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Distribution of Chrysaora quinquecirrha in the York River

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DISTRIBUTION OF *Chrysaora quinquecirrha* IN THE YORK RIVER

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ABSTRACT

Investigations were conducted in the York River from September 1966 to November 1967 to determine the distribution, quantitative abundance, and period of maximum set of the polyp stage of the sea nettle Chrysaora quinquecirrha. In the laboratory, the effects of varying salinity and temperature on the polyp stage were investigated. The distribution and abundance of the medusoid stage were also determined.

Dredged and planted substrate showed the polyp stage to occur generally in a 12-mile area between Y-13.0 and Y-25.0, the greatest abundance occurring at Y-22.0.

Medusae appeared in the creeks 15 to 30 days before their appearance in the river and were more abundant in the creeks in all cases. Medusae appeared in the river between 12 June and 2 October, reaching their peak during the week of 17-21 July.

Polyps had a lower salinity tolerance of approximately 5 to 10 o/oo and an upper limit in excess of 40 o/oo. A gradual temperature rise (1°C/day) between 1 and 29°C caused no mortality of polyps. Strobilation occurred at 20 to 22°C and several methods for inducing the process were determined.

Two new ephyra predators were found.

DISTRIBUTION OF *Chrysaora quinquecirrha* IN THE YORK RIVER

INTRODUCTION

Chrysaora quinquecirrha, the common sea nettle, is a coastal species with a pan-tropical distribution. Various authors have commented on its unusual abundance in the Chesapeake Bay; however, quantitative studies dealing with its distribution and life cycle are lacking. With the increasing use of the Chesapeake Bay and its tributaries for recreation, a greater demand has developed for an understanding of the ecology and possible control of this animal.

Early taxonomic studies of the sea nettle in the Chesapeake Bay were confused by the presence of two apparently different forms of the same species. Agassiz and Mayer noted this phenomenon in 1898 and Mayer (1910) reported finding the "red ones and the white ones" together in Hampton Roads. The red variety, defined as Dactylometra quinquecirrha, was thought by various authors to develop in the high-salinity waters of the ocean and float into the Bay. The white variety, having a lesser number of tentacles, was described as an early maturing, stunted, brackish water form in which the tertiary tentacles did not develop. The white variety was defined as the Chrysaora stage of Dactylometra development. Stiasney (1919, after Littleford, 1939), believing the two to be the same species, reported Chrysaora quinquecirrha cannot be separated from Dactylometra quinquecirrha. Hyman (1942) attempted to describe the two varieties as separate species, the distinction being the number of ephyrae produced during strobilation,

Dactylometra having six and Chrysaora sixteen. The most recent taxonomic study redescribes the genus Chrysaora and broadens the taxonomic base to include both varieties of C. quinquecirrha (Kramp, 1961). This paper will follow the classification of Kramp (1961).

Early life history studies of this organism were fragmentary (Agassiz, 1862; Agassiz and Mayer, 1898; Hadzi, 1907; Mayer, 1910). Papenfus (1934) was the first to publish the main aspects of the animal's life history. This author established that (a) there is metagenesis in the species; (b) the polyp form buds profusely; (c) Chrysaora overwinters in the polyp stage. Work by Truitt (1934), Papenfus (1935), Littleford and Truitt (1937) and Truitt (1939) preceded the most complete publication on the sea nettle's life history by Littleford (1939), who was the first to raise C. quinquecirrha from egg to adult. Various aspects of the sea nettle's life history have been subsequently reviewed by Hyman (1942), Mansueti (1955), and Bailey (1956, 1960).

Cargo and Schultz (1966) were the first to publish on the ecology and distribution of the Chrysaora polyp stage in the Chesapeake Bay. These authors found that oyster shells are the principal substrate on which polyps occur, but they only noted presence or absence of polyps on the substrate and gave no quantitative data.

The purpose of the present investigation conducted in the York River and in the laboratory was to determine (1) the distribution, quantitative abundance and period of maximum set of the polyp (scyphistoma) stage of Chrysaora quinquecirrha; (2) the distribution

and abundance of the medusoid stage; (3) the effects of varying salinity and temperature on the polyp stage in the laboratory.

DESCRIPTION OF THE STUDY AREA

The York River basin extends 140 miles from the divide on the Blue Ridge mountains to the Chesapeake Bay east of Yorktown. Its watershed of approximately 2,660 square miles discharges a mean of 2,200 c.f.s. of freshwater annually into Chesapeake Bay.

The York River extends 28.5 miles from Tue Marsh light to West Point where it is formed by the confluence of the Pamunkey and Mattaponi rivers. The upper portion of the river is characterized by broad shallow flats, and a relatively narrow channel averages 25 to 30 feet in depth. In the lower river, the channel broadens and reaches a maximum depth of 60 to 75 feet.

The area studied was between Bells Rock and Gaines Point (Sarah Creek) (Figure 1). Twenty-eight creeks and one river enter the York in this area: 16 creeks and one river on the southeast shore and 12 creeks on the opposite side. The York River is typical of a horizontal boundary estuary, type B, as classified by Williams (1962), with higher salinities on the right side of the river looking upstream.

Salinity fluctuations during a season are common (Pritchard, 1952). During the present investigation (1966-1967), salinity at Bells Rock (Y-25.0), the upper boundary of the study area, varied from 8.6 o/oo in early April to 16.8 o/oo in mid-August, with a mean of 11.5 o/oo. At Y-5.5, the lower boundary of the study area,

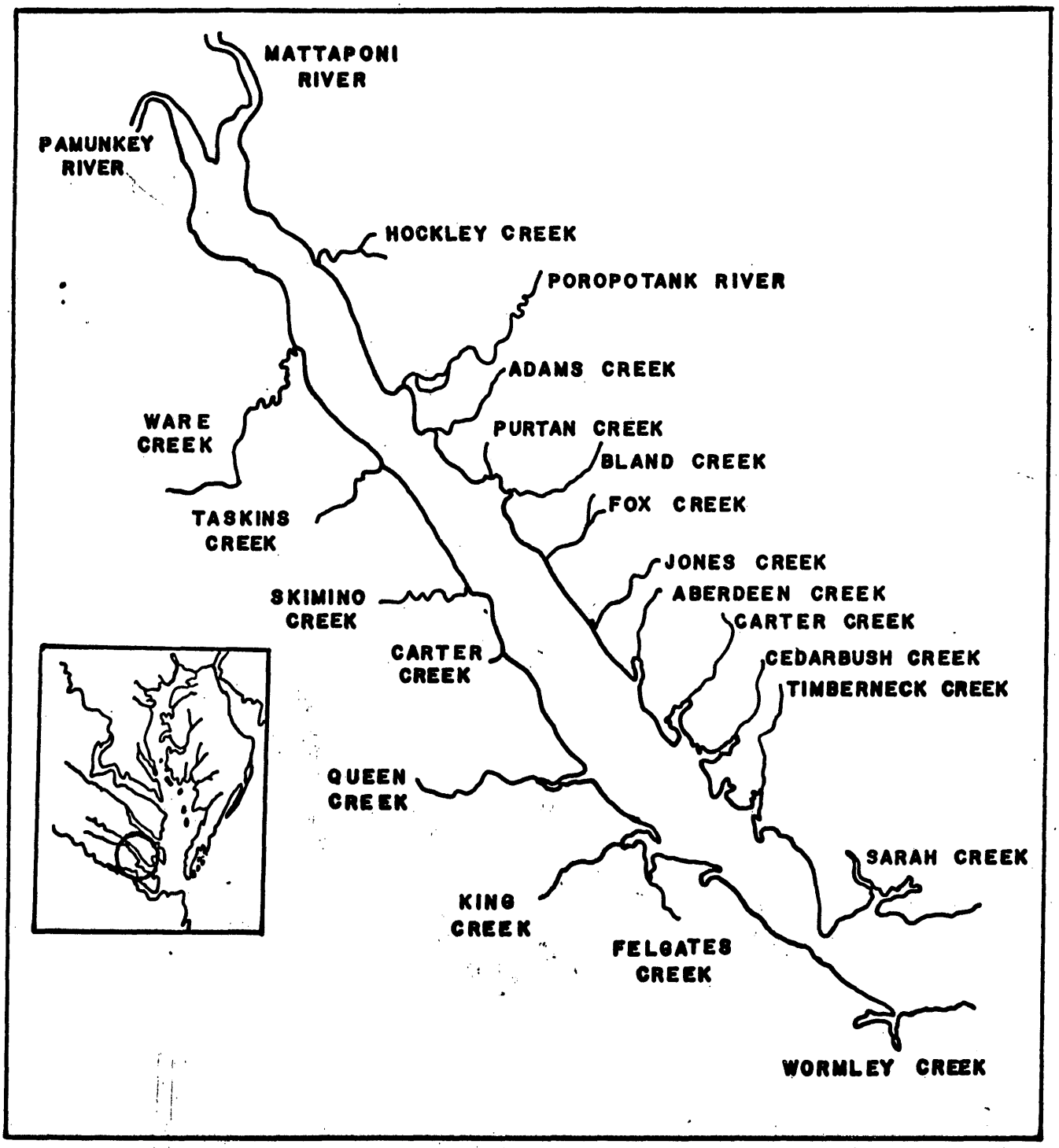

Figure 1. Map of York River showing principal tributaries.

mean salinity was 19.9 o/oo, with a range of 16.5 o/oo to 22.9 o/oo during the same period.

Current velocities were not measured. However, Haight, Finnegan, and Anderson (1930) have reported maximum surface currents in the York range from 0.5 to 1.9 knots, depending on location and tide stage.

Total suspended solids in the York River may vary widely throughout the year with a gradual increase in the upriver direction (Patten, Young, and Roberts, 1963). Mean surface values for nine cruises during 1966 were 17.42 mg l^{-1} at Y-6.0 and 23.34 mg l^{-1} at Y-25.0 (Eayrs, unpublished data).

Oxygen content of the York River approaches saturation under normal conditions (Patten and Warinner, 1961). The water is well mixed and at no time during the present investigation were anaerobic conditions observed at the sampling stations.

MATERIALS AND METHODS

I. Field Studies

A. Setting and polyp distribution on natural substrate

From November 1966 to April 1967 (Winter 1966-67) and again during November 1967 (Winter 1967-68), samples of oysters and shells were dredged from numerous locations in the York River. Areas sampled were generally where large numbers of oysters grew naturally on public rocks or on private grounds where oysters had been planted. Locations were chosen on the basis of quantity of undisturbed shell. Regular winter stations (Figure 2) were Green Rock (Y-8.0), Pages Rock (Y-12.0), Queens Creek mouth (Y-12.5), Aberdeen Creek mouth (Y-13.0), Roane Point (Y-22.0), Pig Rock (Y-24.0), and Bells Rock (Y-25.0). Occasional samples were taken at Ferry Point (Y-16.0) and Mt. Folly (Y-22.5).

