The Ecological Significance of a Ctenophore, Mnemiopsis leidyi (A. Aggasiz), in a Fish Nursery Ground

Victor G. Burrell
College of William and Mary - Virginia Institute of Marine Science

THE ECOLOGICAL SIGNIFICANCE OF A CTENOPHORE,

MNEMIOPSIS LEIDYI (A. AGASSIZ),

IN A FISH NURSERY GROUND

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 Arts

By

Victor G. Burrell, Jr.

1968

APPROVAL SHEET

This thesis is submitted in partial fulfillment of

the requirements for the degree of

Master of Arts

Author

Approved, July 1968

Willard A. Van Engel, Ph.M.

Dexter S. Haven, M.S.

Edwin B. Joseph, Ph.D.

Frank O. Perkins, Ph.D

Marvin L. Wass, Ph.D.

ACKNOWLEDGEMENTS

I am indebted to Mr. Willard A. Van Engel for guidance and encouragement throughout this study. Thanks are also due Dr. Edwin B. Joseph, Mr. Dexter S. Haven and Dr. Marvin L. Wass for suggestions and criticisms and to all of the above as well as Dr. Frank O. Perkins for reading this manuscript. Miss Evelyn C. Wells was kind enough to secure needed reference literature and to review the bibliography and to her I am grateful. Mrs. Evelyn N. White drafted Figure 1 and generously allowed the use of it in this manuscript.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

ABSTRACT

The tentaculate ctenophore, *Mnemiopsis leidyi*, occurred all months of the year in the York River estuary, Virginia. It was present only in higher salinity water (15 ^{o}/oo and above) in winter, but in less than 6 ^{o}/oo in late summer. Numbers of small plankton, such as copepods and the larvae of annelids, mollusks and barnacles, varied inversely with the volume of ctenophores present at each sampling site. Stomodaeum analyses and feeding experiments confirmed *M. leidyi* as a predator of these plankters. Other feeding experiments indicated that the ctenophore was responsible for 3/4 of the total predation by plankton forms. Plankters exceeding 6 mm in length were not preyed upon.

Most of the fish using this estuary as a nursery ground were large enough before entering infested waters to avoid predation. Young fish in the area subsisted chiefly on items not preyed on by this ctenophore.

Another ctenophore, *Beroe ovata*, preyed on the tentaculate form in the summer and fall to such an extent that the tentaculate ctenophores were restricted to areas outside the range of the beroid. The medusa *Chrysaora quinquecirrha* also preyed on the tentaculate form but did not significantly reduce its numbers.

THE ECOLOGICAL SIGNIFICANCE OF A CTENOPHORE,

<u>MNEMIOPSIS</u> <u>LEIDYI</u> (A. AGASSIZ),

IN A FISH NURSERY GROUND

INTRODUCTION

Ctenophores are members of the plankton occurring in waters ranging from mesohaline portions of estuaries to open oceans. Oceanic and coastal ctenophores are sometimes concentrated by currents into large swarms or rafts. These swarms are comparatively short-lived in neritic and oceanic waters, but often persist for months in estuaries (Fraser 1962; Cronin, Daiber and Hulbert 1962).

Ctenophores are divided into two classes, essentially by their means of feeding. Members of Class Tentaculata feed chiefly by drawing tentacles containing entangled food into the mouth, while those which lack tentacles (Class Nuda) engulf food in a large stomodaeum occupying most of the body (Hyman 1940). Tentaculate ctenophores, of which *Mnemiopsis*, *Pleurobrachia*, *Bolinopsis*, and *Mertensia* are common genera, feed on small crustaceans, chaetognaths, fish eggs, and larvae of fish, mollusks, and annelids (Bigelow 1914, 1924; Cronin et al. 1962; Grice and Hart 1962; Hardy 1958; Hyman 1940; Lebour 1922, 1923; Main 1928; Mayer 1912; Nelson 1925; Ralph and Kaberry 1950; Raymont 1962; Russell 1925). The principal genus of the Class Nuda is *Beroe*, which feeds chiefly on other ctenophores. Lebour (1923) found copepods in the stomodaeum of a beroid species, but Kamshilov, as cited by Fraser (1962), thought that these came from the stomodaeum of an ingested tentaculate form.

A drastic reduction in crustacean plankton follows the appearance of tentaculate ctenophores (Cronin et al. 1962; Nelson 1925). Laboratory studies by Williams and Baptist (1966) and Bishop (1967) indicate the predatory capabilities of Mnemiopsis leidyi. Few, if any, studies of seasonal composition of estuarine plankton have taken into account the influence of ctenophores. Indeed, more attention has been directed toward avoiding the collection of these forms (Heinle 1965). Difficulties experienced in preserving ctenophores have contributed to the reluctance of investigators to interest themselves in the group.

In August 1965, the Ichthyology and Crustaceology departments of the Virginia Institute of Marine Science embarked on a study to characterize a low-salinity fish nursery ground. The physical, chemical and biological attributes of a fish nursery ground were examined to determine what made it more suitable than adjacent areas (Joseph and Van Engel 1966). The nursery ground selected for study was the upper 10 miles of the York River and the lower 10 miles of one of its major tributaries, the Pamunkey River.

M. leidyi, present in this nursery ground at certain times of the year, is a biological influence worthy of investigation. The nursery ground project was ideally suited for the study of M. leidyi, as it provided monthly hydrographic, chemical and biological data for over a year and permitted collection and observation of living ctenophores. Pleurobrachia pileus has been reported from this area, but was not seen during this study.

Monthly plankton samples from the entire York-Pamunkey river system were counted by Mrs. Sue Davidson and Mr. Terry R. Sopher. Identifications of the coelenterates were made by Mr. Dale R. Calder, isopods and cumaceans by Mr. Daniel Gibson, amphipods by Mr. James B. Feeley, and fish eggs and larvae by Miss Sarah B. Leonard and Mr. Ronald G. Rinaldo. The remaining groups were my responsibility.

MATERIALS AND METHODS

Procedures of the Fish Nursery Ground Project

The Nursery Ground Project entailed monthly occupation of four stations in the York River and four in the Pamunkey River (Fig. 1). These stations, beginning 10 miles above the mouth of the York, were 5 miles apart, except for the two most up-river stations in the Pamunkey, which were 10 miles apart. Three other stations occasionally occupied were Y00, at the mouth of the York; C10, 10 miles seaward from the mouth of the York; and C00, in the entrance to Chesapeake Bay.

The location of each station was as follows:

Code	Latitude and Longitude	
C00	37 04' N 76 05' W	Mouth of Chesapeake Bay
C10	37 10' N 76 14' W	York River entrance channel
Y00	37 15' N 76 23' W	Mouth of York River
Y10	37 19' N 76 36' W	York River, Pages Rock
Y15	37 23' N 76 39' W	York River, Capahosic
Y20	37 26' N 76 42' W	York River, Poropotank
Y25	37 29' N 76 45' W	York River, Bell Rock
P30	37 33' N 76 50' W	Pamunkey River, Eltham Marsh
P35	37 33' N 76 52' W	Pamunkey River, Lee Marsh
P40	37 33' N 76 53' W	Pamunkey River, White Oak
P50	37 35' N 76 59' W	Pamunkey River, Lester Manor

Temperature, salinity and dissolved oxygen were measured at the surface and 1 meter above the bottom at each station. Light attenuation was measured with a Secchi disc. Plankton tows were made at

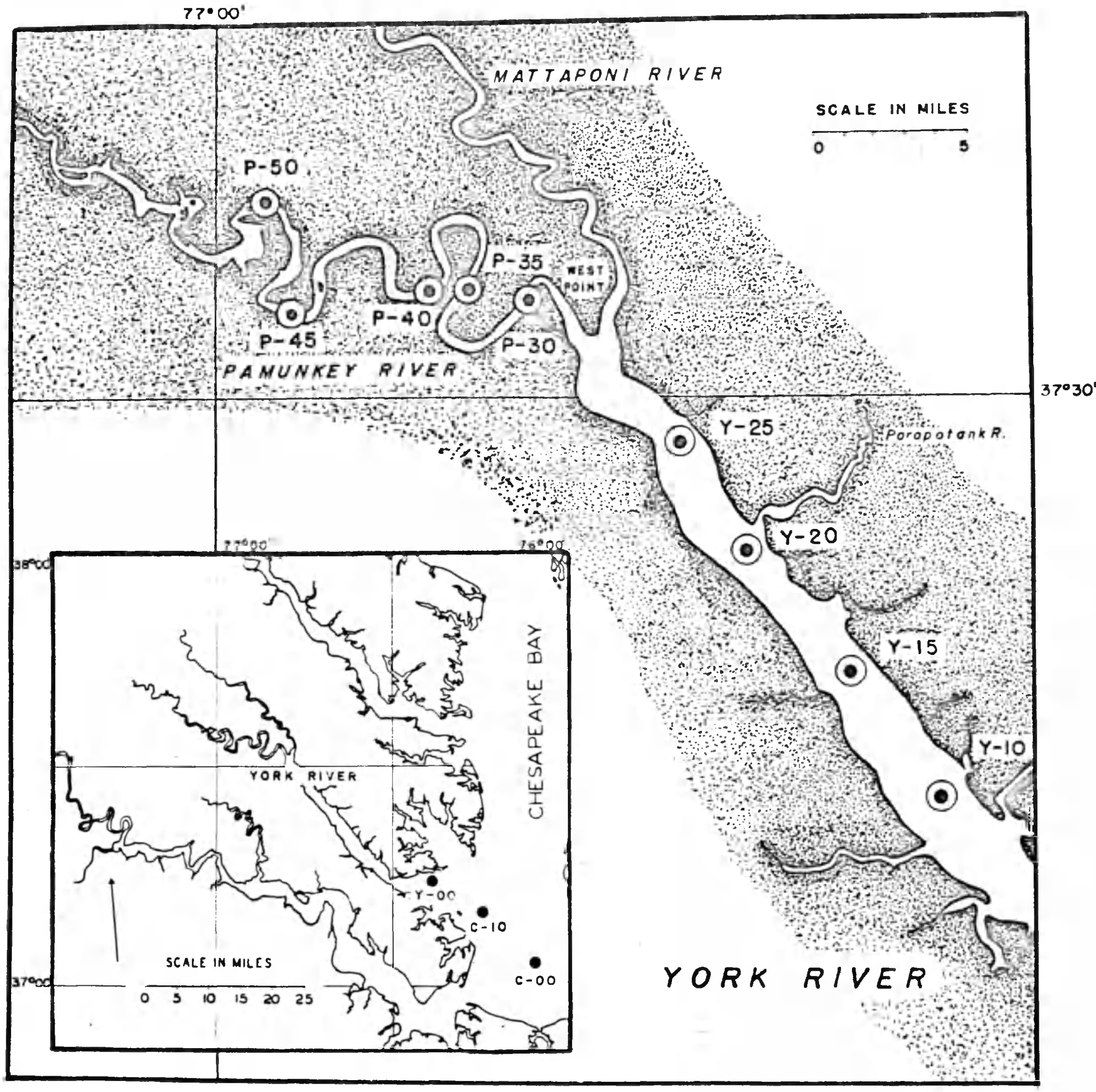

Figure 1. Chart of the area showing stations.

1 meter above the bottom at each station, using a meter net with a 0.75 mm mesh. These tows were of 5 minutes duration. Fish and large invertebrates were sampled with a 30-foot semi-balloon trawl towed for 15 minutes at York River stations and 7.5 minutes at Pamunkey River stations. See Joseph and Van Engel (1966) for details.

The meter net samples were split into smaller subsamples by means of a Folsom splitter (McEwen, Johnson and Folsom 1954). The number of splits varied with the number of fish larvae and the number of copepods. One large aliquot, from 1/8 to the whole sample was examined for fish larvae. Another, usually smaller, subsample was used to estimate the abundance of all species of zooplankters; it was considered adequate for the purpose of estimation if it contained between 200 and 300 copepods, and varied from 1/2000 to the entire sample.

Procedures Providing Supplementary Data

Volume was used as a measure of abundance of M. leidyi. Counting was not feasible due to the fragile nature of ctenophores which resulted in many disintegrated individuals in the samples. Volumes were recorded as less than 0.5 liters, 0.5, 1, 4, 8 and more than 8 liters. Since larger volumes resulted in net clogging and packing of ctenophores, measurement of volumes over 1 liter to an accuracy greater than that stated was not justified.

Ctenophore volume in samples collected prior to June 1966 was extracted from estimates given in cruise log books. When no estimate was logged, plankton samples were re-examined: whenever ctenophores were found these were assigned a volume of less than 0.5 liters. This volume was given because a larger volume would have been noted on the cruise log books. After June 1966, the volume of ctenophores in each meter-net haul was measured in a graduated plastic bucket. Then 25 ctenophores, selected at random, were examined under a dissecting microscope fitted with an ocular micrometer. Total length, from apical end to tips of the oral lobes, was measured and stomach contents were noted. The trawl net was used to monitor the occurrence of large forms such as the nudate ctenophore, Beroe ovata, and the coelenterate, Chrysaora quinquecirrha and, on occasion, M. leidyi when plankton samples were not taken with the meter net. Another Ichthyology department program[1], occupying the same stations on a monthly basis, permitted this sampling to continue through May 1967, after the field phase of the Nursery Ground Project ended in December 1966.

