1969

# Aspects of the Ecology, Life History, and Host-Parasite Relationship of Loxothylacus panopaei (Sacculinidae) in Chesapeake Bay

Seth Jerome Daugherty
*College of William and Mary - Virginia Institute of Marine Science*

# ASPECTS OF THE ECOLOGY, LIFE HISTORY, AND HOST-PARASITE RELATIONSHIP OF *LOXOTHYLACUS PANOPAEI* (SACCULINIDAE) IN CHESAPEAKE BAY

---

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

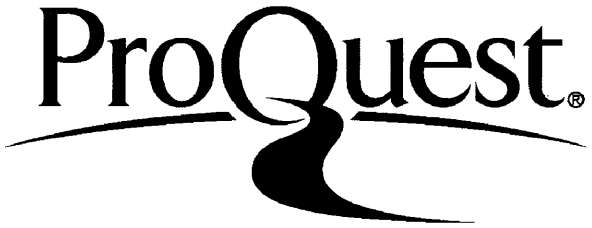
Master of Arts

---

By

Seth J. Daugherty

1969



APPROVAL SHEET

This thesis is submitted in partial fulfillment

of the requirements for the degree of

Master of Arts

Seth J. Daugherty

Seth J. Daugherty

Approved, August 1969

W. A. Van Engel

Willard A. Van Engel, Ph.M.

Marvin L. Wass

Marvin L. Wass, Ph.D.

Jay D. Andrews

Jay D. Andrews, Ph.D.

ACKNOWLEDGMENTS

I am indebted to Mr. W. A. Van Engel for guidance and patience throughout this study. I am further indebted to Dr. Marvin L. Wass and Dr. Jay D. Andrews for valuable criticism of the manuscript and to Mssrs. Alex Marsh and Ronald Hall and Miss Pamela Knowles who assisted in making field collections. The photographic work could not have been done without the assistance of Mr. Roy Terretta.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF PLATES

ABSTRACT

Xanthid crabs were collected in Chesapeake Bay and its tributaries and the ocean side of Virginia from January 1967 to November 1968 and examined for the presence of the sacculinid parasite, Loxothylacus panopaei. Infections were determined by the presence of externae.

Two species, Eurypanopeus depressus and Rhithropanopeus harrisii, were found with sacculinids. During this study prevalence of infection was higher on the eastern shore of the bay than in the York River, but decreased in both areas with time. The parasite was not found on the ocean coast of Virginia. Prevalence of infection of E. depressus was higher on oyster bars than on pilings, and higher intertidally than subtidally. The distribution of L. panopaei appears to be limited by host density and salinities less than 6 °/oo.

The frequency distribution of host size was unimodal, with most parasitized crabs being in the medium size groups. The smallest host was 3.2 mm.

Size of the externae of the adult parasite ranged from 4.8 to 11.2 mm. Nauplii were expelled from May to November in the laboratory. The internal stage was found to last at least 8½ months.

Modifications of the secondary sex characters of the host were carried through one molt after removal of an externa.

# ASPECTS OF THE ECOLOGY, LIFE HISTORY, AND HOST-PARASITE RELATIONSHIP OF *LOXOTHYLACUS PANOPAEI* (SACCULINIDAE) IN CHESAPEAKE BAY

# INTRODUCTION

The sacculinid, Loxothylacus panopaei (Gissler, 1884) is a rhizocephalan parasite of several species of xanthids and a goneplacid crab. L. panopaei has been reported from Eurypanopeus depressus (Smith) from Florida and Texas (Boschma, 1928), Louisiana (Causey, 1954), and Mississippi (Christmas, 1968) and from Rhithropanopeus harrisii (Gould) from Louisiana (Behre, 1950) and Mississippi (Christmas, 1968). Other hosts are: Panopeus herbstii (Gissler) in Florida, Tetraplax quadridentata (Rathbun) in Venezuela, Panopeus occidentalis (Saussure) in the West Indies, Lophopanopeus bellus (Stimpson) in British Columbia, possibly Lophopanopeus diagensis (Rathbun) in Southern California, and Tetraxanthus rathbunae (Chace) from 120 fathoms in the Gulf of Mexico (Boschma, 1955; Reinhard and Reischman, 1958). Reinhard and Reischman (1958) state that this species is one of the most common and widely distributed of North American sacculinids.

The best known sacculinid life cycle is that of Sacculina carcini from Carcinus maenas (Delage, 1884, in Day, 1935; Orton, 1936; Foxon, 1940). Nauplii hatch from eggs in the mantle cavity of the adult and are expelled through the mantle opening. After five or six days the nauplius becomes a cypris larva. The cypris larva attaches itself to the exoskeleton of the host by a style through which an undifferentiated mass of cells passes into the body of the crab. This mass of cells forms a tumor-like growth around the gut, grows posteriorly to the junction of the abdomen and thorax, and sends branches throughout the

body of the crab. After nine to twelve months development as an interna, the parasite penetrates the anteroventral surface of the abdomen of the host and develops an external reproductive body called the externa. The externa of many rhizocephalans is initially light colored and becomes progressively darker with age. The most important effects of sacculinids upon their decapod hosts include 1) a loss of reproductive ability of the host, 2) cessation of growth by rendering the host incapable of molting and 3) possibly making the host less able to compete with other individuals of the same species.

The introduction of L. panopaei to the east coast of North America in 1963 or 1964 was reported by Van Engel, Dillon, Zwerner, and Eldridge (1966), following the first imports of oysters from the Gulf of Mexico to alleviate the scarcity caused by the haplosporidian parasite, Minchinia nelsoni. L. panopaei was first observed in the lower York River on E. depressus and later on R. harrisii (W. A. Van Engel, personal communication). Dillon and Zwerner (1966) described a nauplius, the cypris and the externa of L. panopaei from the York River; their description of the nauplis is in close agreement with that of one of the last of six naupliar stages found and briefly described by Knowles (1968). Three other species of xanthids not attacked by the sacculinid are found in the Chesapeake Bay: Panopeus herbstii (H. Milne Edwards), Neopanope texana sayi (Smith), and Hexapanopeus angustifrons (Benedict and Rathbun). Aids for identification and descriptions of habitats and general distributions of xanthids in the Chesapeake Bay are given by Rathbun (1930) and Ryan (1956).

Wide dispersal of L. panopaei in the lower Chesapeake Bay evidently occurred rapidly. The parasite was found in all the Virginia

rivers on the western shore in 1965 and on the eastern shore in 1966. None were found north of the mouth of the Rappahannock River or on the ocean coast (W. A. Van Engel, personal communication).

There is uncertainty whether the relative abundance of E. depressus, R. harrisii and N. texana sayi changed from 1964 to late 1966. Numbers of E. depressus appeared to have decreased while those of N. texana sayi increased in the vicinity of Gloucester Point (W. A. Van Engel, personal communication). In the Rappahannock River, both E. depressus and R. harrisii decreased abruptly in 1966, and at Gloucester Point E. depressus was replaced by N. texana sayi (J. D. Andrews, personal communication).

At the end of 1966 there was uncertainty of the effects that L. panopaei had had on the xanthid population. It is believed that part of the decrease in numbers of E. depressus, at least at Gloucester Point, was due to a change in sampling procedure. From late 1964 to mid-1965 many of the samples were taken from trays of oysters; later samples were collected from pilings. However, in many instances the small numbers in samples preclude statistical tests for differences.

The role of xanthids in the ecology of Chesapeake Bay is complex but it is known that the crabs are scavengers and predators of Crassostrea virginica (McDermott, 1960; Hoese, 1962) and Mercenaria mercenaria (Landers, 1954) and alternate hosts of the oyster parasite, Nematopsis ostrearum (Prytherch, 1940; Sprague and Orr, 1955; Kenk, 1964). The large numbers of xanthids indicate that they are important in considerations of energy flow.

This study was undertaken to consider aspects of the ecology, life history and host-parasite relationships of L. panopaei in Chesapeake

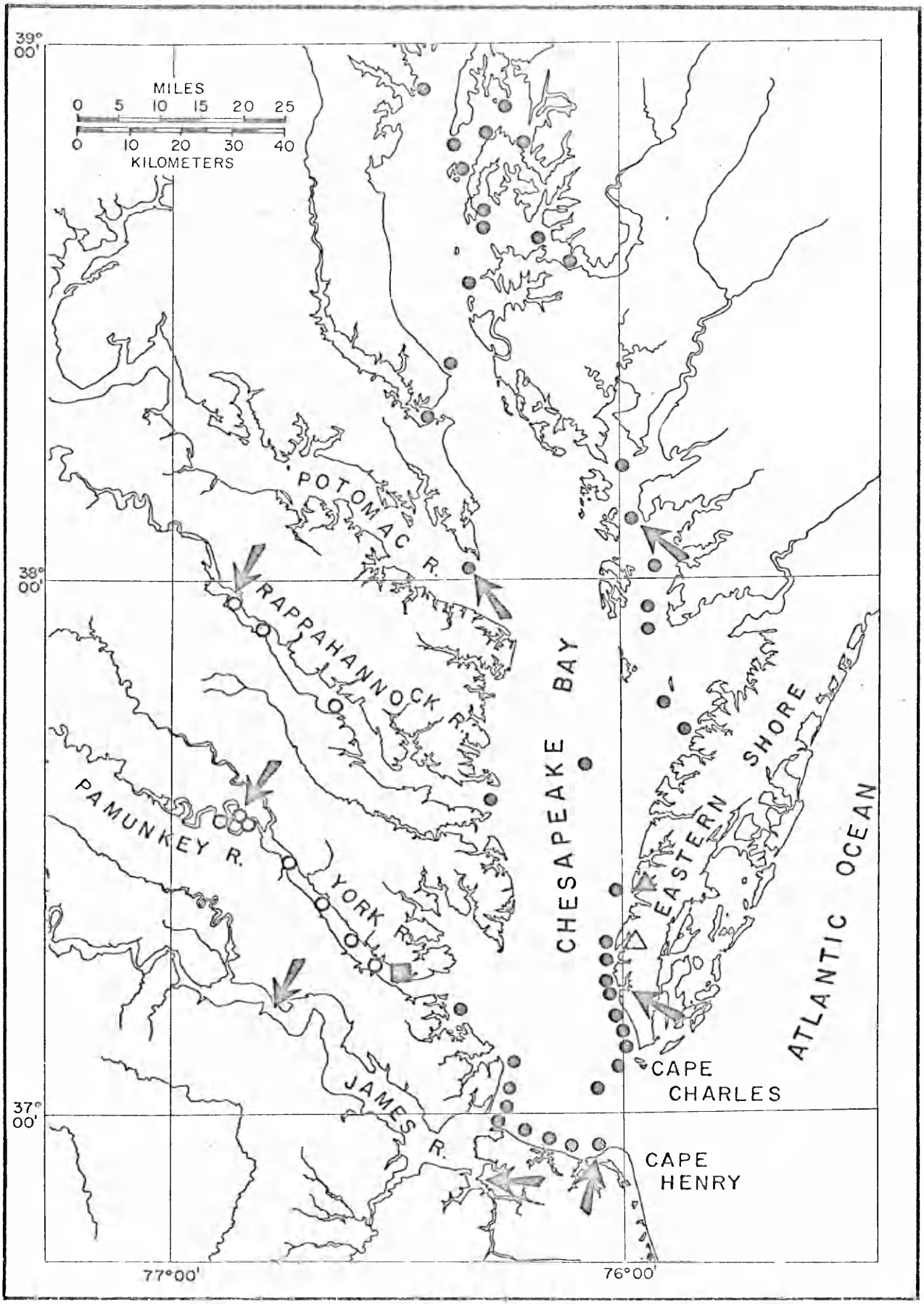
Bay. Special attention has been given to differences between E. depressus and N. texana sayi in habitat preference and relative abundance.

## MATERIALS AND METHODS

Xanthids were collected from January 1967 to November 1968, by hand, dip nets, trawls, and dredges. Most sampling was done in shallow near-shore waters on oyster bars and pilings, as these habitats consistently yield xanthids. Salinity (determined by an RS-7A induction salinometer) and temperature (stem thermometer) data were collected at most sampling sites. The crabs were either preserved or returned to the laboratory alive.

The areas sampled during this study are shown in Fig. 1. The ocean side of the eastern shore of Virginia has large tidal lagoons and extensive salt marshes where salinities range from 28 to 32 °/oo. There most crabs were collected from intertidal oyster bars by hand and dip net. On the bay side of the eastern shore are small brackish creeks and inlets. Here most samples were taken by hand from intertidal oyster bars at Cherrystone and Hungars creeks in salinities of 18 to 22 °/oo. The outstanding features of the southwestern shore of the bay are large rivers and inlets. Most collecting was done by hand and dip net on the subtidal portions of wooden pilings in the York River area, where salinity, as on the eastern shore bay side, varied from 17 to 22 °/oo. Otter trawl stations were also made in the brackish-water areas of the York and Rappahannock rivers. Trawl and dredge stations made in Chesapeake Bay, Eastern Bay, Choptank River, and Back River, on mud and sand bottoms are designated as "Bay Stations" to distinguish them from collections made by nets or by hand on oyster bars and pilings.

Figure 1. Map of the Chesapeake Bay showing locations sampled. Chesapeake Bay trawl and dredge stations, solid dot (●); Southwestern shore trawl stations, open circle (o); Cherrystone Creek, open triangle (△); Hungars Creek, solid triangle (▲); Gloucester Point, solid block (■). Limits of L. panopaei distribution are shown by arrows, those on the south shore and in the James, York and Rappahannock rivers from W. A. Van Engel (personal communication).

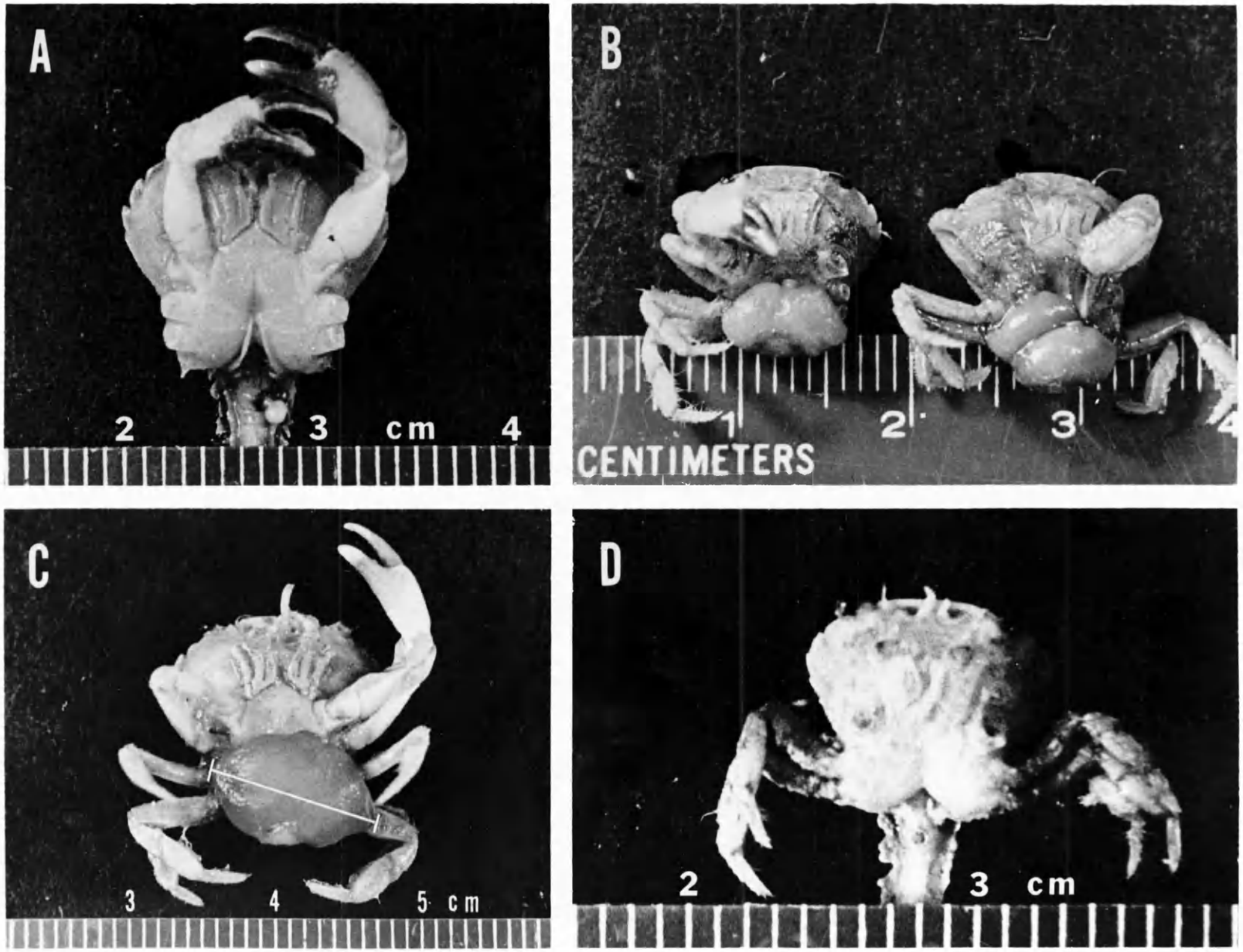

39° 00'
38° 00'
37° 00'
77°00'
76°00'
MILES
0 5 10 15 20 25
0 10 20 30 40
KILOMETERS
POTOMAC R.
RAPPAHANNOCK R.
PAMUNKEY R.
YORK R.
JAMES R.
CHESAPEAKE BAY
EASTERN SHORE
ATLANTIC OCEAN
CAPE CHARLES
CAPE HENRY

In the laboratory crabs were identified and examined for the presence of L. panopaei externae. The carapace width of all crabs was measured to the nearest 0.1 mm by vernier calipers. The sex of infected crabs was often difficult to determine. Except in rare cases, the male abdomen is broadened and fringed with setae to resemble that of the female. The criterion used for sex determination was the number of pairs of pleopods, two on the male and four with plumose exopods on the female. Infection by L. panopaei was determined only by the presence or absence of an externa. The internal stages of the parasite are not apparent upon external examination of the host and were not readily identified from sectioned material.