Substrate samples were collected by towing an oyster dredge for about five minutes at each station. One-quarter to ½ bushel of the dredged material was placed in buckets of river water and transported to the laboratory. Each oyster, oyster shell, or other solid object over 2 cm in length was examined for polyps with an illuminated 4X hand lens and a binocular microscope. Buried shell, identified by its black color, was discarded. Shells or oysters with attached polyps were held in fingerbowls in flowing river water. Data for each sample were recorded as follows:

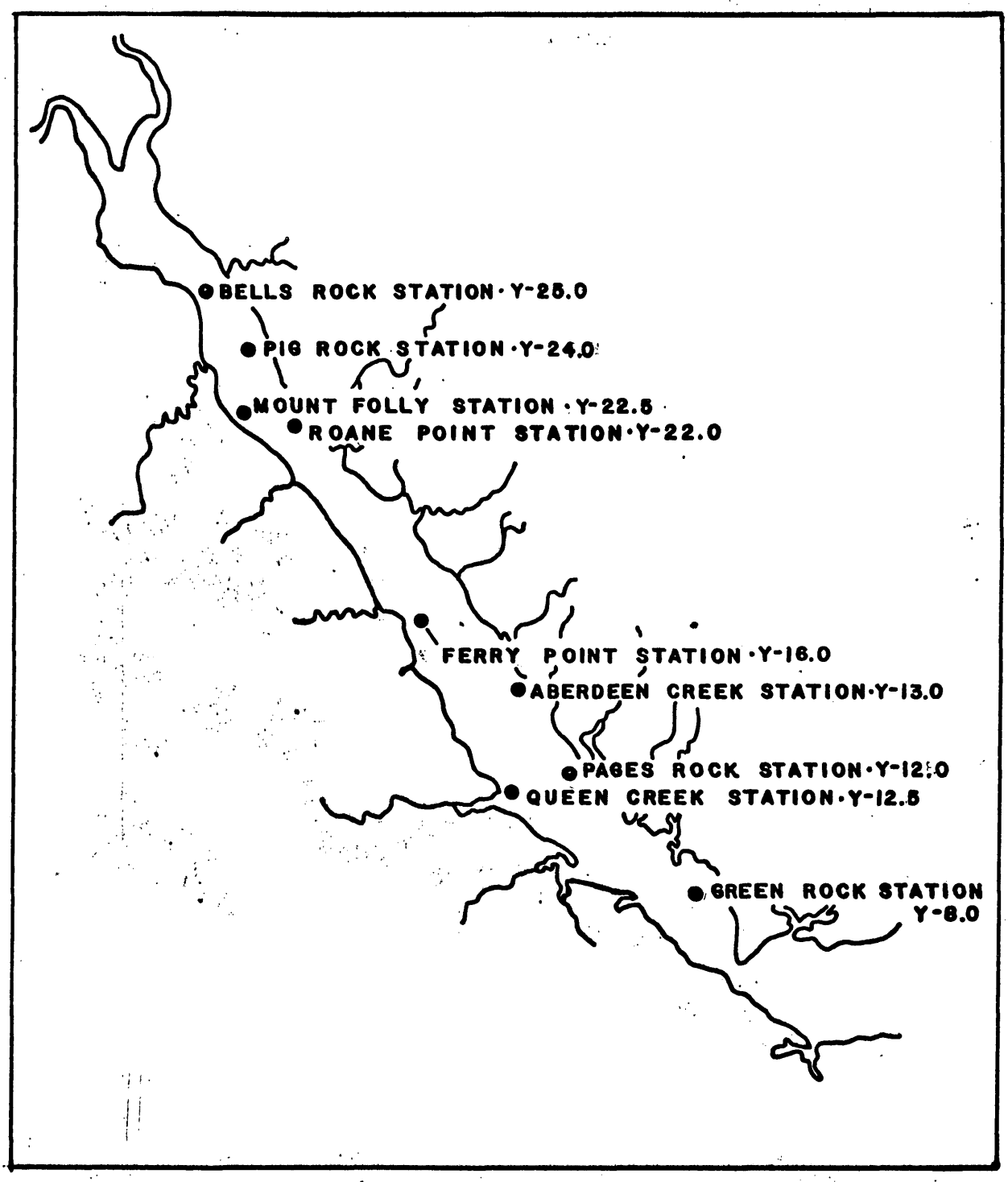

Figure 2. York River winter sampling stations.

A--total number of oysters and shells

B--number of shells

C--number of oysters

D--total number of polyps

E--number of oysters and shells with polyps

F--number of shells with polyps

G--number of oysters with polyps

H--number of polyps on shells

I--number of polyps on oysters.

Data were analyzed as follows:

Mean number of polyps in relation to total units of substrate (D/A)

Percent of units of substrate with polyps in relation to total substrate (E/A)

Mean number of polyps on shells in relation to total shell substrate (H/B)

Percent of shells having polyps (F/B)

Mean density of polyps on a single shell having polyps (H/F)

Mean number of polyps on oysters in relation to total oyster substrate (I/C)

Percent of oysters having polyps (G/C)

Mean density of polyps on a single oyster having polyps (I/G).

Polyp density per unit of bottom area was also measured in the winter of 1966-67 at certain stations. Substrate in unit areas of approximately one square meter was removed with oyster tongs from a boat anchored fore and aft to prevent drifting.

During winter and summer studies the dominant macroscopic fouling organisms and percent area covered by each species were recorded for all samples. Microscopic fouling was not recorded.

B. Seasonal setting of polyps on substrate in wire bags

The set of Chrysaora polyps between March and November 1967 was determined by placing wire bags (shellbags) containing 1/8 to 1/4 bushel of cleaned oyster shells at various locations in the York River and its tributaries. Stations were selected in most instances to be near the winter survey stations. Areas regularly sampled in the summer study (Figure 3) included Gloucester Point (Y-6.0), Pages Rock (Y-12.0), Queens Creek mouth (Y-12.5), Aberdeen Creek mouth (Y-13.0), Ferry Point (Y-16.0), Purtan Bay (Y-19.0), Roane Point (Y-22.0), Mt. Folly (Y-22.5), and Bells Rock (Y-25.0). Additional stations were later established at Sarah Creek (Y-5.5), Timberneck Creek (Y-9.0) and Hockley Creek ($Y\text{-}25.0_a$).

The wire bags were suspended 0.25 m off the bottom on duck blinds or from stakes delimiting private oyster grounds. Water depth varied from 1.5 to 3.0 m. To minimize fouling, bags were exposed for only 15 days and fresh bags substituted at the end of this period. The exposed bags were labeled and returned to the laboratory in river water where the substrate was examined with the hand lens and binocular microscope.

Several bags (survival bags) remained in the water from March through November to indicate accumulated set over the season.

Results for the summer survey were tabulated and analyzed in the same manner as those for the winter survey. In addition, biweekly data were summed to show total theoretical accumulated set for the season.

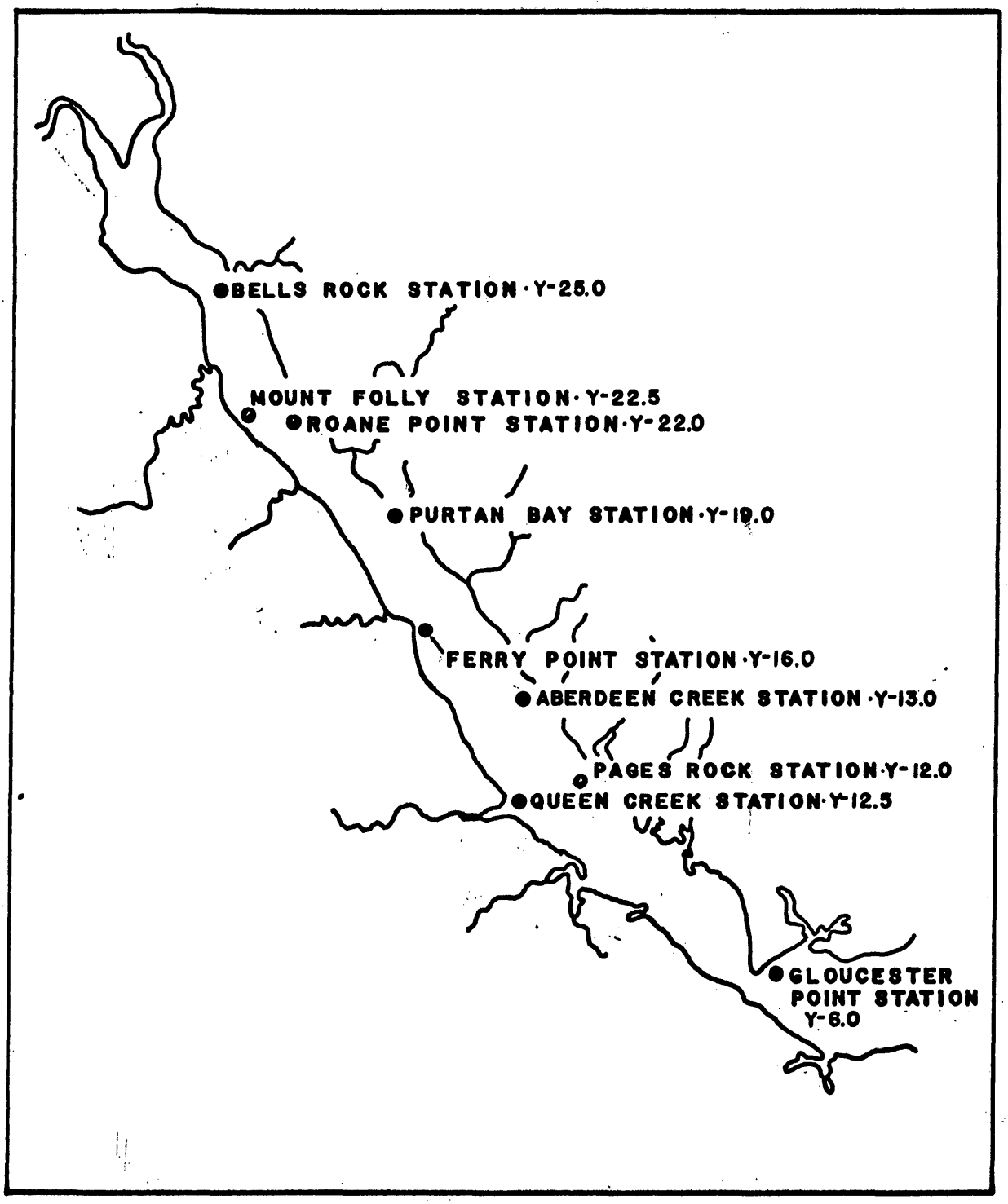

Figure 3. York River summer sampling stations.

C. Abundance of medusae

Four types of surveys were made to determine distribution and abundance of the medusae and time of strobilation of the polyps.

(1) All York River tributaries navigable by an outboard motor boat with a 2½-foot draft were examined on 1 June, 15 June, and 30 June 1967.

(2) More detailed studies were made in certain creeks on the same dates. A floating frame one meter square was used to estimate medusae abundance at specific stations; all visible medusae within the boundaries of the frame were counted. Results were expressed as medusae visible beneath a square meter.

(3) Counts of medusae were made from the pier of the Virginia Institute of Marine Science (VIMS) at Gloucester Point between 12 June and 15 October 1967. These counts were made every Monday through Friday at sometime between 1200 and 1300 hours. All medusae visible within an area 50 feet on either side of the pier were counted. Results were summarized as the number of medusae during five-day periods.

(4) Weekly plankton samples were taken at Gloucester Point from 1 May to 30 October 1967. A 1/8 m plankton net with 1/32" mesh was suspended for 30 minutes from the end of the pier at VIMS during the period of maximum current. Results were expressed as number of ephyrae per thirty-minute period. One- to three-minute plankton tows were made with the same net from boats in other areas of the river at irregular intervals.

II. Laboratory Studies

A. Salinity and temperature tolerance of the polyps

Freshly dredged polyps on their original substrate were placed in fingerbowls containing river water at 20 o/oo and 20°C for several days. At the end of this acclimation period, polyps were transferred to fingerbowls where salinities were adjusted with distilled water to 2.5, 5.0, 10.0, 15.0, 20.0, 25.0, 30.0, and 35.0 o/oo. Ocean water of 36 o/oo brought to a dissolved solids content of 40 o/oo with NaCl was also used. All dilutions were mixed in large quantities to insure constancy during the experiment. Temperatures were maintained at 20°C with a constant temperature water bath. Feeding and survival at various salinities were monitored. Water was changed every 12 hours and polyps were fed newly hatched *Artemia* and enchytraeids at 24-hour intervals. Polyp height was measured every 24 hours with the aid of a calibrated ocular grid and evaluated as percent change from initial size.

Temperature tolerance was determined by placing freshly dredged polyp colonies in a constant temperature bath containing river water of 20 o/oo salinity. After acclimation, the colonies were subjected to fluctuations in temperature. Initially, temperature changes were great to determine approximate maximum and minimum temperature tolerance. Later changes were of small increments to show more precision. The effect of varying rate of temperature change was also studied. The ocular grid was used as previously outlined to measure change from initial size. Percent of change was then calculated.

B. Strobilation of the polyp

Several methods were discovered for inducing strobilation of the polyp during the study. The discovery of these methods, which will be discussed later, made it possible to determine some of the factors inducing strobilation, as well as the observation and description of the strobilation process.

Attempts were made to accelerate the rate of strobilation in polyps that were observed to be strobilating. They were placed in river water several degrees warmer than that in which the process began. Ephyrae were removed and held in aerated tanks of river water kept at 20 to 25°C; they were fed newly hatched Artemia at daily intervals.

RESULTS

I. Polyp Distribution During the Winter of 1966-67 as Shown by Dredge Samples

Polyps occurred on bottom substrate, chiefly oyster shell, between Y-13.0 and Y-25.0, a range of 12 miles (Figures 4 and 5, Table 1). Although living oysters were abundant at most stations, polyps occurred on this substrate only over a 3-mile range above Y-22.0. Samples were not obtained upriver from Y-25.0 due to absence of suitable substrate. Repeated sampling downriver from Y-12.0, where suitable substrate was abundant, yielded no polyps.