An extra bottom plankton net tow provided a means of estimating total predation by plankton as compared with predation by M. leidyi. This tow was made if the first plankton sample contained appreciable numbers of chaetognaths, coelenterate medusae, or larval or juvenile fish. The second sample was split into three equal volumes at once and treated as follows: one part, containing all organisms alive, was diluted to 4 liters and allowed to stand for 24 hours before being preserved with 5% formalin buffered with an excess of sodium carbonate; another subsample, with M. leidyi removed, but all other plankton alive, was diluted to 4 liters and allowed to stand for 24 hours before being preserved; the third, containing all organisms, was preserved at once. The plankters in each aliquot were identified and counted later in the laboratory. The numbers in the first aliquot (all plankters were maintained alive for 24 hours) subtracted from the numbers in the third aliquot gave an estimate of total predation by zooplankton. The numbers in the

[1]Contract Number 14-16-008-801. "Estimation of Parameters of Striped Bass Populations and Description of the Fishery of Lower Chesapeake Bay." Bureau of Sport Fisheries and Wildlife.

first aliquot subtracted from the numbers in the second aliquot (all plankton, except M. leidyi, maintained alive for 24 hours) gave an estimate of predation due to M. leidyi.

The occurrence of M. leidyi, B. ovata and C. quinquecirrha was monitored from the pier at the Virginia Institute of Marine Science at Gloucester Point, Virginia, a point on the York River 6 miles above the mouth. Vertical plankton tows with a nylon net, 0.75 mm mesh aperture and 0.5 meter mouth diameter, provided specimens for total length measurements and stomach analyses. Relative abundance of M. leidyi was estimated volumetrically and abundance of B. ovata by counting those present along one side of the pier. The proximity of this station permitted sampling on an average of 20 days per month and, on occasion, several samplings in a single day.

Feeding experiments were conducted in the laboratory to examine the ecological role of M. leidyi as prey and as predator. In the first set of experiments, the tentaculate ctenophore was fed the same species of zooplankters which appeared in the digestive cavity of field-collected animals or which showed a decrease in those samples taken when the ctenophore was found. If feeding occurred, this indicated that zooplankton found in the digestive apparatus were prey and not ingested accidentally after being confined in the net and that the ctenophore was responsible for a decrease in zooplankters in areas of mutual occurrence. A known number of food organisms was placed in a 1.5 liter finger bowl with a single ctenophore. Stomach contents recorded at regular intervals during the experiments gave information on feeding patterns. Food organisms remaining after 24 hours were counted and subtracted from initial numbers to calculate numbers captured. Experiments were repeated using various sizes of ctenophores.

In the second series of experiments, five M. leidyi were placed in a 15 liter aquarium containing either one specimen of B. ovata or one specimen of C. quinquecirrha. Ctenophores were ranked, from 1st to 5th, according to the sequence in which they were captured. The time lapse from the introduction of the five tentaculate ctenophores to each individual's capture, hereinafter referred to as accumulated capture time, was recorded in order to determine the feeding rate of each predator. Experiments were repeated using different size prey and predators. The geometric mean of accumulated capture time for each rank of ctenophore was used instead of the arithmetic mean since it is less affected by extreme values. The purpose of these tests was to determine the relative ability of individuals of these two species to capture M. leidyi.

In all feeding studies water in the aquaria was at the ambient salinity (19-20 ^{o}/oo) and temperature (19-26 C) of the laboratory's salt water system. An aquarium containing a like number of food organisms, but no predator, served as control for each experiment.

RESULTS AND DISCUSSION

Distribution of *Mnemiopsis leidyi*

The segment of the York-Pamunkey system occupied by *M. leidyi* varied in length from 50 miles in June to 10 miles or less in late winter and again in mid-summer. This ctenophore was present at some stations in the fish nursery ground, designated as the area lying between Y20 and P40, at all times of the year except in the winter and early spring (Fig. 2). Figure 2 also depicts this zone along with the occurrence of *B. ovata*. In the period July to December 1966, the beroid species completely displaced the tentaculate ctenophore at all river stations at which the beroid form occurred; however, *M. leidyi* did appear briefly on several occasions at the Virginia Institute of Marine Science during this time (Fig. 3).

Size of *M. leidyi* varied spatially more than temporally, with the smallest animals occupying the less saline portion of the river (Fig. 4). This suggests that major spawning of *M. leidyi* occurred up river and further indicated that the prey would be smallest at the further-most point of penetration of the estuary by the ctenophore.

Largest volumes of *M. leidyi* were obtained in June 1966 when meter net samples from C00 to Y25 yielded more than 8 liters of ctenophores per 5 minute tow. Vertical tows at the Institute pier also contained the largest volumes of the year during this period (Fig. 3).

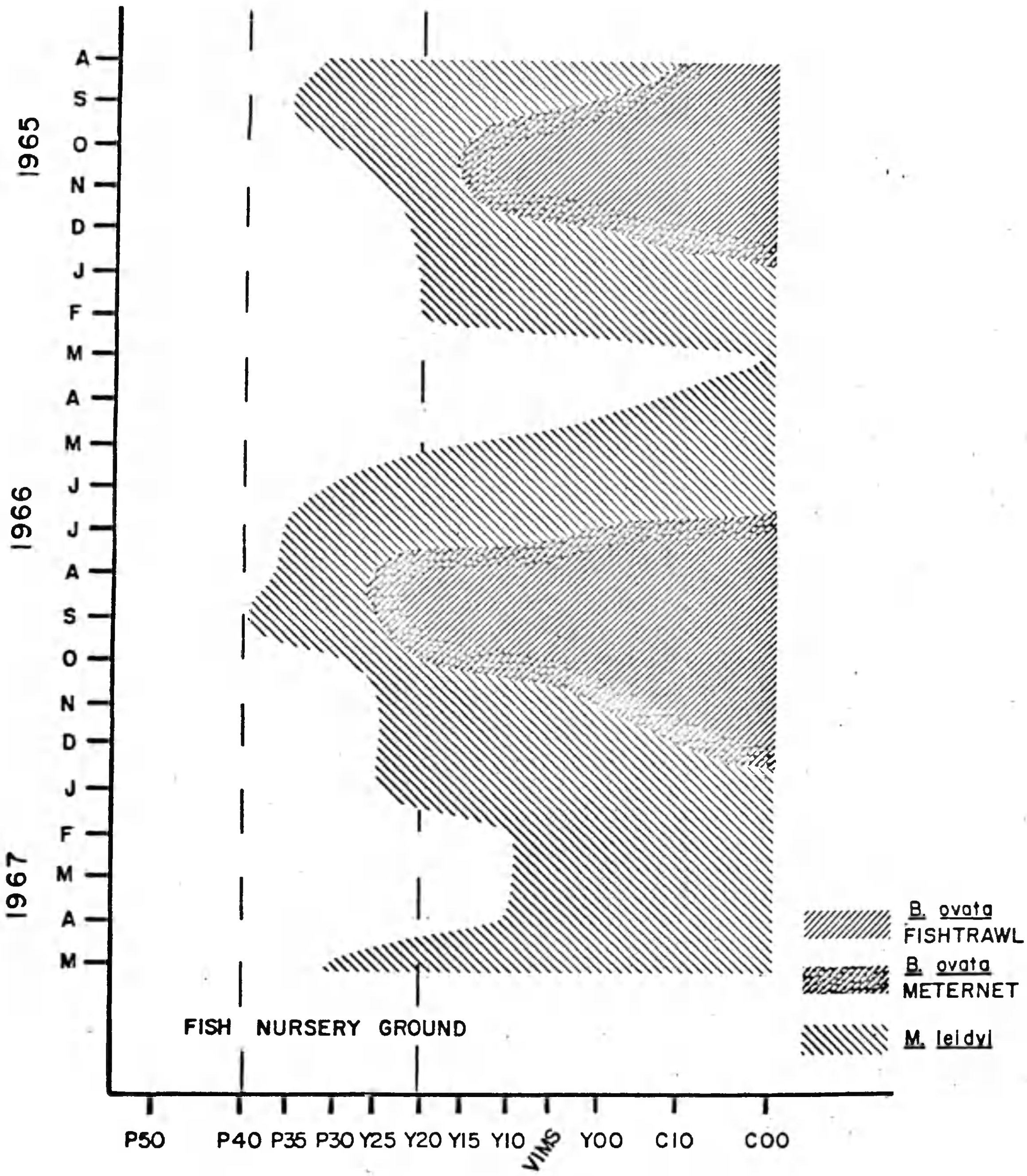

Figure 2. Distribution of M. leidyi and B. ovata from August 1965 to May 1967.

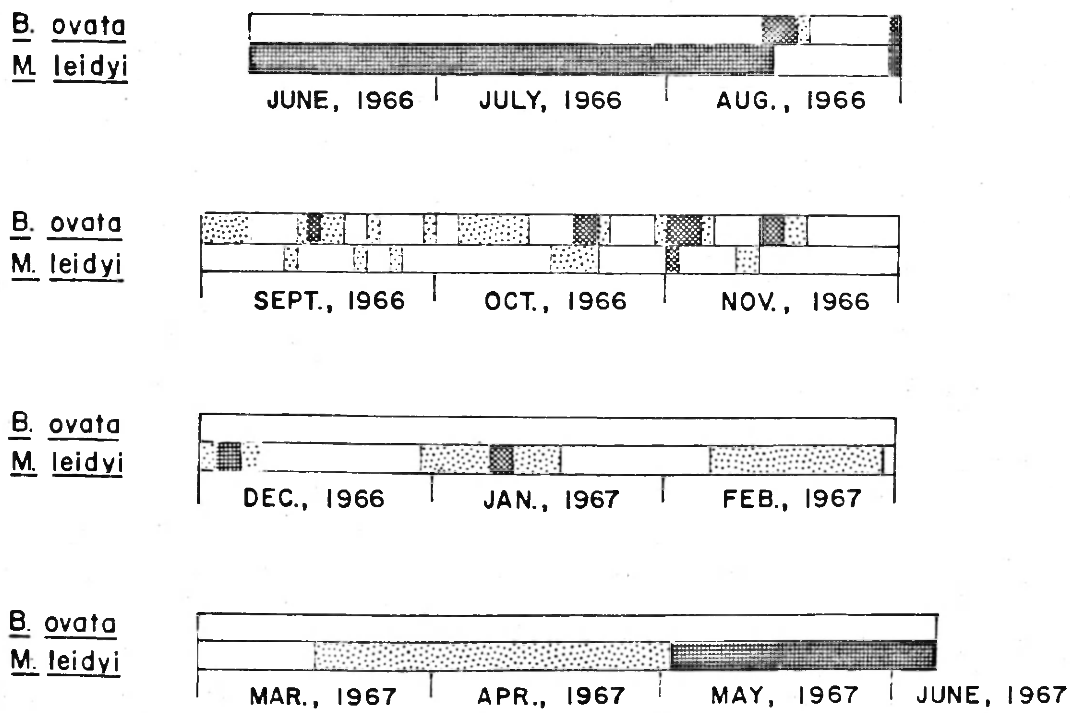

Figure 3. The distribution of *M. leidyi* and *B. ovata* at the Virginia Institute of Marine Science pier from 6 June 1966 to 6 June 1967. For *B. ovata*, dark stippling depicts more than ten animals observed on the left side in one traverse from foot to head (approximately 250 feet); for *M. leidyi*, dark stippling indicates more than 1 ml per liter in a vertical haul with the half meter net. For *B. ovata*, light stippling indicates less than ten animals per traverse and, *M. leidyi*, less than 1 ml per haul. Clear spaces indicate neither ctenophore was present.