Living crabs were held in standing York River water, in 16 oz. jars, on a running-seawater table. These crabs were fed oyster, clam, or fish, and had frequent water changes (filtered to 1 u) that varied from two days in the summer to seven in winter. Jars were examined daily for evidence of expulsions of nauplii. Length of the dorsoventral axis (DVA) of a selected lot of externae was measured by ocular micrometer to the nearest 0.2 mm (Plate 1c), at the time of capture of the crabs and later at frequent intervals.

PLATE 1. L. panopaei externae on E. depressus.

A. Male with immature externa. Note broadened female-type abdomen.
B. Single and double adult externae.
C. Largest externa found showing dorsoventral axis (DVA) of the parasite.
D. Typical scar, the result of a previous infection of an externa.


A
2
3
cm
4
B
1
2
3
CENTIMETERS
C
3
4
5 cm
D
2
3 cm

# RESULTS

## DISTRIBUTION AND OCCURRENCE OF *L. PANOPAEI*

The sacculinid was found on the south shore of the bay from Lynnhaven Bay to the Elizabeth River, on the western shore of the bay from the Elizabeth River to the Potomac River and on the eastern shore of the bay from Old Plantation Creek to Deal Island. It has been found thirty-two miles from the mouth of the James River at Jamestown Island, thirty-five miles from the mouth of the York River in the Pamunkey River, and forty miles from the mouth of the Rappahannock at Naylors Point. None was found on the ocean side of the eastern shore of Virginia.

A summary of the collections is given in Table 1 which shows the prevalence of infection in different areas of the bay from January 1967 to November 1968. Infection ranged from 0 to 70% with an overall prevalence of 27.1% for the entire bay. A more meaningful figure of 36.8% includes only areas where the parasite was known to be present. A significant difference in the total prevalence of infection was found between the eastern and western shores, between zones, and between habitats. More infected crabs and a higher prevalence of infection were found on the eastern shore than on the western shore. Prevalence of infected *E. depressus* was higher on oyster bars than on pilings, and higher in intertidal than in subtidal habitats.

*E. depressus* was more frequently infected and the most common xanthid on oyster bars and in the intertidal habitat on the eastern shore. *N. texana sayi* was the most common xanthid on pilings and in

Table 1. Summary of xanthids collected and prevalence of L. panopaei externae, by area, habitat, and zone. Miscellaneous includes mud flats, eelgrass beds, rocks, experimental oyster trays, and otter trawl hauls.

| | | E. depressus | | | R. harrisii | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | Total | W/parasite | % infected | Total | W/parasite | N. texana sayi | P. herbstii | H. angustifrons |
| CHESAPEAKE BAY | | | | | | | | | |
| York and Rappahannock Rivers | | | | | | | | | |
| Habitat: | pilings | 209 | 24 | 11.5 | 1 | 0 | 897 | 10 | 0 |
| | oyster bars | 10 | 7 | 70.0 | 5 | 0 | 72 | 101 | 0 |
| | miscellaneous | 77 | 10 | 12.9 | 159 | 0 | 51 | 31 | 0 |
| | | 296 | 41 | 13.8 | 165 | 0 | 1020 | 142 | 0 |
| Zone: | subtidal | 271 | 27 | 10.0 | 158 | 0 | 892 | 24 | 0 |
| | intertidal | 25 | 14 | 56.0 | 7 | 0 | 128 | 118 | 0 |
| | | 296 | 41 | 13.8 | 165 | 0 | 1020 | 142 | 0 |
| Eastern Shore | | | | | | | | | |
| Habitat: | pilings | 14 | 2 | 14.3 | 0 | 0 | 148 | 16 | 0 |
| | oyster bars | 461 | 237 | 53.4 | 7 | 3 | 55 | 158 | 0 |
| | miscellaneous | 4 | 2 | 50.0 | 15 | 13 | 9 | 6 | 0 |
| | | 479 | 241 | 48.5 | 22 | 16 | 212 | 181 | 0 |
| Zone: | subtidal | 15 | 3 | 20.0 | 15 | 13 | 64 | 17 | 0 |
| | intertidal | 464 | 238 | 51.3 | 7 | 3 | 148 | 164 | 0 |
| | | 479 | 241 | 48.5 | 22 | 16 | 212 | 181 | 0 |

Table 1. (Continued)

| | | E. depressus | | | R. harrisii | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | Total | W/parasite | % infected | Total | W/parasite | N. texana sayi | P. herbstii | H. angustifrons |
| Bay Stations | | 38 | 17 | 44.7 | 131 | 0 | 2270 | 89 | 6 |
| OCEAN COAST | | | | | | | | | |
| Habitat: | pilings | 7 | 0 | 0 | 0 | 0 | 21 | 0 | 0 |
| | oyster bars | 65 | 0 | 0 | 0 | 0 | 0 | 5 | 0 |
| | miscellaneous | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | | 72 | 0 | 0 | 0 | 0 | 21 | 5 | 0 |
| Zone: | subtidal | 7 | 0 | 0 | 0 | 0 | 21 | 0 | 0 |
| | intertidal | 65 | 0 | 0 | 0 | 0 | 0 | 5 | 0 |
| | | 72 | 0 | 0 | 0 | 0 | 21 | 5 | 0 |

in subtidal habitats on the eastern shore and in both habitats and in both zones on the southwestern shore.

About 10% of the parasitized crabs bore multiple externae. However, on the bay side of the eastern shore multiple externae were found on 22% of the parasitized E. depressus. Most multiple infections showed two or three externae, although as many as six have been found on a single R. harrisii. Scars, (Plate 1d) which indicated previous infection, were found on only four E. depressus and two R. harrisii.

During the two year period there was a significant decline in the prevalence of infection for E. depressus in the lower York River as evidenced by (1) a significant difference between the January 1967 and the November 1968 levels of infection and (2) a declining cumulative percentage of hosts with externae (Table 2). The slight increase in cumulative percentage of infection from August to November 1967 is not statistically significant. The same decreasing trend was observed at Cherrystone and Hungars creeks. There was also a significant difference between the size-frequency distributions of E. depressus at Cherrystone and Hungars creeks in 1967 and 1968 (Fig. 2): the modal size of infected hosts was smaller in 1968 and there were more large infected and uninfected crabs in 1968 than in 1967.

## THE EFFECT OF PHYSICAL FACTORS

### Salinity

The salinity ranges of hosts and parasite are shown in Fig. 3. L. panopaei has been found from 5.9 to 24.3 °/oo in Chesapeake Bay and its tributaries (Van Engel, personal communication) but has never been taken from the higher salinity waters of the ocean coast of the eastern

Table 2. Cumulative prevalence of *E. depressus* with externae for the York River area and Cherrystone and Hungars creeks from January 1967 to November 1968 with 95% confidence limits.

| | LOWER YORK RIVER | | | | CHERRYSTONE AND HUNGARS CREEKS | | | |
|---|---|---|---|---|---|---|---|---|
| | Total | No. with Externae | % with Externae | Cumulative % with Externae | Total | No. with Externae | % with Externae | Cumulative % with Externae |
| 1967 | | | | | | | | |
| January | 26 | 9 | 34.6 ± 17.8 | 34.6 | | | | |
| February | | | | | | | | |
| March | | | | | | | | |
| April | | | | | | | | |
| May | | | | | | | | |
| June | | | | | | | | |
| July | | | | | 70 | 61 | 87.1 ± 8.0 | 87.1 |
| August | 4 | 4 | 100.0 | 43.3 | | | | |
| September | 8 | 4 | 50.0 ± 36.0 | 41.7 | | | | |
| October | 7 | 4 | 57.0 ± 36.0 | 46.6 | | | | |
| November | 10 | 7 | 70.0 ± 29.0 | 50.9 | | | | |
| December | | | | | 25 | 18 | 72.0 ± 18.0 | 83.2 |
| 1968 | | | | | | | | |
| January | | | | | | | | |
| February | | | | | | | | |
| March | 23 | 3 | 13.0 ± 14.0 | 39.7 | | | | |
| April | | | | | | | | |
| May | 4 | 0 | 0.0 | 37.8 | 5 | 1 | 20.0 ± 36.0 | 80.0 |
| June | 13 | 1 | 7.7 ± 14.8 | 33.7 | 201 | 64 | 31.8 ± 6.6 | 47.8 |
| July | | | | | | | | |
| August | | | | | 170 | 74 | 43.5 ± 7.6 | 46.3 |
| September | | | | | | | | |
| October | | | | | | | | |
| November | 115 | 3 | 2.6 ± 2.8 | 16.7 | | | | |
| December | | | | | | | | |

Figure 2. Comparison of the size distribution of E. depressus from Cherrystone and Hungars creeks collected during the summer of 1967 with those collected during the summer of 1968.

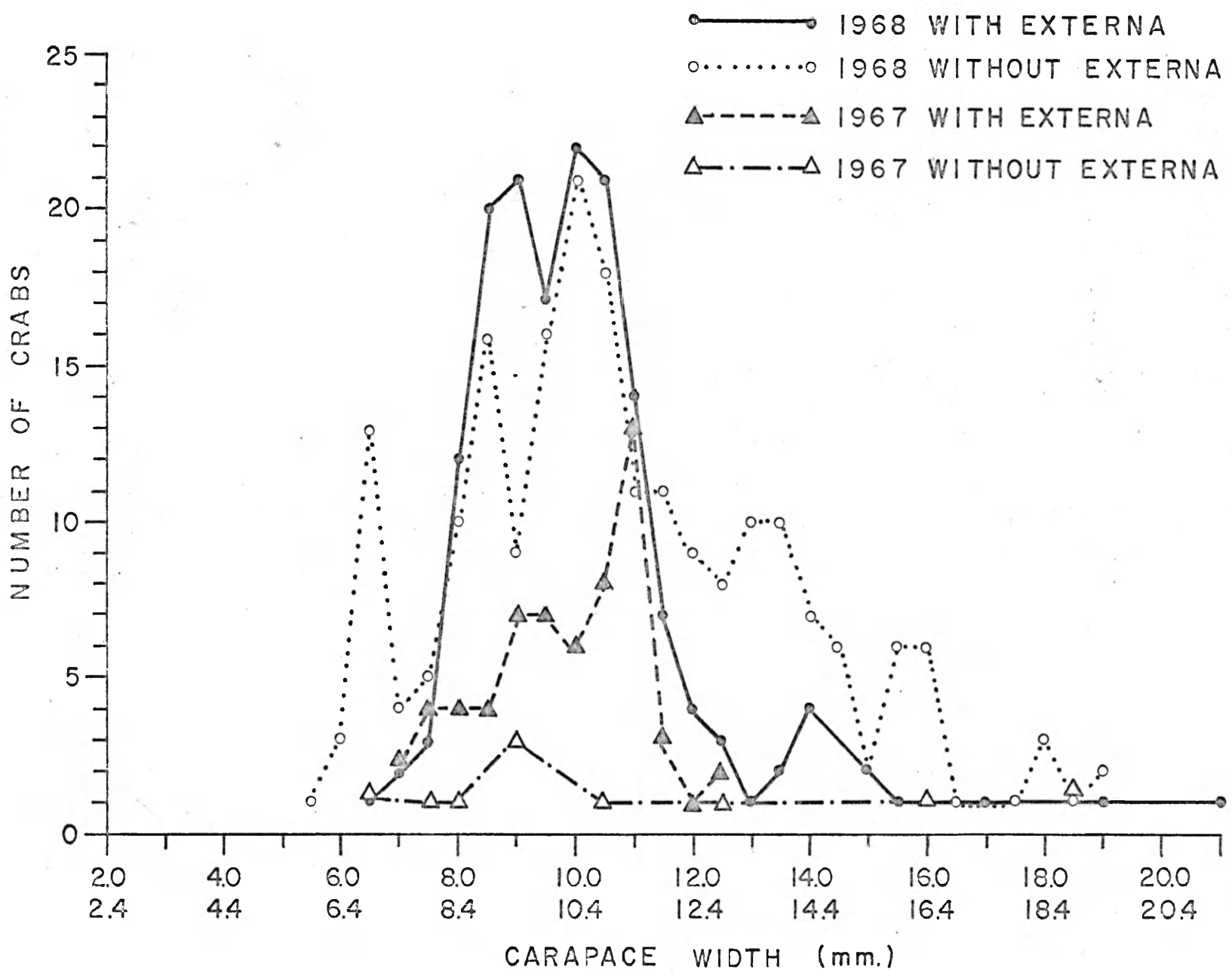
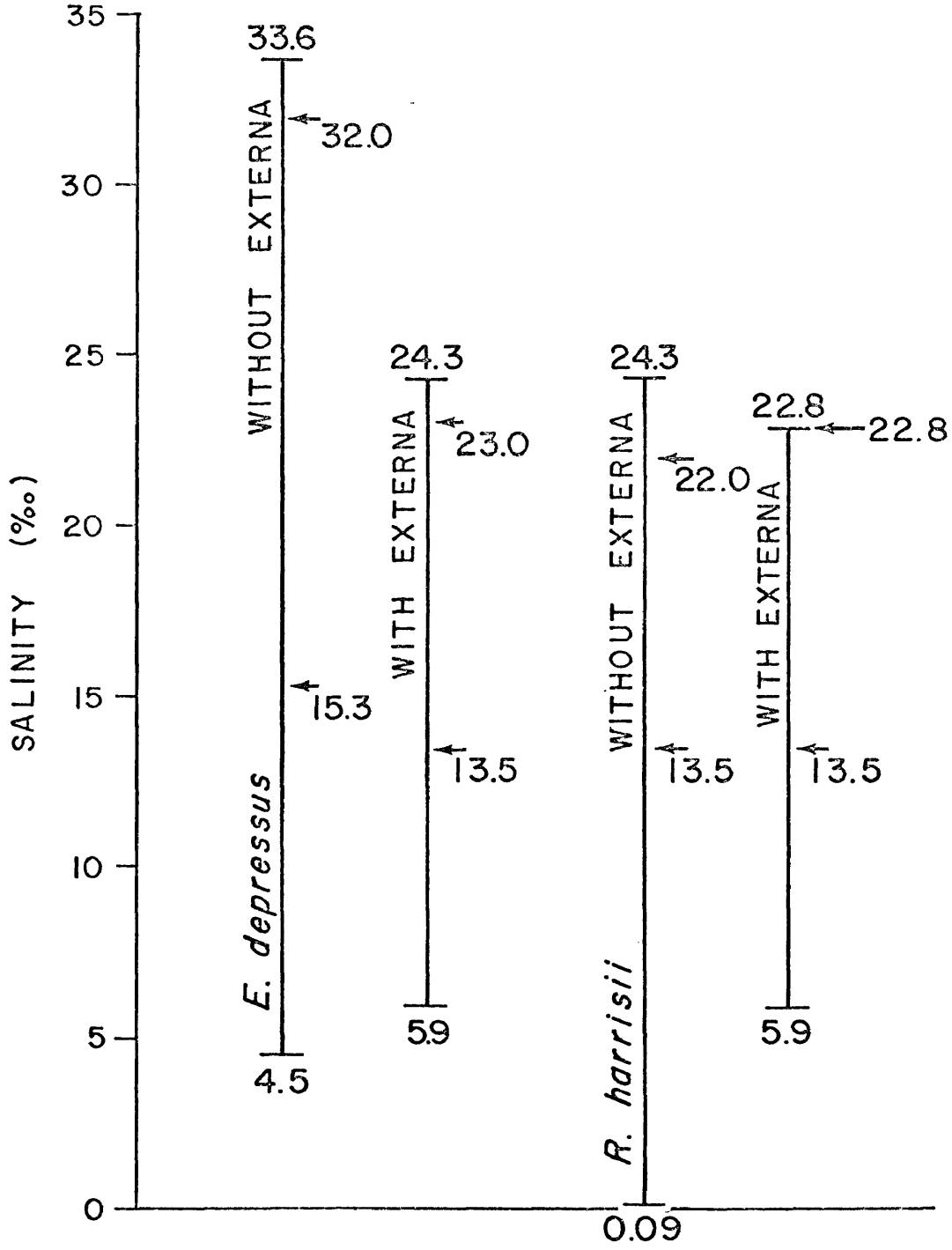

1968 WITH EXTERNA
1968 WITHOUT EXTERNA
1967 WITH EXTERNA
1967 WITHOUT EXTERNA
NUMBER OF CRABS
0
5
10
15
20
25
2.0
2.4
4.0
4.4
6.0
6.4
8.0
8.4
10.0
10.4
12.0
12.4
14.0
14.4
16.0
16.4
18.0
18.4
20.0
20.4
CARAPACE WIDTH (mm.)