Peak values for seven out of eight parameters investigated occurred at Y-22.0. These seven parameters were (Table 1): (I) Mean number of polyps in relation to total units of substrate--0.67 polyp/unit substrate; (II) Percent of substrate with polyps in relation to total units of substrate--7.66%; (III) Mean number of polyps on shells in relation to total shell substrate--0.62 polyp/shell; (IV) Percent of shells having polyps--7.95%; (VI) Mean number of polyps on oysters in relation to total oyster substrate--0.91 polyp/oyster; (VII) Percent of oysters having polyps--6.06%; and (VIII) Mean density of polyps on oysters having polyps--15.0 polyps/oyster.

Mean density of polyps on a single shell having polyps (V) was greatest at Y-25.0 (8.33 polyps/shell).

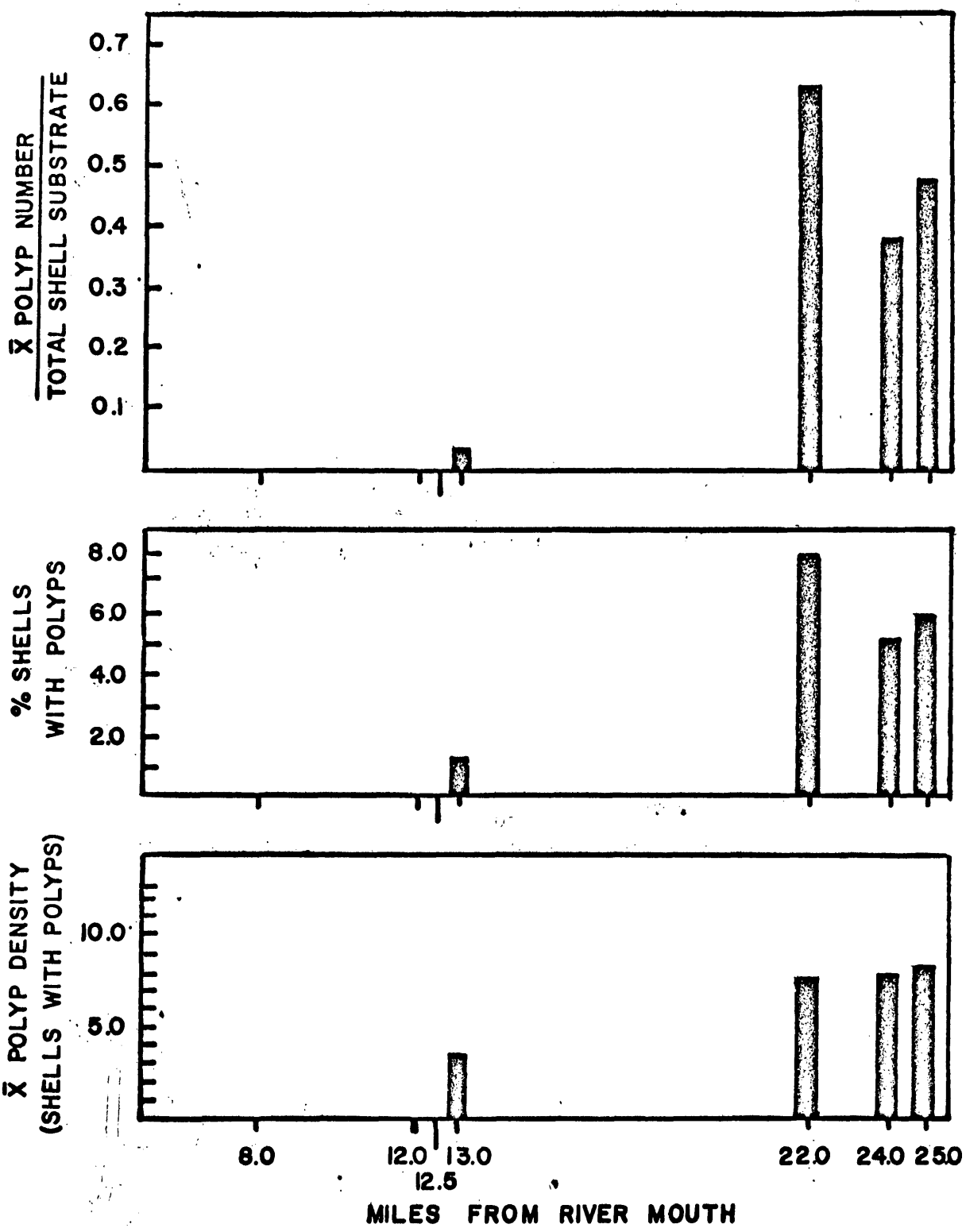

Figure 4. Distribution and abundance of polyps on shells, York River, Winter 1966-1967 dredge samples.

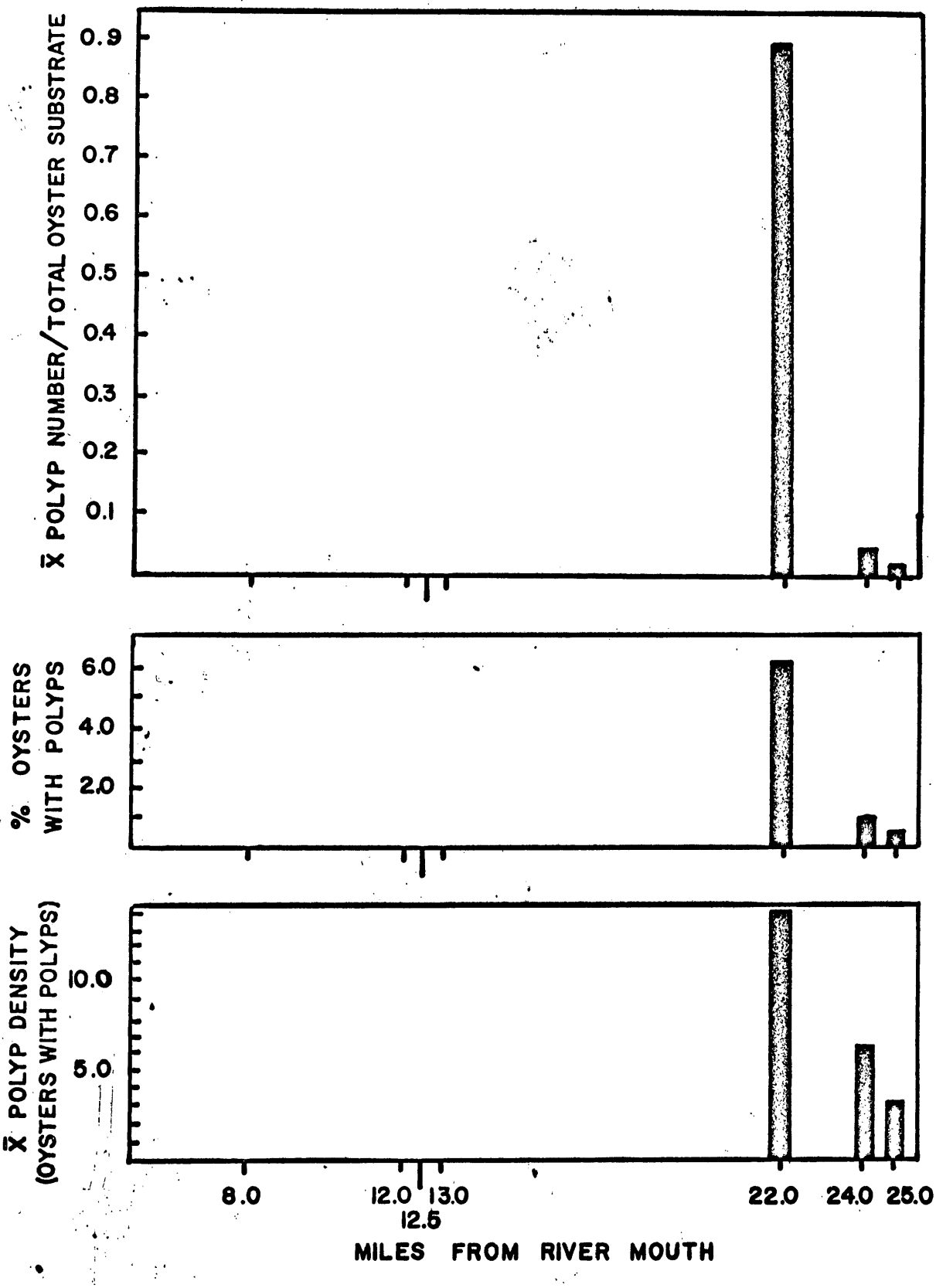

Figure 5. Distribution and abundance of polyps on oysters, York River, Winter 1966-1967 dredge samples.

TABLE 1

TABULATION OF DATA FROM SAMPLES COLLECTED BY DREDGING DURING WINTER 1966-1967

Station	A Total substrate	B Shells	C Oysters	D Total polyps	E Oysters and shells with polyps	F Shells with polyps	G Oysters with polyps
Y-8.0	144	144	0	0	0	0	0
Y-12.0	371	356	25	0	0	0	0
Y-12.5	438	426	12	0	0	0	0
Y-13.0	944	860	84	22	7	7	0
Y-22.0	209	176	33	139	16	14	2
Y-24.0	834	592	242	243	32	30	2
Y-25.0	1007	688	319	328	40	39	1

TABLE 1 CONTINUED

Station	I (D/A)	II (E/A) %	D - I = H III (H/B)	IV (F/B) %	V (H/F)	VI (I/C)	VII (G/C) %	VIII (I/G)
Y-8.0	0	0	0	0	0	0	0	0
Y-12.0	0	0	0	0	0	0	0	0
Y-12.5	0	0	0	0	0	0	0	0
Y-13.0	0.02	0.74	0.03	0.81	3.14	0	0	0
Y-22.0	0.67	7.66	0.62	7.95	7.79	0.91	6.06	15.00
Y-24.0	0.29	3.84	0.39	5.07	7.67	0.05	0.83	6.50
Y-25.0	0.33	3.97	0.47	5.67	8.33	0.01	0.31	3.00

I = Mean number of polyps in relation to total substrate.
II = Percent of substrate with polyps in relation to total substrate.
III = Mean number of polyps on shells in relation to total shell substrate.
IV = Percent of shells having polyps.
V = Mean density of polyps on a single shell having polyps.
VI = Mean number of polyps on oysters in relation to total oyster substrate.
VII = Percent of oysters having polyps.
VIII = Mean density of polyps on a single oyster having polyps.

II. Polyp Distribution During the Winter of 1966-67 as Shown by Tonged Samples

Analysis of data from tonged bottom samples is shown in Figure 6 and Table 2. No polyp-bearing oysters were taken when samples were collected with tongs. This method showed polyps on shells over a 13-mile range between Y-12.0 and Y-25.0.

Peak values were found at Y-16.0 for three of the five parameters investigated. The three were: (I) Mean number of polyps in relation to total shell substrate--0.43 polyp/shell; (III) Mean density of polyps on a single shell having polyps--21.4 polyps/shell; and (IV) Number of polyps per square meter bottom area--53.50 polyps/m^2.

Y-22.0 was found to have peak values for (II) Percent of shells having polyps in relation to total shell substrate--2.48%, and (V) Number of polyp-bearing shells per unit area (m^2)--4.5 polyp-bearing shells/m^2.

III. Polyp Distribution During November 1967 (Winter 1967-68) as Shown by Dredge Samples

This survey was made over the identical range as that of winter 1966-67. Polyps were found on shell substrate over a range of 9 miles between Y-16.0 and Y-25.0 (Figure 7 and Table 3). Polyp-bearing oysters were not found during this period of the study.

Y-22.0 was again the region where most polyps were found on shell. In this location, three out of five parameters had peak values here. These three parameters were: (I) Mean number of polyps in relation to total units of substrate--1.02 polyps/unit substrate; (III) Mean number of polyps on shells in relation to total shell substrate--1.30 polyps/shell; and (V) Mean density of polyps on a single shell having polyps--16.42 polyps/shell.