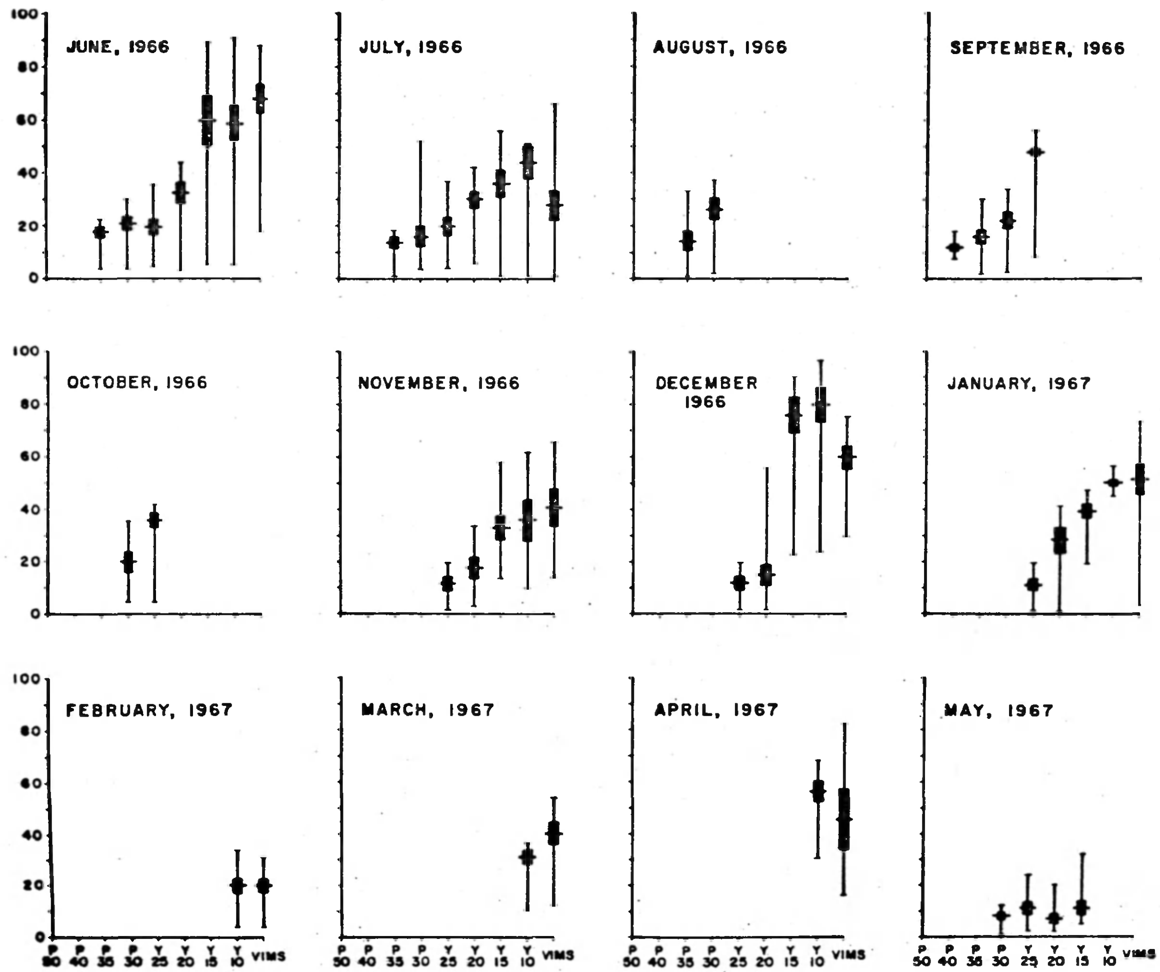

Figure 4. Distribution of M. leidyi by length range, mean length, and $S_{\bar{x}}t_{.05}$.

Factors Controlling the Distribution of *M. leidyi*

Salinity and temperatures

Reduced salinity apparently limited penetration upriver. The lowest salinity at which *M. leidyi* occurred was 5.64 ^{o}/oo at P40 in September 1966 (Appendix Table XIV). No evidence was obtained to indicate that the highest salinity of the York River excluded the ctenophore. The highest salinity was 27.51 ^{o}/oo in March 1966. While the ctenophore was not found at higher salinities in this survey, it is known to frequent coastal marine waters and I have found it in salinities above 32 ^{o}/oo in Wachapreague Inlet, Virginia.

Temperature *per se* was not limiting. The animal was present at Y25 in January 1966 when the water temperature was 1.28 C and at P35 in July when the water temperature reached 28.8 C. These two extremes approximate the maximum range for the York-Pamunkey river system; however, in colder months the ctenophore was present only in higher salinities (Fig. 5). The interaction of temperature and salinity affects the distribution of many estuarine species (Gunter 1957, Pearse and Gunter 1957).

Dissolved Oxygen

Minimum dissolved oxygen, 3.5 mg per liter, occurred at P30 in August 1966 (Appendix Table XIII). The tentaculate ctenophore was present at this station and was in no distress, so it is unlikely that it was limited by low levels of dissolved oxygen in the York River system.

Food

There was no evidence that food limited the distribution of this ctenophore in the York River in 1966. While zooplankton numbers were

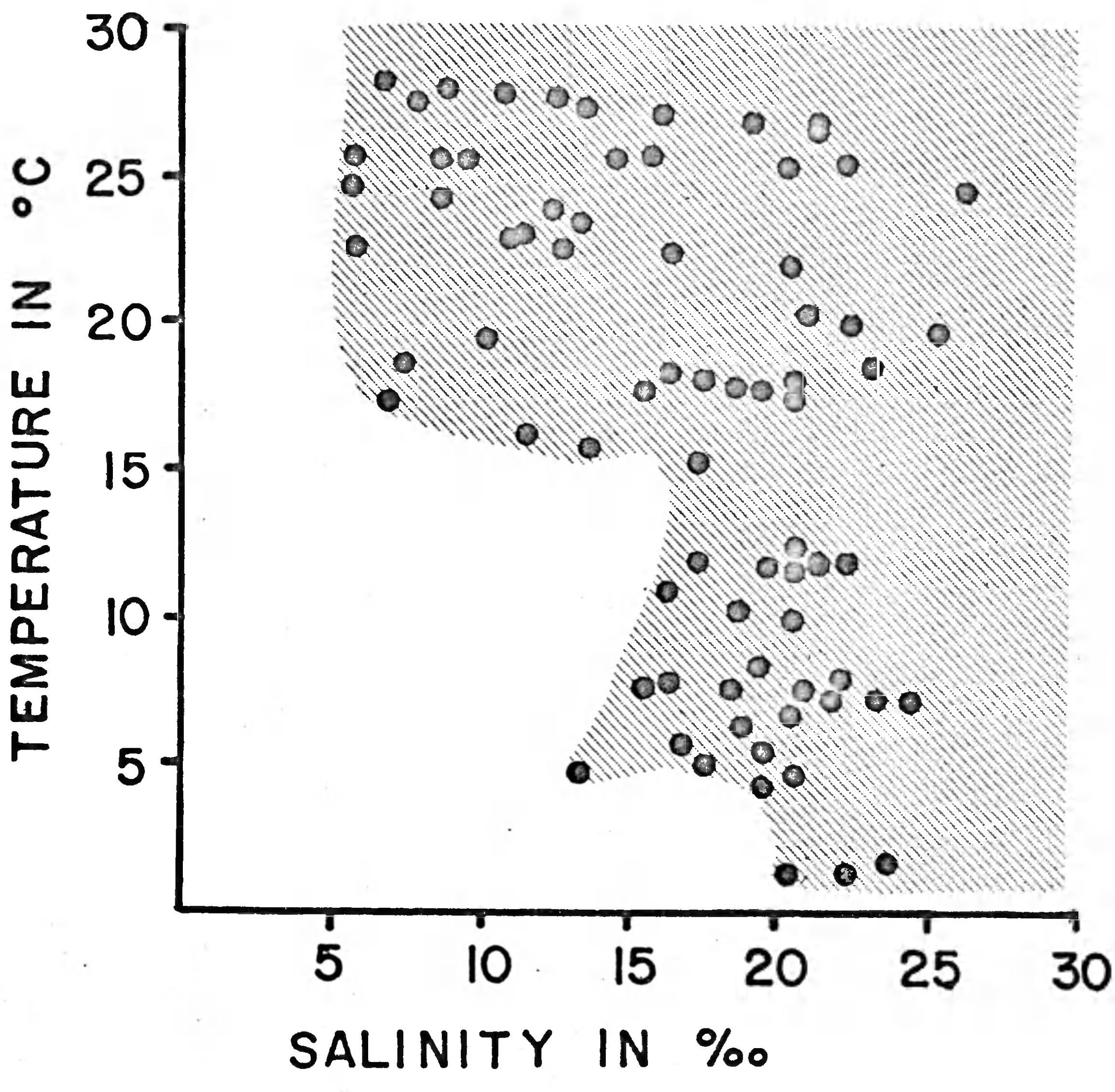

Figure 5. Occurrence of M. leidyi from June 1966 to June 1967 at Chesapeake Bay, York River and Pamunkey River stations according to temperature and salinity. Dark circles are observations and the shadow area indicates salinity and temperature compatible to the ctenophore.

minimal in samples from ctenophore infested areas, volumes of *M. leidyi* in subsequent monthly samples did not reflect a shortage of this food source (Appendix Tables XI, XVI). Volume of ctenophores actually increased in June and November 1966, at stations having very few zooplankters the preceding months. Nelson (1925) postulated that *M. leidyi* may be able to utilize detritus and nannoplankton when zooplankton is scarce.

Predators

M. leidyi has few known predators. Two, *C. quinquecirrha* and *B. ovata*, are found in local waters. *C. quinquecirrha* has been reported to prey on tentaculate ctenophores by Lebour (1922) and Mayer (1910). *Beroe* sp. feeds chiefly on other ctenophores, especially the Tentaculata (Bigelow 1924; Hyman 1940; Lebour 1923; Mayer 1912; Nelson 1925).

Feeding experiments showed that *C. quinquecirrha* captured large numbers of *M. leidyi* in a relatively short time (Table 1, Fig. 6). In 1966 the medusa occurred from June to September (Fig. 7) and usually with *M. leidyi* (Appendix). This medusa occurred when the ctenophore was most abundant, but its presence did not noticeably alter the distribution of the ctenophore. Recruitment of the ctenophore apparently equals or exceeds predation. Conversely, *M. leidyi* may be a limiting factor in the abundance of *C. quinquecirrha* in that the ctenophore is a food source for the stinging nettle. *C. quinquecirrha* was not as abundant in the York River in the late summer of 1966 as in other years. *B. ovata* moved into the estuary in late June or early July, earlier than reported for previous years (Wass 1965), and this resulted in an earlier curtailment of *M. leidyi*. Lambert (1935) reported that a species of *Chrysaora* must feed on ctenophores or coelenterates in order to develop the bell.

Table 1. Speed of capture of *M. leidyi* by *C. quinquecirrha*. Five ctenophores were offered to each medusa. Speed of capture is accumulated time in minutes from the start of the experiment to the instant the ranked individual was captured.

Length range of *M. leidyi* in mm	Diameter of *C. quinquecirrha* in mm	Accumulated capture time, in minutes, for each ranked individual				
		1st	2nd	3rd	4th	5th
Range 14 - 17	40	6	10	10	12	14
	80	2	6	8	9	11
	100	7	12	12	13	18
Range 23 - 25	45	1	1	7	8	16
	75	3	4	6	6	9
	103	1	1	2	4	6
Range 33 - 38	47	31	65	80	180	240
	80	6	60	75	80	120
	100	4	7	15	21	44
	115	3	4	8	30	66