Figure 3. Salinity ranges of E. depressus and R. harrisii including those found with L. panopaei. Arrows show range of salinity sampled during this study. Low salinity end of the range of E. depressus is from Ryan (1956), all others are from Van Engel (personal communication).


SALINITY (‰)
35
30
25
20
15
10
5
0
E. depressus
WITHOUT EXTERNA
33.6
32.0
15.3
4.5
WITH EXTERNA
24.3
23.0
13.5
5.9
R. harrisii
WITHOUT EXTERNA
24.3
22.0
13.5
0.09
WITH EXTERNA
22.8
22.8
13.5
5.9

shore of Virginia. In this study the parasite was collected from salinities of 13.5 to 23.0 °/oo.

From 18 June to 5 August an experiment was conducted to determine the effect of higher salinities on L. panopaei. Fifteen infected and 15 uninfected E. depressus were acclimated from filtered York River water at 20.2 °/oo to filtered and ultraviolet-irradiated ocean water at 31.6 °/oo. Acclimation was conducted over a 6 day period at a rate of approximately 2 °/oo per day. A control group of 13 infected E. depressus was kept at about 20 °/oo. All crabs were kept in individual jars and examined every day for the expulsion of nauplii, until 5 August 1968. Both the control and experimental groups produced viable nauplii (Table 3). The largest number of hosts that expelled nauplii and the largest number of naupliar expulsions were in the experimental group. It is possible that the higher salinities artificially induced some of these expulsions. Releases of nauplii occurred from 18 June to 2 August (although only three occurred after 17 July) in both groups and no difference was observed in their appearance or viability. No difference in condition of the adult parasite was observed in either group except for one externa of the experimental group which expanded to a transparent bulb (from 7.4 mm on 18 June to 10.4 mm on 28 June) which was found with a scar on 17 July. No other differences were observed in the physical appearance of the externae or nauplii of L. panopaei. Mortality of infected crabs was significantly greater in the experimental group than among the controls and the uninfected crabs. This may indicate that infected crabs are more susceptible to stress conditions, but the small number of crabs tested does not justify a more positive statement.

Table 3. The effects of exposure of infected and uninfected E. depressus to ambient high salinity.

| | Salinity (°/oo) | Crabs | Crabs with mature externae | Number of externae | Crab deaths | Number of externae that had at least one expulsion | Total expulsions |
|---|---|---|---|---|---|---|---|
| Control group | 20.2 | | | | | | |
| Infected | | 13 | 12 | 16 | 6 | 8 | 13 |
| Experimental group | 31.6 | | | | | | |
| Infected | | 15 | 15 | 17 | 13 | 14 | 29 |
| Uninfected | | 15 | 0 | 0 | 2 | -- | -- |

Temperature.

Living externae were found at all times of the year and are apparently able to survive the annual temperature variations of 3 to 28 C. However, E. depressus appeared to be scarcer on intertidal oyster bars in the winter, perhaps indicating a seasonal population movement to deeper water.

Depth.

The effect of depth on the parasite is uncertain. Although parasitized E. depressus were found at a depth of 10 meters in the bay, infected crabs are scarce in the channels (5 meters) of the rivers of the southwestern shore (W. A. Van Engel, personal communication).

## REPRODUCTION OF L. PANOPAEI

Thirty-three adult parasites, collected throughout the year, were examined for evidences of reproductive activity by opening their mantle cavities. While nauplii were never seen, some eggs were found in nearly all externae. Embryos with eyespots were seen in only three instances, all in July.

Direct evidence of reproduction was obtained by observing releases of nauplii from parasites held in the laboratory. The DVA sizes of externae observed to expel nauplii ranged from 4.8 to 8.2 mm. In 1967 nauplii were observed from 21 September to 11 November, and in 1968 from 11 May to 8 October. During these periods the water temperature ranged from 11.9 to 29.0 C. The length of the reproductive season may not be accurately defined by these observations as some of the expulsions produced very few nauplii and others probably went undetected. The greatest number of expulsions and those which produced

the greatest number of nauplii occurred in the summer. Again, it is possible that some expulsions may have been induced. Many expulsions occurred soon after crabs were brought to the laboratory in the summer of 1968.

From June to August 1968, 26 infected crabs (carrying 35 externae) were closely monitored for releases of nauplii. The interval between releases varied from 4 to 25 days with an average of 6 days. The process of expelling nauplii was found to last as long as two days. Two externae expelled six times each and nearly all expelled at least three times. Again, these data are not meant to define an interval between expulsions, due to the possibility of induced expulsions and the short time span considered. The externa is nonetheless capable of producing several broods of nauplii each year, with short intervals between expulsions.

## THE IMMATURE EXTERNA

The smallest externa was 0.4 mm. The size at which the parasite reaches sexual maturity is not known. However, the smallest externa observed to expel nauplii was of DVA 4.8 mm, and all those less than this size are considered to be immature (Plate 1a). Immature externae were found throughout the year on both host species, although they occurred most frequently in the summer. Of 21 crabs with immature externae, 13 were collected from June through September.

The minimum time L. panopaei spends as an interna can be estimated in only one case. An externa appeared on a male E. depressus eight and one-half months after it had been brought into the laboratory. In the intervening time the crab had been isolated in filtered seawater.

Externae appeared on several laboratory-held crabs. On 10 and 11 June 1968, 67 E. depressus without externae were collected from Hungars Creek. By 15 August 1968, 15 of these had externae. In 8 of these cases the host molted 1 to 19 days prior to the appearance of the externa. No significant growth of these externae occurred in the first five months (Table 4).

THE ADULT EXTERNA

The DVA of the largest externa was 11.2 mm. The size range of 95 randomly selected adult externae on E. depressus, all taken from hosts with a single externa, was 4.4 to 9.8 mm, with a mean of 6.4 mm and a standard deviation of 1.1 mm.

The color and texture of externae varied from smooth-white in the younger adult parasites, to wrinkled-dark brown or black in the older. The difference between light brown and brown is subject to judgement error but the numbers of white, reddish-brown, and dark brown can be shown with some certainty. Light colored externae were found more often in the summer and the dark brown more often in the late fall (Table 5).

The color and DVA of 19 externae observed during the summer of 1968 are shown in Table 6. Fluctuations in the measurements of a single externa may reflect either contractions, reproductive state, or measurement error, rather than an increase or decrease in size. Nevertheless, a few externae appeared to grow. The DVA of one externa increased from 3.3 to 6.1 mm in one week. No relationship was observed between DVA size and the expulsion of nauplii.

The externa may persist for the life of its host. Only six crabs with scars were collected and very few crabs became scarred in

Table 4. Growth (mm) of immature L. panopaei externa on E. depressus.

| Date externa erupted | Date of last known molt | Size of externa (mm) | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | 17 July | 13 Aug. | 26 Aug. | 5 Sept. | 17 Sept. | 3 Oct. | 15 Oct. | 25 Oct. | 25 Nov. |
| 1 July | 24 June | 0.7 | --- | 0.7 | | | | | | |
| 1 July | unknown | 0.4 | 0.9 | 1.0 | 1.1 | 1.0 | 1.0 | 1.0 | 6.9 | 1.1 |
| 3 July | 2 July | 1.1 | 1.2 | 1.3 | | | | | | |
| 5 July | 26 June | 1.2 | 1.5 | 1.5 | 1.5 | 1.6 | 1.6 | 1.6 | | |
| 5 July | 30 June | 0.8 | 1.1 | 1.5 | 1.5 | 1.5 | | | | |
| 5 July | unknown | 0.9 | 0.9 | 1.0 | 1.0 | 1.1 | 1.1 | | | |
| 15 July | unknown | 1.1 | 0.9 | 0.9 | 1.0 | 1.2 | 1.1 | 1.1 | 0.9 | 1.6 |
| 29 July | 18 July | --- | 0.9 | 1.3 | 1.3 | 1.3 | 1.1 | 1.3 | | |
| 6 August | 26 July | --- | 1.2 | 1.2 | 1.3 | 1.2 | 1.1 | 1.2 | | |

Table 5. Seasonal occurrence of different colored adult externae. Hosts were E. depressus except where noted.

| Date Collected | Number of Externae | | | | |
|---|---|---|---|---|---|
| | White | Reddish-Brown | Light Brown | Brown | Dark Brown |
| 24 January 1967 | 3 | 0 | 2 | 4 | 3 |
| 13 April 1967 | 0 | 0 | 0 | 1 | 0 |
| 6 July 1967 | 8 | 0 | 28 | 3 | 2 |
| 17 August 1967 | 3 | 3 | 0 | 0 | 0 |
| 16 November 1967 | 1 | 1 | 1 | 1 | 1 |
| 31 November 1967 | 0 | 0 | 0 | 0 | 2 |
| 9 & 10 December 1967 | 1 | 1 | 1 | 5 | 12 |
| 9 & 10 December 1967* | 8 | 2 | 0 | 5 | 1 |
| 14 March 1968 | 2 | 0 | 0 | 1 | 0 |
| 14 May 1968 | 3 | 1 | 0 | 0 | 0 |
| 10 & 11 June 1968 | 32 | 2 | 0 | 0 | 0 |
| 4 September 1968 | 3 | 1 | 0 | 0 | 0 |
| 30 October 1968 | 7 | 1 | 2 | 3 | 7 |

* R. harrisii

Table 6. DVA size and color of 19 externae during the summer and early fall of 1968. Asterisk (*) indicates crabs that were held at 31.6 °/oo; all others at 20.2 °/oo. W - white; rb - reddish-brown; lb - light brown; s - scar.

| Host Carapace Width | DVA (mm), color and date measured | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | 14 June | 21 June | 28 June | 17 July | 13 Aug. | 26 Aug. | 5 Sept. | 17 Sept. | 3 Oct. | 15 Oct. | 23 Oct. |
| Males | | | | | | | | | | | |
| 8.1 | 5.6 w | 6.1 rb | 5.5 lb | 5.8 lb | | | | | | | |
| 10.7 | 6.8 w | 7.7 rb | 6.81 lb | 7.2 lb | 7.0 lb | | | | | | |
| 11.2* | 5.0 w | 5.8 w | | | | | | | | | |
| 13.6 | 8.1 lb | 8.0 lb | 8.1 lb | 8.8 lb | 8.2 lb | | | | | | |
| Females | | | | | | | | | | | |
| 8.0* | 5.8 w | 5.9 rb | 5.7 w | 5.5 w | 5.3 w | | | | | | |
| 8.7* | 6.9 w | 6.7 w | | | | | | | | | |
| 8.9 | 3.4 w | 3.3 w | 6.1 w | 5.6 w | 5.0 lb | 5.8 lb | 6.6 lb | 5.3 lb | 6.4 lb | 5.3 lb | |
| 9.0* | 4.9 w | 5.6 w | -- | | | 5.7 lb | | | | | |
| 9.2* | 6.4 w | 6.4 w | 5.0 w | 6.9 w | 5.3 w | | | | | | |
| 10.1 | 4.9 w | 4.7 w | 5.2 w | 4.4 w | 3.6 lb | | 5.2 lb | 5.0 lb | 4.2 lb | 4.4 lb | |
| 10.1 | 5.7 w | 6.2 w | 6.1 w | 6.4 w | 5.7 lb | 5.3 lb | 5.3 b | 5.6 b | 5.5 b | 4.6 b | |
| 10.2* | 7.0 w | 6.4 w | | | | | | | | | |
| 10.5* | 5.4 w | 6.6 w | | | | 6.0 w | | | | | |
| 10.7* | 5.9 w | 6.2 w | | | | | | | | | |
| 10.8 | 4.7 w | 6.6 w | | | | 7.4 w | | | | | |
| 11.4 | 7.2 w | 8.2 w | 10.4 w | s | | | | | | | |
| 11.6* | 5.8 w | 7.0 w | 6.8 w | 7.5 w | 7.0 w | | 7.6 lb | 6.3 lb | 7.0 lb | 6.4 lb | 5.8 lb |
| 11.7* | 7.8 w | 7.1 w | 6.4 lb | | | | | | | | |
| 12.0 | 6.9 w | 7.2 w | | | | 6.9 w | | | | | |

the laboratory.

Regeneration of an externa does not appear to occur. Externae were amputated from 27 E. depressus. Although many of these crabs died soon after amputation, no evidence of regeneration was found, even as long as four months after amputation in eight cases. The typical scar developed within two months on some crabs.

Previous infection does not appear to confer immunity to subsequent infections. Both large and small externae were sometimes found on the same host. Three crabs had a scar and an externa. One host with a mature externa on 17 July was found with a scar and a small immature externa on 24 August.

## PREVALENCE OF INFECTION AND HOST SEX RATIOS

Prevalence of infection differed for males and females. Of 326 E. depressus males, 20.6% were found with a single externa and 1.2% with multiple externae (Table 7). A single externa was found on 30.4% of 559 E. depressus females; while 10.4% carried multiple externae. No difference was observed in the size of the parasite on hosts of different sex. The sex ratio and the prevalence of infection of males and females also varied for different areas. Areas with high levels of infection had higher ratios of females to males than areas with low levels of infection. On the ocean coast of the eastern shore of Virginia, the sex ratio was 0.9 female to 1 male. In the York River the sex ratio was 1.1 female to 1 male, while the levels of infection were 12% for males and 15% for females. On the eastern shore of the bay the sex ratio was 2.5 females to 1 male and the infection levels were 38% for males and 55% for females.

Table 7. Frequency association of sex and sex ratio to prevalence of externae in different areas for *E. depressus*.

| | Total | With one Externa | % With one Externa | With Multiple Externae | % with Multiple Externae | Sex Ratio Female to Male |
|---|---|---|---|---|---|---|
| York River | | | | | | |
| Males | 138 | 15 | 10.9 | 2 | 1.4 | |
| | | | | | | 1.1 to 1 |
| Females | 158 | 20 | 12.7 | 4 | 2.5 | |
| Eastern Shore | | | | | | |
| Males | 135 | 50 | 37.0 | 2 | 1.5 | |
| | | | | | | 2.5 to 1 |
| Females | 344 | 139 | 40.4 | 50 | 14.5 | |
| Ocean Coast | | | | | | |
| Males | 37 | 0 | 0 | 0 | 0 | |
| | | | | | | 0.9 to 1.0 |
| Females | 35 | 0 | 0 | 0 | 0 | |
| Bay Stations | | | | | | |
| Males | 16 | 2 | 12.5 | 0 | 0 | |
| | | | | | | 1.4 to 1 |
| Females | 22 | 11 | 50.0 | 4 | 18.2 | |
| Totals | | | | | | |
| Males | 326 | 67 | 20.6 | 4 | 1.2 | |
| | | | | | | 1.7 to 1 |
| Females | 559 | 170 | 30.4 | 58 | 10.4 | |

## SIZE RELATIONSHIPS

Hosts with externae were found throughout the entire size range of sexually mature crabs (Table 8). The minimum and maximum carapace widths of infected E. depressus were 5.0 to 21.6 mm for males and 4.5 to 18.7 mm for females. The range of carapace widths of infected R. harrisii was 3.2 to 12.6 mm for males and 4.8 to 14.3 mm for females.