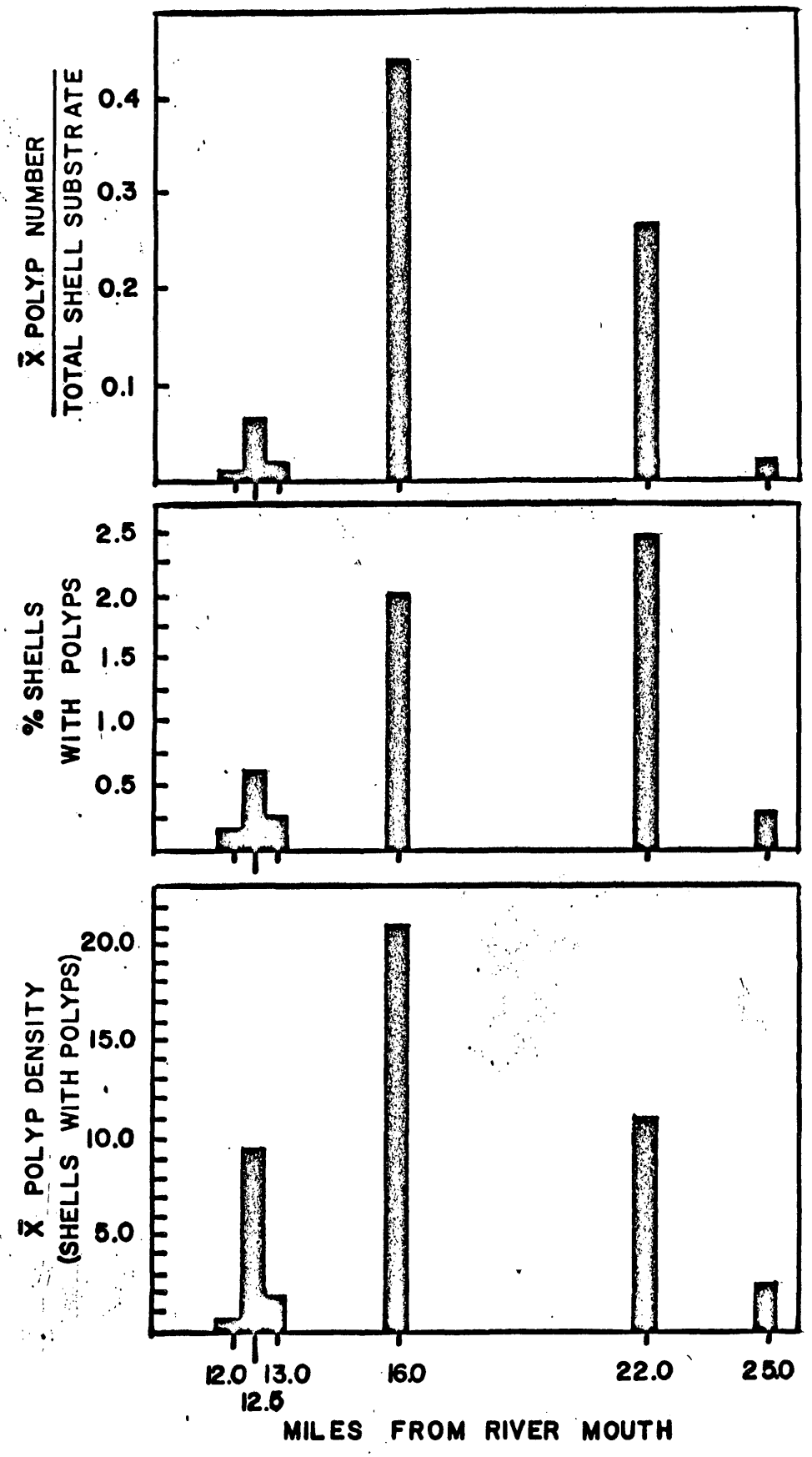

Figure 6. Distribution and abundance of polyps on shells, York River, Winter 1966-1967 tong samples.

TABLE 2

TABULATION OF DATA FROM SAMPLES COLLECTED WITH OYSTER TONGS DURING WINTER 1966-1967

Station	A Substrate	B Shells with polyps	C Polyp number	Areas sampled	Approximate area (m^2)	D Total area (m^2)
Y-12.0	1120	2	2	5	4.0	0.8
Y-12.5	152	1	10	1	1.5	1.0
Y-13.0	820	2	4	5	1.5	1.0
Y-16.0	248	5	107	2	1.5	1.0
Y-22.0	363	9	100	2	1.5	1.0
Y-25.0	1523	5	12	5	1.5	1.0

TABLE 2 CONTINUED

Station	I (C/A)	II (B/A) %	III (C/B)	IV (C/D)	V (B/D)
Y-12.0	0.002	0.18	1.00	0.67	0.67
Y-12.5	0.07	0.66	10.00	10.00	1.00
Y-13.0	0.01	0.24	2.00	0.80	0.40
Y-16.0	0.43	2.02	21.40	53.50	2.50
Y-22.0	0.28	2.48	11.10	50.00	4.50
Y-25.0	0.01	0.33	2.40	2.40	1.00

I = Mean number of polyps in relation to total shell substrate.
II = Percent of shells having polyps in relation to total shell substrate.
III = Mean density of polyps on a single shell having polyps.
IV = Number of polyps per square meter bottom area.
V = Number of polyp-bearing shells per unit area (m^2).

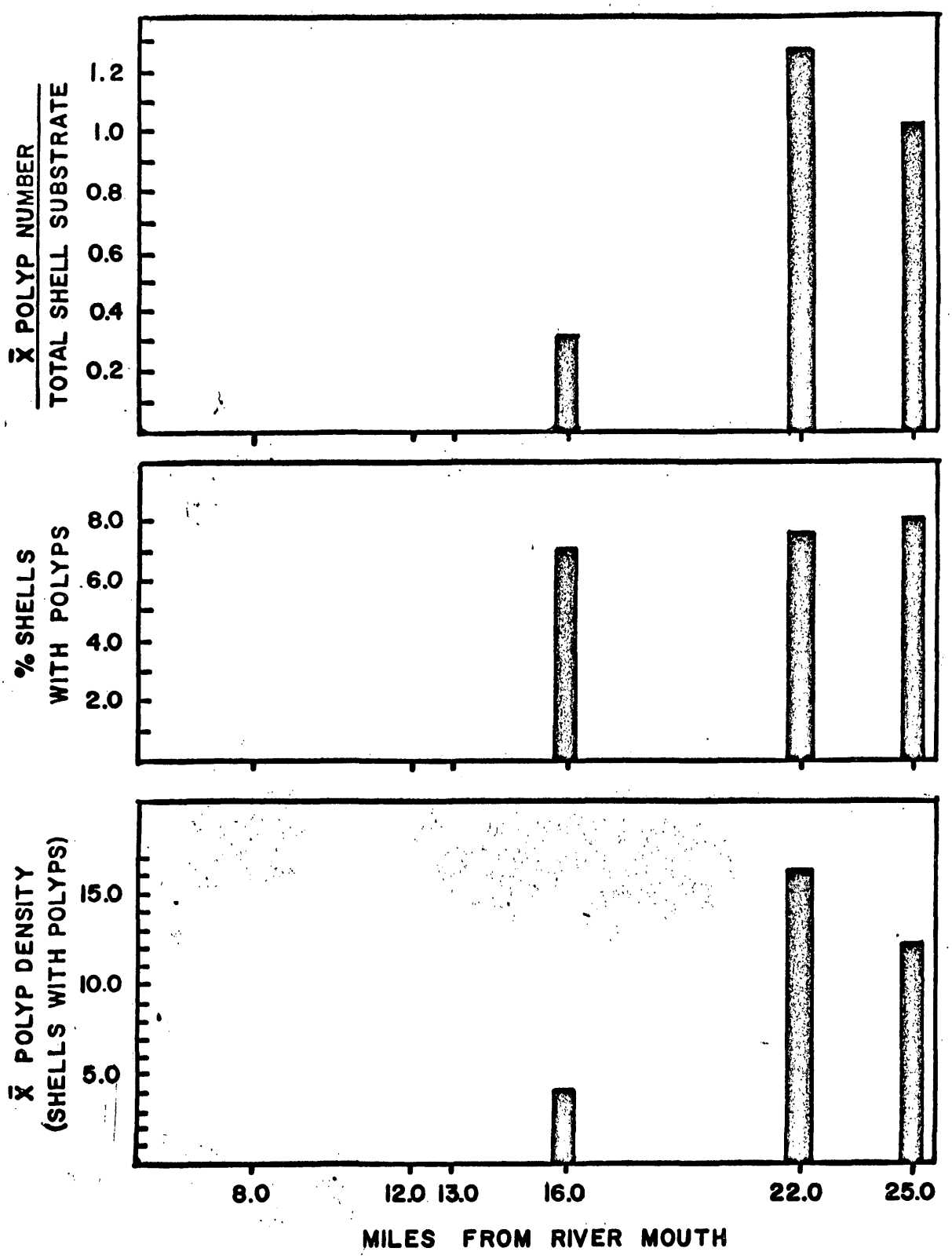

Figure 7. Distribution and abundance of polyps on shells, York River, Winter 1967-1968 dredge samples.

TABLE 3

TABULATION OF DATA FROM SAMPLES COLLECTED BY DREDGING DURING WINTER 1967-1968

Station	A Total substrate	B Shells	C Oysters	D Total polyps	E Oysters and shells with polyps	F Shells with polyps	G Oysters with polyps
Y-8.0	194	194	0	0	0	0	0
Y-12.0	90	89	1	0	0	0	0
Y-13.0	109	92	17	0	0	0	0
Y-16.0	92	82	10	26	6	6	0
Y-22.0	194	152	42	197	12	12	0
Y-25.0	180	168	12	171	14	14	0

TABLE 3 CONTINUED

Station	I (D/A)	II (E/A) %	III (H/B)	IV (F/B) %	D - I = H V (H/F)
Y-8.0	0	0	0	0	0
Y-12.0	0	0	0	0	0
Y-13.0	0	0	0	0	0
Y-16.0	0.27	6.52	0.32	7.32	4.33
Y-22.0	1.02	6.20	1.30	7.80	16.42
Y-25.0	0.95	7.70	1.02	8.30	12.21

I = Mean number of polyps in relation to total substrate
II = Percent of substrate with polyps in relation to total substrate.
III = Mean number of polyps on shells in relation to total shell substrate.
IV = Percent of shells having polyps.
V = Mean density of polyps on a single shell having polyps.

IV. Relation of Polyp Set to Winter Fouling

The majority of the polyps collected on bottom substrate during the winters of 1966-67 and 1967-68 were found within the protected umbo of oyster shell in association with a diatom film and organic dirt. Other habitats favored by the polyps were niches, cracks, and other depressions on the shell. Observations suggested that the unexposed surface of the substrate was preferred; polyps were never found on heavily fouled surfaces.

The dominant macroscopic organisms on the shell and oysters were sponges, hydroids, anemones, barnacles, and tunicates (Table 4).

The boring sponge, Cliona sp., was the most common winter fouling organism at Y-13.0 and below, often covering 20 to 25% of the shell surface. Chrysaora polyps were not observed on shells having boring sponge. Another common sponge at the downriver stations was the red finger sponge Microciona prolifera, often covering 5 to 10% of the sample.

The most abundant macroscopic winter hydroid was Sertularia argentea. In most cases, fouling due to this organism was light and it did not seem to inhibit attachment of polyps.

Fouling by tunicates was moderate at all stations sampled. In the upper river during early winter, it was common to find 5 to 10% of the substrate covered with Molgula manhattensis. Polyps were rarely present on substrate covered by this tunicate.

V. Polyp Distribution During the Summer of 1967 as Shown by Shellbags

The summer polyp distribution as determined by exposing shellbags is shown in Figures 8 and 9 and Tables 5-8.

