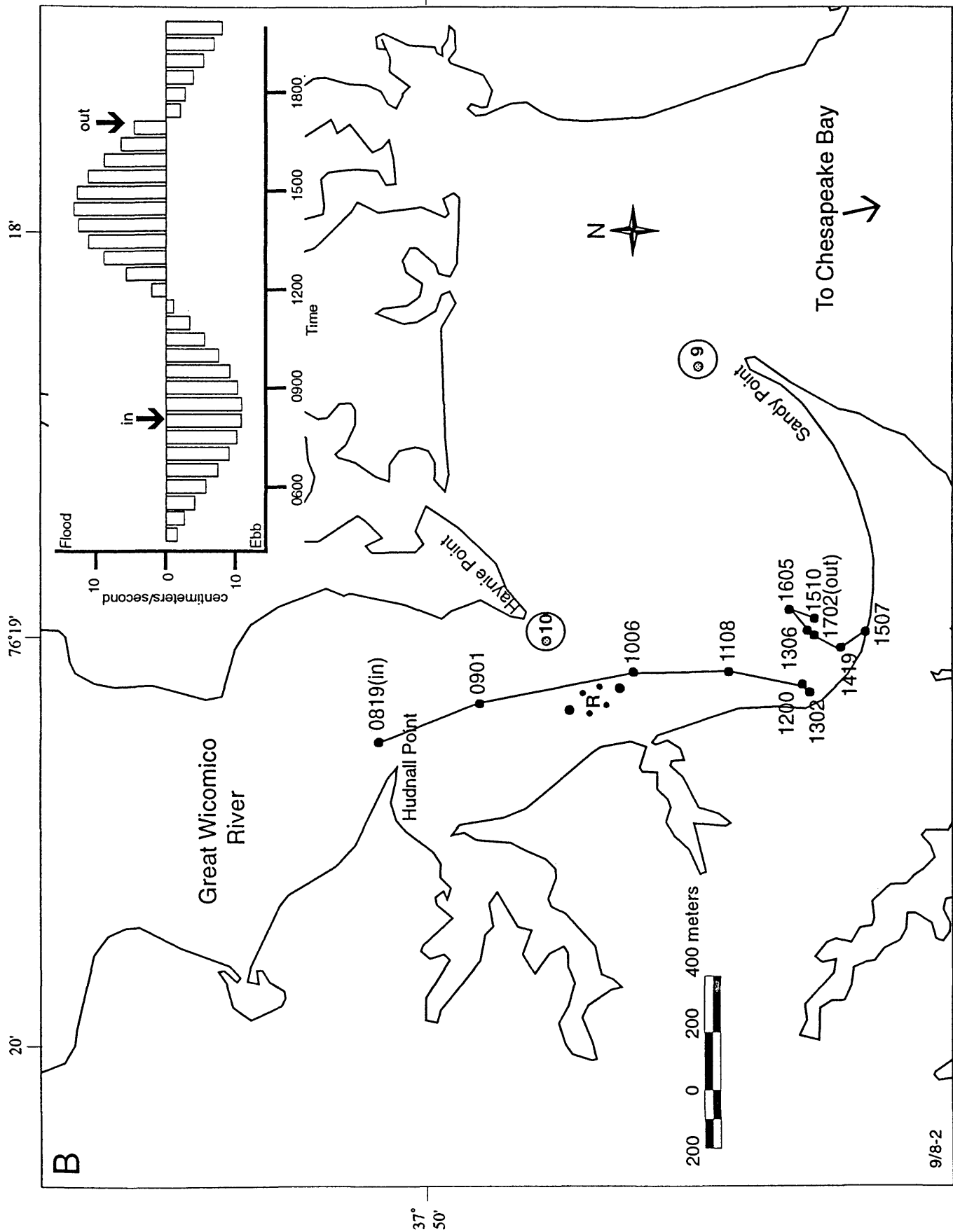
E

8/25-5

Figure 19: Drifter tracks for September 8, 1997. (A-E) represent drifters 1-5 respectively. Inset shows predicted tidal currents for Sandy Point, with arrows representing approximate times of deployment (in) and retrieval (out) of the drifters. Time is reported as Eastern Standard (E.S.) Military time. R denotes the location of the reef and 9 and 10 mark the main channel in the river.