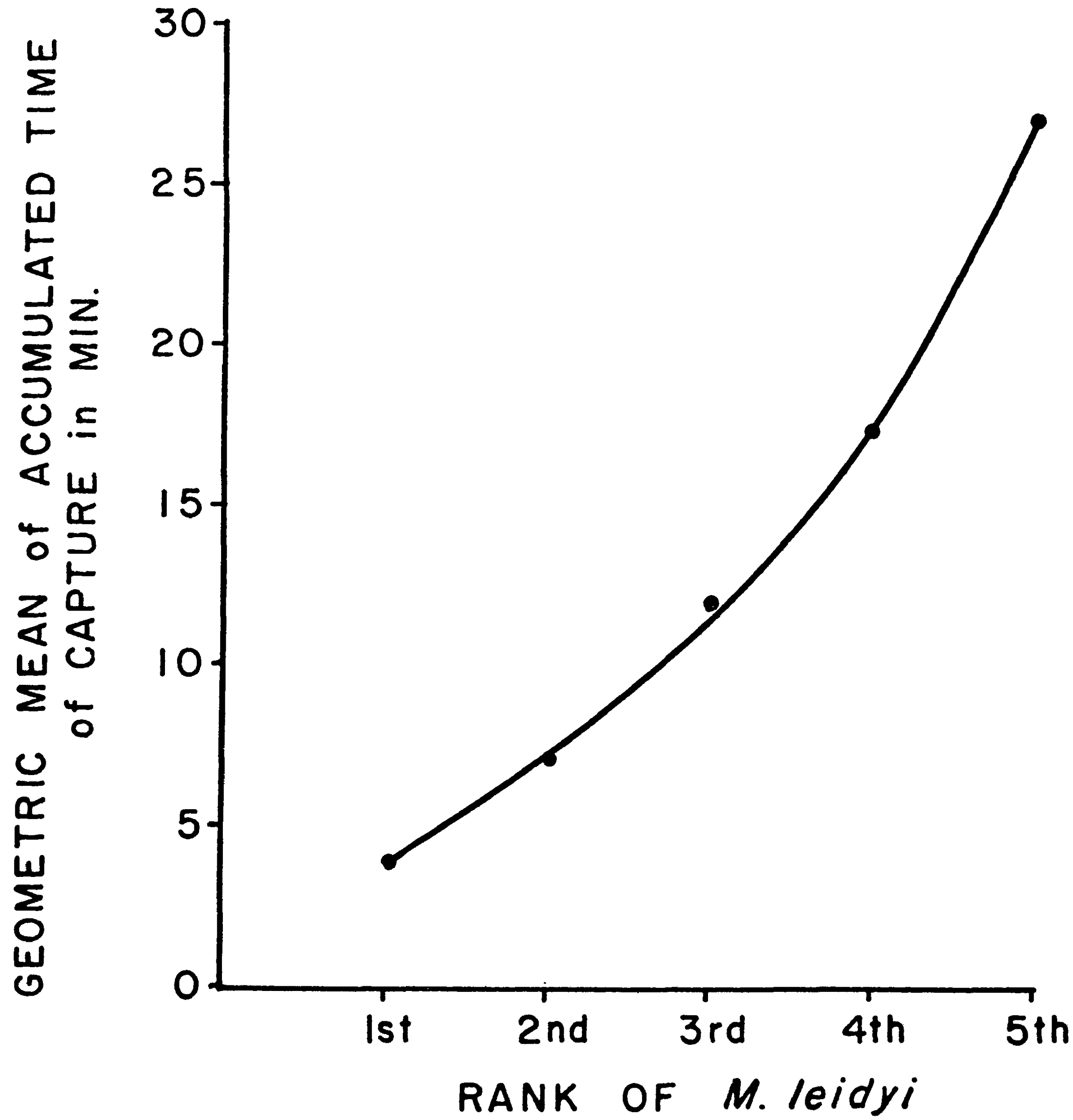

Figure 6. The time required for Chrysaora quinquecirrha to capture 5 Mnemiopsis leidyi, expressed as the mean of 10 experiments.

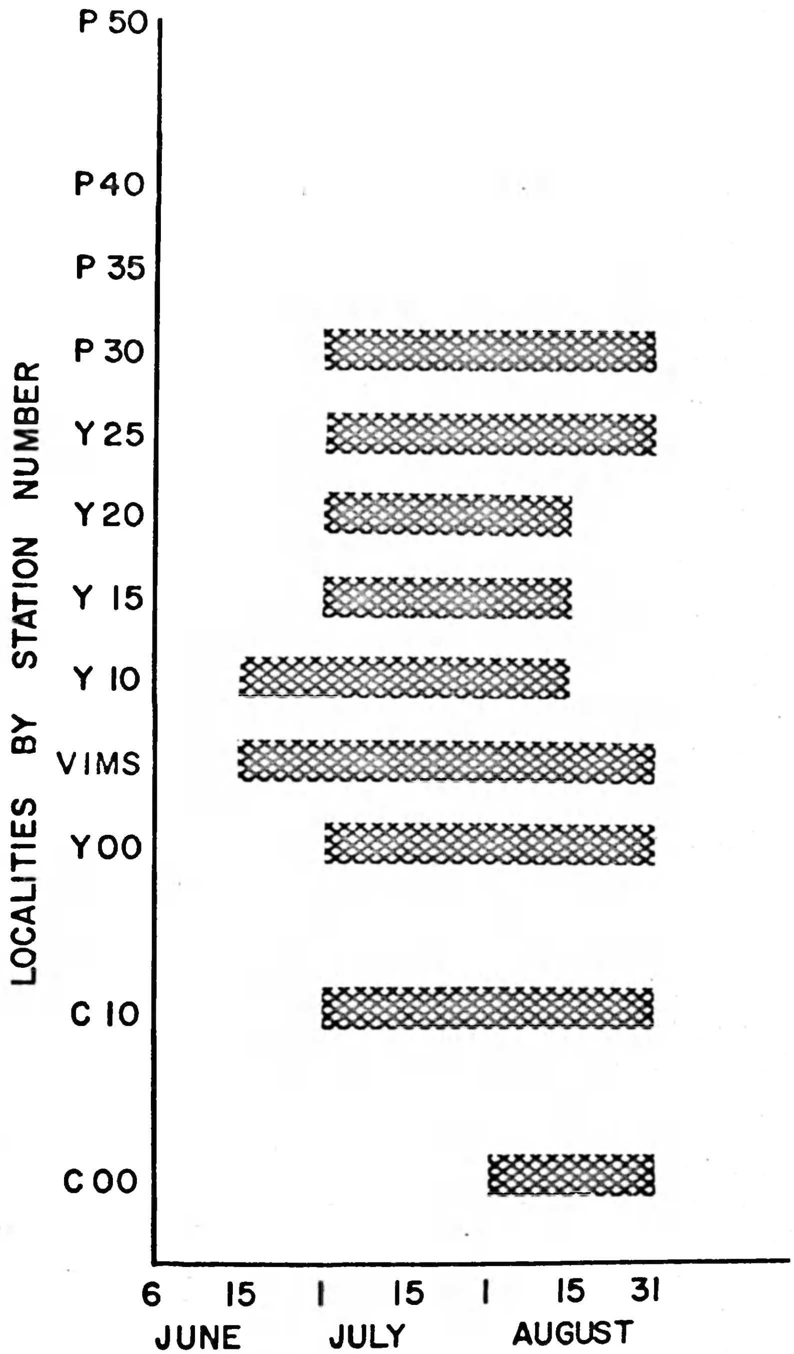

Figure 7.
DISTRIBUTION OF *Chrysaora quinquecirrha* IN 1966
Cross hatching indicates medusae present.

B. ovata appeared at Station C00 in Chesapeake Bay in late June or early July 1966, and moved up the estuary until it reached Y25 in August (Fig. 2). As *B. ovata* moved into an area, *M. leidyi* disappeared, often within hours. Daily sampling at the Institute pier revealed that *B. ovata* ate *M. leidyi*: stomodaea of 101 out of 700 a-tentaculate forms contained specimens of *M. leidyi*. No other food items were detected in the beroid ctenophores. Seven *M. leidyi* ingested by one *Beroe* was the maximum number observed. Observations from the pier revealed that when *M. leidyi* was present, *B. ovata* would orient its mouth first in one direction and then another as if seeking its prey. If *M. leidyi* was not present, *B. ovata* drifted with the tide, usually with the oral end directed down current.

The distribution of the two ctenophores indicated the effectiveness of B. ovata in controlling *M. leidyi* (Fig. 2). As *B. ovata* superseded *M. leidyi*, plankton counts rose sharply (Appendix Tables XIII and XIV). A similar relationship was found in coastal waters of Northern Europe where, in years of *Beroe cucumis* abundance, *Pleurobrachia pileus* was curtailed and crustacean plankton was more abundant (Kamshilov, in Fraser 1962).

Largest numbers of *Beroe* occurred at the pier when *Mnemiopsis* was present (Fig. 3). A similar situation seemed to exist in the river. Evidence for this was the presence of *Beroe* in meter net samples just below stations with *M. leidyi* present (Fig. 2), whereas at stations downstream further removed from concentrations of the tentaculate ctenophore, the beroid was scarce, occurring in fish trawl catches but not in meter net samples. The zone of overlap of the two species did not coincide with any river stations; however, this zone was observed on several occasions and many more *Beroe* were observed on the surface there than at any other point in the river.

In the feeding experiments *B. ovata* captured *M. leidyi* initially at a rate equal to that of *C. quinquecirrha* (Table 2, Fig. 8). In a majority of cases, the beroid stopped feeding before capturing all of the tentaculate forms offered and would not resume feeding even after all traces of food were gone from the stomodaeum. Only beroids brought immediately from the river were used in the feeding test as those kept in aquaria for only a day often would not feed at all. *Chrysaora*, however, actively approached *Mnemiopsis* at any time both animals were in the same aquarium. The difference in behavior of the two predators may result from the ability of *Chrysaora* and the inability of *Beroe* to adjust to confinement and therefore not reflect the situation in the river.

Effect of *Mnemiopsis* on Crustacean Plankton

Total numbers of zooplankton in the York-Pamunkey river system were found to be inversely proportional to volumes of ctenophores (Fig. 9). The possibility that the stations low in plankton numbers are normally so is unlikely. The major constituents of the crustacean plankton were the mysid, *Neomysis americana*, and the copepods, *Acartia tonsa*, *A. clausii*, *Centropages hamatus*, *Labidocera aestiva*, and *Pseudodiaptomus coronatus*. These species are euryhaline and would normally occupy stations where *Mnemiopsis* was present (Jeffries 1965; Tattersall 1951; Wass 1965; Wilson 1932). When *M. leidyi* was not present the numbers of plankton were comparable to those at other stations. Numbers in samples from Y25 through Y10 immediately rose when *Beroe* supplanted *Mnemiopsis* in August and September 1966.

In two instances at P30 and P35 in August 1966 total zooplankton

Table 2. Speed of capture of M. leidyi by B. ovata. Five ctenophores were offered each beroid ctenophore. Speed of capture is accumulated time in minutes from the start of the experiment to the instant the ranked individual was captured. *No further captures for the duration of the experiment (24 hours).

Length range of M. leidyi in mm	Length of B. ovata in mm	Accumulated capture time, in minutes, for each ranked individual				
		1st	2nd	3rd	4th	5th
Range 13 - 15	16	4	16	45	105*	
	30	3	31	75	116	132
	66	7	20	31*		
	80	5	11	37	40*	
	105	4	7	10	11*	
Range 18 - 21	20	2*				
	30	5	8	180*		
	58	3	7	8	10	20
	78	7	9	11	29	38
	100	2	6	10	15	30
Range 30 - 40	40	3	41*			
	62	6	14*			
	77	4	10	15*		
	96	2	8	12	38*	

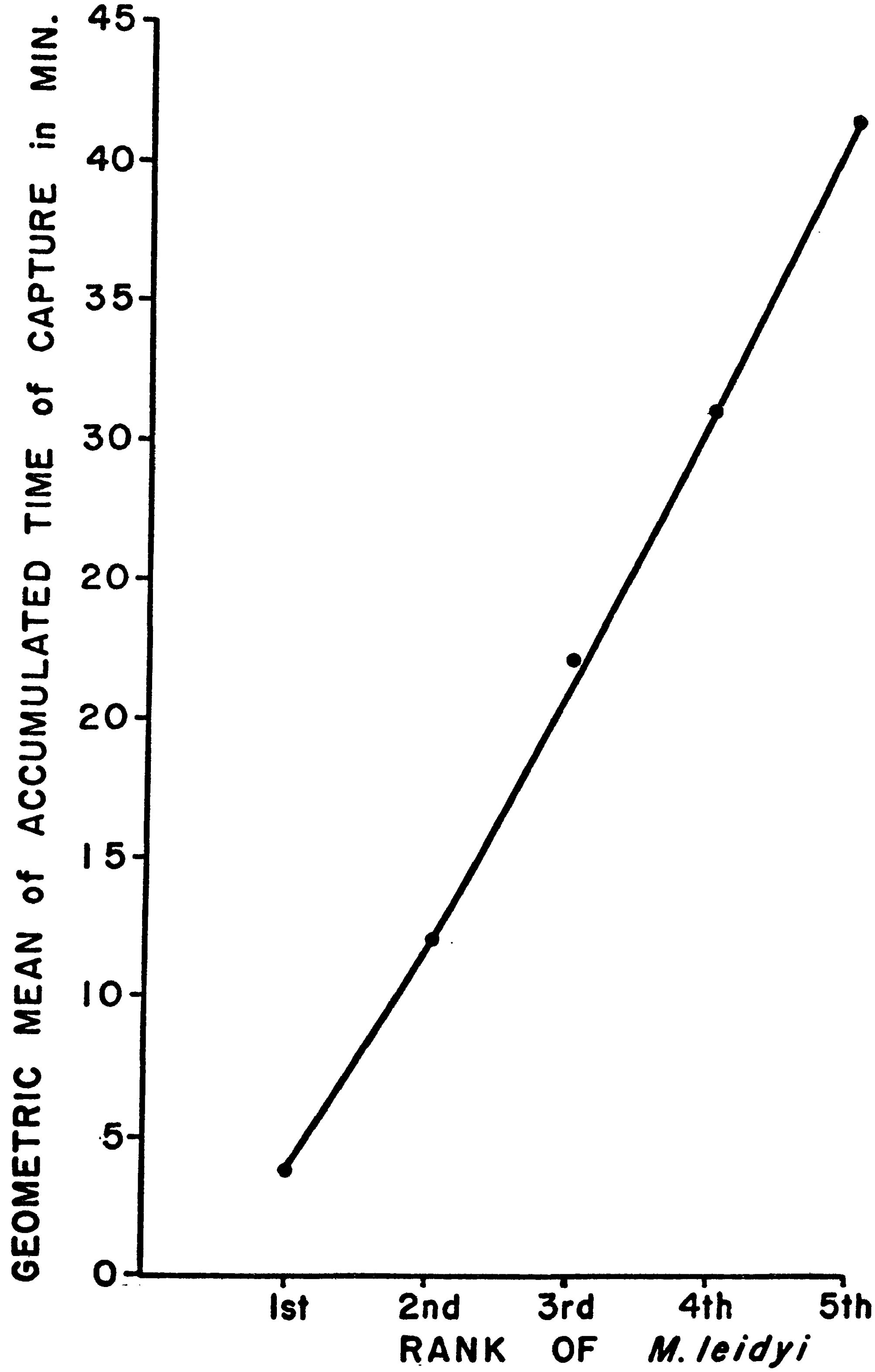

Figure 8. The time for Beroe ovata to capture 5 M. leidyi, expressed as the mean of 14 experiments.

abundance increased in the presence of the ctenophore. This apparent discrepancy may be reconciled by an analysis of the zooplankton at these stations. The organism occurring in greatest number in the samples was Neomysis americana, whose mean length of 10 mm exceeded the upper size limit of food selected by Mnemiopsis (Table 3, Appendix Table XII).