TABLE 4

PERCENT COVERAGE OF SUBSTRATE BY FOULING ORGANISMS AT YORK RIVER STATIONS IN 1967

Month	Y-6.0	% Coverage	Y-12.0	% Coverage
January	Molgula	5	Cliona	20
			Microciona	10
February	Molgula	5	Cliona	20
			Microciona	5
March	Molgula	5	Cliona	5
			Microciona	5
April	Balanus	80	Balanus	80
May	Molgula	90	Molgula	90
	Balanus	50	Balanus	40
June	Molgula	80	Molgula	70
July	Molgula	80	Molgula	80
August	Molgula	80	Diadumene	30
			Calyptospadix	5
September	Molgula	70	Molgula	20
October	Molgula	40	Molgula	20
			Cliona	10
November	Molgula	5	Molgula	10
			Cliona	10
December	Molgula	5	Cliona	15

TABLE 4 CONTINUED

Month	Y-12.5	% Coverage	Y-13.0	% Coverage
January	Molgula	3	Cliona	20
February	Molgula	3	Cliona	20
March	Molgula	5	Cliona	20
April	Balanus	80	Balanus	85
May	Molgula	100	Molgula	100
	Balanus	50	Balanus	50
June	Molgula	70	Molgula	70
July	Diadumene	40	Molgula	40
	Molgula	40		
August	Diadumene	30	Molgula	20
September	Diadumene	10	Molgula	15
	Calyptospadix	5	Calyptospadix	5
October	Molgula	10	Molgula	10
November	Molgula		Cliona	10
			Molgula	5
December	Molgula		Molgula	5

TABLE 4 CONTINUED

Month	Y-16.0	% Coverage	Y-19.0	% Coverage
January	Molgula	5		
February	Molgula	5		
March	Molgula	5		
April	Balanus	85	Balanus	80
May	Molgula	100	Molgula	60
	Balanus	30	Balanus	10
June	Molgula	70	Molgula	20
	Calyptospadix	5		
July	Molgula	40	Molgula	20
August	Molgula	20	Diadumene	20
	Calyptospadix	5	Calyptospadix	5
September	Molgula	10	Diadumene	5
	Calyptospadix	5	Calyptospadix	5
October	Molgula	5	Molgula	5
November	Molgula	5	Molgula	5
December	Molgula	5	Molgula	5

TABLE 4 CONTINUED

Month	Y-22.0	% Coverage	Y-22.5	% Coverage
January	Molgula	5	Molgula	5
February	Molgula	5	Molgula	5
March	Molgula	5	Molgula	5
April	Balanus	90	Balanus	90
May	Molgula	70	Molgula	60
	Balanus	40	Balanus	40
June	Molgula	40	Molgula	40
July	Molgula	20	Molgula	20
August	Diadumene	50	Diadumene	30
	Calyptospadix	5	Calyptospadix	5
September	Diadumene	20	Diadumene	10
	Calyptospadix	5	Calyptospadix	5
October	Molgula	5	Molgula	5
November	Molgula	5	Molgula	5
December	Molgula	5	Molgula	5

TABLE 4 CONTINUED

Month	Y-25.0	% Coverage
January	Molgula	5
February	Molgula	5
March	Molgula	5
April	Balanus	90
May	Molgula	60
	Balanus	50
June	Molgula	30
July	Diadumene	20
	Molgula	10
August	Diadumene	20
	Calyptospadix	5
September	Diadumene	10
	Calyptospadix	5
October	Molgula	5
November	Molgula	5
December	Molgula	5

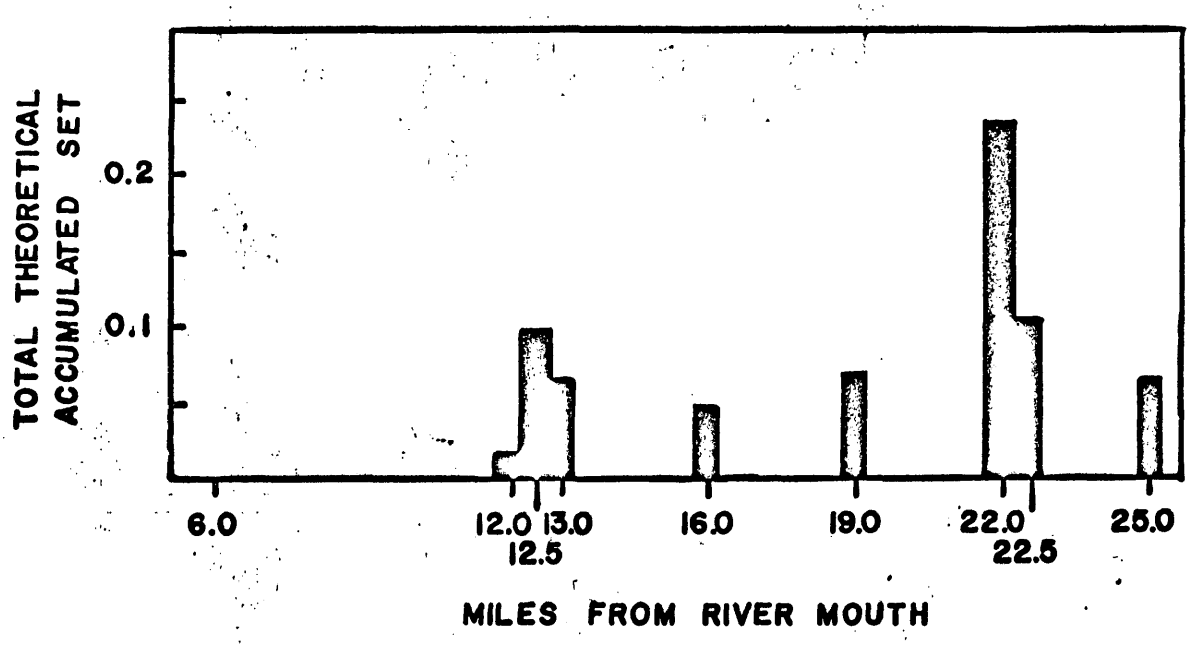

Figure 8. Total theoretical accumulated set of polyps in wire bags, York River, 1967 setting season.

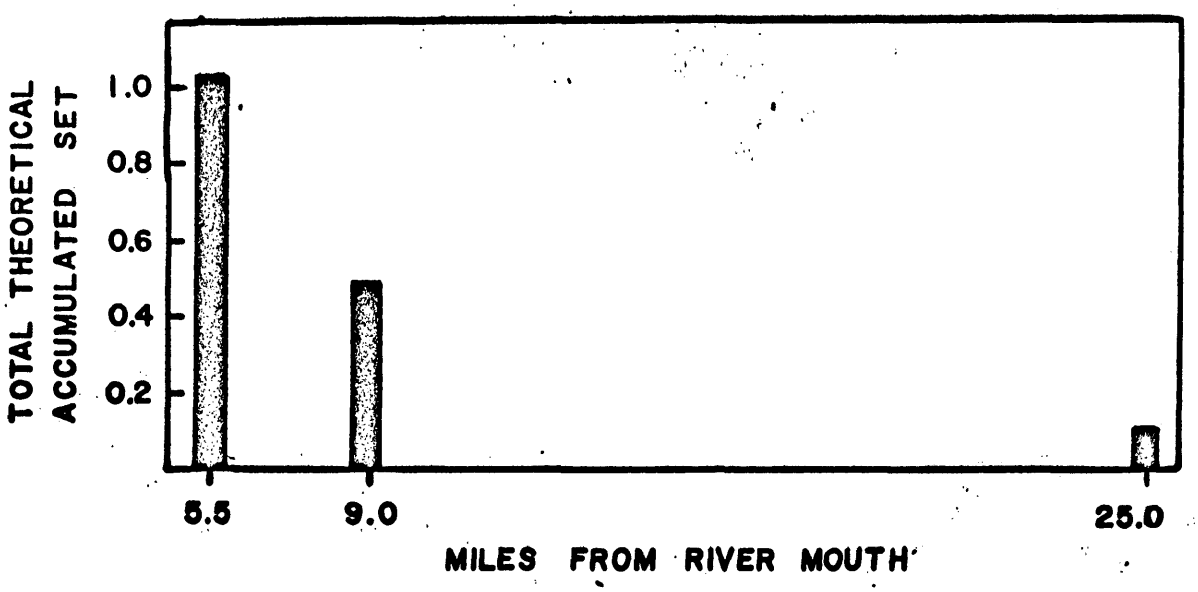

Figure 9. Total theoretical accumulated set of polyps in wire bags, selected York River tributaries, 1967 setting season.

TABLE 5

NUMBER OF POLYPS ON SHELLS IN WIRE BAGS (SET OUT 4 IV) AT YORK RIVER STATIONS IN 1967

Station	2 V	1 VI	14 VI	5 VIII	17 VII	1 VIII	14 VIII	5 IX	19 IX	5 X	29 XI
Y-6.0	190^{0}	128^{0}	210^{0}	138^{0}	130^{0}	117^{0}	99^{0}	122^{0}	118^{0}	124^{0}	109^{0}
Y-12.0	186^{0}	230^{0}	200^{0}	120^{0}	110^{0}	144^{0}	122^{0}	137^{3}	135^{0}	121^{0}	132^{0}
Y-12.5	204^{0}	180^{0}	-	131^{0}	159^{0}	111^{1}	142^{2}	126^{1}	142^{2}	132^{0}	141^{0}
Y-13.0	197^{0}	184^{0}	197^{0}	104^{0}	144^{0}	162^{2}	119^{1}	148^{4}	113^{2}	118^{0}	126^{0}
Y-16.0	134^{0}	204^{0}	176^{0}	118^{0}	128^{4}	104^{0}	136^{0}	111^{1}	113^{0}	117^{0}	137^{0}
Y-19.0	-	-	-	126^{0}	109^{0}	111^{1}	138^{0}	118^{2}	126^{3}	144^{2}	118^{0}
Y-22.0	165^{0}	165^{0}	184^{0}		210^{0}	146^{3}	110^{6}	131^{8}	132^{6}	125^{2}	131^{0}
Y-22.5	189^{0}	208^{0}	228^{0}		208^{0}	124^{4}	164^{0}	141^{1}	150^{3}	107^{1}	126^{0}
Y-25.0	207^{0}	200^{0}	207^{0}	-	195^{0}	105^{0}	178^{7}	114^{0}	145^{3}	132^{1}	134^{0}

000^{x}: 000 = number of shells in sample; x = polyp number.

TABLE 6

TOTAL THEORETICAL ACCUMULATED SET FOR 1967 BASED ON MEAN NUMBER OF POLYPS PER SHELL IN WIRE BAGS (SET OUT 4 IV) AT YORK RIVER STATIONS

Station	2 V	1 VI	14 VI	5 VII	17 VII	1 VIII	14 VIII	5 IX	19 IX	5 X	29 XI	TTAS*
Y-6.0	0	0	0	0	0	0	0	0	0	0	0	0
Y-12.0	0	0	0	0	0	0	0	0.02	0	0	0	0.02
Y-12.5	0	0	0	0	0	0.01	0.06	0.01	0.01	0	0	0.09
Y-13.0	0	0	0	0	0	0.01	0.01	0.03	0.02	0	0	0.07
Y-16.0	0	0	0	0	0.04	0	0	0.01	0	0	0	0.05
Y-19.0	0	0	0	0	0	0.01	0	0.02	0.02	0.02	0	0.07
Y-22.0	0	0	0	0	0.01	0.03	0.07	0.06	0.05	0.02	0	0.24
Y-22.5	0	0	0	0	0	0.03	0	0.01	0.06	0.01	0	0.11
Y-25.0	0	0	0	0	0	0	0.05	0	0.02	0.01	0	0.08

* TTAS = Total Theoretical Accumulated Set.

TABLE 7

NUMBER OF POLYPS ON SHELLS IN WIRE BAGS (SET OUT 1 VI) AT CREEK STATIONS IN 1967

Station	14 VI	5 VII	17 VII	1 VIII	14 VIII	5 IX	19 IX	5 X	29 XI
Sarah Creek (Y-5.5)	139^{0}_{0}	126^{0}_{0}	142^{21}_{24}	134^{28}_{34}	129^{32}_{41}	140^{36}_{39}	128^{18}_{21}	136^{2}_{2}	109^{0}_{0}
Timberneck Creek (Y-9.0)	111^{0}_{0}	136^{0}_{0}	123^{8}_{8}	156^{19}_{21}	132^{14}_{16}	141^{21}_{21}	140^{12}_{26}	132^{3}_{3}	126^{0}_{0}
Hockley Creek (Y-25.0)	137^{0}_{0}	114^{0}_{0}	111^{0}_{0}	138^{9}_{9}	138^{4}_{6}	122^{2}_{3}	114^{2}_{2}	124^{0}_{0}	112^{0}_{0}

$000^{(A)}_{(B)}$: 000 = number of shells in sample; (A) = shells with polyps; (B) = polyp number on (A).

TABLE 8

TOTAL THEORETICAL ACCUMULATED SET FOR 1967 BASED ON MEAN NUMBER OF POLYPS PER SHELL IN WIRE BAGS (SET OUT 1 VI) AT CREEK STATIONS

Station	14 VI	5 VIII	17 VII	1 VIII	14 VIII	5 IX	19 IX	5 X	29 XI	TTAS*
Sarah Creek (Y-5.5)	0	0	0.15	0.22	0.25	0.26	0.14	0.02	0	1.04
Timberneck Creek (Y-9.0)	0	0	0.06	0.12	0.11	0.15	0.09	0.02	0	0.55
Hockley Creek ($Y\text{-}25.0_a$)	0	0	0	0.06	0.03	0.02	0.02	0	0	0.13

* TTAS = Total Theoretical Accumulated Set.