No correlation was found between the carapace widths of 95 E. depressus bearing a single adult externa and DVA of the parasite. Nor was any correlation found between the wet weights of 15 hosts and their parasites.

The size-class distribution of infected E. depressus from nearly all collections is unimodal (Fig. 4). Unimodality was observed for data from both eastern and western shores of Chesapeake Bay (Figs. 5 & 6). The distributions shown in Figs. 4 & 5 are mainly due to the infected female crabs collected in the summer of 1968 from Cherrystone and Hungars creeks.

Hosts with externae were frequently found in the 7.5 to 12.0 mm size ranges. Above 12 mm a decreasing prevalence of infection with increasing host size was observed. None with an externa was smaller than 6.8 mm. Cumulative percentages of infection increased rapidly from 7.5 to 11.5 mm and 90% of all crabs with an externa were less than 12.0 mm (Fig. 7).

## NOTE ON MODIFICATIONS OF THE SECONDARY SEX CHARACTERS

The most frequently reported morphological modifications of brachyurans infected with sacculinids have been the degeneration of the pleopods in both sexes and the broadening of the abdomen of the male to

Table 8. Carapace width, mm, of parasitized and unparasitized hosts.

| | Size at sexual maturity | | Maximum size | | Smallest size, with externa | | Largest size, with externa | |
|---|---|---|---|---|---|---|---|---|
| E. depressus | ♂ | ♀ | ♂ | ♀ | ♂ | ♀ | ♂ | ♀ |
| Daugherty, 1967-1968 | - | 6.8 | 23.7 | 21.5 | 7.0 | 6.8 | 21.2 | 18.5 |
| Ryan (1956) | 5.1-6.0 | 5.5-6.4 | 26.2 | 20.6 | - | - | - | - |
| Van Engel, before 1967 | - | 7.2 | 26.1 | 20.5 | 5.0 | 4.5 | 21.6 | 18.7 |
| R. harrisii | | | | | | | | |
| Daugherty, 1967-1968 | - | 6.3 | 16.2 | 16.4 | 7.2 | 5.4 | 12.6 | 14.3 |
| Ryan (1956) | 4.5 | 4.4-5.5 | - | - | - | - | - | - |
| Van Engel, before 1967 | - | 5.9 | 19.1 | 18.5 | 3.2 | 4.8 | 12.2 | 12.2 |

Figure 4. Size class distribution of E. depressus collected in Chesapeake Bay and its tributaries, January 1967 to November 1968.

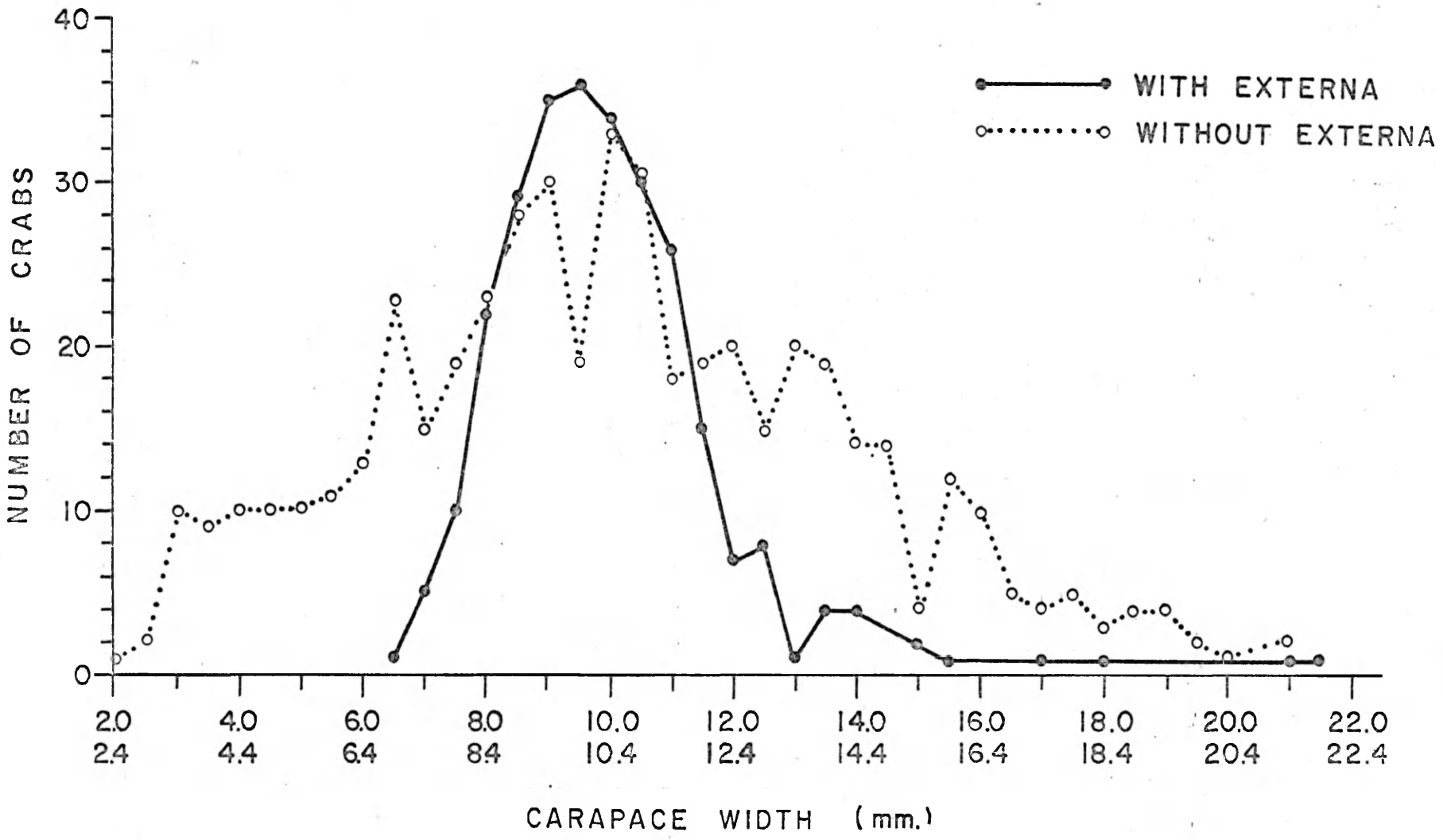

WITH EXTERNA
WITHOUT EXTERNA
NUMBER OF CRABS
0
10
20
30
40
2.0
2.4
4.0
4.4
6.0
6.4
8.0
8.4
10.0
10.4
12.0
12.4
14.0
14.4
16.0
16.4
18.0
18.4
20.0
20.4
22.0
22.4
CARAPACE WIDTH (mm.)

Figure 5. Size class distribution of E. depressus from the eastern shore of Chesapeake Bay, January 1967 to November 1968.

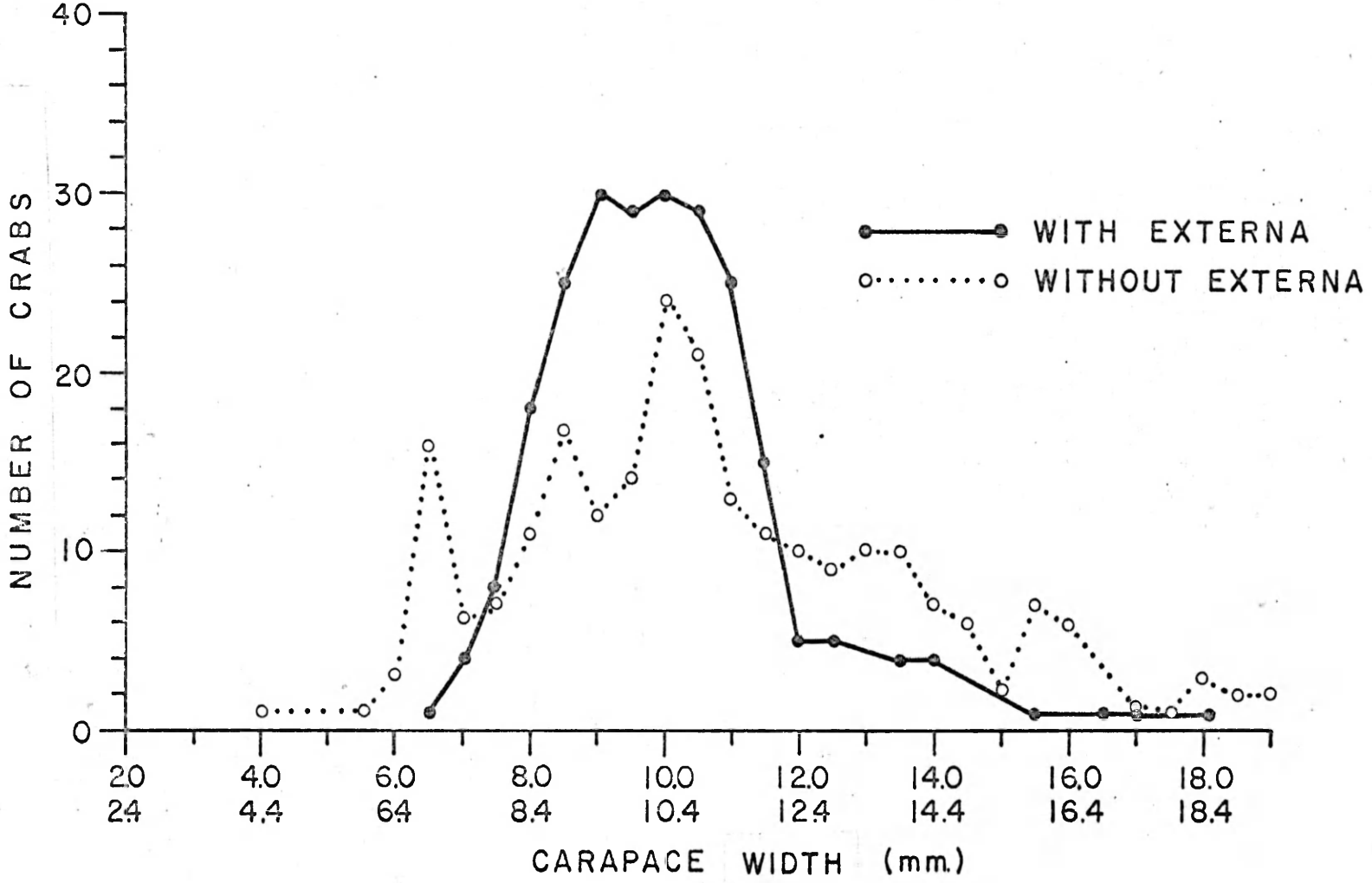

NUMBER OF CRABS
40
30
20
10
0
WITH EXTERNA
WITHOUT EXTERNA
2.0
2.4
4.0
4.4
6.0
6.4
8.0
8.4
10.0
10.4
12.0
12.4
14.0
14.4
16.0
16.4
18.0
18.4
CARAPACE WIDTH (mm.)

Figure 6. Size class distribution of E. depressus from the York River, January 1967 to November 1968.

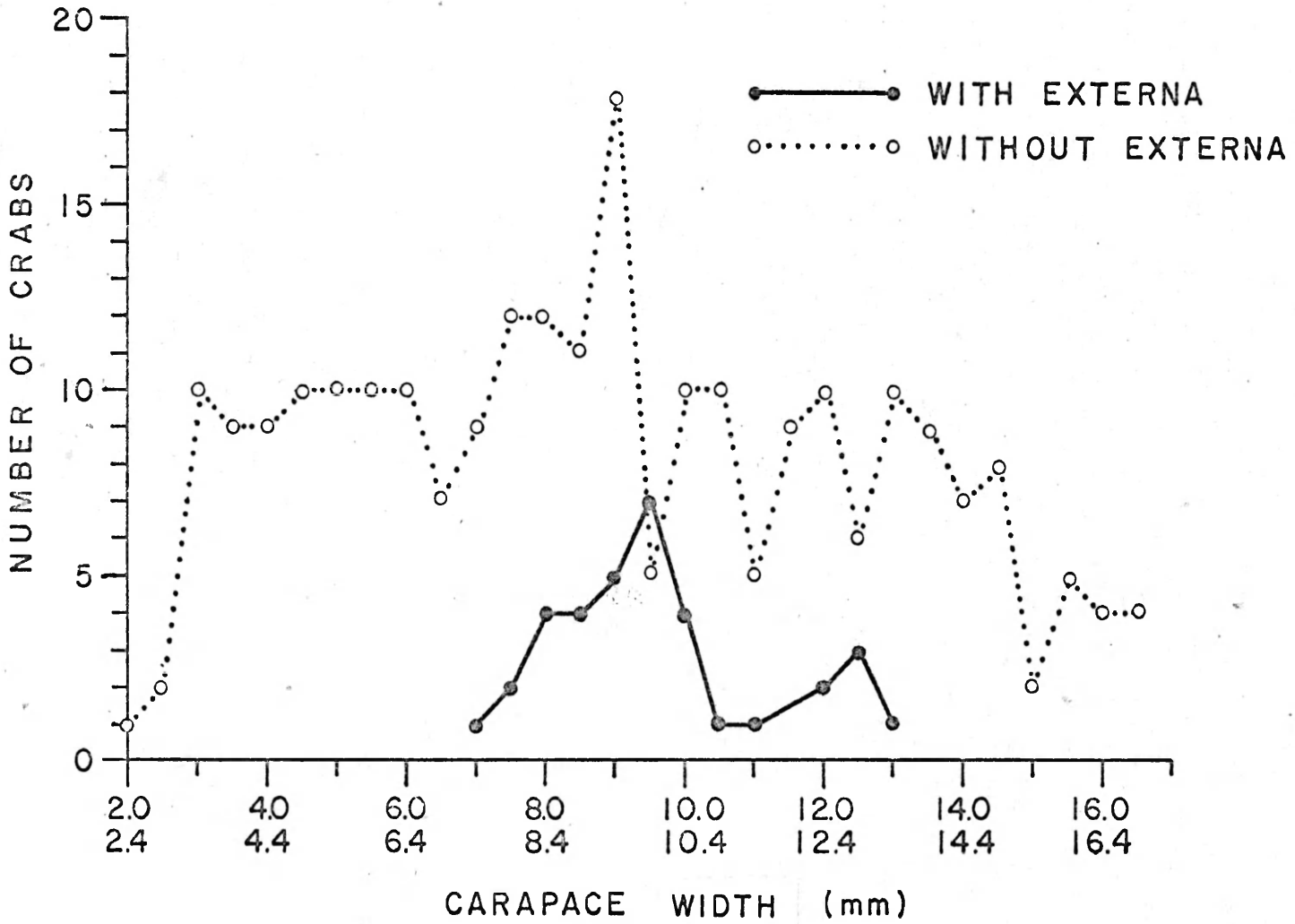
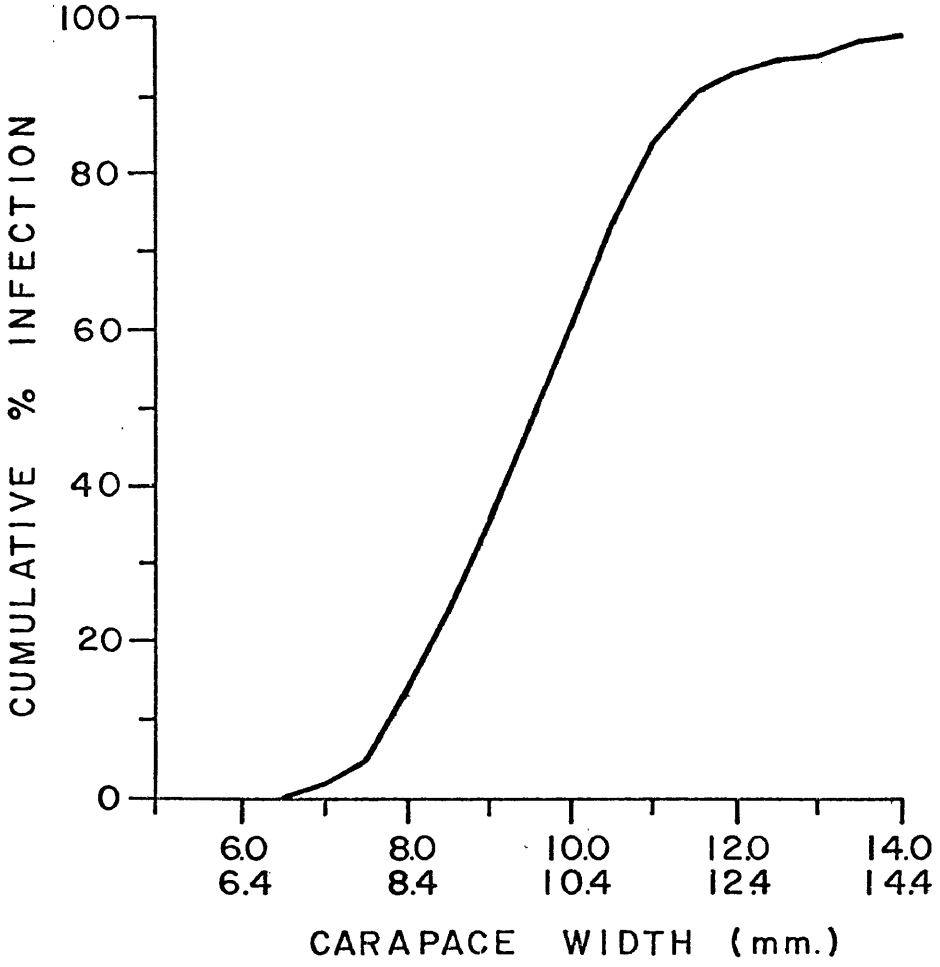