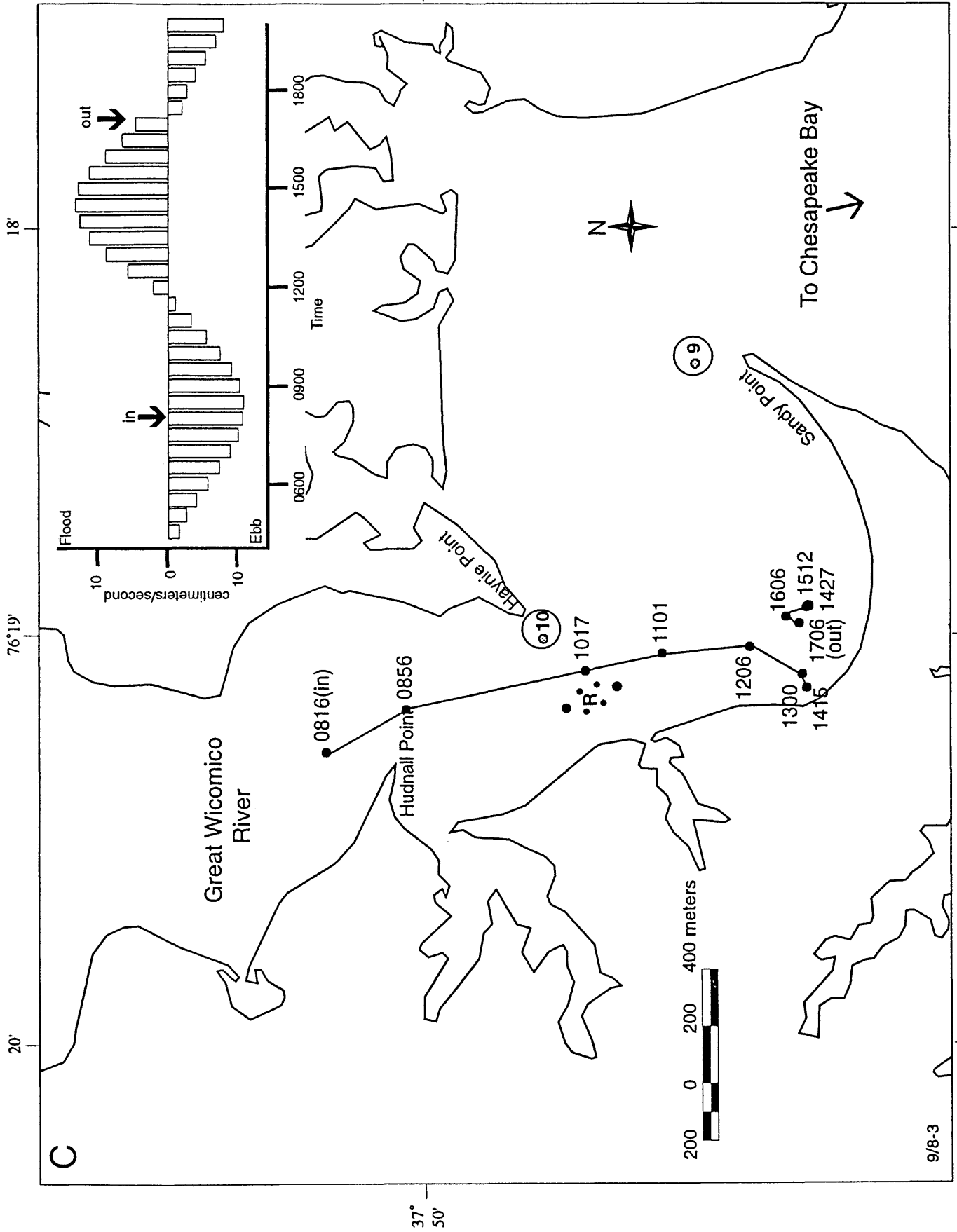


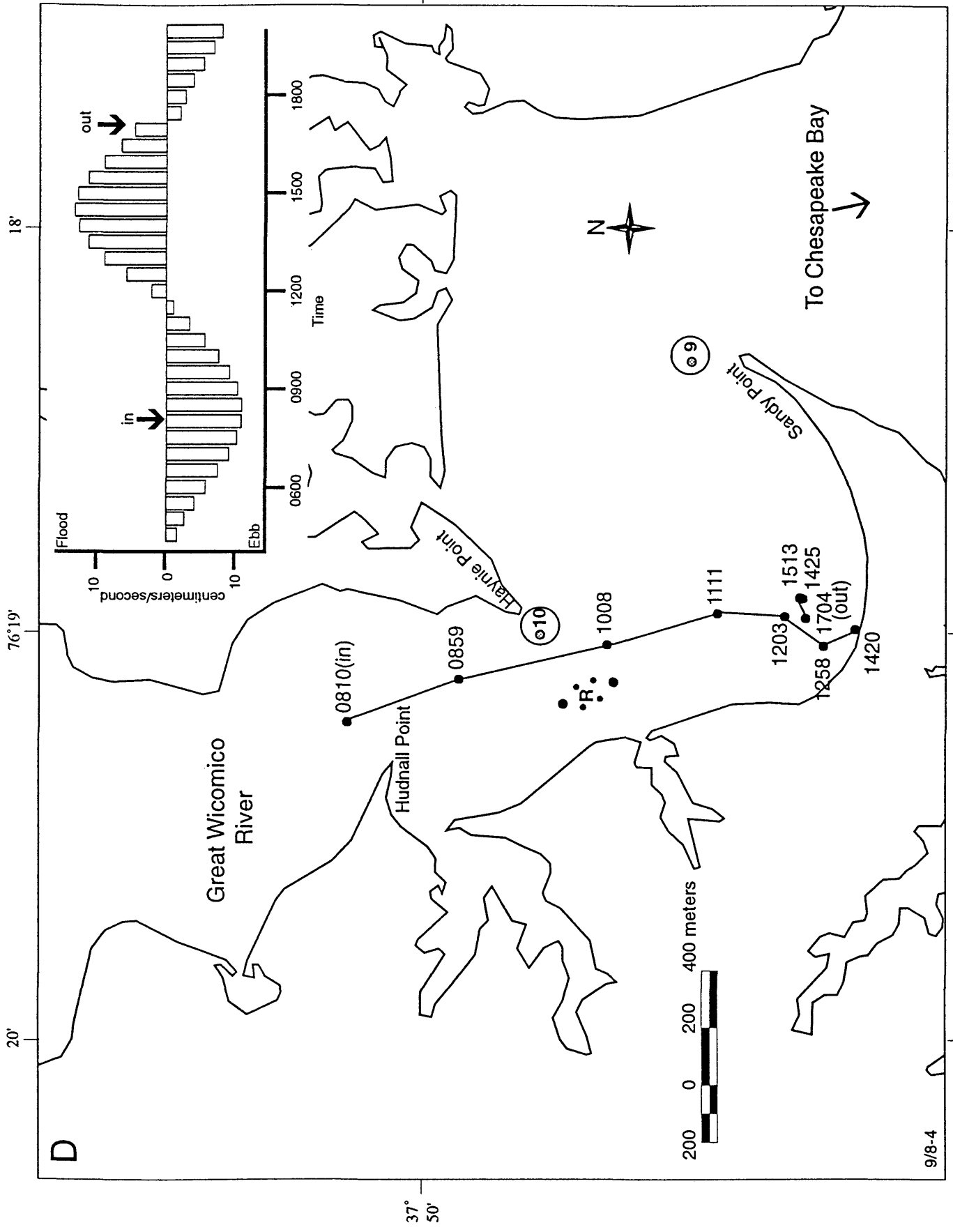
A



B

9/8-2





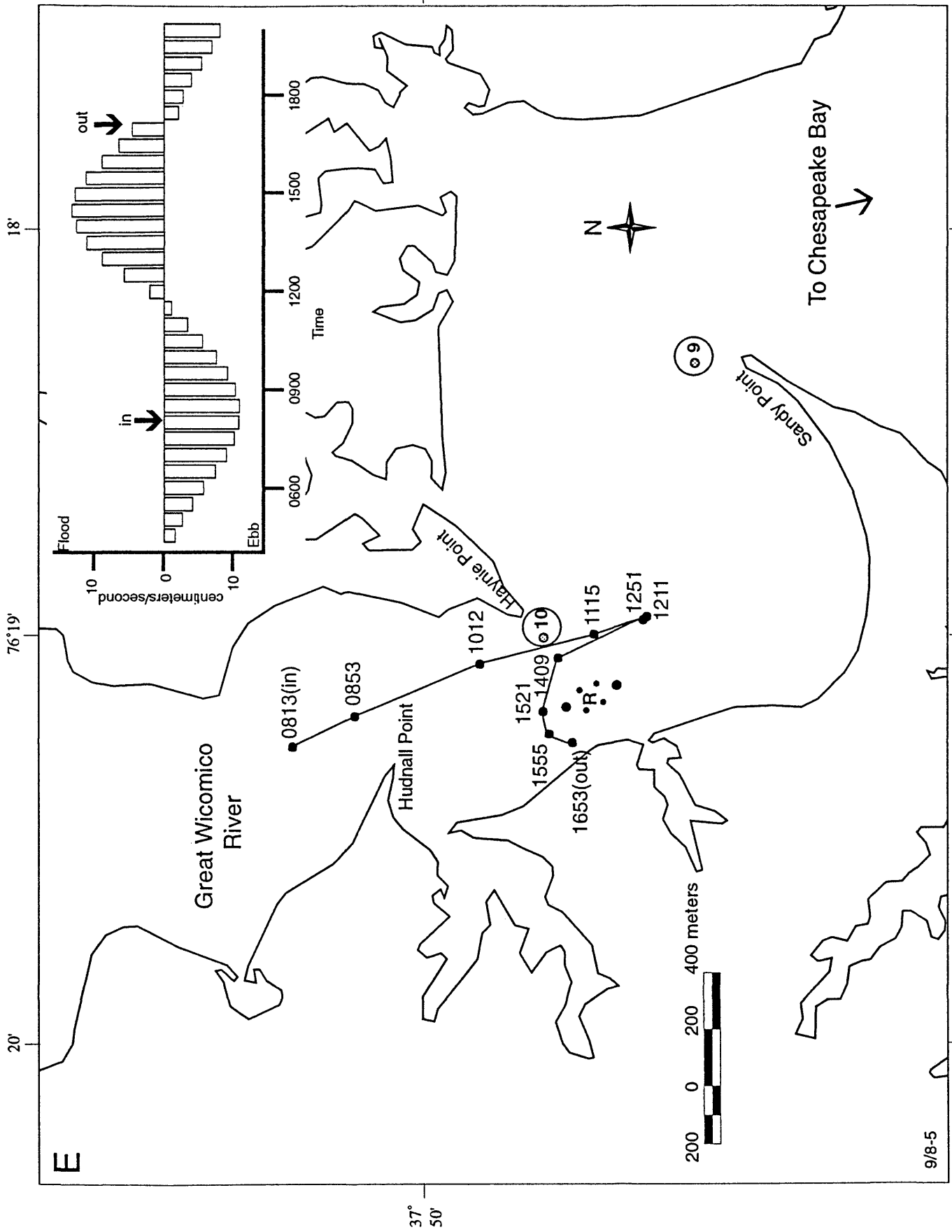