Newly set polyps which appeared as pink "buttons" with 2-16 tentacles were found on shell in wire bags throughout the same range as determined by the winter surveys (Figure 8 and Tables 5 and 6). Polyp setting began in 1967 between 5 July and 17 July. Setting first occurred at two mid-river stations (Y-16.0 and Y-22.0) and had spread throughout the range by the next sampling period (1 August). Generally the upriver stations were last to receive set. The last polyps were found on the 5 October samples. The period of maximum set varied slightly at each station but generally it occurred between 14 August and 19 September when 5 out of 8 stations received over 60% of their total annual set. Seasonality of Chrysaora polyp set in the York River is shown by all set occurring in a three-month period between 5-17 July and 5 October.

Setting as shown by shell bags was generally higher in the three creeks sampled (Sarah Creek, Y-5.5; Timberneck Creek, Y-9.0; and Hockley Creek, Y-25.0_a) than it was in the river during comparable periods (Figure 9 and Tables 7 and 8). The majority of the set occurred as individual polyps; however, some aggregation and early colony formation was evident. The setting period in the creeks generally ranged from 17 July to 5 October. The period of maximum set occurred between 1 August and 5 September when all stations received over 50% of their total annual set and 2 of 3 stations received over 70% of their total annual set. Y-25.0_a, the most upriver creek, had the shortest set range, from 1 August to 5 October.

Biweekly setting data of mean polyp number in relation to total shell substrate were summed for the river and the sampled tributaries and expressed as total theoretical accumulated set for each station.

Analysis showed Y-22.0 to be the peak river station with 0.24 polyp/shell and Y-5.5 to be the peak creek station with 1.04 polyps/shell.

VI. Survival of Polyps on Wire Bags at the End of the 1967 Setting Season

Survival bags which remained in the water for seven months were retrieved only at Queens Creek (Y-12.5), Aberdeen Creek (Y-13.0), Ferry Point (Y-16.0), and Roane Point (Y-22.0). At other stations, the wire had corroded and the shells had fallen from the bag. Results of the retrieved bags are shown in Figure 10 and Table 9.

The peak number of polyps (0.14 polyp/shell) occurred on shell substrate at Y-22.0 as did the percent of shells bearing polyps (3.80%). Mean density of polyps on shells having polyps (5.00 polyps/shell) peaked at Y-13.0.

VII. Relation of Polyp Set to Summer Fouling on Shellbags

Summer fouling on shellbags exposed in the creeks and in the river was heavier than that found on bottom substrate during the winter. In most cases, shells at the outer surface of the bags were thickly fouled; those toward the center were relatively free of fouling.

The most common macroscopic fouling organism was the tunicate Molgula manhattensis. During June through August, the period of maximum Molgula set, the entire outer surfaces of the shellbags were often covered by this organism (Table 4).

The most abundant hydroid was Calyptospadix cerulea. C. cerulea was often dense on the suspending ropes and on the wire bags but was found infrequently on the shell material within the bags.

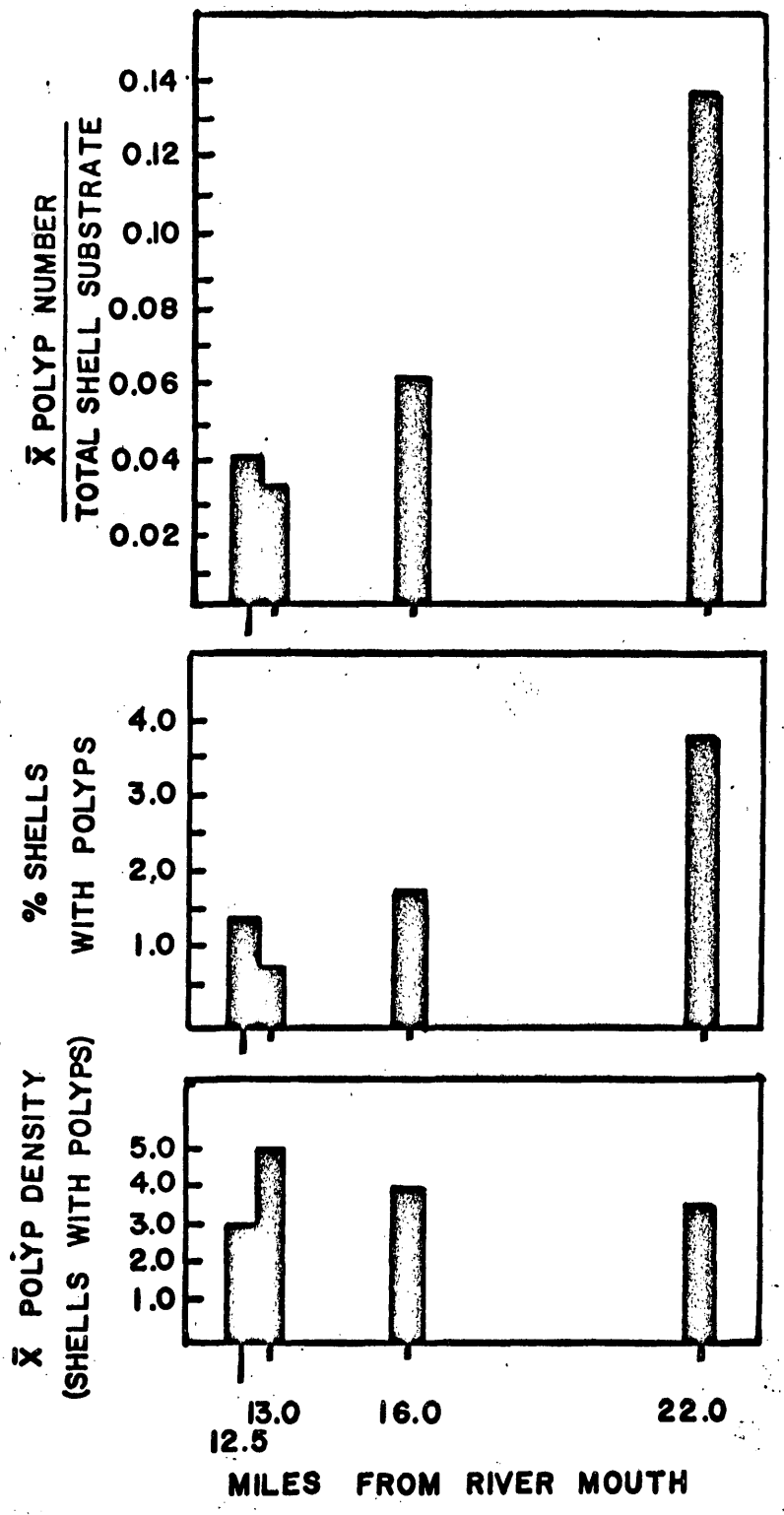

Figure 10. Distribution and abundance of polyps on survival bags, York River, 1967 setting season.

TABLE 9

TABULATION OF DATA FROM SURVIVAL BAGS AT YORK RIVER STATIONS IN 1967

Station	DATA A Substrate	DATA B Shells with polyps	DATA C Polyp number	CALCULATIONS I (C/A)	CALCULATIONS II (B/A) %	CALCULATIONS III (C/B)
Y-12.5	142	2	6	0.04	1.40	3.00
Y-13.0	151	1	5	0.03	0.70	5.00
Y-16.0	120	2	8	0.07	1.70	4.00
Y-22.0	132	5	18	0.14	3.80	3.60

I = Mean number of polyps in relation to total substrate.

II = Percent of shells having polyps in relation to total substrate.

III = Mean density of polyps on a single shell having polyps.

During August and September, the sea anemone Diadumene leucolena was common. This organism would often cover 15 to 25% of a single shell at the upriver stations. Chrysaora polyps were not observed on substrate when D. leucolena exceeded approximately ten or more individuals per shell.

The period of maximum set for Balanus eburneus occurred early in the study in mid-May 1967 at all river stations. During this period, virtually all oyster shells on the outside surfaces of the bags were covered with small barnacles. The shells within the bags generally escaped fouling by this organism. By early July barnacle fouling decreased in intensity, and for the rest of this study, the animal covered only about 10% of the shell surface.

Due to the short exposure time of the bags, many fouling organisms never became a problem.

VIII. Abundance of Medusae in the York River and Its Tributaries

Medusae were observed in the creeks for a period of at least 15 days before they first appeared in the river. The entire York River system appeared to be devoid of medusoid Chrysaora on 1 June 1967. By 15 June, medusae were observed in five downriver creeks in about equal abundance. These creeks, entering York River between Y-5.0 and Y-12.0, were Wormley, Sarah, Timberneck, Cedarbush, and Carter's Creek. By 30 June, all creeks surveyed contained approximately equal numbers of Chrysaora medusae in various stages of development; however, on this same date they were still scarce in the river and only scattered individuals were observed at the sampling stations (Table 10).

Chrysaora medusae were first observed from the VIMS pier on 12 June 1967, but the next sighting did not occur until 28 June

TABLE 10

MEDUSAE COUNTS MADE IN 1967 WITH A 1 M^2 FLOATING FRAME

Location	Miles above mouth		1 June	15 June	30 June	15 July
Wormley Creek (Y-5.0)	0		0	9	6	
	0.10		0	2	4	
	0.20		0	9	9	
	0.30		0	10	14	
	0.20		0	18	17	
	0.40		0	16	18	
			0	64	68	
		$\bar{x}$	0	10.66	11.33	
Sarah Creek (Y-5.5)	0		0	0	0	
	0.10		0	7	1	
	0.20		0	6	7	
	0.30		1?	20	4	
	0.40		0	18	12	
	0.50		0	20	20	
	0.80		0	20	20	
	0.50		1?	12	20	
	0.70		0	14	18	
			2	117	102	
		$\bar{x}$		13.00	11.30	
Timberneck Creek (Y-9.0)	0			6	8	
	0.20			14	12	
	0.40			12	14	
	0.50			12	15	
	0.70			19	19	
				63	63	
		$\bar{x}$		12.60	12.60	
Carter Creek (Y-11.5)	0		0	0	1	
	0.30		0	1	5	
	0.50		0	7	10	
	1.00		0	20	14	
	1.35		0	23	23	
	1.65		0	21	20	
	1.70		0	23	14	

TABLE 10 CONTINUED

Location	Miles above mouth		1 June	15 June	30 June	15 July
Carter Creek continued	1.95		0	14	12	
	2.25		0	7	2	
	2.95		0	0	0	
	3.15		0	0	0	
			0	116	101	
		$\bar{x}$	0	10.50	9.18	
York River	6.0		0	0	0	2
	12.0		0	0	0	1
	12.5		0	0	0	5
	13.0		0	0	0	3
	16.0		0	0	0	6
	19.0		0	0	0	4
	22.0		0	0	0	3
	22.5		0	0	0	5
	25.0		0	0	0	6

(Figure 11). There was a gradual increase in abundance after this date until a peak was reached during the week of 17-21 July when a total of 97 medusae was recorded. This maximum was followed by a gradual decline until 2 October when the last medusa was observed. After this, medusae were still observed at upriver stations, but none were seen after the week of 14-21 October.

IX. Abundance of Ephyrae in the York River and Its Tributaries

Ephyrae were scarce in the river, often none or only a single individual being taken at a station (Table 11). In contrast, it was common to take 2 to 27 ephyrae in a single tow at the creek stations. Ephyrae were obtained only on three occasions at the VIMS pier--on 29 May, 24 July, and 12 August 1967. At these times only single individuals were collected.

X. Salinity Tolerance of the Polyp

Salinity tolerance results are shown in Table 12. When water with a salinity higher or lower than that to which the polyps had been acclimated was introduced into a dish containing polyps, the immediate reaction was a contraction and clumping of the tentacles. Secondary reactions varied with the various salinities. Results are summarized as follows:

2.5 o/oo--Polyps failed to recover from initial shock reaction. Gradual decline in size until total encystment after 11 days.

5.0 o/oo--Polyps encysted after 4 days.

10.0 o/oo--All polyps recovered from salinity shock in 24 hours and regained normal health. Some stolon formation.