Animals found in captured Mnemiopsis are listed in Table 4. The list corresponds very closely to that of plankters that decreased in numbers at stations where ctenophores were present (Appendix Tables I through XVII). Copepods, the most numerous zooplankters in the York-Pamunkey system, were most often observed in the digestive cavity of the tentaculate ctenophore; however, bivalve larvae, barnacle nauplii, and annelid larvae were present in many more instances than would be expected by their relative abundance as indicated from plankton tows (Appendix Tables I through XVII). Mysids, also abundant plankters of the York system, were observed in large numbers of ctenophores; however, only smaller individuals appeared vulnerable to capture by this predator, as the largest observed in a stomodaeum was only 5.7 mm long. Size therefore appears to be a major factor in determining prey of M. leidyi, with smallest zooplankters most vulnerable to capture. Zoeae of a xanthid crab, Rhithropanopeus harrisii, were present in large numbers coincident with M. leidyi in the summer of 1966 (Appendix Tables XII, XIII, and XIV), but did not appear to be preyed on by this ctenophore even though they were among the smallest (0.7 mm mean length) planktonic animals. The long rostral spines of the zoea may have served to discourage this predator.

Gammarid amphipod numbers were much larger at up river stations than from areas of ctenophore concentrations. Those gammarid species

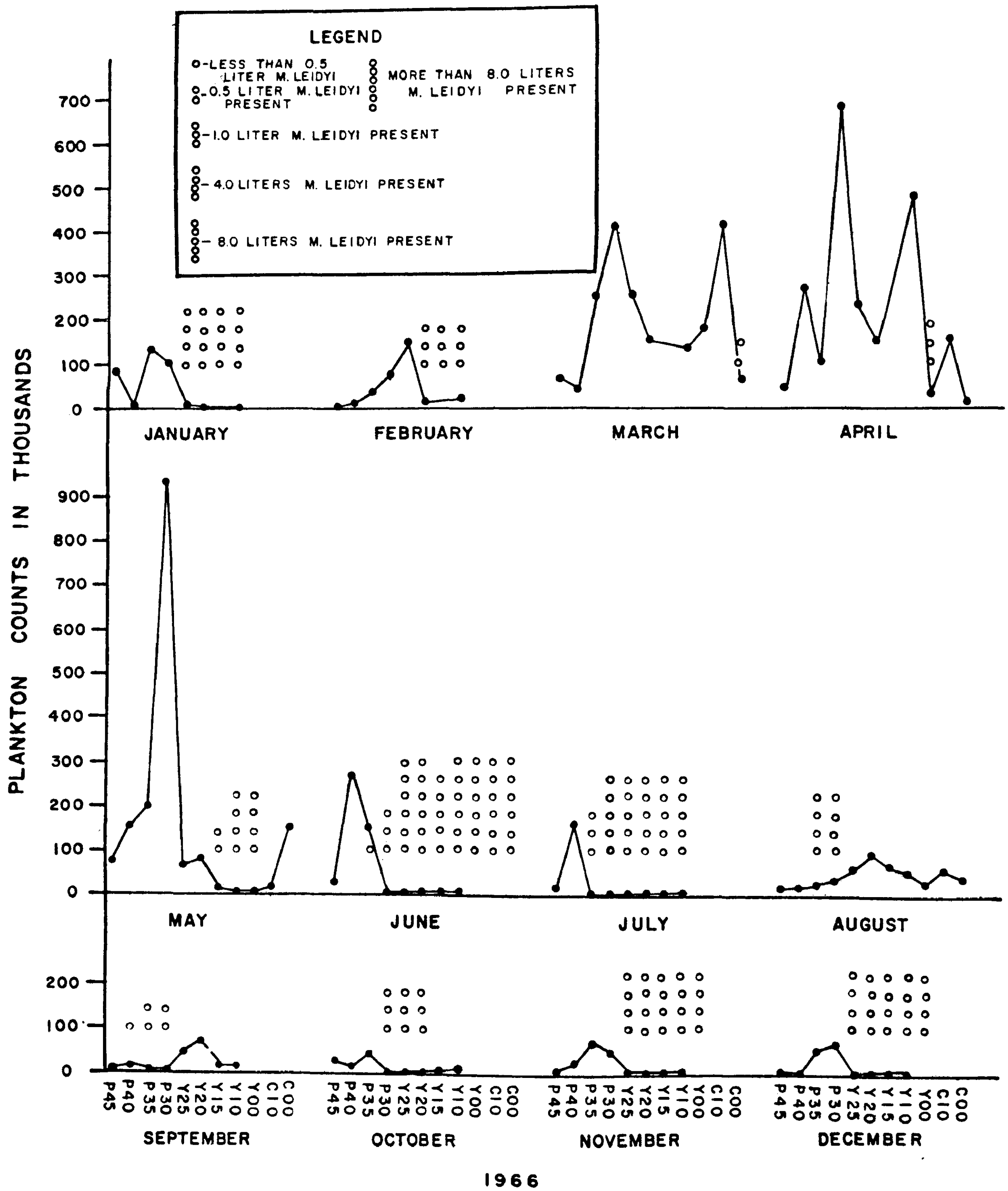

Figure 9. Zooplankton counts as compared with volume of M. leidyi present. Plankton counts presented as line graphs and ctenophore volumes depicted by open dots are plotted from totals per 5 minute meter net tow at two and one half knots. These values multiplied by 0.0033 would be reduced to numbers and volumes per cubic meter.

Table 3. Capture of zooplankters by *M. leidyi*

Prey	Mean length in mm	No. at start of test	1-3	4-8	9-14	15-20	21-30	31-40	41-50
			Size of *M. leidyi* in mm — Percent consumed						
Crassostrea virginica larvae	0.2	1000	16	97	84	82	84	91	99
Acartia tonsa copepodids	0.2	150	22	91	90	83	75	99	94
Artemia salina nauplii	0.4	150	20	89	87	67	74	91	86
Penilia avirostris	0.7	150	- *	60	100	93	99	91	96
Rhithropanopeus harrisii zoeae	0.7	150	0	0	0	0	0	0	0
Balanus nauplii	0.8	150	0	0	24	97	92	97	97
Acartia clausii	1.1	150	-	46	81	90	90	91	93
Eurytemora affinis	1.2	150	-	84	76	75	89	87	91
Acartia tonsa	1.3	150	2	52	75	99	99	96	94
Polydora ligni	1.3	100	0	20	80	90	82	87	72
Cymadusa compta	1.4	50	-	-	10	12	14	16	14
Pseudodiaptomus coronatus	1.4	100	6	80	96	82	86	91	78
Centropages hamatus	1.6	150	0	3	27	41	93	86	95
Roccus saxatilis larvae	3.0	10	-	-	0	0	70	100	90
Gobiesox strumosus larvae	3.0	25	-	-	0	16	20	92	88
Neomysis americana	3.4	150	-	45	46	84	84	89	91
Menidia sp.	5.6	25	-	-	-	0	4	28	32+
Neomysis americana	5.9	150	-	-	-	0	0	0	3#
Sagitta tenuis	8.0	20	0	0	0	0	0	0	0

* Dash (-) indicates that no test was made
\+ The largest *Menidia* larva captured was 6.0 mm
\# The largest mysid captured was 6.2 mm

Table 4. Food items found in *M. leidyi* stomodaea.

M. leidyi examined 3300

Stomodaeum empty 806

Items present	Number of occurrences	Longest measurement in mm
Copepods	2101	2.3
Barnacle nauplii	414	0.8
Mysids	412	5.7
Annelid larvae	338	1.45
Bivalve larvae	316	0.15
Cladocerans	60	0.9
Fish eggs	36	1.0
Cumaceans	26	1.6
Amphipods	23	3.0
Caridean larvae	16	2.1
Fish larvae	16	5.2
Decapod zoeae	11	0.6

prevalent in the river channel were not found in the stomodaea of ctenophores and it must be assumed that *M. leidyi* did not prey on them. Size of the channel forms probably was too great for the ctenophore to ingest, as a small-sized species, *Cymadusa compta*, found over *Zostera* beds in shallow water, was observed in ctenophore stomodaea. Increased light penetration down river, coincident with salinities suitable to ctenophores, may have caused the gammarids to remain more closely associated with the bottom, thereby reducing their vulnerability to capture by the meter net and thus explain the apparent reduction in numbers in samples from ctenophore occupied waters.

The present feeding studies revealed that relatively active plankters, such as fish larvae, copepods, and small mysids are vulnerable to *M. leidyi* (Table 3), whereas Main (1928) concluded from studies of the feeding mechanism of *Mnemiopsis* that it is capable of capturing only small weak swimmers such as polychaete and bivalve larvae. An explanation for the different observations probably lies in the size of vessels used in the two studies. Main used a watch crystal [sic], presumably rather confining, while a 1.5 liter finger bowl which allowed the ctenophore to move about more freely was used in this study. *M. leidyi* was observed to use two distinct methods of capturing and ingesting food. If the concentration of prey was relatively dense, it was entangled in mucus and the resulting bolus pushed into the stomodaeum by contraction of the oral lobes. Often part of the food ball would not be taken into the digestive cavity, or, in some instances, would be ejected after being taken in. Sometimes the ctenophore would retrieve an ejected food ball and reingest it. This was also observed by Williams and Baptist (1966). The second mode of feeding occurred when prey were small and less abundant. Individual animals were caught in the tentacles and passed into the mouth via the labial ridge and trough as described by Main (1928).

These studies confirmed that M. leidyi would feed on all of the organisms found in its stomodaeum in field collections. Percentage capture increased with a decrease in size of food items. Percent capture of smaller forms such as copepods, cladocerans, barnacle nauplii, and oyster larvae did not increase in ctenophores above 9 mm mean length. Larger prey were captured by larger ctenophores up to a maximum of 6.2 mm length in mysids and 6.0 mm length in silversides. The mysids and fish larvae taken in aquaria were slightly larger than observed captured in the field due probably to restrictions imposed on them by confinement in the tanks.

Predation on Fish Larvae

Larval fish were incidental items in the diet of M. leidyi in the York River in 1966 as only 16 fish were seen in the stomodaea. In feeding experiments Mnemiopsis consumed larvae of Roccus saxatilis, Gobiosoma bosci and Menidia sp., but only if they were smaller than 6.0 mm. Thus in areas of large concentrations of this ctenophore, it appears that size of the fish larvae would determine the amount of predation by M. leidyi.

Effect of Other Zooplankton Predators on the Zooplankton

Predation by other zooplankters on the zooplankton, as revealed by counts of three-way splits of extra meter net tows, constituted a much smaller percentage (27%) of predation than M. leidyi (73%) (Table 5). These data are biased in that extra tows were made only when the regular sample contained forms considered predators of the zooplankton, such as chaetognaths, coelenterates, and larval fishes, as defined by

Table 5. Percent zooplankton predation due to *M. leidyi* as compared with percent zooplankton predation by other zooplankters estimated from field samples maintained alive for 24 hours.