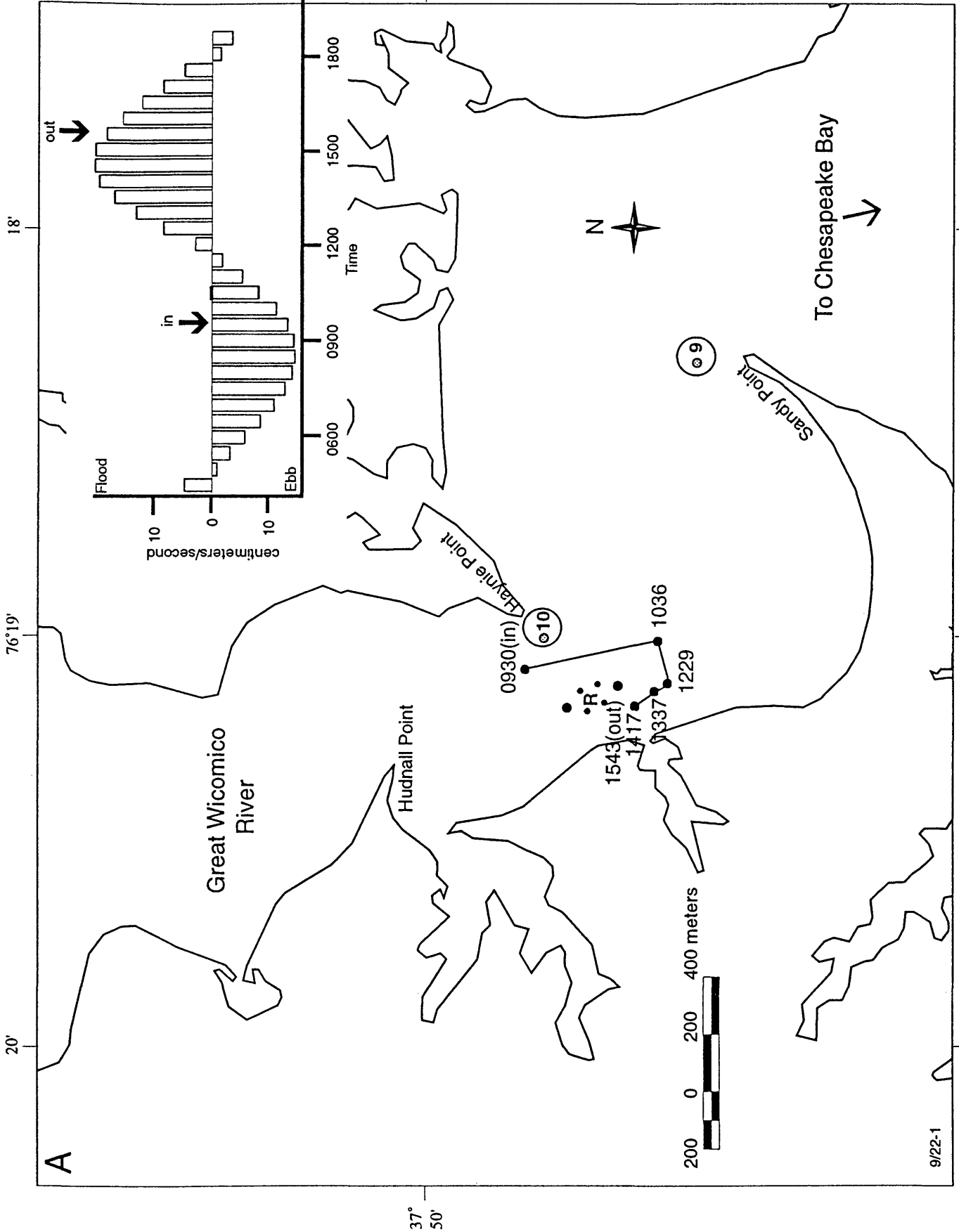
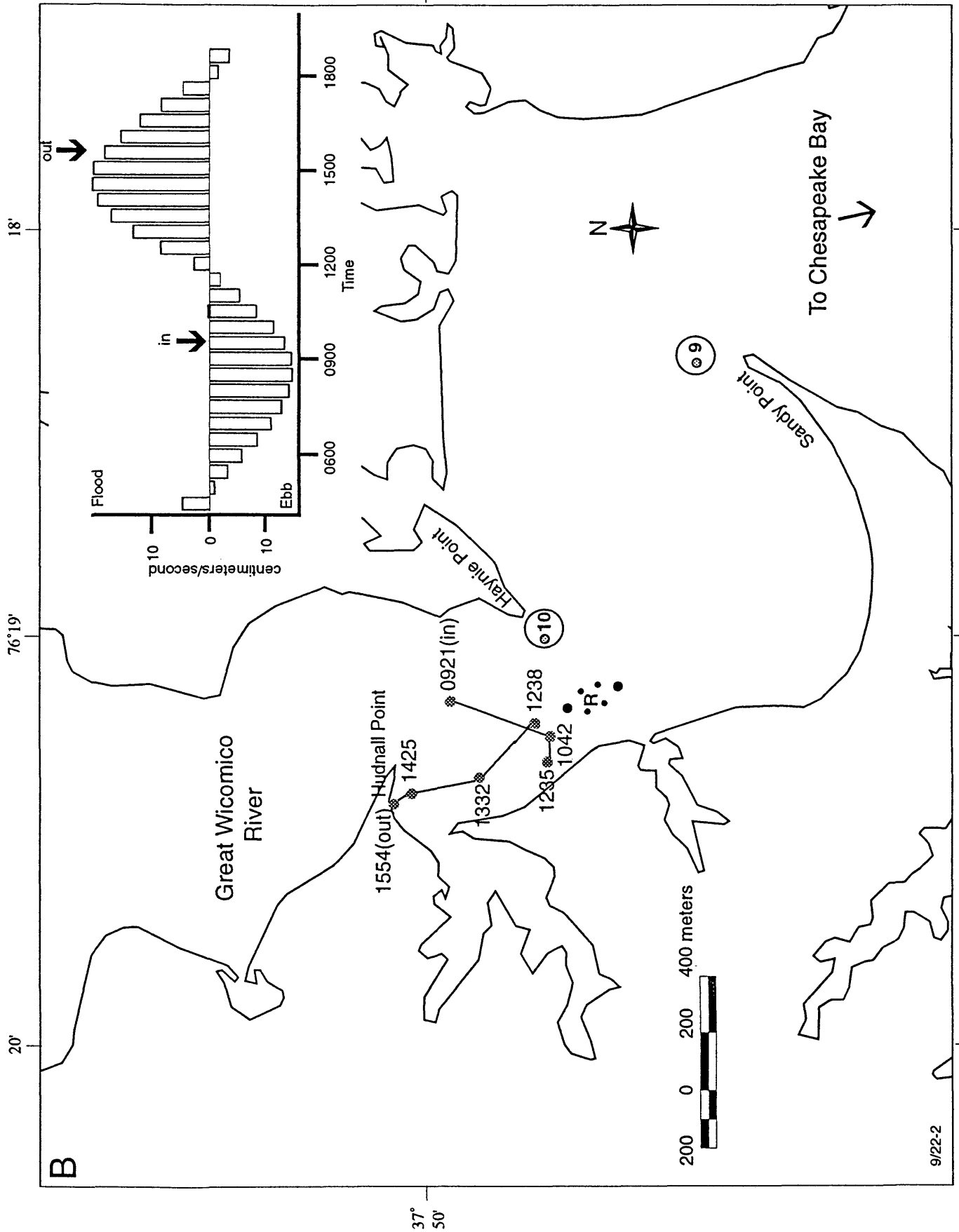
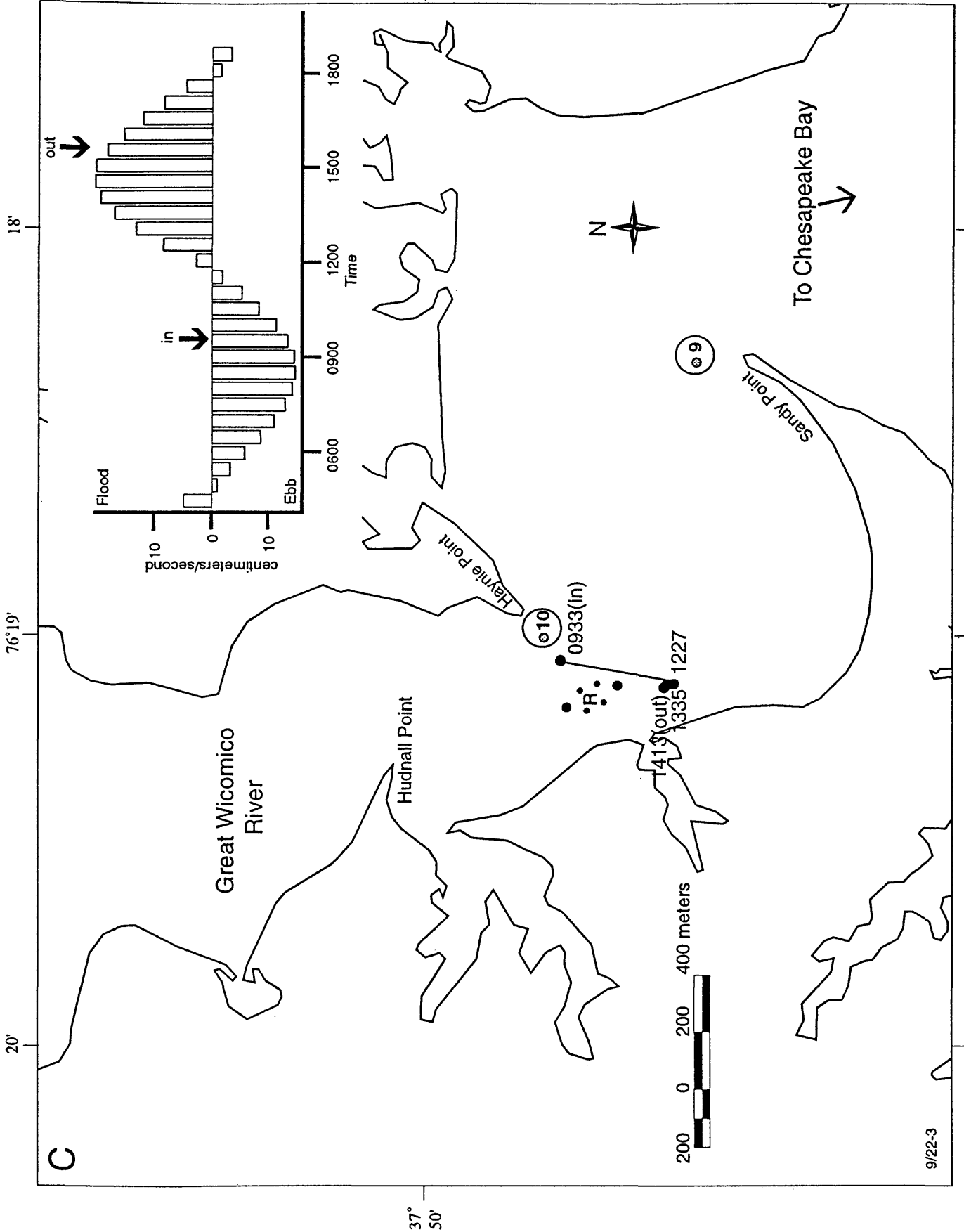