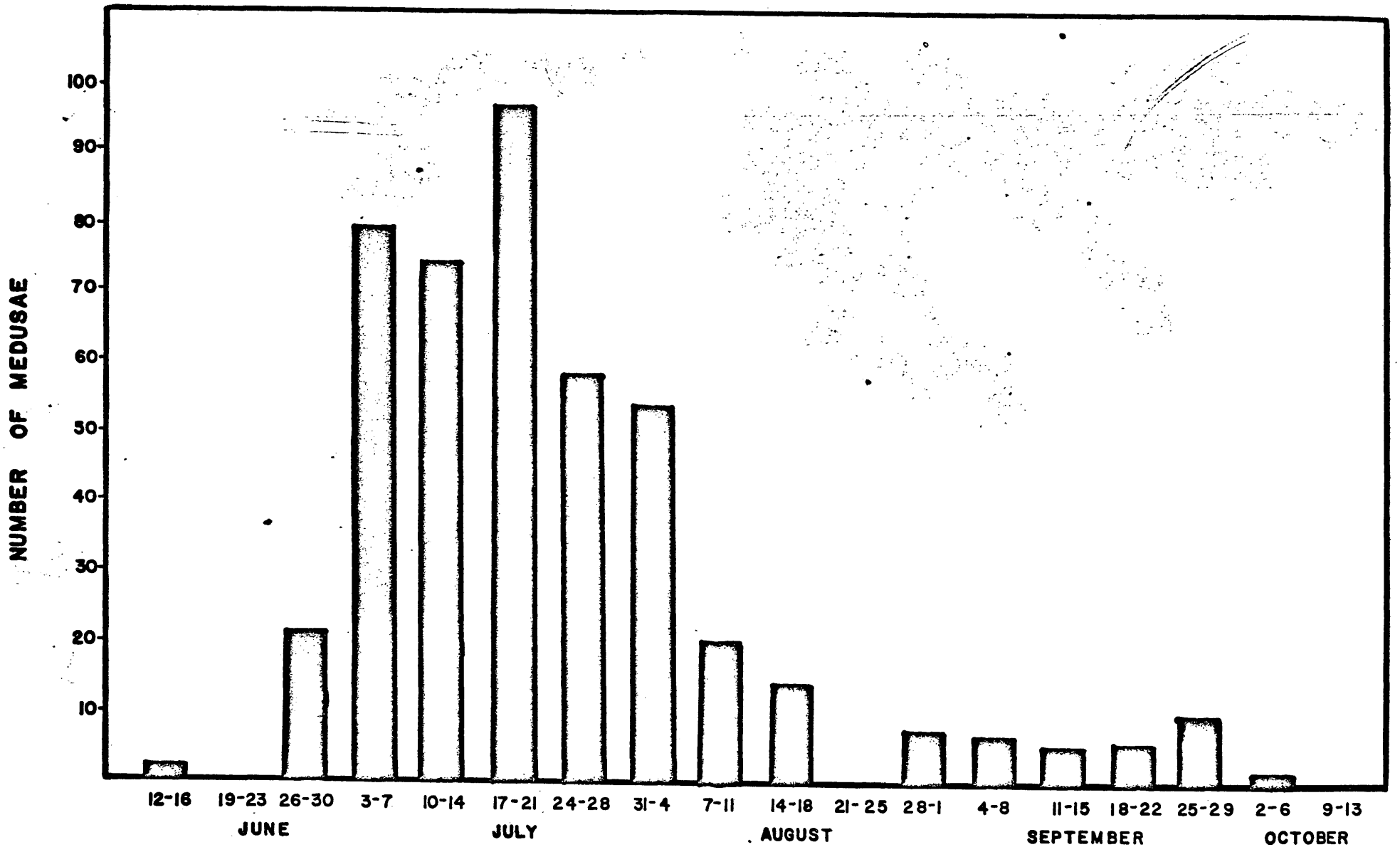

Figure 11. Seasonal abundance of medusae, Virginia Institute of Marine Science Pier, 1967.

TABLE 11

NUMBER OF EPHYRAE PER TOW COLLECTED IN 1967 WITH A 1/8 M NET

Location	Miles from mouth	29 May	15 June	17 June	30 June	1 July	15 July	24 July	12 August
Sarah Creek (Y-5.5)	0		4		10				
	0.10		7		18				
	0.20		9		12				
	0.30		21		22				
	0.40		19		26				
	0.50		26		25				
	0.80		14		21				
	0.50		12		20				
	0.70		1		14				
			113		168				
$\bar{x}$			12.55		18.66				
Carter Creek (Y-11.5)	0		0		2				
	0.30		4		2				
	0.50		21		12				
	1.00		20		19				
	1.35		13		24				
	1.65		19		12				
	1.70		27		20				
	1.95		14		4				
	2.25		10		8				
	2.95		0		1				
	3.15		0		0				
			128		104				
$\bar{x}$			11.63		9.46				

TABLE 11 CONTINUED

Location	Miles from mouth	29 May	15 June	17 June	30 June	1 July	15 July	24 July	12 August
York River	12.0			0		0	1		
	13.0			0		1	0		
	22.0			0		1	1		
	24.0			0		0	0		
	25.0			0		0	1		
				0		2	3		
$\bar{x}$				0		0.40	0.60		
VIMS Pier		1						1	1

TABLE 12

SALINITY TOLERANCE OF POLYPS AS EVIDENCED BY

PERCENT CHANGE FROM ORIGINAL HEIGHT

Day		2.5	5.0	10.0	15.0	20.0	25.0	30.0	35.0	40.0
0	% of original size	100	100	100	100	100	100	100	100	100
1		60	60	60	80	"	90	90	90	90
2		50	40	80	100	"	95	100	100	100
3		45	20	100	"	"	100	"	"	"
4		40	10	"	"	"	"	"	"	"
5		35	0	"	"	"	"	"	"	"
6		30	"	"	"	"	"	"	"	"
7		25	"	"	"	"	"	"	"	"
8		20	"	"	"	"	"	"	"	"
9		15	"	"	"	"	"	"	"	"
10		10	"	"	"	"	"	"	"	"
11		5	"	"	"	"	"	"	"	"
12		0	"	"	"	"	"	"	"	"
13		"	"	"	"	"	"	"	"	"
14		"	"	"	"	"	"	"	"	"

" indicates no change.

15.0 o/oo--Recovery from salinity shock complete in 12 hours. Very little change occurred.

20.0 o/oo--(Control) No change.

25.0 o/oo--Salinity shock compensated for in 18 hours. Very little change occurred.

30.0 o/oo--Recovery from salinity shock was slow, taking 48 to 56 hours. Three of 8 polyps entered pre-strobilation stages but progressed no further.

35.0 o/oo--Recovery from salinity shock was complete in 48 hours. Two of 9 polyps began stolon formation and 4 of 9 budded. Three cysts opened. All polyps remained healthy.

40.0 o/oo--Salinity shock compensated for in 36 hours. All polyps formed stolons or buds and after 8 days appeared healthier than when study began. After 65 days, polyp colony had increased in size and general health.

XI. Temperature Tolerance of the Polyp

Temperature extremes similar to those encountered in the York River during one year (1°C-29°C) were found to have no lethal effect on the polyps. Temperatures above 35.5°C, however, induced encystment in all individuals.

Polyps were found to tolerate a gradual increase in temperature (1°C/day) better than a rapid increase (4°C/day). A gradual increase often induced strobilation at 20 to 22°C in polyps previously acclimated to temperatures of 4 to 9°C. In contrast, a rapid temperature rise often resulted in encystment at 28 to 30°C, with no indication of strobilation at 20 to 22°C.

XII. Strobilation of the Polyp

Strobilation of the polyp was induced by several techniques in the laboratory. These methods proved effective about 40% of the time.

One method consisted of slowly raising the water temperature from 6 to 18°C over a period of ten to twelve days. At the end of this time, a further sudden, sharp rise in temperature of 4 to 6°C would induce strobilation of the polyp within 48 hours. Water of ambient salinity (17.2-19.5 o/oo) was used in this procedure. A second technique utilized temperature and salinity shock. Once the polyps had become conditioned to a specific salinity, a sudden increase of 5 to 15 o/oo, along with a 4 to 6°C temperature rise, often resulted in strobilation within 72 to 96 hours.

Occasional feeding with Artemia or enchytraieds, water changes, and aeration were all that was needed to maintain polyps in good health for extended periods of time at 20°C. When needed for experimentation, polyp-bearing shells were removed from storage, and strobilation was attempted by one of the above methods.

Polyps which had been induced to encyst by unfavorable conditions could again be made to excyst by placing them in a 25°C constant temperature bath for seven to ten days. In some cases, excystment initiated strobilation within 96 hours. Occasionally excystment could be produced by placing the cysts in 40 o/oo water at 20°C.

XIII. Polyp Predators

Two new predators of the ephyrae were discovered during the study. The common sea anemone of the upper York River, Diadumene

leucolena, was observed in the laboratory on several occasions to catch and actively feed on newly strobilated ephyrae. Digestion time varied from 30 minutes to one hour, depending on the size of the individual. Previously fed anemones could catch and digest large numbers of ephyrae with little difficulty. The rapid contractions of the ephyrae stopped immediately upon contact with the tentacles of D. leucolena.

The second predator was the Ivory barnacle Balanus eburneus, also common in the York River. During their cirripedial sweepings, several barnacles were observed to catch and take into their carapace newly strobilated ephyrae. The ephyrae were not rejected and it is assumed they were digested.

One instance of predation of the polyp stage was observed on 2 August 1967. The common annelid worm Nereis succinea was observed to bite and masticate a single Chrysaora polyp. Fragments of the polyp were scattered over a wide area of the shell but were not ingested by the worm. It is felt this was not typical behavior since Nereis often were seen to graze among polyps without any apparent harm to either.

DISCUSSION

Polyp distribution determined during the 1966-67 and 1967-68 winter surveys was essentially the same, with the region of maximum set occurring between Y-22.0 and Y-25.0. Mean abundance (mean number of polyps in relation to total units of substrate), however, was about four times greater at Y-25.0 in winter 1967-68 than during 1966-67. A decrease in polyp abundance toward the river mouth was observed during both winters, with mean polyp per shell reaching zero at Y-12.0 in winter 1966 and at Y-13.0 in winter 1967-68.

Mean polyp density on shells having polyps was greatest between Y-22.0 and Y-25.0 in both winters. Similarly, the percent of shells bearing polyps and percent of substrate with polyps was highest between these regions. Polyps were not found at river stations below Y-12.0. They were found, however, in creeks with mouths located at Y-9.0 and Y-6.0. In these downriver creeks, polyps were not found in the high-salinity areas at the mouth, but rather in upcreek regions where the salinity varied from 12 to 18 o/oo.

Polyp distribution as observed during the winters of 1966-67 and 1967-68 was probably related to salinity, but the exact limits and relations are not clear. In the upriver direction, polyp number decreased at Y-25.0. Lack of available substrate prevented sampling above this region; however, it is probable that even if substrate were available above Y-25.0, abundance would have decreased

rapidly. This hypothesis is based on hydrographic studies (Van Engel and Joseph, 1968) which show a rapidly diminishing salinity gradient in the upper end of the York with a mean salinity of 6 o/oo over a ten-year period at P30 (Y-30.0). Cargo and Schultz (1966) found that polyps did not survive at salinities lower than 5 o/oo.

In the downriver region, distribution also appeared limited by salinity. Hydrographic data over a ten-year period (Van Engel and Joseph, 1968) showed that at Y-12.0 and Y-13.0 (the lower limit of polyp distribution), mean salinity ranged from 15.2 to 16.3 o/oo. These data agree in general with results obtained by Cargo and Schultz (1966) which showed polyps to be absent in Chesapeake Bay areas where salinities exceeded 19 to 25 o/oo.

Salinity tolerances determined in the laboratory did not always agree with distribution of polyps as observed in the river. Before comparing these results, however, it must be emphasized that there may be a major difference in setting of polyps and survival of established polyps in relation to salinity.

Studies conducted in the laboratory during 1967 demonstrated a lower salinity tolerance at salinities between 5 to 10 o/oo. The upper tolerance limit was shown to exceed 40 o/oo. Polyps in water of 40 o/oo grew faster and colony size increased through stolon formation at a faster rate than the controls maintained at 20 o/oo.

Temperature did not appear to be a major factor in limiting polyp distribution in the upper or lower river during any single season. It also appears that differences in polyp abundance between years cannot be attributed to this factor. During the entire study period, river water temperatures varied from 1 to 25°C and living polyps were found over this range. However, on comparable dates,

temperature differences between the head of the river and the mouth seldom exceeded 2 to 3°C. A comparison of the two setting seasons shows the temperature ranges to be similar. Ranges for 1966 during the July to October setting period varied from 29.4 to 13.3°C, while 1967 values ranged from 27.8 to 14.6°C (VIMS thermograph).