	No. of samples	Individuals present at start	Survivors (*M. leidyi* removed)	Survivors (*M. leidyi* present)	% predation by other plankters	% predation by *M. leidyi*	% surviving
Gastropod larvae	4	5	3	3	40.0	0.0	60.0
Acartia tonsa	6	2070	1437	61	30.6	66.5	2.9
Labidocera aestiva	3	127	84	19	33.8	51.2	15.0
Pseudodiaptomus coronatus	2	44	27	2	38.6	56.8	4.6
Cladocerans	1	47	36	6	23.4	63.8	12.8
Carideans	5	252	301	286	0.0	0.0	113.5
Gammarus sp.	1	1	2	1	0.0	0.0	100.0
Neomysis americana	5	2870	2668	1842	7.0	28.8	64.2
Balanus nauplii	2	23	25	1	0.0	0.0	4.4
Decapod zoeae	5	717	699	684	2.5	2.1	95.4
Sagitta tenuis	4	57	53	58	0.0	0.0	101.8
Fish eggs	4	33	27	11	18.2	48.4	33.3
Microgobius thalassinus	2	18	19	17	0.0	5.0	94.4
Syngnathus fuscus	2	8	5	9	0.0	0.0	112.5
Anchoa mitchilli	4	73	63	48	13.7	20.5	65.8
Gobiosoma bosci	5	82	82	58	0.0	29.2	70.8
Chrysaora quinquecirrha	1	2	2	*	0.0	0.0	100.0

* *C. quinquecirrha* removed from sample containing *M. leidyi* to prevent predation on *M. leidyi*.

Total number of zooplankters	6429
Total number of zooplankters eaten	3323
Number of zooplankters eaten by other forms	896
Number of zooplankters eaten by *M. leidyi*	2427
Predation by all forms as a percent of total zooplankton	51.6
Predation by *M. leidyi* as a percent of total zooplankton	37.7
Predation by other forms as a percent of total zooplankton	13.9
Survival as a percent of total zooplankton	48.4
Percent of predation by *M. leidyi*	73.0
Percent of predation by other forms	27.0

Hildebrand and Schroeder (1928), Hyman (1940), and Lebour (1922). Usually when ctenophores were present, few of these forms were present and therefore an extra tow was not made, thus predation by *M. leidyi* would be expected to constitute an even greater percentage of the total. Conversely, this estimate did not take into account predation by large fish, which, however, is probably negligible, for contents of fish stomachs taken from these stations showed gammarids and large mysids to be eaten more often than smaller crustaceans (Joseph and Van Engel 1968). Further, confining the animals to a container created a highly artificial environment. Copepods, cladocerans and barnacle nauplii showed the greatest reduction in numbers. *M. leidyi* removed roughly twice as many copepods and cladocerans as did other predators and accounted for all of predation on barnacle nauplii. Inspection of both prey and predator species at the termination of the holding period did not reveal excessive mortality in either group so it was assumed predation remained proportional.

ECOLOGICAL CONCLUSION

Food habit investigations on several fish utilizing the York-Pamunkey nursery ground indicated that small fish did not enter the segment of the river occupied by tentaculate ctenophores until a change in the fish's diet had occurred. This shift was from small crustaceans such as copepods and cladocerans to larger plankters such as mysids or amphipods, or to benthic infauna as annelids or mollusks (Joseph and Van Engel 1968). The young fish were large enough by this time to avoid capture by the ctenophores. Therefore, the ctenophore had little detrimental effect on fish populations using this nursery ground. Actually, the presence of *Mnemiopsis leidyi* might well have been beneficial to fish populations successfully using this nursery ground in that other species of fish were likely excluded from the area if spawning time and site or the small plankton feeding phase coincided with an abundance of the ctenophore. Thus, some competition for the available food could have been eliminated.

SUMMARY

1. Mnemiopsis leidyi was present in the York River system at all times in 1966, being confined to higher salinity in colder months.
2. Size of M. leidyi decreased with distance up river.
3. Major spawning appeared to be in the lower salinity portion of its range.
4. Mnemiopsis appeared to be an important item in the diet of Chrysaora quinquecirrha.
5. Beroe ovata entered the York River in the summer and preyed on M. leidyi to such an extent that M. leidyi was limited to stations above the range of Beroe.
6. Mnemiopsis preyed on small crustaceans, and molluscan and annelid larvae and its presence at a station signalled a drastic reduction in numbers of these plankters. Mnemiopsis was unable to eat organisms larger than 5.7 mm according to field observations. Maximum size of ingested food items in laboratory experiments was 6.2 mm.
7. Feeding experiments confirmed the role of Mnemiopsis as a predator of zooplankton.
8. Mnemiopsis accounted for 73 per cent of the predation on zooplankton, when it occurred with coelenterate medusae, chaetognaths and larval fish.
9. Crustacean plankton numbers increased as Beroe replaced Mnemiopsis.
10. Fishes using the low salinity nursery ground were not preyed on by Mnemiopsis to any great extent, because they exceeded the upper size limit of food items taken by the ctenophore.

11. Fishes using the York-Pamunkey nursery ground were not dependent on small crustacean plankters when they moved into ctenophore-infested waters but fed on larger, more abundant invertebrates.

APPENDIX

Plankton counts estimated from meter net tows made one meter from the bottom are listed with hydrographic data from each station. All values have been adjusted to tows of five minutes duration at a speed of 2.5 knots. These figures more clearly indicate the impact of *M. leidyi* on other zooplankton than if reduced to numbers per cubic meter. These values can be reduced to numbers per cubic meter by multiplying by 0.0033. T records the presence of an animal in an otter trawl sample. M records the presence of an animal in a meter net sample.

TABLE I. BOTTOM METER NET SAMPLES

August 1965	P50	P40	P35	P30	Y25	Y20	Y15	Y10	Y00	C10	C00
Sal. $^{o}/oo$	0.09	1.07	2.03	10.08	13.39	16.02	16.02	21.27	26.10	28.91	26.10
Temp. ^{o}C	28.22	27.76	27.54	27.77	27.64	27.28	27.00	26.32	24.16	20.88	24.16
D.O. mg/liter			4.9								
Coelenterata											
Chrysaora quinquecirrha				T	T	T		T	T		
Moerisia lyonsi				M							
Obelia sp.									T		
Ctenophora											
Mnemiopsis leidyi vol. in liters				4	4	T		T	T		
Beroe ovata											
Cladocera											
Diaphanosoma brachyurum			304								
Ostracoda			16		288						
Mysidacea											
Neomysis americana			5344	1152	832						
Amphipoda											
Gammarus sp.			256	64							
Monoculodes edwardsi			96								
Corophium lacustre				32							
Isopoda			16		32						
Copepoda											
Acartia tonsa			10287	1056	2976						
Eurytemora hirundoides and *E. affinis*			337								
Cirripedia nauplii					256						
Decapoda											
Palaemonetes larvae			352	64	198						
Caridean larvae					320						
Rhithropanopeus harrisii zoea			5856	288	5856						
Fish Eggs				96							

TABLE II. BOTTOM METER NET SAMPLES

September 1965	P50	P40	P35	P30	Y25	Y20	Y15	Y10	Y00	C10	C00
Sal. $^{o}/oo$	1.79	2.24	5.79	9.64	14.72	16.80	20.16	22.16	25.06	27.48	25.99
Temp. ^{o}C	25.82	25.36	25.50	25.54	25.60	25.64	25.24	25.16	23.71	24.16	25.0
D.O. mg/liter	6.7	4.8	4.6	2.7	5.4	5.6	5.5	5.5			
Ctenophora											
Mnemiopsis leidyi vol. in liters			0.5	4		4		4			
Beroe ovata									M		
Cladocera											
Penilia avirostris									80		
Leptodora kindtii	720										
Ostracoda									8		
Mysidacea											
Neomysis americana		256	6784	60	64	6		312	8		
Amphipoda											
Gammarus sp.		128	512	12	96	4		12			
Monoculodes edwardsi		1024	2048	20							
Corophium lacustre		256	768	28		12					
C. tuberculatum								36			
Cumacea			3072	52	64	16		120			
Copepoda											
Acartia tonsa	445	1664	11008	6	112	272		287	115		
Eurytemora hirundoides and *E. affinis*								53			
Labidocera aestiva	371			6					13		
Cirripedia nauplii								21	16		
Decapoda									36		
Palaemonetes larvae	560					20			60		
Porcellanid larvae									90		
Rhithropanopeus harrisii zoea	304		1028	12		16		270			
Chaetognatha											
Sagitta tenuis									12		
Fish Eggs		128									

TABLE III. BOTTOM METER NET SAMPLES

October 1965	P50	P40	P35	P30	Y25	Y20	Y15	Y10	Y00	C10	C00
Sal. °/oo	0.30	2.31	7.28	10.12	18.59	20.52		23.14	26.16	28.28	32.36
Temp. °C	18.2	18.4	18.48	19.4	17.9	17.9		18.4	18.36	18.12	18.72
D.O. mg/liter	7.5	6.9	6.3								
Coelenterata											
Moerisia lyonsi				M							
Obelia sp.											
Ctenophora											
Mnemiopsis leidyi vol. in liters			4	4	4	4		4			
Beroe ovata											
Ostracoda	128										
Mysidacea											
Neomysis americana	384	6400	448	496	1288	352		640			
Amphipoda											
Gammarus sp.	10112	2048	64	198	104						
Monoculodes edwardsi			64								
Corophium lacustre				10							
Ampelisca abdita						16		192			
Elasmopus pocillimanus						8					
Cumacea	2176	384	128	80	232	48		256			
Copepoda											
Acartia tonsa	1700	3883	2687	1076	6639	2188		3678			
Eurytemora hirundoides and E. affinis	1756	2373		215	16						
Pseudodiaptomus coronatus				516	1073	167		919			
Labidocera aestiva						83		459			
Temora turbinata			65								
Cirripedia nauplii			256								
Decapoda											
Caridean larvae					48	32		64			
Rhithropanopeus harrisii zoea	128										
Chaetognatha											
Sagitta tenuis								64			

TABLE IV. BOTTOM METER NET SAMPLES

November 1965	P50	P40	P35	P30	Y25	Y20	Y15	Y10	Y00	C10	C00
Sal. $^{o}/oo$			10.37	16.02	18.75	21.56		24.01	24.32	25.32	28.88
Temp. ^{o}C			10.50	10.16	10.22	9.98		11.24	13.48	13.52	13.80
D.O. mg/liter	9.3	8.8	7.9	7.1	8.5	8.5		10.1			
Ctenophora											
Mnemiopsis leidyi vol. in liters					1	1					
Beroe ovata								M	M	M	M
Cladocera											
Penilia avirostris										8	1645
Podon sp.											99
Ostracoda											8
Mysidacea											
Neomysis americana	2816	2048	2048	4069	64	16		2144		16	8
Amphipoda											
Gammarus sp.		1024	1024								
Monoculodes edwardsi			2848								
Corophium lacustre		1024									
Ampelisca abdita								244			
Isopoda										24	
Cumacea						32		32		8	
Copepoda											
Acartia tonsa	131688	146976	525726	402761	30831	14640		64684	2008	8250	8762
Eurytemora hirundoides and E. affinis	24782	102880	33378	14007							
Pseudodiaptomus coronatus	5829							564			
Labidocera aestiva					329				60	518	550
Cirripedia nauplii										8	144
Decapoda											
Crangon larvae									2	40	48
Caridean larvae					2						16
Porcellanid larvae										112	576
Chaetognatha											
Sagitta tenuis									2	640	784

TABLE V. BOTTOM METER NET SAMPLES

December 1965	P50	P40	P35	P30	Y25	Y20	Y15	Y10	Y00	C10	C00
Sal. $^{o}/oo$	0.61	5.52	11.58	15.64	18.77	20.42	21.77	23.01	24.38		
Temp. ^{o}C	6.30	6.66	6.99	6.34	6.37	6.74	7.04	7.12	7.10		
D.O. mg/liter											
Ctenophora											
Mnemiopsis leidyi vol. in liters					0.5	4	4	4	4		
Beroe ovata											
Annelids								32			
Gastropods			1024								
Mysidacea											
Neomysis americana	384	512	17408	15360	384	448	1232	24			
Amphipoda											
Monoculodes edwardsi						64					
Ampelisca abdita							48				
Cumacea	158			5400	2304	1088	112				
Copepoda											
Acartia tonsa	43531	166252	233128	353441	133363	11695	17900	1520	10865		
Eurytemora hirundoides and E. affinis	34544	50578	466257	6741							
Pseudodiaptomus coronatus					6925	3217	2164				
Caprellids							16				
Decapoda											
Crangon larvae									464		
Caridean larvae								8			

TABLE VI. BOTTOM METER NET SAMPLES

January 1966	P50	P40	P35	P30	Y25	Y20	Y15	Y10	Y00	C10	C00
Sal. $^{o}/_{oo}$	0.52	4.00	10.04	15.56	20.16	22.36		23.92			
Temp. ^{o}C	1.96	2.56	2.68	2.08	1.28	1.48		1.64			
D.O. mg/liter	12.2	11.4	10.4	10.2	10.9	10.9		10.6			
Ctenophora											
Mnemiopsis leidyi vol. in liters					4	4		4			
Cladocera											
Daphnia pulex	128										
Mysidacea											
Neomysis americana		448	256	64							
Amphipoda											
Gammarus sp.			256								
Monoculodes edwardsi	128			64							
unidentified											
Copepoda											
Acartia tonsa	9806	519	30358	98270	5202	1530		812			
A. clausii					2159	510					
Eurytemora hirundoides and E. affinis	76201	2873	104223	3170	102						