WITH EXTERNA
WITHOUT EXTERNA
NUMBER OF CRABS
0
5
10
15
20
2.0
2.4
4.0
4.4
6.0
6.4
8.0
8.4
10.0
10.4
12.0
12.4
14.0
14.4
16.0
16.4
CARAPACE WIDTH (mm)

Figure 7. Cumulative percentages of parasitized E. depressus from the eastern shore of Chesapeake Bay, January 1967 to November 1968.


100
80
60
40
20
0
CUMULATIVE % INFECTION
6.0
6.4
8.0
8.4
10.0
10.4
12.0
12.4
14.0
14.4
CARAPACE WIDTH (mm.)

resemble the female form (Reinhard, 1956). Both of these effects were observed in E. depressus and R. harrisii parasitized by L. panopaei.

During the course of the study one male and one female E. depressus became scarred and later molted. The female scarred naturally and molted about four months later without any increase in size. The male had its externa amputated, molted two and one-half months later, and increased in carapace width from 11.6 to 12.5 mm. No trace of a scar was found on either crab after the molt. Modification of the secondary sex characters was observed on both crabs. The male retained the broadened abdomen and had two female pleopods on the second abdominal segment and one on the fifth. One pair of male pleopods was found on the first segment and these appeared to be normal. In the female the endopods of all four pairs of pleopods were reduced.

## DISCUSSION

The large number of hosts reported for L. panopaei from past studies seems excessive. Although L. panopaei was originally described from P. herbstii, and has since been reported to occur on this host, the parasite has been in Chesapeake Bay for nearly six years and has never been found on P. herbstii or N. texana sayi. These xanthids are present in the same habitats as infected E. depressus and R. harrisii. Christmas (1968) has tentatively identified L. panopaei only on E. depressus and R. harrisii in Mississippi Sound. It is possible that there are different species, subspecies or genetic stocks of either host or parasite, [Foxon (1940) has suggested different "biological races" of Sacculina carcini] or that the hosts or parasites have been previously misidentified.

The externa was the only indicator of infection used in this study and the numbers of infected crabs are thus relative and do not represent total infection. Parasites in the internal stage may be present in a significant number of crabs. Of the 95 E. depressus collected at Hungars Creek on 10 and 11 June, 1968, fifteen originally without externa were known to have been infected. These crabs represent a 15.8% increase in total infection.

The levels of rhizocephalan infection vary by species and area. Christmas (1968) reported that the Loxothylacus texanus infection, parasitic upon Callinectes sapidus, varied from 0 to 50% in Mississippi and Alabama. Daugherty (1952) found L. texanus prevalence to be 16.4%

in Aransas Bay, Texas. Day (1935) found 13 to 73% Portunus holsatus infected with S. carcini, depending upon the time of year and size of the host. Ricketts and Calvin (1962) reported 1 to 10% Pugettia producta infected with Heterosaccus californicus in California, while 25% of Lophopanopeus bellus were parasitized by Sacculina sp. in Alaska. Reinhard (1942) reported 8.6 to 15% (overall 13.7%) Pagurus pubescens with Peltogaster paguri in different areas of Frenchmans Bay, Maine. MacKay (1943) found only 0.1% sacculinid infection of Cancer pagurus at Plymouth, England. Drepanorchis neglecta was reported by Hartknoll (1962) to infect 0.8% of Inachus leptochirus and 4.6% Macropodia longirostris at the Isle of Man. Okada and Miyashita (1935) found about 10% of young Eriocheir japonicus with Sacculina gregaria in the River Yura, Japan. In the lower York River, Van Engel et al (1966) found 54% E. depressus to be infected with L. panopaei.

The abundance of a parasite often varies directly with host density. High levels of infection and the greater number of hosts with multiple infection found on the oyster bars of the eastern shore of Chesapeake Bay may reflect the large host densities found in this habitat. Alternatively, or in addition, there may be better conditions for the dispersal of larvae and for survival of any life stage in this area.

Some species of introduced parasites reach high density levels shortly after introduction and then subside to lower density levels as they become established (Elton, 1958). The differences in levels of infection between the eastern shore and the York River may reflect the history of the parasite in the bay since it could have been first introduced to the western shore and spread to the east. Thus the higher

levels of infection of the eastern side of the bay may represent a more recent introduction or outbreak of the parasite. This assumption is supported by the gradual reduction of the levels of infection over the last few years in both areas, in particular the decrease from an infection of 54% of 595 E. depressus in the lower York River in 1964 (Van Engel et al, 1966) to 2.6% of 115 crabs in November, 1968.

The test of this hypothesis would be in a monitoring of the levels of infection on the eastern and western shores to see if they continue to decline, and a study of the levels of infection on the ocean coast of Virginia if the parasite spreads to that area. Whether it has been in the bay for some time and an unusual combination of biological and physical conditions resulted in an outbreak of L. panopaei, it appears that the parasite began its population increase on the western side and spread to the east. Thus the levels of infection on the eastern shore of the bay should continue to decline.

Although there is some evidence that sacculinid infections increase with increasing latitude (Ricketts and Calvin, 1962) and decreasing temperature (Knudsen, 1960), the levels of infection of L. panopaei for other areas are not known.

L. panopaei appears to exist in nearly the same salinity range as both of its host species. Although they were not shown to be infective, nauplii and externae may be able to live in salinities as high as 30 °/oo. Darnell (1959) and Gunter (1950) found L. texanus infection to be higher in more saline waters. The apparent absence of L. panopaei from the ocean coast of Virginia may be due to the prevailing water currents which could transport larvae away from the shore. The studies of Harrison, Norcross, Pore, and Stanley (1967) and of the

Chesapeake Bay Institute (1953) indicated that the currents flow from the ocean into the bay at the Cape Charles area. However, their studies are not detailed enough to be certain of current structure. Another explanation could be based on the low density of host species in the Cape Charles area. Neither host has been collected from this area and there are no intertidal oyster bars, a major habitat of E. depressus, from Cape Charles to Old Plantation Creek. Thirdly, the parasite may not yet have had time to spread to the ocean side. There is a further possibility that the parasite may be transported to the ocean side by the transfer of infected hosts on oysters or oyster shells from areas in which it is now present.

Delage (1884, in Day, 1935) found nauplii in the externa of S. carcini on Carcinus maenas from April to November at Roscoff, France. Orton (1936) showed a similar seasonal occurrence at Plymouth, England. In the Mersey Estuary, England, Day (1935) found S. carcini on Portunus holsatus producing nauplii from May to July. In the Clyde Sea, Foxon (1940) concluded that the breeding of S. carcini parasitizing C. maenas occurs over the entire year with a maximum from August through December and a minimum from January to March. The reproductive season of L. panopaei was at least from May to November in Chesapeake Bay. Delage (1884, in Day, 1935) concluded that S. carcini spends 20 to 21 months as an interna. However, later work by Day (1935), Orton (1936) and Foxon (1940) indicated that the normal length of the life cycle for this parasite, from cypris to mature externa, is nine months to one year. The internal stage of L. panopaei was shown to last at least eight and one-half months in one case.

The size range of hosts with externae indicates that infection may take place at or before sexual maturity and any size thereafter in the life of the hosts. Although there were many hosts in the 7.5 to 12.0 mm size range, it is impossible to determine the age of maximum infection on this basis. E. depressus and N. texana sayi reared from zoeae in the laboratory have varied in size from 4.8 to 11.0 mm in ten to eleven months (W. A. Van Engel, personal communication). As xanthids undergo little or no winter growth (December through March), potential hosts could have been hatched and infected in late summer and the externa could appear the following spring when the host is quite large. These possibilities, and the variability in growth rates observed in the laboratory, make it difficult to relate host size and life stage (or age) at which infection took place.

The externae of several rhizocephalans have been found to exhibit different colors, which are related to the age of the parasite (Foxon, 1940; Reinhard, 1942). In general, the darker the color of the externa the older or more mature the parasite. In L. panopaei, Van Engel et al (1966) noted that the colors varied from white in the smallest to brown in the largest. Dillon and Zwerner (1967) stated that in hosts with multiple infections the largest externa was always the darker.

Light colored externae were found more frequently in the summer while older, darker externae were more common in the winter, suggesting an annual cycle. The factors which determine the color and condition of the externa are unknown. The sequence begins with white and progresses to dark brown or black, the position of the reddish-brown stage being uncertain but probably occurring between white and light brown. However, the actual age of these externae is unknown and the

presence of fouling organisms, such as barnacles, is also a poor indication of age due to variations in their growth rates.

The occurrence of many young white and light brown externae in June and July suggests that many crabs were infected from May to November, assuming an interna stage lasting eight to thirteen months. Several dark brown (old) externae found in November and December suggest that the externa may exist for six months, a year and six months, or longer. Crabs with dark externae have been held five and one-half months in the laboratory. However, both white and dark brown externae were found throughout the year. Many small, white externae were found on R. harrisii in December, suggesting infection from November to April of the preceding winter, again assuming an internal stage of eight to thirteen months. The breeding season of L. panopaei may this extend from mid-April through mid-November.

The small number of crabs with scars could be taken as evidence that the externa persists for the life of the host, but if the host molts after a previous infection all traces of a scar will be removed.

No pattern of growth was observed for mature or immature externae. The lack of growth of immature externae may be due to experimental conditions, normal growth patterns, or the absence of cypris males. Development and maturation of Peltogaster and Sacculina depend on cypris males that attach to the mantle opening of juvenile externae and inject cells into the mantle cavity (Ichikawa and Yanagimachi, 1960). These cells produce spermatozoa for fertilization. If cypris males of L. panopaei exist, they had no opportunity to come in contact with immature externae as all crabs were held in filtered seawater. The

relatively constant size of the adult externae may represent a natural stability, although color and texture changes of the adult externae suggests some change in size. Irregularities of shape and the contractions of the parasite may have prevented accurate and precise measurements.

Rhizocephalans have been reported to parasitize females more frequently than males (Perez, 1927, 1931b; Reinhard, 1942), although the reverse has been noted (Perez, 1931a). Van Engel et al (1966) found males and females to be about equally infected. In this study the prevalence of infection was found to be higher for females than for males.

However, this may not imply a greater susceptibility of females or resistance of males, but rather a greater mortality of infected males. The highest prevalence of infection was found on the eastern shore of the bay, an area which also had the highest ratio of females to males (Table 7). In areas where infection was lower the sex ratio was essentially 1:1.

Perez (1931b) found an unimodal distribution of the frequency of infection by Chlorogaster sulcatus and the size of Eupagurus cuanensis. Reinhard (1942) states that most Pagurus pubescens parasitized by Peltogaster paguri fell into the medium size classes. An unimodal distribution among the larger crabs and an increasing percentage of infection with increasing host size was shown by Day (1935). Finally, Christmas (1968) found the relationship between the number of L. texanus and the size of C. sapidus to be multimodal. The frequency distribution of L. panopaei on the carapace width of E. depressus was unimodal and most crabs with externae were of medium size (Fig. 4). The small number of crabs of carapace width greater than 12 mm with externae suggests

resistance to infection or increased liability of death due to the parasite.

Current theory favors an explanation of the effects produced by rhizocephalan parasitism based on the androgenic gland. Hormones of the androgenic gland cause development of all sex characters of male crustaceans. Rhizocephalans presumably remove the androgenic hormone, causing feminization of the male (Charniaux-Cotton, 1960). The term parasitic castration is thus a misnomer.

One important effect of sacculinids upon their decapod hosts is a loss of reproductive ability. Even if the gonad remains intact, mating could probably not occur due to mechanical interference by the externa. Further, if a previously infected individual rids itself of the externa, assuming the gonad is still intact and can produce viable gametes, the male would still be unable to copulate due to pleopod degeneration or modification, while the female would be unable to retain eggs for the same reason. My observations demonstrate that some modifications of the secondary sex structures can be carried through at least one molt after the externa is removed. The parasite also causes a cessation of growth by rendering the host incapable of molting thereby allowing the accumulation of fouling organisms, erosion of the exoskeleton, and perhaps preventing the elimination of other parasites, expecially those which infest the exoskeleton or gills. All of these effects could affect the scavenging roles of the infected hosts. L. panopaei could also render the host less able to compete with uninfected individuals of the same or related species or become more liable to predation or other stress conditions by physiological weakening or mechanical interference. Thus the effects of sacculinid infection on

the individual host may be quite profound.

It is difficult to determine the effect of the parasite on the xanthid population. Xanthids exhibit a clumped distribution and the habitats in which they are most commonly found (pilings, oyster bars, among sponges) are difficult to sample quantitatively. Other factors, such as the mobility of the crabs and possible offshore migrations in the winter, compound the difficulties of making accurate population estimates.

The effects of L. panopaei on the xanthid populations of the bay are uncertain. The relative abundance of E. depressus may have decreased while that of N. texana sayi may have increased since the parasite was introduced, at least in the York and Rappahannock rivers (J. D. Andrews and W. A. Van Engel, personal communications). Cowles (1930) found N. texana sayi to be the most abundant crab in Chesapeake Bay. Ryan (1956) found E. depressus to be the most abundant xanthid on oyster bars while N. texana sayi was so scarce that he concluded a decline in numbers since Cowles' study. However, Ryan made very few stations in the deeper waters of southern Chesapeake Bay where both Cowles and I have found N. texana sayi to be very abundant. All patterns of distribution and abundance are questionable due to difficulties of consistently obtaining large numbers of xanthids from their diverse habitats and the great variability often found in species composition in similar habitats and areas.

I have found the relative abundance of xanthid species to differ by salinity in the case of N. texana sayi and R. harrisii, and by general area and habitat in the case of E. depressus and N. texana sayi. E. depressus was more abundant on both sides of the eastern shore of

Virginia while N. texana sayi was more abundant in the rivers of the western shore and the southern part of Chesapeake Bay. Further differences in the relative abundance of these two species were observed between habitats and tidal zones. E. depressus was more common intertidally and on oyster bars while N. texana sayi was more common subtidally and on pilings. In nearly every collection site more than one species of xanthid was found. Seasonal differences in abundance were also indicated, at least in the case of E. depressus on oyster bars. Feng (1957) found E. depressus to be the most abundant xanthid in the Rappahannock River. From the mouth of the York River to Gloucester Point P. herbstii and N. texana sayi were more abundant, but E. depressus and R. harrisii more abundant farther upstream. Uncertainties of distribution make statements of absolute abundance of any xanthid species questionable at this time.