Figure 20: Drifter tracks for September 22, 1997. (A-E) represent drifters 1-5 respectively. Inset shows predicted tidal currents for Sandy Point, with arrows representing approximate times of deployment (in) and retrieval (out) of the drifters. Time is reported as Eastern Standard (E.S.) Military time. R denotes the location of the reef and 9 and 10 mark the main channel in the river.

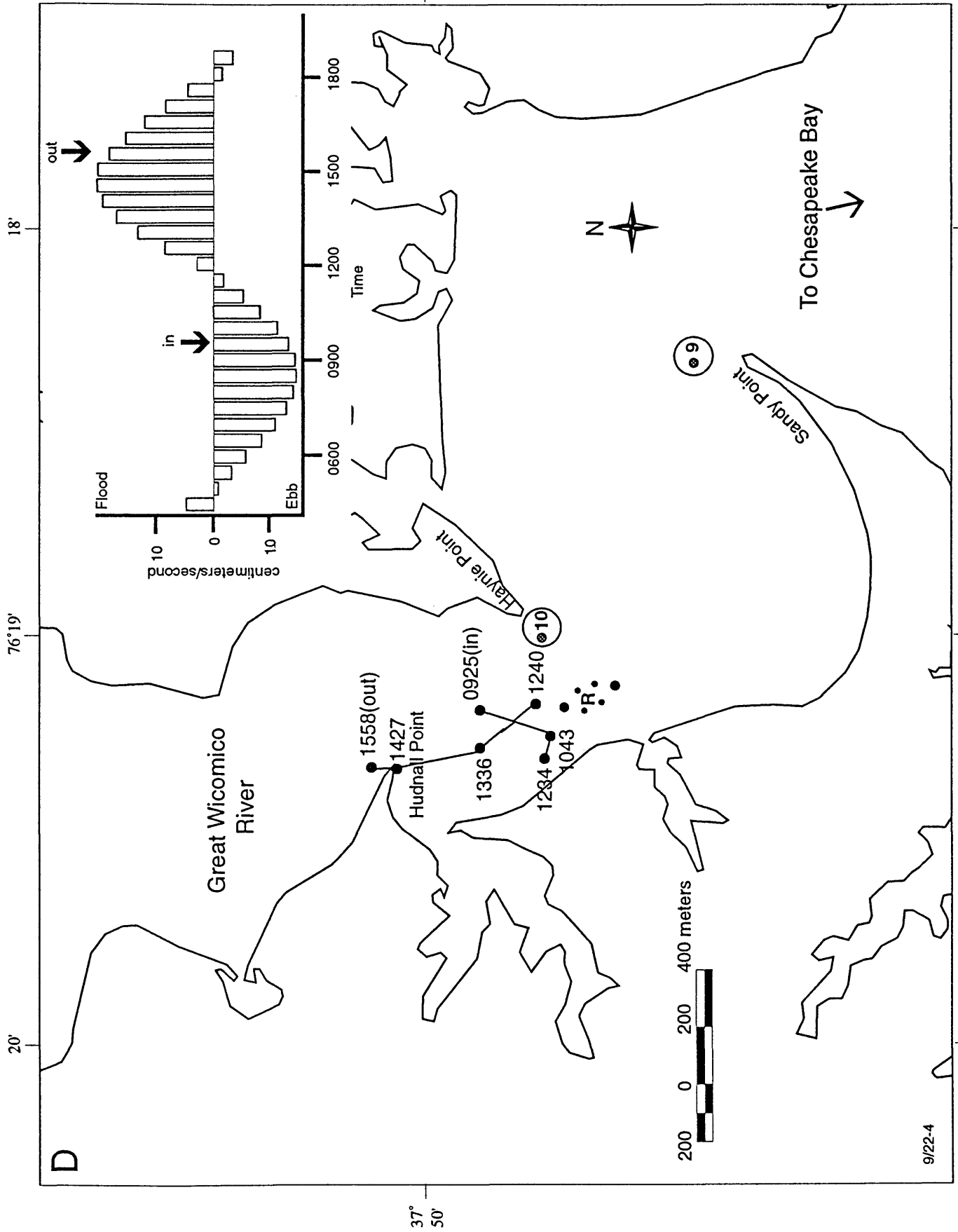






C

9/22-3



D

9/22-4

37° 50'

18'

76°19'

20'

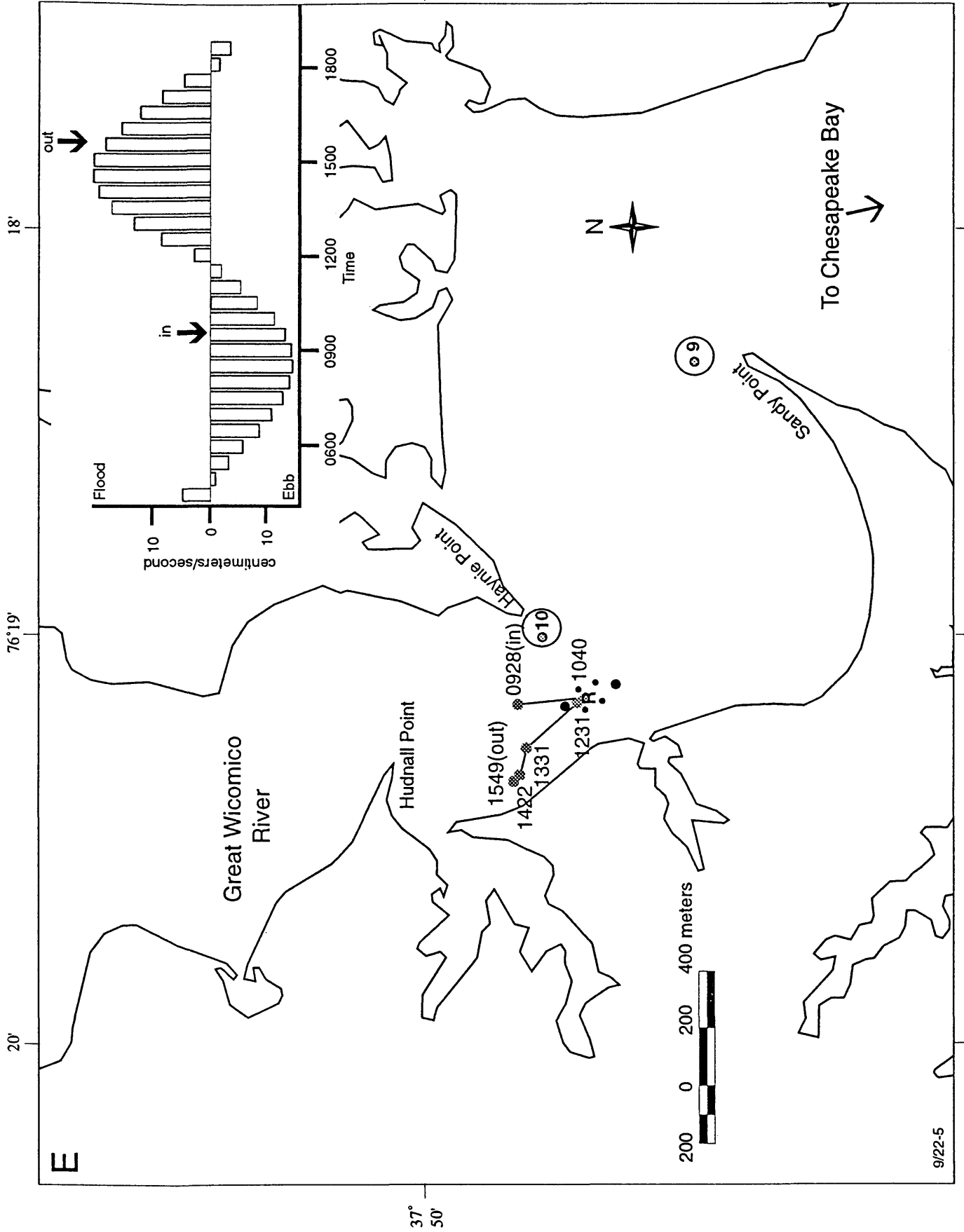


Figure 21: Location of shellstring stations in the Great Wicomico River, in 1997, showing the average number of spat / week measured at each site.