TABLE VII. BOTTOM METER NET SAMPLES

February 1966	P50	P40	P35	P30	Y25	Y20	Y15	Y10	Y00	C10	C00
Sal. °/oo	0.13	0.17	0.58	10.00	16.73	19.35		19.39	23.14	23.27	26.23
Temp. °/C	4.5	4.1	4.2	5.1	5.6	5.5		5.4	3.4	2.3	2.8
D.O. mg/liter	11.1	11.4	11.4	9.8	10.3	10.4		10.8	11.0	11.3	11.0
Coelenterata											
Nemopsis bachei										M	M
Ctenophora											
Mnemiopsis leidyi vol. in liters					1			1			
Annelida	24							16		8	
Cladocera											
Daphnia pulex	536	264		64							
Ostracoda	16										
Mysidacea											
Neomysis americana					128	16		32			
Amphipoda											
Gammarus sp.	8		896								
Monoculodes edwardsi		32									
Corophium lacustre		32	890								
Batea catharinensis											16
Copepoda											
Acartia tonsa				18909	111182	13981		13004	51475		
A. clausii				325	2515	184		3207	13428	69828	27000
Eurytemora hirundoides and *E. affinis*		9536	33536	54118	32921	2606		802	5397		
Pseudodiaptomus coronatus								1096			
Mesocyclops leukarti	376			549							
Centropages hamatus						797		4811	6977	1435	3003
Decapoda											
Crangon larvae									224	224	1200

TABLE VIII. BOTTOM METER NET SAMPLES

March 1966	P50	P40	P35	P30	Y25	Y20	Y15	Y10	Y00	C10	C00
Sal. °/oo	0.06	0.09	3.34	7.73	14.19	15.41		19.22	19.65	25.19	27.51
Temp. °C	9.0	9.6	9.3	9.5	8.8	8.6		7.8	8.5	7.4	7.4
D.O. mg/liter	9.3	9.3	8.2	8.2	9.3	9.5		10.0	10.1	9.4	10.1
Coelenterata											
Nemopsis bachei									M		
Ctenophora											
Mnemiopsis leidyi vol. in liters											0.5
Cladocera											
Daphnia pulex	196	384									
D. longispina			512								
Mysidacea											
Neomysis americana	32			189							
Amphipoda											
Gammarus sp.		288	252	128							
Monoculodes edwardsi		96									
Corophium lacustre			512	128							
Copepoda											
Acartia tonsa				375102	198706	119657		38792			
A. clausii				20226	14570	3284		73678	175817	375460	
Eurytemora hirundoides and *E. affinis*	59176	33362	233711	9347	31551	10403		15261			
Pseudodiaptomus coronatus					16690	10130		7631			
Mesocyclops leukarti	3787										
Centropages hamatus					9006	4927			3639	16221	
Pseudocalanus minutus						1094				5820	31212
Decapoda											
Crangon larvae						128			2394	15872	5376
Caridean larvae								256			
Chaetognatha											
Sagitta elegans											128
Fish Eggs											
Scophthalmus aquosus											18

TABLE IX. BOTTOM METER NET SAMPLES

April 1966	P50	P40	P35	P30	Y25	Y20	Y15	Y10	Y00	C10	C00
Sal. °/oo	0.06	1.27	7.07	11.89	15.89	17.34		19.67	20.54	20.65	29.27
Temp. °C	10.5	10.5	11.0	11.4	14.0	11.2		10.9	11.6	10.4	10.4
D.O. mg/liter	9.0	8.4	7.0	7.5	8.3	8.7		8.9	9.1	8.1	8.9
Coelenterata											
Nemopsis bachei								M	M		
Ctenophora											
Mnemiopsis leidyi vol. in liters									1		
Annelids	32										
Cladocera											
Evadne nordmanni											448
Ostracoda	640										
Mysidacea											
Neomysis americana		8192	768	4096							
Amphipoda											
Gammarus sp.	1024	1536	1536								
Monoculodes edwardsi		512									
Isopoda								2			
Copepoda											
Acartia tonsa			94078	286717	126292	33028				4285	
A. clausii		1998	49663	81915	75775	106540		467968	28597	132605	6451
Eurytemora hirundoides and *E. affinis*	41253	250921	270845	327674	25258	5326					
Mesocyclops leukarti	2683										
Centropages hamatus										5625	
C. typicus											1630
Pseudocalanus minutus									715		
Decapoda											
Crangon larvae								3072	640	11764	768
Caridean larvae	32										
Fish Eggs											
Scophthalmus aquosus											58

cont.

TABLE IX (Cont.).

April 1966	P50	P40	P35	P30	Y25	Y20	Y15	Y10	Y00	C10	C00
Fish larvae											
Roccus americanus	1936	1640	16								
R. saxatilis		8									
Alosa sp.	24	8									
Anguilla rostrata (elvers)	2										
Brevoortia tyrannus (juveniles)	2										
Perca flavescens	216	40									

TABLE X. BOTTOM METER NET SAMPLES

May 1966	P50	P40	P35	P30	Y25	Y20	Y15	Y10	Y00	C10	C00
Sal. $^{o}/oo$	0.08	0.09	2.04	6.42	11.57	12.89	15.34	16.35	20.75	21.07	25.82
Temp. ^{o}C	18.4	18.3	18.9	18.8	18.7	18.9	17.7	18.1	17.2	17.7	16.1
D.O. mg/liter	8.4	8.4	7.3	6.0	7.6	7.8	7.8	8.2	6.9	8.0	7.9
Ceolenterata											
Nemopsis bachei								M	M		
Ctenophora											
Mnemiopsis leidyi vol. in liters								0.5	4	4	
Cladocera											
Evadne nordmanni									48	4096	17920
Daphnia pulex		4796									
Sida crystallina		86340									
Leptodora kindtii		7168	320								
Ostracoda	69632										
Mysidacea											
Neomysis americana			163840	37552	256						
Amphipoda											
Gammarus sp.		27726	4069	1536		128					
Monoculodes edwardsi		947	6144								
Copepoda											
Acartia tonsa				696376	64512	79592	15492	2435	273	2521	
Eurytemora hirundoides and *E. affinis*			10480	147382							
Mesocyclops leukarti	4096	18432									
Centropages hamatus							299	685	31		110453
Labidocera aestiva								304			4774
Decapoda											
Crangon larvae							64	48			
Caridean larvae						128				1240	12288
Fish Eggs											
Anchoa mitchilli					240	416	1022	468	324	8800	4996
A. hepsetus										10	136
Pogonias cromis										30	176
Bairdiella chrysura									12	54	104

cont.

TABLE X (Cont.).

May 1966	P50	P40	P35	P30	Y25	Y20	Y15	Y10	Y00	C10	C00
Fish Larvae											
Anchoa mitchilli										102	
A. sp.											68
Gobiesox strumosus					16	32	20	8		4	
Syngnathus fuscus					16	8	10	2		14	12
Menidia sp.					4		2				
Alosa sp.	1088	186									
Roccus saxatilis		368									
R. americanus		320									
R. sp.	1328		896								
Gobiosoma bosci	672										

TABLE XI. BOTTOM METER NET SAMPLES

June 1966	P50	P40	P35	P30	Y25	Y20	Y15	Y10	Y00	C10	C00
Sal. $^{o}/oo$	0.06	0.02	5.84	8.68	12.36	13.33	16.69	20.10	22.45	21.06	25.59
Temp. ^{o}C	24.8	24.0	24.7	24.1	23.9	23.5	22.3	21.9	19.9	20.3	19.6
D.O. mg/liter	6.5	6.4	5.3	4.9	6.0	6.0	5.0	3.7	5.4	7.4	7.4
Secchi disk meters	0.7	0.2	0.4	0.7	0.7	0.8	0.9	1.1	2.8	2.5	2.4
Coelenterata											
Chrysaora quinquecirrha			T	T	T	T	T	T	T		
Ctenophora											
Mnemiopsis leidyi vol. in liters			0.5	1	8	8	8	8	8	8	8
Cladocera											
Diaphanosoma brachyurum	19916	221184									
Simocephalus exspinosus	948										
Leptodora kindtii	6400										
Mysidacea											
Neomysis americana			79872	2816							
Amphipoda											
Gammarus sp.		6144	512	384							
Cerapus tubularis							160	10	22		
Isopoda					32	12			4		
Copepoda											
Acartia tonsa			53248	128					428		
Eurytemora hirundoides and *E. affinis*		9984	4095								
Mesocyclops leukarti	512	29952	2047								
Labidocera aestiva									18		547
Decapoda											
Caridean larvae					64	260	1602		90		176
Porcellanid larvae								32			2096
Zoea								12	332		
Fish Eggs											
Anchoa mitchilli			144	228	206	72	88	24		470	90
A. hepsetus										6	48
Trinectes maculatus								4			

cont.

TABLE XI. (Cont.)

June 1966	P50	P40	P35	P30	Y25	Y20	Y15	Y10	Y00	C10	C00
Fish Larvae											
Roccus americanus	72	1412	128								
R. saxatilis		116	64								
Alosa sp.	2	4									
Anchoa mitchilli				80	22	4	240	24			
Gobiosoma bosci			5712	612	82	48	72	12			
Syngnathus fuscus						2	16			2	
Microgobius thalassinus							16	4			

TABLE XII. BOTTOM METER NET SAMPLES

July 1966	P50	P40	P35	P30	Y25	Y20	Y15	Y10	Y00	C10	C00
Sal. $^{o}/oo$	0.16	2.0	5.76	8.92	13.48	16.05	19.22	21.15			
Temp. ^{o}C	28.48	27.7	28.2	27.9	27.3	27.0	26.7	26.6			
D.O. mg/liter	5.6	5.4	4.2	3.3	4.4	5.4	5.5	4.9			
Secchi Disk meters	0.4	0.6	0.4	0.2	0.8	0.8	0.8	0.9	1.8	1.5	1.5
Coelenterata											
Chrysaora quinquecirrha				T	T	T	T	T			
Ctenophora											
Mnemiopsis leidyi vol. in liters				8	8	8	8	8			
Beroe ovata									T	T	T
Cladocera											
Diaphanosoma brachyurum	13440										
Leptodora kindtii	896										
Mysidacea											
Neomysis americana			704	448		160		12			
Amphipoda											
Gammarus sp.		8192						4			
Monoculodes edwardsi				64				2			
Ericthonius brasiliensis							1				
Cerapus tubularis								8			
Isopoda			320	192	6		2	10			
Copepoda											
Acartia tonsa		143360	384		8		118	24			
Pseudodiaptomus coronatus											
Mesocyclops leukarti	1152										
Cirripedia nauplii								2			
Decapoda											
Caridean larvae			1344	640	16	53	332				
Zoea			1880	1280	8	95	414				
Chaetognatha						1					

cont.

TABLE XII. (Cont.)

July 1966	P50	P40	P35	P30	Y25	Y20	Y15	Y10	Y00	C10	C00
Fish Eggs											
Anchoa mitchilli			800	6		6	65	12			
Trinectes maculatus							6				
Fish Larvae											
Anchoa mitchilli	6	128	56	32	8	20	16	T			
Gobiosoma bosci		384	464	48	62	42	28	T			
Microgobius thalassinus							20	T			

TABLE XIII. BOTTOM METER NET SAMPLES

August 1966	P50	P40	P35	P30	Y25	Y20	Y15	Y10	Y00	C10	C00
Sal. $^{o}/oo$	0.36	2.43	7.99	8.73	15.45	18.36	19.79	22.48			
Temp. ^{o}C	27.64	27.0	27.5	25.5	25.7	27.7	27.5	26.9			
D.O. mg/liter	6.3	6.0	4.6	3.5	5.6	6.0	5.4	5.2			
Secchi Disk meters	0.8	0.4	0.4	0.6	1.0	0.6	1.1	1.0	2.2	2.1	3.6
Coelenterata											
Chrysaora quinquecirrha				T	T						
Liriope tetraphylla							M	M	M		
Obelia sp.									M		
Lovanella sp.									M		
Ctenophora											
Mnemiopsis leidyi vol. in liters			4	4							
Beroe ovata					M	T	T	T	T	T	T
Cladocera											
Evadne nordmanni								32			
Penilia avirostris									1408		
Ostracoda	5		128								
Mysidacea											
Neomysis americana			8576	18048	1280	1280					
Amphipoda											
Gammarus sp.	3994	1536	128								
Monoculodes edwardsi											
Corophium lacustre			256	384							
Copepoda											
Acartia tonsa			8960	128	48111	73554	16492		4118		
Eurytemora hirundoides and *E. affinis*	2000										
Pseudodiaptomus coronatus				256		313					
Mesocyclops leukarti	491										
Labidocera aestiva				128	529	2704	4694		6442		
Harpacticoid			1								
Decapoda											
Caridean larvae			896	2944		6144	4672		2304		
Zoea		512	740	9472	512	2304	6848	13760	6400		

cont.