High prevalence of infection was found at Cherrystone and Hungars creeks in the summers of 1967 and 1968, yet there appeared to be no decline in the abundance of E. depressus. Although L. panopaei could conceivably have profound effects on its host populations and there is some evidence of a recent decline in E. depressus, there exists a considerable body of evidence that environmental factors are more important in controlling the abundance of some species than the size of the brood stock (Pearson, 1948; Ricker, 1958; Kinne, 1967). In conclusion, on the basis of my data no evidence of a decline of E. depressus was observed in 1967 or 1968.

The observations of J. D. Andrews, along with the data of Feng (1957), indicate a decline of E. depressus in the Rappahannock River, possibly due to L. panopaei. However, variations in abundance of

xanthids reported in the literature and observed by W. A. Van Engel and J. D. Andrews may indicate natural fluctuations of xanthids. The existence of an epizootic wave of L. panopaei may have been obscured in the York River and the eastern shore of the bay during 1967-68. L. panopaei may have already decimated the E. depressus population in the York River. On the eastern shore the epizootic may now be reaching a peak of infection before the decline of the host population.

Appendix 1. List of xanthids collected by area and chronological order with salinity, temperature, prevalence of externa, habitat, and zone indicated. S = scar; B = oyster bar; P = piling; M = mud; OT = oyster tray; A = algae (mostly Agardhiella); I = intertidal; S = subtidal; E = E. depressus; R = R. harrisii; P = P. herbstii; N = N. texana sayi; H = Hexapanopeus angustifrons.

| AREA | Date | Water Temperature (°C) | Salinity (°/oo) | Number, Sex, and Species | Number with Externa | Number with Multiple Externa | Number with Scars | Habitat or water Depth (Meters) | Zone |
|---|---|---|---|---|---|---|---|---|---|
| CHESAPEAKE BAY | | | | | | | | | |
| Western Shore | 1967 | | | | | | | | |
| Gloucester Point | 24 Jan. | 8.0 | 18.5 | 9E♂ | 3 | 0 | 0 | P | S |
| Area | | 8.0 | 18.5 | 17E♀ | 6 | 1 | 1 | P | S |
| | | 8.0 | 18.5 | 50N♂ | | | | P | S |
| | | 8.0 | 18.5 | 53N♀ | | | | P | S |
| | | 8.0 | 18.5 | 2P♂ | | | | P | S |
| | | 8.0 | 18.5 | 1P♀ | | | | P | S |
| Indian Field Cr. | 19 July | 25.7 | 19.5 | 1P♂ | | | | M | I |
| | | 25.7 | 19.5 | 1P♀ | | | | M | I |
| Felgates Creek | 19 July | 26.5 | 18.7 | 2R♂ | 0 | 0 | 0 | M | I |
| | | 26.5 | 18.7 | 2R♀ | 0 | 0 | 0 | M | I |
| | | 26.5 | 18.7 | 1P♂ | | | | M | I |
| Upper Perrin R. | 17 Aug. | 26.0 | 21.0 | 1R♀ | 0 | 0 | 1 | P | S |
| Mid Perrin R. | 17 Aug. | 26.0 | 21.4 | 1E♀ | 1 | 0 | 0 | P | S |
| | | 26.0 | 21.4 | 2N♂ | | | | P | S |
| | | 26.0 | 21.4 | 10N♀ | | | | P | S |
| | | 26.0 | 21.4 | 1P♂ | | | | P | S |
| | | 26.0 | 21.4 | 1P♀ | | | | P | S |

Appendix 1. (Continued)

| AREA | Date | Water Temperature (°C) | Salinity (°/oo) | Number, Sex, and Species | Number with Externa | Number with Multiple Externa | Number with Scars | Habitat or water Depth (Meters) | Zone |
|---|---|---|---|---|---|---|---|---|---|
| | 1967 | | | | | | | | |
| Perrin R. Mouth | 17 Aug. | 26.2 | 21.6 | 2E♂ | 2 | 0 | 0 | P | S |
| | | 26.2 | 21.6 | 1E♀ | 1 | 0 | 0 | P | S |
| | | 26.2 | 21.6 | 1N♂ | | | | P | S |
| | | 26.2 | 21.6 | 7N♀ | | | | P | S |
| | | 26.2 | 21.6 | 3P♂ | | | | P | S |
| York R. Mouth | 17 Aug. | 27.6 | 21.2 | 8E♂ | 0 | 0 | 0 | P | S |
| | | 27.6 | 21.2 | 11E♀ | 0 | 0 | 0 | P | S |
| | | 27.6 | 21.2 | 14N♂ | | | | P | S |
| | | 27.6 | 21.2 | 27N♀ | | | | P | S |
| Gloucester Point | 7 Sept. | -- | -- | 1E♀ | 0 | 0 | 0 | P | S |
| | | -- | -- | 6N♂ | | | | P | S |
| | | -- | -- | 22N♀ | | | | P | S |
| | 21 Sept. | 22.9 | -- | 2E♂ | 0 | 0 | 0 | P | S |
| | | 22.9 | -- | 1E♀ | 1 | 0 | 0 | P | S |
| | | 22.9 | -- | 1N♂ | | | | P | S |
| | | 22.9 | -- | 3N♀ | | | | P | S |
| | 23 Sept. | -- | 19.5 | 1E♂ | 1 | 0 | 0 | P | S |
| | | -- | 19.5 | 2E♀ | 1 | 0 | 0 | P | S |
| | | -- | 19.5 | 1N♂ | | | | P | S |
| | | -- | 19.5 | 9N♀ | | | | P | S |
| | 25 Sept. | 20.1 | 20.2 | 1E♂ | 1 | 0 | 0 | P | S |
| | | 20.1 | 20.2 | 53N♂ | | | | P | S |
| | | 20.1 | 20.2 | 119N♀ | | | | P | S |

Appendix 1. (Continued)

| AREA | Date | Water Temperature (°C) | Salinity (°/oo) | Number, Sex, and Species | Number with Externa | Number with Multiple Externa | Number with Scars | Habitat or water Depth (Meters) | Zone |
|---|---|---|---|---|---|---|---|---|---|
| | 1967 | | | | | | | | |
| York R. Mouth | 19 Oct. | 16.5 | 20.7 | 3E♂ | 0 | 0 | 0 | P | S |
| | | 16.5 | 20.7 | 3E♀ | 0 | 0 | 0 | P | S |
| | | 16.5 | 20.7 | 1N♀ | | | | P | S |
| Perrin R. Mouth | 19 Oct. | -- | 20.7 | 1E♂ | 0 | 0 | 0 | P | S |
| | | -- | 20.7 | 3E♀ | 2 | 0 | 0 | P | S |
| | | -- | 20.7 | 2N♂ | | | | P | S |
| | | -- | 20.7 | 5N♀ | | | | P | S |
| Gloucester Point | 25 Oct. | 17.3 | 20.2 | 4N♂ | | | | P | I |
| | | 17.3 | 20.2 | 9N♀ | | | | P | I |
| | | -- | 20.1 | 1E♂ | 0 | 0 | 0 | P | I |
| | | -- | 20.1 | 1N♂ | | | | P | I |
| | | -- | 20.1 | 1N♀ | | | | P | I |
| | | -- | 18.1 | 1E♂ | 1 | 0 | 0 | B | I |
| | | -- | 18.1 | 1E♀ | 1 | 1 | 0 | B | I |
| | | -- | 18.1 | 1N♂ | | | | B | I |
| | | -- | 18.1 | 1N♀ | | | | B | I |
| | | -- | 18.1 | 1P♂ | | | | B | I |
| | | -- | 18.1 | 1P♀ | | | | B | I |
| Yorktown | 14 Nov. | 12.5 | 19.9 | 9N♂ | | | | P | S |
| | | 12.5 | 19.9 | 23N♀ | | | | P | S |
| Queens Creek | 30 Nov. | 5.6 | 18.8 | 2E♀ | 2 | 1 | 0 | B | I |
| | | 5.6 | 18.8 | 6N♂ | | | | B | I |
| | | 5.6 | 18.8 | 8N♀ | | | | B | I |

Appendix 1. (Continued)

| AREA | Date | Water Temperature (°C) | Salinity (°/oo) | Number, Sex, and Species | Number with Externa | Number with Multiple Externa | Number with Scars | Habitat or water Depth (Meters) | Zone |
|---|---|---|---|---|---|---|---|---|---|
| | 1967 | | | | | | | | |
| Queens Creek | 30 Nov. | 5.6 | 18.8 | 6P♂ | | | | B | I |
| (Cont.) | | 5.6 | 18.8 | 2P♀ | | | | B | I |
| Gloucester Point | 16 Nov. | -- | -- | 5E♂ | 3 | 1 | 0 | M | I |
| | | -- | -- | 5E♀ | 4 | 0 | 0 | M | I |
| | | -- | -- | 2N♀ | | | | M | I |
| | | -- | -- | 7P♂ | | | | M | I |
| | 1968 | | | | | | | | |
| Gloucester Point | 14 Mar. | 5.3 | 20.5 | 7E♂ | 2 | 0 | 0 | P | S |
| | | 5.3 | 20.5 | 16E♀ | 1 | 0 | 0 | P | S |
| | | 5.3 | 20.5 | 32N♂ | | | | P | S |
| | | 5.3 | 20.5 | 39N♀ | | | | P | S |
| | | 5.3 | 20.5 | 1P♂ | | | | P | S |
| Rappahannock R. | 2 Apr. | 11.9 | 4.6 | 10R♂ | 0 | 0 | 0 | 6 | - |
| (R-35) | | 11.9 | 4.6 | 21R♀ | 0 | 0 | 0 | 6 | - |
| Rappahannock R. | 2 Apr. | 12.3 | 0.6 | 38R♂ | 0 | 0 | 0 | 6 | - |
| (R-40) | | 12.3 | 0.6 | 28R♀ | 0 | 0 | 0 | 6 | - |
| York River | 18 Apr. | 13.9 | 16.1 | 31N♂ | | | | 9 | - |
| (Y-10) | | 13.9 | 16.1 | 37N♀ | | | | 9 | - |
| York River | 18 Apr. | 14.7 | 14.1 | 3N♂ | | | | 10 | - |
| (Y-15) | | 14.7 | 14.1 | 1R♀ | 0 | 0 | 0 | 10 | - |
| York River (Y-20) | 18 Apr. | 14.8 | 11.1 | 1N♂ | | | | 6 | - |
| York River (Y-25) | 18 Apr. | 15.2 | 8.5 | 1P♂ | | | | 10 | - |

Appendix 1. (Continued)

| AREA | Date | Water Temperature (°C) | Salinity (°/oo) | Number, Sex, and Species | Number with Externa | Number with Multiple Externa | Number with Scars | Habitat or water Depth (Meters) | Zone |
|---|---|---|---|---|---|---|---|---|---|
| | 1968 | | | | | | | | |
| Pamunkey R. | 18 Apr. | 15.7 | 3.4 | 23R♂ | 0 | 0 | 0 | 6 | - |
| (P-30) | | 15.7 | 3.4 | 41R♀ | 0 | 0 | 0 | 6 | - |
| Pamunkey R. (P-40) | 16 Apr. | 16.6 | 0.1 | 1R♀ | 0 | 0 | 0 | 6 | - |
| Queens Creek | 25 Apr. | 17.7 | 15.9 | 6N♂ | | | | B | I |
| | | 17.7 | 15.9 | 5N♀ | | | | B | I |
| | | 17.7 | 15.9 | 3P♂ | | | | B | I |
| | | 17.7 | 15.9 | 2P♀ | | | | B | I |
| | | 17.7 | 15.9 | 1R♂ | 0 | 0 | 0 | B | I |
| Gloucester Point | 11 May | -- | -- | 2E♂ | 0 | 0 | 1 | M | I |
| | | -- | -- | 2E♀ | 0 | 0 | 0 | M | I |
| | | -- | -- | 4P♂ | | | | M | I |
| | | -- | -- | 4P♀ | | | | M | I |
| | 21 June | 23.5 | 18.2 | 1N♂ | | | | P | S |
| | | 23.5 | 18.2 | 1N♀ | | | | P | S |
| York River Mouth | 21 June | 25.5 | 18.7 | 21E♂ | 0 | 0 | 0 | P | S |
| | | 25.5 | 18.7 | 23E♀ | 0 | 0 | 0 | P | S |
| | | 25.5 | 18.7 | 5N♂ | | | | P | S |
| | | 25.5 | 18.7 | 9N♀ | | | | P | S |
| Perrin R. Mouth | 21 June | 24.5 | 18.5 | 7E♂ | 0 | 0 | 0 | P | S |
| | | 24.5 | 18.5 | 6E♀ | 1 | 0 | 0 | P | S |
| | | 24.5 | 18.5 | 2N♂ | | | | P | S |
| | | 24.5 | 18.5 | 2N♀ | | | | P | S |

Appendix 1. (Continued)

| AREA | Date | Water Temperature (°C) | Salinity (°/oo) | Number, Sex, and Species | Number with Externa | Number with Multiple Externa | Number with Scars | Habitat or water Depth (Meters) | Zone |
|---|---|---|---|---|---|---|---|---|---|
| | 1968 | | | | | | | | |
| Mid Perrin R. | 21 June | 25.0 | -- | 1N ♂ | | | | P | S |
| | | 25.0 | -- | 1N ♀ | | | | P | S |
| Queens Creek | 4 Sept. | 26.5 | 20.4 | 5E ♂ | 3 | 1 | 0 | B | I |
| | | 26.5 | 20.4 | 1E ♀ | 0 | 0 | 0 | B | I |
| | | 26.5 | 20.4 | 13N ♂ | | | | B | I |
| | | 26.5 | 20.4 | 32N ♀ | | | | B | I |
| | | 26.5 | 20.4 | 44P ♂ | | | | B | I |
| | | 26.5 | 20.4 | 42P ♀ | | | | B | I |
| | | 26.5 | 20.4 | 2R ♂ | 0 | 0 | 1 | B | I |
| | | 26.5 | 20.4 | 2R ♀ | 0 | 0 | 0 | B | I |
| Gloucester Point | 10 Oct. | -- | -- | 7N ♂ | | | | M | I |
| | | -- | -- | 7N ♀ | | | | M | I |
| | 15 Oct. | -- | -- | 4N ♂ | | | | M | I |
| | | -- | -- | 5N ♀ | | | | M | I |
| | 8 Nov. | 16.4 | 22.8 | 26E ♂ | 0 | 0 | 0 | P | S |
| | | 16.4 | 22.8 | 26E ♀ | 1 | 1 | 0 | P | S |
| | | 16.4 | 22.8 | 135N ♂ | | | | P | S |
| | | 16.4 | 22.8 | 118N ♀ | | | | P | S |
| | | 16.4 | 22.8 | 118N ? | | | | P | S |
| | | 16.4 | 22.8 | 1P ♀ | | | | P | S |
| | | 16.4 | 22.8 | 37E ♂ | 1 | 0 | 0 | OT | S |
| | | 16.4 | 22.8 | 26E ♀ | 2 | 0 | 0 | OT | S |
| | | 16.4 | 22.8 | 4N ♀ | | | | OT | S |

Appendix 1. (Continued)

| AREA | Date | Water Temperature (°C) | Salinity (°/oo) | Number, Sex, and Species | Number with Externa | Number with Multiple Externa | Number with Scars | Habitat or water Depth (Meters) | Zone |
|---|---|---|---|---|---|---|---|---|---|
| | 1968 | | | | | | | | |
| Gloucester Point (Cont.) | 8 Nov. | 16.4 | 22.8 | 2N ? | | | | OT | S |
| | | 16.4 | 22.8 | 7P ♂ | | | | OT | S |
| | | 16.4 | 22.8 | 6P ♀ | | | | OT | S |
| | 14 Nov. | -- | -- | 1N ♂ | | | | M | I |
| | | -- | -- | 3N ♀ | | | | M | I |
| | 28 Nov. | -- | -- | 5N ♂ | | | | M | I |
| | | -- | -- | 7N ♀ | | | | M | I |
| Eastern Shore | 1967 | | | | | | | | |
| Cherrystone Creek | 6 July | 26.2 | 21.8 | 3E ♂ | 3 | 1 | 0 | B | I |
| | | 26.2 | 21.8 | 16E ♀ | 14 | 8 | 0 | B | I |
| | | 26.2 | 21.8 | 5N ♂ | | | | B | I |
| | | 26.2 | 21.8 | 1N ♀ | | | | B | I |
| | | 26.2 | 21.8 | 3P ♂ | | | | B | I |
| | | 26.2 | 21.8 | 1P ♀ | | | | B | I |
| | | 26.2 | 21.8 | 1R ♀ | 1 | 0 | 0 | B | I |
| Hungars Creek | 6 July | 28.2 | 21.5 | 15E ♂ | 13 | 2 | 0 | B | I |
| | | 28.2 | 21.5 | 36E ♀ | 31 | 12 | 0 | B | I |
| | | 28.2 | 21.5 | 2N ♂ | | | | B | I |
| | | 28.2 | 21.5 | 2N ♀ | | | | B | I |
| | | 28.2 | 21.5 | 8P ♂ | | | | B | I |
| | | 28.2 | 21.5 | 6P ♀ | | | | B | I |
| | | 28.2 | 21.5 | 1R ♂ | 1 | 0 | 0 | B | I |
| | | 28.2 | 21.5 | 1R ♀ | 0 | 0 | 0 | B | I |