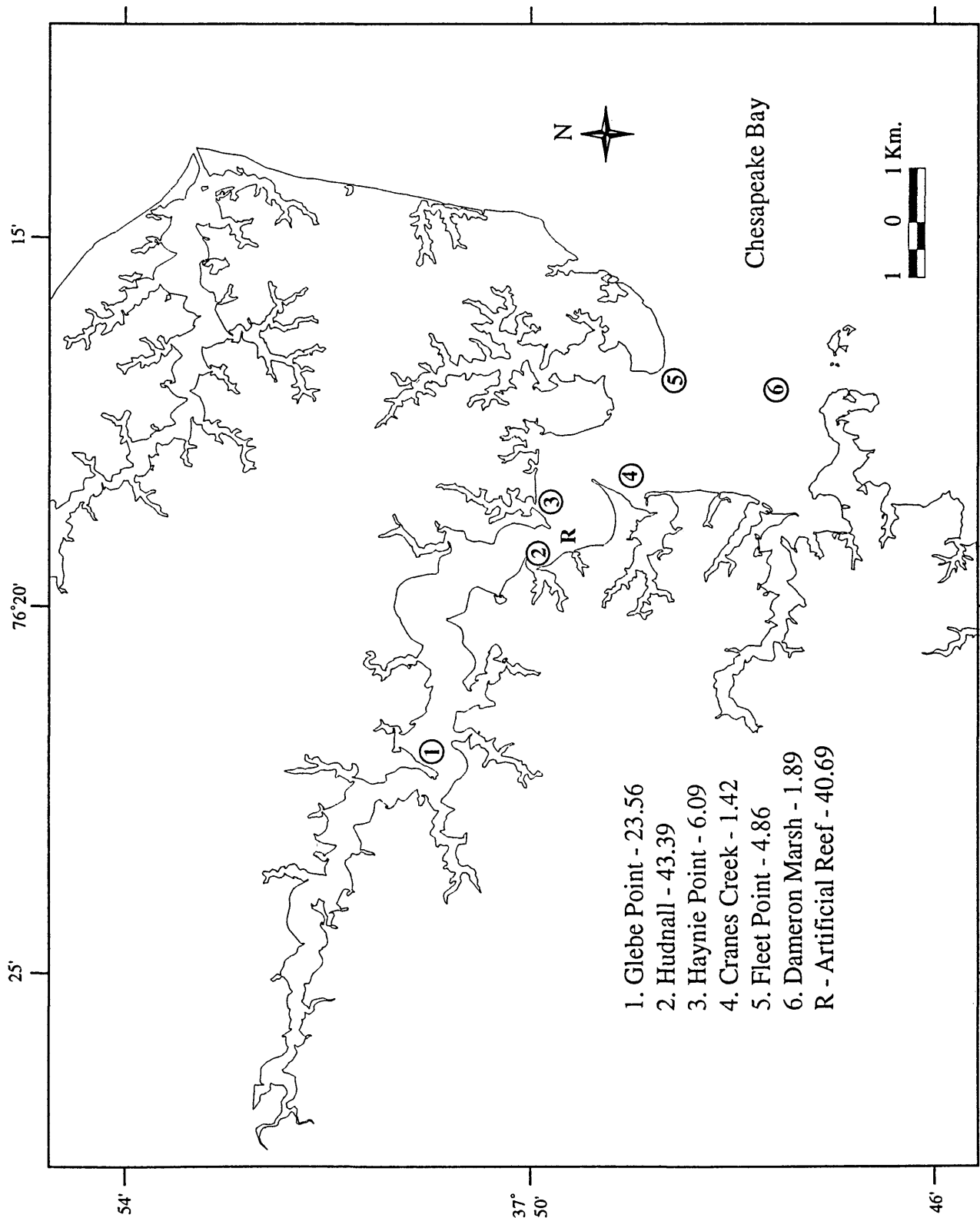
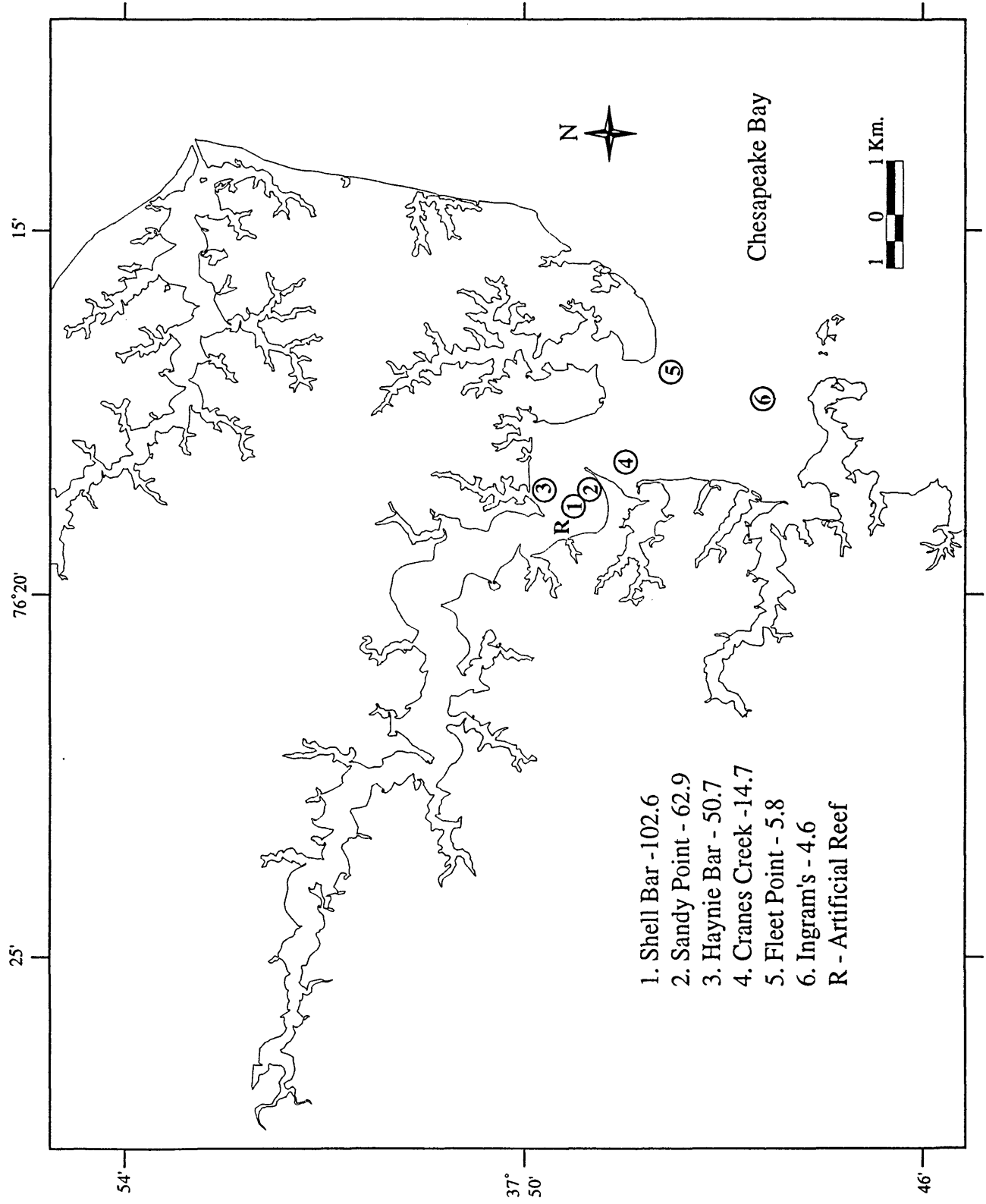


Figure 22: Location of patent tong survey stations in the Great Wicomico River, in 1997, showing the average spat / m² measured at each site.