TABLE XIII. (Cont.)

August 1966	P50	P40	P35	P30	Y25	Y20	Y15	Y10	Y00	C10	C00
Chaetognatha											
Sagitta tenuis					768	1280	32				
Fish Eggs											
Anchoa mitchilli			48		320	480	2268	2656	2112	80	12
Trinectes maculatus						28	72	96	48		88
Fish larvae											
Anchoa mitchilli	64	32	524	2	832	776	812	1376	48		
Gobiosoma bosci			176	12	1216	1776	292	480			
Microgobius thalassinus						60	52	192	16		
Syngnathus fuscus								16			
Alosa aestivalis (juvenile)	16										

TABLE XIV. BOTTOM METER NET SAMPLES

September 1966	P50	P40	P35	P30	Y25	Y20	Y15	Y10	Y00	C10	C00
Sal. °/oo	1.25	5.64	11.54	12.72	18.71	20.65	22.5	23.25			
Temp. °C	22.6	22.7	23.0	22.5	22.1	22.1	22.6	22.6			
D.O. mg/liter	6.2	5.6	4.8	4.2	6.1	3.6	5.8	6.1			
Secchi Disk meters		0.7	0.7	0.7	0.7	0.7	1.0	1.2			
Ctenophora											
Mnemiopsis leidyi vol. in liters		0.5	4	4							
Beroe ovata					M	T	T	T	T	T	T
Cladocera											
Ilyocryptus sordidus	256										
unidentified						512					
Mysidacea											
Neomysis americana	64		512	80	13056	12288					
Amphipoda											
Gammarus sp.	64	512									
Corophium lacustre	1216	1024									
Monoculodes edwardsi		512		16							
Isopoda	1280	2560									
Cumacea			512		1024						
Copepoda											
Acartia tonsa	1600		512	672	18935	46665	14001	725			
Eurytemora hirundoides and *E. affinis*	1120										
Pseudodiaptomus coronatus					996	4241	274				
Mesocyclops leukarti	480										
Labidocera aestiva					7972	8484	5628	15			
Decapoda											
Caridean larvae					2560	1536	9800				
Rhithropanopeus harrisii zoea			512	48	256		2300				
Chaetognatha											
Sagitta tenuis							1184				
Fish Eggs											
Anchoa mitchilli							16				

cont.

TABLE XIV. (Cont.)

September 1966	P50	P40	P35	P30	Y25	Y20	Y15	Y10	Y00	C10	C00
Fish Larvae											
Anchoa mitchilli	90		32	8	600	960	198	52			
Gobiosoma bosci				2	40	32	4	2			
Microgobius thalassinus					8	96	64	12			
Syngnathus fuscus					8	32	8	4			
Micropogon undulatus	2										

TABLE XV. BOTTOM METER NET SAMPLES

October 1966	P50	P40	P35	P30	Y25	Y20	Y15	Y10	Y00	C10	C00
Sal. $^{o}/oo$	0.10	0.38	6.91	10.21	15.56	17.32	19.46	20.42			
Temp. ^{o}C	16.91	17.5	18.5	17.9	17.7	18.0	17.6	17.5			
D.O. mg/liter	6.2	6.2	6.1	5.6	6.9	7.0	7.0	7.0			
Secchi Disk meters	0.5	0.3	0.4	0.5	0.8	1.1	1.3		2.2	3.2	3.4
Ctenophora											
Mnemiopsis leidyi vol. in liters						1	1				
Beroe ovata								M	T	T	T
Mysidacea											
Neomysis americana	256		28672	1408	32			544			
Amphipoda											
Corophium lacustre			2040					96			
Isopoda							1	32			
Copepoda											
Acartia tonsa	941	2793	922		688	288	5965	6819			
Eurytemora hirundoides and E. affinis	13180	7819									
Pseudodiaptomus coronatus						421	1116				
Labidocera aestiva			102				301				
Decapoda											
Caridean larvae					16	144	37	896			
Zoea								64			
Chaetognatha											
Sagitta tenuis					16						
Fish Larvae											
Anchoa mitchilli			128			64	1	58			
Microgobius thalassinus							4	2			
Syngnathus fuscus								4			

TABLE XVI. BOTTOM METER NET SAMPLES

November 1966	P50	P40	P35	P30	Y25	Y20	Y15	Y10	Y00	C10	C00
Sal. $^o/oo$	0.07	0.71	4.09	16.00	19.79	20.40	21.33	22.21			
Temp. ^oC	10.1	10.9	11.8	11.6	11.9	12.3	11.8	11.9			
D.O. mg/liter	8.6	8.5	6.8	7.4	7.8	8.1	8.3	8.1			
Secchi Disk meters		0.3	0.6	0.8	1.0	1.8	1.9	3.3	0.3		
Ctenophora											
Mnemiopsis leidyi vol. in liters					4	4	4	4	T		
Beroe ovata										T	T
Mysidacea											
Neomysis americana			3	704		8	1				
Amphipoda											
Gammarus sp.	2624	512									
Monoculodes edwardsi	1728										
Isopoda				64							
Copepoda											
Acartia tonsa	204		55821	23776	2	115	110				
Eurytemora hirundoides and E. affinis		23040	16114	3999	12	11					
Mesocyclops leukarti	800										
Labidocera aestiva								4			
Decapoda											
Palaemonetes sp. larvae								3			
Caridean larvae					6						
Fish Larvae											
Anchoa mitchilli			8		2		1				

TABLE XVII. BOTTOM METER NET SAMPLES

December 1966	P50	P40	P35	P30	Y25	Y20	Y15	Y10	Y00	C10	C00
Sal. °/oo	0.20	0.45	4.90	4.66	15.41	18.42	20.92	22.13			
Temp. °C	8.3	8.2	8.3	7.7	7.6	7.6	7.5	7.9			
D.O. mg/liter	10.2	9.9	8.5	8.4	9.3	9.6	9.5	9.4			
Secchi Disk meters			0.4	0.4	0.7	0.7	1.1	1.1	1.7	1.8	1.8
Ctenophora											
Mnemiopsis leidyi vol. in liters					4	4	4	4	T		
Beroe ovata										T	T
Ostracoda											
Mysidacea											
Neomysis americana			5952	22		2	11				
Isopoda								1			
Copepoda											
Acartia tonsa		8	8754	14086	9	186	78				
Eurytemora hirundoides and *E. affinis*		8	38605	51577	1						
Pseudodiaptomus coronatus							10				
Labidocera aestiva								6			
Decapoda											
Caridean larvae							1	2			
Fish larvae											
Anchoa mitchilli			24	6	8	8	4	1			

LITERATURE CITED

Bigelow, H. B. 1914. Explorations in the Gulf of Maine, July and August 1912, by the U. S. Fisheries Schooner Grampus. Oceanography and notes on the plankton. Bull. Mus. Comp. Zool., Harvard, 58(2):31-147.

Bigelow, H. B. 1924. Plankton of the offshore waters of the Gulf of Maine. Bull. U. S. Bur. Fish. (1924) 40(2):1-509.

Bishop, J. W. 1967. Feeding by ctenophores and its effect on zooplankton. Assoc. Southeast Biol. Bull. 14(2):23 (Abst.).

Cronin, L. E., J. C. Daiber and E. M. Hulbert. 1962. Quantitative seasonal aspects of zooplankton in the Delaware River Estuary. Chesapeake Sci. 3(2):63-93.

Fraser, J. H. 1962. The role of ctenophores and salps in zooplankton production and standing crop. Intern. Counc. Explor. Sea, Rapp. Verb., 153:121-123.

Grice, G. D. and A. D. Hart. 1962. The abundance and distribution of the epi-zooplankton between New York and Bermuda. Ecol. Monog. 32:287-309.

Gunter, G. 1957. Temperature, p. 159-184. In J. W. Hedgepeth ed. Treatise on Marine Ecology and Paleoecology. Vol. 1. Ecology. Geol. Soc. Amer. Memoir 67.

Hardy, A. C. 1958. The open sea--its natural history. Vol. 1. The world of plankton. Houghton Mifflin, Boston. 335 p.

Heinle, D. R. 1965. A screen for excluding jellyfish and ctenophores from Clarke-Bumpus plankton samples. Chesapeake Sci. 6(4):231-232.

Hildebrand, S. F. and W. C. Schroeder. 1928. The fishes of Chesapeake Bay. Bull. U. S. Bur. Fish. (1927) 43; pt. 1:1-365.

Hyman, L. H. 1940. The invertebrates: Vol. 1. Protozoa through Ctenophora. McGraw-Hill, New York. 726 p.

Jeffries, H. P. 1962. Succession of two _Acartia_ species in estuaries. Limnol. Oceanog. 7(3):354-364.

Joseph, E. B. and W. A. Van Engel. 1966. The characterization of coastal and estuarine fish nursery grounds as natural communities. Va. Inst. Mar. Sci. Quart. Prog. Rep. Nov. to Dec. 1965. Contract No. 14-17-0007-531. Commercial Fish Research and Development Act. 27 p.

Joseph, E. B. and W. A. Van Engel. 1968. The characterization of coastal and estuarine fish nursery grounds as natural communities. Va. Inst. Mar. Sci. Final Rep. Nov. 1965 - Aug. 1967. Contract No. 14-17-0007-531. Commercial fish Research and Development Act. Mimeogr. 43 p., 48 tables, 56 fig.

Lambert, F. J. 1935. Jellyfish, the difficulties of the study of their life history and other problems. Essex Nat. 25:70-86.

Lebour, M. V. 1922. The food of plankton organisms. I. Jour. Mar. Biol. Ass. U. K. 12(4):644-677.

Lebour, M. V. 1923. The food of plankton organisms II. Jour. Mar. Biol. Ass. U. K. 13(1):70-92.

Main, R. J. 1928. Observations on the feeding mechanisms of a ctenophore, _M. leidyi_. Biol. Bull. 55(2):69-78.

Mayer, A. G. 1910. Medusae of the World. Vol. III. The Scyphomedusae. Carnegie Inst. Wash. Pub. 109:495-735.

McEwen, G. F., M. W. Johnson and T. R. Folsom. 1954. A statistical analysis of the performance of the Folsom plankton sample splitter, based on test observations. Contr. Scripps Inst. Oceanog. N. S. No. 649:502-527.

Nelson, T. C. 1925. On the occurrence and food habits of ctenophores in New Jersey inland coastal waters. Biol. Bull. 48(2):92-111.

Mayer A. G. ~~Pearse, A. S. and G. Gunter.~~ 1912. Ctenophores of the Atlantic Coast of North America. Carnegie Inst. Wash. Pub. 162. 57 p.

Pearse, A. S. and G. Gunter. 1957. Salinity, p. 129-158. In J. W. Hedgepeth [ed.] Treatise on Marine Ecology and Paleoecology. Vol. 1. Ecology. Geol. Soc. Amer. Mem. 67.

Ralph, P. M. and C. Kaberry. 1950. New Zealand coelenterates and ctenophores from Cook Strait. Zool. Pub. Victoria Univ. Coll. 3:1-11.

Raymont, J. E. G. 1963. Plankton and productivity in the oceans. McMillan Co., New York. 660 p.

Russell, F. S. 1935. Seasonal abundance and distribution of the young teleostean fishes caught in the ring trawl in offshore water in the Plymouth area. Pt. II. Jour. Mar. Biol. Assoc. U. K. 20(2): 147-179.

Tattersall, W. M. 1951. A review of the Mysidacea of the United States National Museum. U. S. Nat. Mus. Bull. 201:1-292.

Wass, M. L. 1965. Check list of marine invertebrates of Virginia. Va. Inst. Mar. Sci. Spec. Sci. Rept. No. 24 (3rd rev.). 55 p.

Williams, R. B. and J. P. Baptist. 1966. Physiology of Mnemiopsis in relation to its role as a predator. Assoc. Southeast Biol. Bull. 13(3):48 (abst.).

Wilson, C. B. 1932. The copepods of the Woods Hole region Massachusetts. U. S. Nat. Mus. Bull. 158:1-635.

VITA

Victor Gregory Burrell, Jr.

Born in Wilmington, North Carolina, September 12, 1925. Graduated from Florence High School, Florence, South Carolina, June 1942. Received a B. S. in English from the College of Charleston, Charleston, South Carolina, June 1949. Attended Coker College, Hartsville, South Carolina, September 1962 to May 1963 and Duke University, Durham, North Carolina, the summer of 1964 as an unclassified graduate student.

Entered the Graduate program of the College of William and Mary in June 1965.

Served in the United States Navy 1943 to 1946. Owned and operated an oyster distributorship and a commercial fishing vessel, 1950 to 1966. Traveled as a salesman for a meat-packer 1949 to 1963. Taught in the public schools of Florence, South Carolina, 1963 to 1966.