Appendix 1. (Continued)

| AREA | Date | Water Temperature (°C) | Salinity (°/oo) | Number, Sex, and Species | Number with Externa | Number with Multiple Externa | Number with Scars | Habitat or water Depth (Meters) | Zone |
|---|---|---|---|---|---|---|---|---|---|
| | 1967 | | | | | | | | |
| Onancock Creek | 10 Dec. | 7.5 | 17.5 | 1R ♂ | 1 | 0 | 0 | A | S |
| | | 7.5 | 17.5 | 1R ♀ | 1 | 0 | 0 | A | S |
| Messongo Creek | 10 Dec. | 7.5 | 13.5 | 1E ♂ | 1 | 0 | 0 | A | S |
| | | 7.5 | 13.5 | 1P ♂ | | | | A | S |
| | | 7.5 | 13.5 | 3R ♂ | 3 | 3 | 0 | A | S |
| | | 7.5 | 13.5 | 9R ♀ | 8 | 5 | 0 | A | S |
| Hungars Creek | 10 Dec. | 9.0 | 19.9 | 6E ♂ | 5 | 1 | 0 | B | I |
| | | 9.0 | 19.9 | 5E ♀ | 5 | 0 | 0 | B | I |
| | | 9.0 | 19.9 | 2P ♂ | | | | B | I |
| | | 9.0 | 19.9 | 3P ♀ | | | | B | I |
| | | 9.0 | 19.9 | 1R ♂ | 1 | 0 | 0 | B | I |
| | | 9.0 | 19.9 | 1R ♀ | 0 | 0 | 0 | B | I |
| Cherrystone Creek | 10 Dec. | 10.5 | 21.9 | 3E ♂ | 3 | 1 | 0 | B | I |
| | | 10.5 | 21.9 | 11E ♀ | 5 | 2 | 1 | B | I |
| | | 10.5 | 21.9 | 1N ♀ | | | | B | I |
| | | 10.5 | 21.9 | 2R ♀ | 0 | 0 | 0 | B | I |
| | 1968 | | | | | | | | |
| Hungars Creek | 2 May | 17.9 | 20.2 | 1E ♀ | 0 | 0 | 0 | B | I |
| Smiths Beach | 2 May | 18.0 | 20.8 | 2E ♂ | 0 | 0 | 0 | P | S |
| | | 18.0 | 20.8 | 7N ♂ | | | | P | S |
| | | 18.0 | 20.8 | 12N ♀ | | | | P | S |

Appendix 1. (Continued)

| AREA | Date | Water Temperature (°C) | Salinity (°/oo) | Number, Sex, and Species | Number with Externa | Number with Multiple Externa | Number with Scars | Habitat or water Depth (Meters) | Zone |
|---|---|---|---|---|---|---|---|---|---|
| | 1968 | | | | | | | | |
| Cherrystone Creek | 2 May | 20.5 | 21.4 | 2E ♂ | 0 | 0 | 0 | A | I |
| | | 20.5 | 21.4 | 1E ♀ | 1 | 0 | 0 | A | I |
| | | 20.5 | 21.4 | 4N ♂ | | | | A | I |
| | | 20.5 | 21.4 | 5N ♀ | | | | A | I |
| | | 20.5 | 21.4 | 3P ♂ | | | | A | I |
| | | 20.5 | 21.4 | 2P ♀ | | | | A | I |
| Old Plantation Cr. | 10 June | 25.3 | 22.9 | 2E ♂ | 0 | 0 | 0 | B | I |
| | | 25.3 | 22.9 | 4E ♀ | 1 | 0 | 0 | B | I |
| | | 25.3 | 22.9 | 1N ♂ | | | | B | I |
| | | 25.3 | 22.9 | 2P ♂ | | | | B | I |
| Cherrystone Creek | 10 June | 29.4 | 26.1 | 6E ♂ | 0 | 0 | 0 | B | I |
| | | 29.4 | 26.1 | 12E ♀ | 9 | 3 | 0 | B | I |
| | | 29.4 | 26.1 | 9N ♂ | | | | B | I |
| | | 29.4 | 26.1 | 1N ♀ | | | | B | I |
| | | 29.4 | 26.1 | 10P ♂ | | | | B | I |
| | | 29.4 | 26.1 | 6P ♀ | | | | B | I |
| | | 29.4 | 26.1 | 3E ♂ | 1 | 0 | 0 | P | S |
| | | 29.4 | 26.1 | 9E ♀ | 1 | 0 | 1 | P | S |
| | | 29.4 | 26.1 | 21N ♂ | | | | P | S |
| | | 29.4 | 26.1 | 28N ♀ | | | | P | S |
| | | 29.4 | 26.1 | 10P ♂ | | | | P | S |
| | | 29.4 | 26.1 | 6P ♀ | | | | P | S |

Appendix 1. (Continued)

| AREA | Date | Water Temperature (°C) | Salinity (°/oo) | Number, Sex, and Species | Number with Externa | Number with Multiple Externa | Number with Scars | Habitat or water Depth (Meters) | Zone |
|---|---|---|---|---|---|---|---|---|---|
| | 1968 | | | | | | | | |
| Hungars Creek | 10 June | 28.5 | 19.6 | 26E ♂ | 6 | 0 | 0 | B | I |
| | | 28.5 | 19.6 | 58E ♀ | 21 | 3 | 0 | B | I |
| | | 28.5 | 19.6 | 4N ♂ | | | | B | I |
| | | 28.5 | 19.6 | 3N ♀ | | | | B | I |
| | | 28.5 | 19.6 | 26P ♂ | | | | B | I |
| | | 28.5 | 19.6 | 36P ♀ | | | | B | I |
| | 11 June | 28.4 | 19.9 | 2E ♂ | 0 | 0 | 0 | B | I |
| | | 28.4 | 19.9 | 9E ♀ | 1 | 0 | 0 | B | I |
| | | 28.4 | 19.9 | 18P ♂ | | | | B | I |
| | | 28.4 | 19.9 | 14P ♀ | | | | B | I |
| Chesapeake Bay Bridge | 11 June | 23.7 | 30.4 | 18N ♂ | | | | P | S |
| | | 23.7 | 30.4 | 10N ♀ | | | | P | S |
| Fishermans Island (North Side) | 11 June | 23.8 | 30.0 | 16N ♂ | | | | P | S |
| | | 23.8 | 30.0 | 23N ♀ | | | | P | S |
| Cape Charles | 11 June | 21.9 | 29.3 | 6N ♂ | | | | P | S |
| | | 21.9 | 29.3 | 7N ♀ | | | | P | S |
| Cherrystone Creek | 28 June | -- | 20.8 | 7E ♂ | 2 | 1 | 0 | B | I |
| | | -- | 20.8 | 32E ♀ | 23 | 8 | 0 | B | I |
| | | -- | 20.8 | 6N ♂ | | | | B | I |
| | | -- | 20.8 | 15N ♀ | | | | B | I |
| Hungars Creek | 28 June | -- | 19.5 | 7E ♂ | 2 | 0 | 0 | B | I |
| | | -- | 19.5 | 30E ♀ | 19 | 0 | 0 | B | I |

Appendix 1. (Continued)

| AREA | Date | Water Temperature (°C) | Salinity (°/oo) | Number, Sex, and Species | Number with Externa | Number with Multiple Externa | Number with Scars | Habitat or Water Depth (Meters) | Zone |
|---|---|---|---|---|---|---|---|---|---|
| | 1968 | | | | | | | | |
| Hungars Creek | 2 Aug. | -- | 21.3 | 50E ♂ | 16 | 1 | 0 | B | I |
| | | -- | 21.3 | 120E ♀ | 58 | 13 | 0 | B | I |
| | | -- | 21.3 | 4N ♂ | | | | B | I |
| | | -- | 21.3 | 1N ♀ | | | | B | I |
| | | -- | 21.3 | 10P ♂ | | | | B | I |
| | | -- | 21.3 | 14P ♀ | | | | B | I |
| Bay Stations | 1968 | | | | | | | | |
| Bay East | | | | | | | | | |
| 1 | 24 Sept. | 23.3 | 21.1 | 20N ♂ | | | | 14 | - |
| | | 23.3 | 21.1 | 32N ♀ | | | | 14 | - |
| 2 | 24 Sept. | 23.4 | 26.9 | 9N ♂ | | | | 24 | - |
| | | 23.4 | 26.9 | 3N ♀ | | | | 24 | - |
| 3 | 25 Sept. | 22.9 | 24.7 | 27N ♂ | | | | 7 | - |
| | | 22.9 | 24.7 | 41N ♀ | | | | 7 | - |
| 4 | 25 Sept. | 23.3 | 28.8 | 4N ♂ | | | | 26 | - |
| 5 | 25 Sept. | 23.4 | 26.8 | 1N ♀ | | | | 5 | - |
| | | 23.4 | 26.8 | 1N ♂ | | | | 5 | - |
| 6 | 25 Sept. | 23.8 | 30.9 | 1N ♀ | | | | -- | - |
| 7 | 25 Sept. | 23.3 | 27.5 | 1N ♂ | | | | 10 | - |
| Bay South | | | | | | | | | |
| 8 | 25 Sept. | 23.0 | 28.3 | 2N ♂ | | | | 8 | - |
| | | 23.0 | 28.3 | 3N ♀ | | | | 8 | - |
| | | 23.0 | 28.3 | 1H ♀ | | | | 8 | - |

Appendix 1. (Continued)

| AREA | Date | Water Temperature (°C) | Salinity (°/oo) | Number, Sex, and Species | Number with Externa | Number with Multiple Externa | Number with Scars | Habitat or water Depth (Meters) | Zone |
|---|---|---|---|---|---|---|---|---|---|
| | 1968 | | | | | | | | |
| Bay South | | | | | | | | | |
| 9 | 25 Sept. | 23.9 | 26.9 | 43N ♂ | | | | 5 | - |
| | | 23.9 | 26.9 | 65N ♀ | | | | 5 | - |
| | | 23.9 | 26.9 | 14N ? | | | | 5 | - |
| 10 | 26 Sept. | 23.0 | 23.6 | 74N ♂ | | | | 4 | - |
| | | 23.0 | 23.6 | 105N ♀ | | | | 4 | - |
| | | 23.0 | 23.6 | 5N ? | | | | 4 | - |
| | | 23.0 | 23.6 | 1P ♂ | | | | 4 | - |
| | | 23.0 | 23.6 | 5P ? | | | | 4 | - |
| 11 | 26 Sept. | 23.2 | 23.3 | 142N ♂ | | | | 4 | - |
| | | 23.2 | 23.3 | 170N ♀ | | | | 4 | - |
| | | 23.2 | 23.3 | 2P ♂ | | | | 4 | - |
| | | 23.2 | 23.3 | 1P ♀ | | | | 4 | - |
| 12 | 26 Sept. | 22.8 | 22.9 | 79N ♂ | | | | 5 | - |
| | | 22.8 | 22.9 | 81N ♀ | | | | 5 | - |
| | | 22.8 | 22.9 | 1N ? | | | | 5 | - |
| | | 22.8 | 22.9 | 1P ♀ | | | | 5 | - |
| 13 | 26 Sept. | 22.9 | 22.9 | 53N ♂ | | | | 10 | - |
| | | 22.9 | 22.9 | 59N ♀ | | | | 10 | - |
| | | 22.9 | 22.9 | 2P ♂ | | | | 10 | - |
| | | 22.9 | 22.9 | 1P ♀ | | | | 10 | - |
| | | 22.9 | 22.9 | 1H ♂ | | | | 10 | - |
| | | 22.9 | 22.9 | 1H ♀ | | | | 10 | - |

Appendix 1. (Continued)

| AREA | Date | Water Temperature (°C) | Salinity (°/oo) | Number, Sex, and Species | Number with Externa | Number with Multiple Externa | Number with Scars | Habitat or water Depth (Meters) | Zone |
|---|---|---|---|---|---|---|---|---|---|
| | 1968 | | | | | | | | |
| Bay West | | | | | | | | | |
| 14 | 26 Sept. | 23.1 | 22.8 | 7N ♂ | | | | 7 | - |
| | | 23.1 | 22.8 | 8N ♀ | | | | 7 | - |
| 15 | 26 Sept. | 23.2 | 24.1 | 414N ♂ | | | | 5 | - |
| | | 23.2 | 24.1 | 437N ♀ | | | | 5 | - |
| | | 23.2 | 24.1 | 16N ? | | | | 5 | - |
| | | 23.2 | 24.1 | 2P ♂ | | | | 5 | - |
| | | 23.2 | 24.1 | 1P ♀ | | | | 5 | - |
| Back River | | | | | | | | | |
| 16 | 26 Sept. | 24.1 | 21.9 | 32N ♂ | | | | 5 | - |
| | | 24.1 | 21.9 | 36N ♀ | | | | 5 | - |
| | | 24.1 | 21.9 | 1E ♀ | 1 | 1 | 0 | 5 | - |
| Poquoson R. Mouth | | | | | | | | | |
| 17 | 26 Sept. | 23.4 | 21.4 | 29N ♂ | | | | 6 | - |
| | | 23.4 | 21.4 | 29N ♀ | | | | 6 | - |
| | | 23.4 | 21.4 | 3P ♂ | | | | 6 | - |
| | | 23.4 | 21.4 | 2P ♀ | | | | 6 | - |
| | | 23.4 | 21.4 | 1P ? | | | | 6 | - |
| Bay West | | | | | | | | | |
| 18 | 28 Oct. | 15.9 | 20.1 | 1E ♂ | 1 | 0 | 0 | 11 | - |
| | | 15.9 | 20.1 | 1E ♀ | 0 | 0 | 0 | 11 | - |
| | | 15.9 | 20.1 | 5N ♂ | | | | 11 | - |
| | | 15.9 | 20.1 | 3N ♀ | | | | 11 | - |

Appendix 1. (Continued)

| AREA | Date | Water Temperature (°C) | Salinity (°/oo) | Number, Sex, and Species | Number with Externa | Number with Multiple Externa | Number with Scars | Habitat or water Depth (Meters) | Zone |
|---|---|---|---|---|---|---|---|---|---|
| | 1968 | | | | | | | | |
| Bay West | | | | | | | | | |
| 18 | 28 Oct. | 15.9 | 20.1 | 1P ♂ | | | | 11 | - |
| | | 15.9 | 20.1 | 1P ♀ | | | | 11 | - |
| Bay Center | | | | | | | | | |
| 19 | 28 Oct. | 15.8 | 21.8 | 11N ♂ | | | | 13 | - |
| | | 15.8 | 21.8 | 7N ♀ | | | | 13 | - |
| | | 15.8 | 21.8 | 3N ? | | | | 13 | - |
| Bay East | | | | | | | | | |
| 20 | 28 Oct. | 14.1 | 20.5 | 38N ♂ | | | | 9 | - |
| | | 14.1 | 20.5 | 42N ♀ | | | | 9 | - |
| | | 14.1 | 20.5 | 1P ♂ | | | | 9 | - |
| 21 | 28 Oct. | 14.7 | 26.5 | 2N ♂ | | | | 3 | - |
| | | 14.7 | 26.5 | 6N ♀ | | | | 3 | - |
| | | 14.7 | 26.5 | 1P ♂ | | | | 3 | - |
| | | 14.7 | 26.5 | 1P ♀ | | | | 3 | - |
| 22 | 29 Oct. | 14.2 | 18.9 | 1E ♂ | 0 | 0 | 0 | 4 | - |
| | | 14.2 | 18.9 | 1E ♀ | 0 | 0 | 0 | 4 | - |
| | | 14.2 | 18.9 | 3N ♂ | | | | 4 | - |
| | | 14.2 | 18.9 | 8N ♀ | | | | 4 | - |
| | | 14.2 | 18.9 | 2P ♂ | | | | 4 | - |
| | | 14.2 | 18.9 | 2P ♀ | | | | 4 | - |
| 23 | 29 Oct. | 13.6 | 18.8 | 4E ♀ | 4 | 0 | 0 | 6.5 | - |
| | | 13.6 | 18.8 | 8N ♂ | | | | 6.5 | - |