Laboratory studies support the hypothesis that temperature in the York River was not associated with observed distributional patterns. These studies, conducted in 1967, showed that the polyp stage can withstand the mean York River minimum (1°C) and maximum (29°C) temperatures as well as a gradual temperature change (1°C/day) between the two extremes with no mortality or encystment. Rapid temperature changes (3 to 4°C/day), however, were found to cause encystment.

A summation of the biweekly summer shellbag data showed polyp range to be essentially the same as that found in the two winter studies. The cumulative polyp set, however, showed totals less than those observed during the two winter studies. Lower numbers of polyps may be attributed to the fact that after initial polyp setting, additional colonies are often budded. In this study, bags were removed on a biweekly basis before colony formation could begin. All polyps on the summer bags in the river occurred as single individuals rather than in colonies as was most often encountered in the winter samples. Some early colony formation was evident in the creek bags. The proliferation of the polyps after initial setting is suggested from comparing total theoretical accumulated set during summer 1967 with the number of polyps per total shell substrate in winter 1966-67. This comparison shows the total theoretical accumulated set is lower than the winter values. In the creeks,

summer shellbags yielded total theoretical accumulated sets two to three times greater than similar data for river stations.

A definite seasonality of polyp set in the York River is suggested by the summer shellbag data in that set was limited to a three-month period between 5-17 July and 5 October.

Effects of fouling on polyp distribution must be carefully evaluated. Cargo and Schultz (1966) found polyps would set on all surfaces of a substrate if it were clean and free of fouling. However, fouling on oyster shells begins quickly after immersion. Most macroscopic fouling occurred on exposed surfaces of the substrate. Careful examination of substrate collected during the winter surveys showed Chrysaora polyps were more frequently attached to the less exposed surfaces of the substrate where macroscopic fouling was lightest. Similar results were reported by Fraser (1962) for polyps of Aurelia. Polyps were most often found within the umbo of oyster shells. The possibility exists that polyps are found on less exposed surfaces since those setting on exposed areas are smothered by fouling. Polyps found in the biweekly shellbags occurred most frequently in the umbo.

The effect of fouling on the winter distribution is difficult to determine with available data; number surviving at the end of the setting season (winter distribution) had already been influenced by fouling during the preceding summer.

Instances of polyp setting on live oysters were small; consequently, the percent of oysters having polyps and the average density of polyps on oysters having polyps were small. It is possible that the rapid filter feeding of the oyster ingested the planulae before they could attach to the shell.

The presence or absence of predators in the York River may influence survival and distribution of the polyps, but little work has been done with this problem. One group of animals has been shown to actively feed on the polyps. Cargo (personal communication) found certain nudibranchs (Coryphella sp.) feeding regularly on Chrysaora polyps. This genus was not observed on sampled material during the present investigation; however, it does occur in the York River (Wass, 1965). Two new ephyra predators were observed during this study. These were D. leucolena and B. eburneus. Agassiz and Mayer (1898), Mayer (1910), Littleford (1939), Mansueti (1963), and Cargo and Schultz (1966) reported on predators of the adult medusae. Several instances of predation of the medusa by the orange file fish Alutera schoepfi were observed during this study.

Creeks and tributaries may be important nursery grounds for C. quinquecirrha. Adult medusae and ephyrae were more abundant in the creeks during the investigation than in the river. Creek summer polyp set was found to be much higher on planted substrate than river summer polyp set on the same substrate.

The greater polyp abundance on shellbags in creeks presents an interesting paradox. Although the river contained an abundance of suitable substrate in the form of oysters or shell, there was a definite deficiency of similar material in the creeks. Many contained only scattered or partially buried shells which were entirely free of polyps. This scarcity led to a search for other substrates.

Obvious choices would be the Ruppia, Spartina, and Zostera which are abundant in the creeks during the summer months. Smith (1964) and Whitcomb (personal communication) report finding numbers

of Chrysaora polyps on these grasses in the Woods Hole region. On several occasions, individual polyps were observed on Zostera. However, these grasses die back during the winter, thereby eliminating the substrate and in all probability destroying attached polyps.

Pilings, sea walls, and boundary poles were examined periodically and an occasional polyp was found. However, numbers were not sufficient to account for the tremendous number of medusae which occurred in the creeks during spring. Tin cans, bottles, tires, sunken boat hulls and debris were also examined with negative results. The question of suitable creek substrate must for the present remain unanswered.

During early summer 1967, medusae in all stages of development were observed in the small tributaries 15 to 30 days before they were observed in the river. It is probable that medusae observed in the creeks originated from polyps attached to substrate in these locations. Early strobilation in these regions would account for the observed concentrations several weeks before their appearance in the open river.

Other investigators have observed early concentrations of medusae in creeks. Papenfus (1935) was the first to suggest the possibility of this phenomenon. Later, Littleford and Truitt (1937) reported observing sea nettles in the creeks prior to their appearance in the rivers. Cargo and Schultz (1966) confirmed these observations and found Chrysaora medusae in the creeks of the St. John River, Maryland, several weeks before they were found in the river.

A combination of factors may produce strobilation in the creeks several weeks before it occurs in the river. Lambert (1935) suggested suitable food, a "certain" temperature, and oxygenation

at the critical period. Cargo and Schultz (1966) found the apparent onset of strobilation in the St. John River to correspond with a sharp temperature rise and a decrease in salinity in spring 1965. During the present investigation, water temperature was found to be 1 to 3°C warmer in the creeks than in the river at the onset of strobilation; however, no sharp salinity change was noted.

Tides and currents undoubtedly are a major factor in influencing distribution of planulae, ephyrae, and medusae. The feeble swimming ability of these stages may be such that their distribution is determined to a great extent by these hydrographic features.

SUMMARY

1. The polyp stage of the sea nettle Chrysaora quinquecirrha was confined generally to a 12-mile range in the York River between Y-13.0 and Y-25.0. Within this range, Y-22.0 had the highest values for the majority of the parameters investigated. The principal factor affecting these boundaries appeared to be salinity.
2. There was a definite seasonality in polyp setting in the York River. All setting during 1967 occurred over a 3-month period between 5-17 July and 5 October.
3. It appears that many medusoid Chrysaora in the river originate in the tributaries. However, there is a deficiency of polyp substrate in the latter locations. Medusae in all stages of development were found in creeks 15 to 30 days before they appeared in the river.
4. Salinity tolerance of polyps determined in the laboratory showed a lower tolerance of 5 to 10 o/oo and an upper limit in excess of 40 o/oo.
5. In the laboratory, polyps tolerated a slow change of temperature from 1 to 30°C without appreciable mortality.
6. Strobilation may be induced in polyps by a gradual (1°C/day) increase in temperature from 5 to 10°C to 18 to 19°C, then raising it rapidly to 20 to 22°C. Strobilation may also be

induced by a sudden change in salinity or by inducing excystment of the encysted polyp.

7. The anemone Diadumene leucolena and the barnacle Balanus eburneus are predators on the ephyra stage of Chrysaora reproduction.

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APPENDIX

STROBILATION

It was possible during this study to observe all phases of strobilation in the Chrysaora polyp. Since a concise description of this phenomenon has not been published, it is included here.

The normal polypoid form of Chrysaora quinquecirrha possesses 16 long knotted tentacles surrounding a raised square mouth. Normal polyp height ranges between 1.9 mm and 4.8 mm. The body is goblet shaped, the slender base broadening at the bottom to form a basal disc.

A definite color change occurs in the polyps several days before strobilation. The typical off-white color changes to pale pink and this gradually deepens to red or crimson.

During this color change, and approximately 72 hours before the budding off of the first ephyra, visible clefts begin to appear at five places radially along the length of the polyp. Within 24 to 48 hours, these clefts deepen until five distinct discs become visible, each connected by a thin filament. With the deepening of these clefts, tentacles are resorbed.

With the formation of five distinct plates or discs, the terminal disc develops eight bifid arms and begins spasmodic pulsations. The characteristic jerking motion of strobilation does not occur in the entire polyp but originates within the terminal disc and appears to be the normal swimming pulsation of the ephyra.

The contractions vary in number from a single pulse to five or six in succession, the total series taking between three and five seconds.

The discs become smaller the closer they are to the base of the polyp, the terminal disc being one-third larger than the disc directly beneath it.

Approximately one hour before separation of the terminal disc, the disc immediately beneath it begins to enlarge and starts pulsations, often in unison with the terminal disc but not always.

When only two strobile discs remain, polyp tentacles begin to reappear beneath the last disc and enlarge throughout the strobilation of the remaining ephyrae so that they are near normal size when the last disc has separated. The pulse period for the last disc is usually somewhat longer than for the previous four, being three to eight seconds in duration. Frequency of contractions is not abnormal immediately after separation; the three to eight second pulses continue until separation of the disc is complete. The polyps assume their normal appearance in 24 to 72 hours after the separation of the last disc.

Each strobile disc takes a period of at least four hours to separate. Since five discs are present on each polyp, a total time of 20 to 25 hours is required for the completion of strobilation of a single polyp after clefting.

After the clefting of the polyp, the region between the disc appears clear with a bright red fiber in the middle connecting the disc. Spangenberg (1965) reported this thin red fiber in Aurelia to be the gastric filament. Although the region between the disc appears thick, actual connection is only at the gastric filament. As the discs pulsate, the gastric filament holding the terminal disc

becomes very thin and finally parts as the ephyra breaks free. The remaining clear, thick portion of the stalk appears to become the manubrium of the next ephyra. Several hours before separation, this manubrium-like structure begins to twitch and eventually splits.

When polyps were kept in deoxygenated water for several hours, the rate of polyp contractions was noticeably slower but returned to normal upon addition of freshly oxygenated water. Lambert (1935), working with a British species of Chrysaora, found oxygen necessary for continuation of strobilation once it had begun.

All individuals observed, with the exception of one, produced five ephyrae each; the exception produced six. After strobilation was completed, many of the polyps gave rise to stolons and a general increase in colony size was noted.

The newly strobilated ephyra is inverted as compared to the adult; that is, it swims with the manubrium in a dorsal position rather than ventral. They are light pink with several very prominent deep-red regions. Lambert (1935) believes the intensity of this color is dependent on the intensity of the light reaching the polyp at the time of strobilation. The prominent red portions of the animal are the tentaculocysts, the manubrium, and the tips of the bifid arms. At the time of release, the ephyra has no tentacles and propels itself with a series of rapid pulses (five or six) alternated with slight pauses equal in length of time to two or three contractions. Each pulse propels the ephyra approximately 0.75 mm.

Immediately after release from the polyp, the ephyra moved to the surface of the container and attempted to maintain its position there. Several authors (Lambert, 1935; Cargo and Schultz, 1966)

have suggested this to be a phototactic response. Slight currents induced by the introduction of a small stream of air bubbles aided the ephyra in maintaining its position in the water column.

Approximately 96 to 120 hours after release, the red regions became more prominent and the main body of the animal cleared, taking more the appearance of a miniature adult. In about two weeks, the red regions fade and assume their adult milky-white color.

All developing stages were found to ingest a wide variety of organisms. Foods shown by other authors to be acceptable for coelenterate life stages include Artemia, plankton, liquid Nereis, small nereids, Dendroboena subrubicunda (a worm), Obelia, young jellyfishes, small copepods, Clione, small Limacina, and hamburger (Delap, 1905a, 1905b; Lambert, 1935; Littleford, 1939; Spangenberg, 1965; Cargo and Schultz, 1966). During the present investigation, all stages fed actively on Artemia, enchytraeids, polychaete larva, and strained ctenophores. Lambert (1935) found the ephyrae of a British species of Chrysaora to be cannibalistic. He also found ctenophores to be the only food accepted by Chrysaora ephyrae larger than 1/3 inch.

Unpublished work by Victor Burrell of the Virginia Institute of Marine Science suggests an interesting feeding relationship between Chrysaora medusae and the summer ctenophores of the York River. Papenfuss (1934) and McNamara (1955) recognized that Chrysaora actively feed on ctenophores of the genus Mnemiopsis. This fact was supported in laboratory experiments and field observations conducted by Mr. Burrell and the present author in the early summer, 1967. Mr. Burrell's quantitative studies in the field showed Chrysaora numbers to be large in regions of ctenophore (Mnemiopsis)

shoals. In the early fall another ctenophore, Beroe, appears which also feeds on Mnemiopsis. At this time there is a rapid decline in the Mnemiopsis population and a parallel decline in the Chrysaora population. Beroe, although not feeding on Chrysaora medusa directly, can remove large numbers of the smaller Mnemiopsis and rapidly deplete a large population, thus destroying a valuable sea nettle food supply. No account of Chrysaora feeding on Beroe was found.

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