DISCUSSION

Egg Production

Egg production estimates on the reef were found to be similar to estimates of production seen throughout the entire system in historic times (when oysters were abundant in the river). While the important thing in these estimates is the similar orders of magnitude, the estimates themselves should be viewed with caution. One concern is the inability to offer good values for disease and salinity related modifiers of fecundity. These are both widely acknowledged in the literature as having major effects on the bioenergetics of oysters, and yet they are still poorly described in a quantitative sense.

The model used in the calculation of fertilization efficiency taken from Levitan's work on echinoderms (1991), involves a series of assumptions concerning synchrony and completeness of spawning, half life of gametes in the water column, dispersal or dilution, and probability of fertilization given absolute concentrations of sperm and eggs. There are no good models for sessile bivalves in the literature describing fertilization efficiency. The current model was used based on the similarities in small scale hydrodynamic conditions seen in both Levitan's model and estuarine oyster reefs. Other options for models are discussed by Levitan et al. (1991), Oliver and Babcock (1992), and Benzie et al. (1994). Based on the hydrodynamics of the Great Wicomico, contrasting models such as the one for high-energy environments seen in Denny and Shibata (1989) are inappropriate for use in the Great Wicomico system. The current model used (Levitan, 1991), assumes synchrony in spawning throughout the entire oyster population; however, local synchrony is more appropriate when discussing these populations. The lack of synchrony throughout the population is demonstrated by the

variation in developmental stage seen in my study and variation in settlement (Haven and Fritz, 1985). Localized synchrony in spawning on the other hand is highly probable, so the cumulative effect of these localized events approximates in magnitude to that of a single synchronous spawning in the entire population. In other words, the cumulative output from multiple spawnings that occur throughout the reproductive season (2-3 per season) are within an order of magnitude of the single synchronous spawning event estimate of production.

Spawning

The transplanted broodstock oysters on the reef did spawn. Based on the larval abundance data, and the estimated 14 to 21 days spent in the water column by *C. virginica* larvae, inferences can be made about the timing of spawning. Oysters from the reef probably spawned continuously from mid-June to the end of July, with a few late spawnings occurring in the beginning of August. *C. virginica* populations in the Chesapeake Bay have been reported to spawn from June to August (Kennedy and Krantz, 1982). Gonad data from broodstock oysters on the reef support this observation. While evidence of spawning was not present until mid July, a percentage of both males and females were ripe by the middle of June (the beginning of our sampling period). Evidence of spawned individuals may not have been observed for several reasons. Given the large estimated number of broodstock oysters present on the reef (approximately 1.1×10^6 , Olsen and Wesson, 1997), 25 oysters per sampling day is a very small proportion of the overall population. Also, a majority of the samples were taken from the same portion of the reef. Cox and Mann, (1992) demonstrated that asynchrony in gonadal development and spawning activity between individuals located on the same reef can occur. Combining all of these factors, the sample size used may not have been large enough to adequately estimate spawning activity, until a larger proportion of the animals had already spawned.

Survival

Perkinsus infections progressed through the broodstock population throughout the summer, but did not result in catastrophic mortalities. The effect of *Perkinsus* on adult oysters, mainly reduced fecundity, increases as intensity of the disease increases (Choi et al., 1994). In the broodstock oysters, intensity was highest toward the end of the sampling season, after the majority of the spawning had already taken place. Given this, disease was probably not a limiting factor in the production of larvae.

Larval Abundance and Retention in an Estuary

Larval concentrations at the surface were found to be significantly higher during the flood tidal stage. This is important because it suggests the larvae are acting as more than just passive particles. By depth regulating with changes such as density and salinity, associated with a change in tidal stage, a net transport of larvae upriver is possible (Hidu and Haskin, 1978; Mann, 1988). On most of the sampling days in this study, there was some stratification occurring in the water column at stations N2 and N3 (in the channel). The apparent lack of stratification at N1 may have been due to the shallower depths at this station. Samples at N2 and N3 were taken at twice the depth of those found at N1. Despite the apparent lack of or reduced stratification at N1, the larvae still depth regulated with the changes in tidal stage. This is supported by the absence of a significant interaction between tidal stage and station.

It is believed that larval retention in a system and subsequent movement up river is brought about through a combination of passive transport and active larval swimming (Carriker, 1951; Kunkle, 1957; Haskin, 1964). Oyster larval concentrations reported in the literature over the past 75 years range from 12 m⁻³ to 660,000 m⁻³ (Table 3). Wood and Hargis, (1971) report larval abundance at the surface during maximum flood tide in the James River, with concentrations of larvae ranging between 300 and 800 m⁻³. They found that minimum concentrations (< 100 m⁻³) were encountered during

Table 3: Oyster larval concentrations reported in the literature over the past century.

Larval Concentration m ⁻³	Location	Year	Source
125,000	Barnegat Bay, NJ	1927	Nelson, 1927
660,000	Barnegat Bay, NJ	1931	Nelson and Perkins, 1931
16,680	Lanoka Lagoon, NJ	1938	Carriker, 1951
13,360 - 37,300	Great Bay, NJ	1939	Carriker, 1951
625 - 2400	Delaware Bay, NJ	1956	Haskin, 1964
300 - 800	James River, VA	1965	Wood and Hargis, 1971
12 - 113	James River, VA	1985	Mann, 1988
17,000 - 37,500	Great Wicomico River, VA	1997	This study

slack water, following the ebb tide. The highest larval concentrations reported in the literature were recorded in Delaware Bay as 660,000 m⁻³ (Nelson and Perkins, 1931) and 125,500 m⁻³ (Nelson, 1927). While these numbers seem extremely large compared to concentrations found in this study, the date of the observations must be taken into account. In a more recent study by Mann, (1988) in the James River, much lower concentrations ranging between 12 and 113 m⁻³ were reported. Comparing the concentrations seen in recent years (after the onset of disease and decimation of broodstock oyster populations), the concentration of larvae found in my study is extremely high. While not of the same order of magnitude seen in historical times, the concentration of larvae in the Great Wicomico is still several orders of magnitude higher than that found in the James River, which is considered to be the most important oyster producing river in the Chesapeake Bay. While a few James River reefs have similar densities of broodstock oysters as that found on Shell Bar Reef (unpublished stock assessment data, 1993), the difference in larval abundance probably lies in the differences in size and fecundity between the two broodstocks. The average size of oysters found in the James is between 45 and 60 mm with only a few reaching above 85 mm (unpublished stock assessment data, 1993). In contrast, average sizes found on Shell Bar Reef are between 85 and 95 mm. Given that fecundity and size have a non-linear relationship (Mann and Evans, in press), small differences in broodstock size and hence fecundity can lead to vast differences in larval production.

Settlement

Higher settlement was found upriver of the sand spit in both the patent tong and shellstring surveys. The number of spat m⁻² on the bottom recorded from the patent tong survey were at least 3 times higher at stations up river compared to the stations down river. There was also a difference seen in shellstring data, but the differences were not as great. However, as stated previously, patent tongs have been shown to be

a more accurate predictor of stock size and an overall better stock assessment tool (Chai et al., 1992). The higher recruitment of larvae up river of the sand spit, suggests that some local retention of larvae produced by the broodstock oysters on the reef was occurring.

Circulation

While it has been shown that oyster larvae can depth regulate to aid in the retention in an estuary (Carriker, 1951; Wood and Hargis, 1971), the circulation of a system is also a critical component of the retention mechanism (Pritchard, 1953; Ruzecki and Hargis, 1989). The general trend of the current tracks in this study suggest that circulation in the system is favorable for the retention of larvae. The majority of the tracks had a tendency to turn away from the channel, prior to tidal current change, thus the drifters remained up river of the sand spit, in the general area of the reef. In several instances, at least one of the drifters started out traveling down the channel. On only one occasion however, did the drifter continue traveling in the channel toward the mouth of the river.

The Great Wicomico River, has historically been termed a trap-type estuary (Andrews, unpublished data), along with the Piankatank River also in Virginia and the St. Mary's River in Maryland (Manning and Whaley, 1954). Andrews (1979), defines a trap-type estuary as one that has a low-flushing rate, small tidal amplitudes, and restricted entrances. While these characteristics are important, local circulation, dictated by both topography and tidal currents has been shown to be an important component of larval retention (Carter, 1967). Larval retention is not, however, limited to trap-type estuaries. The James River, for example, has proved to be a good seed producing river, with larvae that is produced in the lower reaches being moved upstream and subsequently settling on upstream oyster beds (Ruzecki and Hargis, 1989; Mann, 1988). The James gyre-like circulation in Hampton Roads is the key to retention in that

system. The retention of larvae in the James, occurs despite that its estuarine characteristics are in direct contrast to the “typical” trap-type estuary.

Impact of Broodstock Seeding from a Management Perspective

The addition of broodstock to the reef in the Great Wicomico River doubled the monetary cost (i.e. half of the cost was adding the broodstock), but the impact on replenishment was immediate. This impact is especially evident when compared with non-seeded areas. In just one year, settlement of spat was comparable to historic conditions. While this is ecologically important, an economic aspect involves the increase in private leases that occurred in 1998, due to the promising spatfall numbers in 1997. This “extra” money could be used to help pay for some of the initial seeding costs.

Recommendations for Management

While the typical definition of a trap-type estuary is useful, one should use caution in deciding where artificial oyster reefs and broodstock are going to be placed for replenishment purposes. The most important resource that should be utilized, is the knowledge of the location of historic oyster reefs. The fact that certain areas in the Chesapeake Bay and its tributaries were once productive oyster grounds, suggest that conditions (such as salinity, temperature, circulation ect.) in these areas are favorable for oysters. Beyond that, circulation studies of a system should become common practice when making these types of management decisions.

After the location of the reef is chosen, stocking density of broodstock on the reef needs to be considered. Based on calculations in this study, 300 m² seems like a reasonable density (i.e. the impact was immediate and comparable to historic conditions). Reproduction in the system should then be monitored to estimate the success of adding the broodstock.

CONCLUSIONS

1. The broodstock oysters were capable of spawning after transfer to the reef.
Spawning occurred between mid-June and mid-August.
2. Mortality due to disease were at a minimum.
3. Larval abundance in the system was several orders of magnitude higher than that seen in recent years in natural systems.
4. The larvae in the system were actively swimming (depth regulating), thus aiding in the retention up river of the sand spit.
5. Settlement was highest upriver of the sand spit, suggesting some local retention.
6. Circulation in the system was favorable for retention of the larvae up river of the sand spit.
7. Caution should be used when choosing a site for reef placement and broodstock enhancement. Circulation, location of historic oyster reefs, and local topography should be considered.

APPENDIX I

The following table summarizes the average hourly speeds (calculated as Δ distance / Δ time) and directions recorded by the drifters. “Fix” refers to GPS readings marking drifter locations taken at regular intervals. UD means the direction was indeterminable. See the text for derivation of tidal stage abbreviations.

Date	Drifter #	Fix	Tidal stage	Drifter speed cm/s	Approximate direction	
28 July	1	1	S-E	7.93	170	
		2	E	11.17	165	
		3	E	2.58	200	
		4	E	0.65	200	
		5	reposition			
		6	S-F	5.03	000	
		7	F	4.45	310	
		2	1	S-E	12.38	160
			2	E	1.79	145
			3	E	8.36	170
	4		E	3.36	190	
	5		reposition			
	6		E-S	7.13	345	
	7		reposition			
	8		F	11.84	325	
	9		reposition			
	10		F	15.89	330	
	3	1	S-E	10.33	160	
		2	E	14.29	160	
		3	E	3.47	170	
		4	E	1.83	300	
		5	E	2.61	020	
		6	E-S	0.84	020	
		7	S	3.35	020	
		8	S-F	4.16	010	
		9	F	7.49	345	
		10	F	5.05	290	
	4	1	S-E	11.09	150	
		2	E	14.07	165	
		3	E	4.73	165	
4		E	1.47	180		
5		reposition				
6		E-S	0.92	220		
7		S	4.03	300		
8		F	3.22	330		
9		F	5.15	355		
10		F	4.71	320		
11 August	1	1	E	6.84	150	
		2	E	7.46	160	
		3	E	2.10	200	
		4	E-S	2.79	230	
		5	S	3.96	315	
		6	F	6.77	350	

Date	Drifter #	Fix	Tidal stage	Drifter speed cm/s	Approximate direction	
11 August	1	7	F	1.84	155	
		8		reposition		
		9	F	2.04	230	
		10	F	0.57	130	
		11	F	2.58	080	
		12	S	1.91	020	
		2	1	E	6.84	145
			2	E	4.58	150
			3	E	3.83	180
			4	E-S	2.56	230
			5	S	6.23	315
			6	S-F	1.62	340
	7			reposition		
	8		F	10.47	335	
	9			reposition		
	10		F	9.92	330	
	11		F	8.31	330	
	3		1	E	2.32	150
		2		reposition		
		3	E	0.94	170	
		4		reposition		
		5	E	0.97	UD	
		6	E-S	1.28	340	
		7		reposition		
		8	S-F	8.30	330	
		9	F	13.75	330	
		10	F	2.14	010	
		11		reposition		
		12	F	8.57	325	
		13	F	8.33	335	
		14	F-S	2.69	005	
	4	1	E	11.75	150	
		2	E	8.21	160	
		3	E	4.49	175	
		4	E-S	2.99	240	
		5	S	5.85	310	
		6	S-F	5.91	255	
		7	F	0.10	UD	
		8		reposition		
		9	F	6.12	325	
		10	F	3.04	320	
		11		reposition		
		12	F	2.26	310	

Date	Drifter #	Fix	Tidal stage	Drifter speed cm/s	Approximate direction
25 August	1	1	S-E	7.55	130
		2	E	7.98	165
		3	E	15.28	140
		4	E	9.23	110
		5	E	4.75	110
		6	E-S	7.60	060
		7	S-F	5.95	000
		8	F	8.69	320
		9	F	7.40	290
	2	1	S-E	4.75	135
		2	E	11.07	165
		3	E	16.78	150
		4	E	7.77	150
		5	E	1.73	190
		6	E-S	2.84	220
		7	S-F	5.92	225
		8	F	4.54	290
		9	F	1.84	050
	3	1	E	14.93	160
		2	E	16.52	160
		3	E	8.35	155
		4	E	4.68	175
		5	E	4.22	225
		6	S	4.42	245
		7	S-F	2.70	260
		8	F	2.61	315
		9	F	0.48	UD
	4	1	E	11.25	185
		2	E	9.20	160
		3	E	11.08	155
		4	E	6.46	160
		5	E	3.84	210
		6	S	5.66	280
		7	S	1.65	240
		8	F	1.95	330
		9	F	0.35	UD
	5	1	E	11.23	170
		2	E	11.10	165
		3	E	6.36	160
		4	E	3.51	235
		5	E	3.58	235
		6	S	3.93	330
7		S	4.61	340	

Date	Drifter #	Fix	Tidal Stage	Drifter speed cm/s	Approximate direction
25 August	5	8	F	1.85	030
		9	F	0.21	UD
8 September	1	1	E	12.85	170
		2	E	7.72	170
		3	reposition		
		4	E-S	7.65	180
		5	S	2.85	185
		6	F	0.51	005
		7	F	3.99	000
		8	F	2.93	005
		9	F	1.27	UD
		10	F	2.34	180
	2	1	E	14.47	160
		2	E	13.91	170
		3	E-S	8.78	180
		4	S	8.06	190
		5	S-F	1.06	220
		6	reposition		
		7	F	3.00	200
		8	F	3.37	140
		9	reposition		
10		F	2.68	010	
3	1	E	13.05	150	
	2	E	12.97	170	
	3	E	10.16	170	
	4	S	7.68	175	
	5	F	6.25	205	
	6	F	1.12	240	
	7	reposition			
	8	F	0.73	UD	
	9	F	2.25	340	
	10	F	1.33	220	
4	1	E	13.91	160	
	2	E	12.74	165	
	3	E-S	7.90	160	
	4	S	7.48	180	
	5	F	5.01	220	
	6	F	2.51	155	
	7	reposition			
	8	F	0.36	UD	
	9	F	1.16	250	
5	1	E	9.82	155	

Date	Drifter #	Fix	Tidal Stage	Drifter speed cm/s	Approximate direction
8 September	5	2	E	9.71	160
		3	E-S	10.72	165
		4	S	5.93	160
		5	F	1.10	UD
		6	F	6.87	335
		7	F	4.48	290
		8	F	4.05	235
		9	F	2.46	205
		22 September	1	1	E
2	S			2.25	260
3	F			1.33	325
4	F			3.46	325
5	F			0.00	UD
2	1		E	7.53	200
	2		S	1.32	270
	3		reposition		
	4		F	9.90	310
	5		F	6.48	340
	6		F	1.86	330
3	1		E-S	3.83	190
	2		F	0.23	UD
	3		F	0.00	UD
	4		F	0.00	UD
4	1		E	5.61	210
	2		S	1.22	280
	3		reposition		
	4		F	8.90	320
	5		F	8.01	350
	6		F	1.63	005
5	1		E	5.32	175
	2		S	0.41	UD
	3		F	6.51	320
	4		F	3.00	290
	5	F	0.63	UD	

APPENDIX II

The following are the field sampling schedules for June 23 - September 22, 1997 in the Great Wicomico River, Virginia.

Field Schedule
 Great Wicomico Trip #1
 23-Jun-97

Time	Tidal Stage	Activity
0515		Meet @ VIMS, load truck etc.
0530		Leave VIMS
0800		Launch @ Public Ramp on Wicomico
0900	Max Ebb	ZP Tows 1-9 (3 per site)
1015		Gather/Tong oysters for disease and gonad data
1130		Lunch
1200	Slack before Flood	ZP Tows 10-18
1330		Deploy nest substrates on reef
1500	Flood	ZP Tows 19-27
1700		Dinner
1800	Slack before Ebb	ZP Tows 28-36
2200		Pull boat
0030		Return VIMS/clean boat etc.

Field Schedule
 Great Wicomico Trip #2
 30-Jun-97

Time	Tidal Stage	Activity
0625		Meet @ VIMS, load truck etc.
0630		Leave VIMS
0845		Launch @ Public Ramp on Wicomico
0912	Max Flood	ZP Tows 1-9 (3 per site)
1015		Gather/Tong oysters for disease and gonad data
1130		Lunch
1200	Slack before Ebb	ZP Tows 10-18
1330		Deploy nest substrates on reef
1500	Max Ebb	ZP Tows 19-27
1700		Dinner
1800	Slack before Flood	ZP Tows 28-36
1900		Pull boat
2130		Return VIMS/clean boat etc.

Field Schedule
 Great Wicomico Trip #3
 14-Jul-97

Time	Tidal Stage	Activity
0515		Meet @ VIMS, load truck etc.
0530		Leave VIMS
0700		Launch @ new ramp off Wicomico
0730	Max Flood	ZP Tows 1-9
0830		Gather/Tong oysters for disease and gonad data
1030	Slack before Ebb	ZP Tows 10-18
1130		Lunch
1215		Check nest substrates on reef
1345	Max Ebb	ZP Tows 19-27
1700	Slack before Flood	ZP Tows 28-36
1830		Pull boat
2000		Return VIMS/clean boat etc.

Field Schedule
 Great Wicomico Trip #4
 28-Jul-97

Time	Tidal Stage	Activity
0515		Meet @ VIMS, load truck etc.
0530		Leave VIMS
0700		Launch @ new ramp off Wicomico
0730		<i>Deploy drifters</i>
0749	Max Flood	ZP Tows 1-9
0830		<i>Drifter check 1</i>
0900		Tong for oysters
0930		<i>Drifter check 2</i>
1030		<i>Drifter check 3</i>
1045	Slack before Ebb	ZP Tows 10-18
1130		<i>Drifter check 4</i>
1200		Lunch
1230		<i>Drifter check 5</i>
1330		<i>Drifter check 6</i>
1404	Max Ebb	ZP Tows 19-27
1430		<i>Drifter check 7</i>
1530		<i>Drifter check 8</i>
1600		Check nest substrates on reef
1630		<i>Drifter check 9</i>
1715	Slack before Flood	ZP Tows 28-36
1745		<i>Drifter check 10</i>
1830		<i>Drifter check 11/recovery</i>
1900		Pull boat
2100		Return VIMS

Field Schedule
 Great Wicomico Trip #5
 11-Aug-97

Time	Tidal Stage	Activity
0500		Meet @ VIMS, load truck etc.
0530		Leave VIMS
0700		Launch @ new ramp off Wicomico
0830		<i>Deploy drifters</i>
0900	Slack onto Ebb	ZP Tows 10-18
0930		<i>Drifter check 1</i>
1000		Tong for oysters
1030		<i>Drifter check 2</i>
1100		Pre-lunch
1115		Shell strings @ reef
1130		<i>Drifter check 3</i>
1145		Niskin bottles
1200	Max Ebb	ZP Tows 19-27
1230		<i>Drifter check 4</i>
1300		Nest substrate check
1330		<i>Drifter check 5</i>
1400		Lunch/continued snacking
1430		<i>Drifter check 6</i>
1500	Slack onto Flood	ZP Tows 28-36
1530		<i>Drifter check 7</i>
1600		Niskin bottles
1630		<i>Drifter check 8</i>
1730		<i>Drifter check 9</i>
1823	Max Flood	ZP Tows 37-45
1930		<i>Drifter check 10/recovery</i>
2000		Pull boat
2200		Return VIMS

Field Schedule
 Great Wicomico Trip #6
 25-Aug-97

Time	Tidal Stage	Activity
0400		Meet @ VIMS, load truck etc.
0430		Leave VIMS
0600		Launch @ new ramp off Wicomico
0622	Max Flood	ZP Tows 1-9
0700		<i>Deploy drifters</i>
0800		<i>Drifter check 1</i>
0830		Tong for oysters
0900		<i>Drifter check 2</i>
0930	Slack onto Ebb	ZP Tows 10-18
1000		<i>Drifter check 3</i>
1030		Niskin bottles
1100		<i>Drifter check 4</i>
1130		Shellstrings @ reef
1200		<i>Drifter check 5</i>
1215		Lunch
1238	Max Ebb	ZP Tows 19-27
1300		<i>Drifter check 6</i>
1340		Nest substrate check
1400		<i>Drifter check 7</i>
1430		Niskin bottles
1500		<i>Drifter check 8</i>
1545	Slack onto Flood	ZP Tows 28-36
1600		<i>Drifter check 9</i>
1700		<i>Drifter check 10/recovery</i>
1730		Pull boat
1930		Return VIMS

Field Schedule
 Great Wicomico Trip #7
 8-Sep-97

Time	Tidal Stage	Activity
0500		Meet @ VIMS, load truck etc.
0530		Leave VIMS
0700		Launch @ new ramp off Wicomico
0735	Slack onto Ebb	ZP Tows 1-9
0800		<i>Deploy drifters</i>
0900		<i>Drifter check 1</i>
0930		Tong for oysters / 75 to measure
1000		<i>Drifter check 2</i>
1020		Niskin bottles
1040	Max Ebb	ZP Tows 10-18
1100		<i>Drifter check 3</i>
1130		Shellstrings @ reef
1200		<i>Drifter check 4</i>
1230		Lunch
1300		<i>Drifter check 5</i>
1320		Nest substrate check
1350	Slack onto Flood	ZP Tows 19-27
1400		<i>Drifter check 6</i>
1500		<i>Drifter check 7</i>
1530		Niskin bottles/GPS in channel markers
1600		<i>Drifter check 8</i>
1652	Max Flood	ZP Tows 28-36
1700		<i>Drifter check 9</i>
1800		<i>Drifter check 10/recovery</i>
1830		Pull boat
2000		Return VIMS

Field Schedule
 Great Wicomico Trip #8
 22-Sep-97

Time	Tidal Stage	Activity
0530		Meet @ VIMS, load truck etc.
0600		Leave VIMS
0730		Launch @ new ramp off Wicomico
0800		<i>Deploy drifters</i>
0810	Slack onto Ebb	ZP Tows 1-9
0900		<i>Drifter check 1</i>
0930		Tong for oysters / 75 to measure
1000		<i>Drifter check 2</i>
1030		Niskin bottles
1045		Snack
1100		<i>Drifter check 3</i>
1115	Max Ebb	ZP Tows 10-18
1200		<i>Drifter check 4</i>
1230		Nest substrate check
1300		<i>Drifter check 5</i>
1400		<i>Drifter check 6</i>
1420	Slack onto Flood	ZP Tows 19-27
1500		<i>Drifter check 7</i>
1530		Late lunch
1600		<i>Drifter check 8</i>
1630		Niskin bottles
1700		<i>Drifter check 9</i>
1730	Max Flood	ZP Tows 28-36
1830		<i>Drifter check 10/recovery</i>
1900		Pull boat
2030		Return VIMS

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