Appendix 1. (Continued)

| AREA | Date | Water Temperature (°C) | Salinity (°/oo) | Number, Sex, and Species | Number with Externa | Number with Multiple Externa | Number with Scars | Habitat or water Depth (Meters) | Zone |
|---|---|---|---|---|---|---|---|---|---|
| | 1968 | | | | | | | | |
| Bay East | | | | | | | | | |
| 23 | 29 Oct. | 13.6 | 18.8 | 11N♀ | | | | 6.5 | - |
| | | 13.6 | 18.8 | 6P♂ | | | | 6.5 | - |
| | | 13.6 | 18.8 | 8P♀ | | | | 6.5 | - |
| 24 | 29 Oct. | 13.8 | 18.2 | 3E♀ | 3 | 1 | 0 | 9 | - |
| | | 13.8 | 18.2 | 15N♂ | | | | 9 | - |
| | | 13.8 | 18.2 | 15N♀ | | | | 9 | - |
| | | 13.8 | 18.2 | 23P♂ | | | | 9 | - |
| | | 13.8 | 18.2 | 27P♀ | | | | 9 | - |
| 25 | 29 Oct. | 13.9 | 17.8 | 1E♂ | 1 | 0 | 0 | 7 | - |
| | | 13.9 | 17.8 | 7E♀ | 7 | 1 | 0 | 7 | - |
| | | 13.9 | 17.8 | 2N♂ | | | | 7 | - |
| | | 13.9 | 17.8 | 4N♀ | | | | 7 | - |
| | | 13.9 | 17.8 | 2P♂ | | | | 7 | - |
| | | 13.9 | 17.8 | 4P♀ | | | | 7 | - |
| 26 | 29 Oct. | 12.7 | 17.3 | 1P♀ | | | | -- | - |
| Bay Center | | | | | | | | | |
| 27 | 30 Oct. | 14.0 | 17.4 | 2E♂ | 0 | 0 | 0 | 3.5 | - |
| | | 14.0 | 17.4 | 2E♀ | 0 | 0 | 0 | 3.5 | - |
| | | 14.0 | 17.4 | 1R♂ | 0 | 0 | 0 | 3.5 | - |
| | | 14.0 | 17.4 | 5R♀ | 0 | 0 | 0 | 3.5 | - |
| Choptank R. Mouth | | | | | | | | | |
| 28 | 30 Oct. | 12.5 | 15.4 | 1R♂ | 0 | 0 | 0 | 7 | - |

Appendix 1. (Continued)

| AREA | Date | Water Temperature (°C) | Salinity (°/oo) | Number, Sex, and Species | Number with Externa | Number with Multiple Externa | Number with Scars | Habitat or water Depth (Meters) | Zone |
|---|---|---|---|---|---|---|---|---|---|
| | 1968 | | | | | | | | |
| Mid Choptank R. | | | | | | | | | |
| 29 | 30 Oct. | 11.9 | 15.3 | 2R♂ | 0 | 0 | 0 | 7 | - |
| | | 11.9 | 15.3 | 5R♀ | 0 | 0 | 0 | 7 | - |
| Poplar Isl. Narrows | | | | | | | | | |
| 30 | 31 Oct. | 12.4 | 16.2 | 2E♂ | 0 | 0 | 0 | 5 | - |
| | | 12.4 | 16.2 | 4R♂ | 0 | 0 | 0 | 5 | - |
| | | 12.4 | 16.2 | 13R♀ | 0 | 0 | 0 | 5 | - |
| Bloody Pt. Bar | | | | | | | | | |
| 31 | 31 Oct. | 13.6 | 16.8 | 8E♂ | 0 | 0 | 0 | 6 | - |
| | | 13.6 | 16.8 | 2E♀ | 0 | 0 | 0 | 6 | - |
| | | 13.6 | 16.8 | 1R♀ | 0 | 0 | 0 | 6 | - |
| Parson Isl. | | | | | | | | | |
| 32 | 31 Oct. | 11.5 | 15.9 | 42R♂ | 0 | 0 | 0 | 6 | - |
| | | 11.5 | 15.9 | 55R♀ | 0 | 0 | 0 | 6 | - |
| | | 11.5 | 15.9 | 1P♂ | | | | 6 | - |
| Miles R. Mouth | | | | | | | | | |
| 33 | 31 Oct. | 13.6 | 15.3 | 1E♂ | 0 | 0 | 0 | 10 | - |
| | | 13.6 | 15.3 | 1E♀ | 0 | 0 | 0 | 10 | - |
| Ocean Coast | 1967 | | | | | | | | |
| Floyds Bay | 5 July | 25.4 | 31.7 | 4E♂ | 0 | 0 | 0 | P | S |
| | | 25.4 | 31.7 | 3E♀ | 0 | 0 | 0 | P | S |

Appendix 1. (Continued)

| AREA | Date | Water Temperature (°C) | Salinity (°/oo) | Number, Sex, and Species | Number with Externa | Number with Multiple Externa | Number with Scars | Habitat or Water Depth (Meters) | Zone |
|---|---|---|---|---|---|---|---|---|---|
| | 1967 | | | | | | | | |
| Upshurs Bay | 5 July | -- | 30.0 | 2E ♂ | 0 | 0 | 0 | B | I |
| | | -- | 30.0 | 3E ♀ | 0 | 0 | 0 | B | I |
| Willis Wharf | 6 July | -- | 31.2 | 1E ♂ | 0 | 0 | 0 | B | I |
| | | -- | 31.2 | 2E ♀ | 0 | 0 | 0 | B | I |
| Oyster, Va. | 6 July | 24.4 | 31.2 | 29E ♂ | 0 | 0 | 0 | B | I |
| | | 24.4 | 31.2 | 27E ♀ | 0 | 0 | 0 | B | I |
| | | 24.4 | 31.2 | 3N ♂ | | | | P | S |
| | | 24.4 | 31.2 | 3N ♀ | | | | P | S |
| | | 24.4 | 31.2 | 5P ♀ | | | | B | I |
| Wachapreague Inlet | 6 July | 23.5 | 32.1 | 3N ♂ | | | | P | S |
| | | 23.5 | 32.1 | 12N ♀ | | | | P | S |

Appendix 2. Geographic coordinates of stations listed in Appendix 1.

| AREA | | LATITUDE Deg. | LATITUDE Min. | LONGITUDE Deg. | LONGITUDE Min. |
|---|---|---|---|---|---|
| Western Shore | | | | | |
| York R. Mouth | | 37 | 16.0 | 76 | 22.9 |
| Perrin R. Mouth | | 37 | 15.6 | 76 | 25.0 |
| Mid Perrin R. | | 37 | 16.0 | 76 | 25.5 |
| Upper Perrin R. | | 37 | 16.2 | 76 | 26.1 |
| Yorktown | | 37 | 14.4 | 76 | 30.6 |
| Gloucester Point | | 37 | 14.7 | 76 | 30.0 |
| Indian Field Creek | | 37 | 16.5 | 76 | 33.4 |
| Felgates Creek | | 37 | 16.5 | 76 | 35.2 |
| Queens Creek | | 37 | 13.5 | 76 | 36.7 |
| York R. (Y-10) | | 37 | 19.2 | 76 | 53.8 |
| York R. (Y-15) | | 37 | 23.0 | 76 | 39.2 |
| York R. (Y-20) | | 37 | 26.3 | 76 | 42.9 |
| York R. (Y-25) | | 37 | 29.1 | 76 | 45.3 |
| Pamunkey R. (P-30) | | 37 | 32.7 | 76 | 49.8 |
| Pamunkey R. (P-40) | | 37 | 32.8 | 76 | 53.4 |
| Eastern Shore | | | | | |
| Fishermans Island | | 37 | 06.3 | 75 | 58.4 |
| Chesapeake Bay Bridge | | 37 | 06.9 | 75 | 58.2 |
| Cape Charles | | 37 | 07.5 | 75 | 58.2 |
| Old Plantation Creek | | 37 | 13.8 | 76 | 00.1 |
| Cherrystone Creek | | 37 | 18.4 | 76 | 00.2 |
| Smiths Beach | | 37 | 22.1 | 75 | 59.1 |
| Hungars Creek | | 37 | 24.4 | 75 | 58.4 |
| Onancock Creek | | 37 | 43.2 | 75 | 48.2 |
| Messongo Creek | | 37 | 54.2 | 75 | 41.2 |
| Bay Stations | | | | | |
| Bay East | 1 | 37 | 24.2 | 76 | 01.7 |
| | 2 | 37 | 16.8 | 76 | 05.3 |
| | 3 | 37 | 13.8 | 76 | 02.0 |
| | 4 | 37 | 10.8 | 76 | 01.0 |
| | 5 | 37 | 10.0 | 75 | 59.5 |
| | 6 | 37 | 07.1 | 76 | 02.1 |
| | 7 | 37 | 03.8 | 76 | 07.3 |
| Bay South | 8 | 36 | 55.3 | 76 | 04.8 |
| | 9 | 36 | 55.5 | 76 | 07.3 |
| | 10 | 36 | 56.1 | 76 | 11.1 |
| | 11 | 36 | 57.8 | 76 | 15.5 |
| | 12 | 36 | 59.4 | 76 | 17.6 |

Appendix 2. (Continued)

| AREA | | LATITUDE Deg. | LATITUDE Min. | LONGITUDE Deg. | LONGITUDE Min. |
|---|---|---|---|---|---|
| Bay South | 13 | 37 | 00.1 | 76 | 16.6 |
| Bay West | 14 | 37 | 02.4 | 76 | 15.7 |
| | 15 | 36 | 05.8 | 76 | 14.8 |
| Back River | 16 | 37 | 06.2 | 76 | 18.7 |
| Poquoson R. Mouth | 17 | 37 | 11.2 | 76 | 21.8 |
| Bay West | 18 | 37 | 35.2 | 76 | 14.5 |
| Bay Center | 19 | 37 | 36.9 | 76 | 04.8 |
| Bay East | 20 | 37 | 43.9 | 75 | 53.8 |
| | 21 | 37 | 47.0 | 75 | 53.8 |
| | 22 | 37 | 54.0 | 75 | 56.2 |
| | 23 | 37 | 56.9 | 75 | 55.4 |
| | 24 | 38 | 02.5 | 75 | 54.9 |
| | 25 | 38 | 06.9 | 75 | 58.4 |
| | 26 | 38 | 12.2 | 75 | 58.4 |
| Bay Center | 27 | 38 | 35.4 | 76 | 23.2 |
| Choptank R. Mouth | 28 | 38 | 39.4 | 76 | 16.6 |
| Mid Choptank | 29 | 38 | 39.0 | 76 | 10.2 |
| Poplar Isl. Narrows | 30 | 38 | 46.5 | 76 | 21.1 |
| Bloody Pt. Bar | 31 | 38 | 49.3 | 76 | 22.6 |
| Parson Island | 32 | 38 | 53.5 | 76 | 14.2 |
| Miles R. Mouth | 33 | 38 | 49.5 | 76 | 13.0 |
| Ocean Coast | | | | | |
| Floyds Bay | | 37 | 38.9 | 75 | 38.9 |
| Upshurs Bay | | 37 | 32.8 | 75 | 43.8 |
| Willis Wharf, Va. | | 37 | 30.7 | 75 | 48.3 |
| Oyster, Va. | | 37 | 17.2 | 75 | 54.1 |
| Wachapreague Inlet | | 37 | 36.2 | 75 | 41.2 |

## LITERATURE CITED


Behre, E. H. 1950. Annotated list of the fauna of the Grand Isle region, 1929-1946. Louisiana State Univ., Occas. Pap. Mar. Lab. 6:1-66.

Boschma, H. 1928. Two common species of parasitic Crustacea (Sacculinidae) of the West Indies. U. S. Nat. Mus., Proc. 73:1-10.

Boschma, H. 1955. The described species of the family Sacculinidae. Zool. Verhandel., Leiden, 27:1-76.

Causey, D. 1954. Parasitic barnacles. Educ. Focus, (Rochester), 25: 9-10.

Charniaux-Cotton, H. 1960. Sex determination, Vol. I, p. 411 to 447. In T. H. Waterman (ed.) The physiology of Crustacea. Academic Press, New York. 2 Vols.

Chesapeake Bay Institute. 1953 (?). Data Report. Lower Chesapeake Bay and shelf area off-shore from Chesapeake Bay. Ms. 96 p.

Christmas, J. Y. 1968. Parasitic barnacles in Mississippi estuaries with special reference to Loxothylacus texanus Boschma in the blue crab (Callinectes sapidus). Presented at the 22nd Annu. Conf. Southeast. Ass. Game & Fish Comm. Baltimore, Oct. 21-23, 1968. 7 p.

Cowles, R. P. 1930. A biological survey of the offshore waters of Chesapeake Bay. U. S. Bur. Fish. Bull. 46:277-381.

Darnell, R. M. 1959. Studies of the life history of the blue crab (Callinectes sapidus Rathbun) in Louisiana waters. Amer. Fish. Soc., Trans. 88:294-304.

Daugherty, F. M., Jr. 1952. The blue crab investigation, 1949-50. Texas J. Sci. 1:77-84.

Day, J. H. 1935. The life history of Sacculina. Quart. J. Microscop. Sci. 77:549-583.

Elton, C. S. 1958. The ecology of invasions by animals and plants. John Wiley & Sons, New York. 181 p.

Feng, S. Y. 1957. Ecological and epidemiological studies of Nematopsis ostrearum, a sporozoan parasite of the oyster Crassostrea virginica, in lower Chesapeake Bay and its tributaries. M.A. Thesis, College of William and Mary, Williamsburg, Va. 33 p.

Foxon, G. E. H. 1940. Notes on the life history of Sacculina carcini Thompson. J. Mar. Biol. Ass. U. K. 24:253-264.

Gissler, C. F. 1884. The crab parasite, Sacculina. Amer. Natur. 18: 225-229.

Gunter, G. 1950. Seasonal population changes and distributions as related to salinity, of certain invertebrates of the Texas coast, including the commercial shrimp. Univ. Texas, Inst. Mar. Sci. Publ. 1(2):7-51.

Harrison, W., J. J. Norcross, N. A. Pore, and E. M. Stanley. 1967. Circulation of shelf waters off the Chesapeake Bight. Surface and bottom drift of continental shelf waters between Cape Henlopen, Delaware and Cape Hatteras, North Carolina. June 1963 - December 1964. U. S. Dep. Com., ESSA Prof. Pap. 3. 82 p.

Hartknoll, R. G. 1962. Parasitic castration of Macropodia longirostris (Fabricius) by a sacculinid. Crustaceana 4(4):295-300.

Hoese, H. D. 1962. Studies on oyster scavengers and their relation to the fungus Dermocystidium marinum. Nat. Shellfish. Ass., Proc. 53:161-173.

Ichikawa, A. and R. Yanagimachi. 1960. Studies on the sexual organization of the Rhizocephala. II. The reproductive function of the larval (cypris) males of Peltogaster and Sacculina. Annot. Zool. Japon. (Tokyo), 33(1):42-56.

Kenk, V. C. 1964. A new crab host of the gregarine Nematopsis ostrearum. Nat. Shellfish. Ass., Proc. 55:87-88.

Kinne, O. 1967. Physiology of estuarine organisms with special reference to salinity and temperature: General aspects, p. 525-540. In G. H. Lauff (ed.) Estuaries. Amer. Ass. Adv. Sci. Publ. 83, Washington, D. C.

Knowles, Pamela 1968. A study of larval development in Loxothylacus panopaei (Gissler, 1884) Boschma, 1928, a sacculinid parasite reared in the laboratory. Virginia Inst. Mar. Sci. Ms. 66 p.

Knudsen, J. W. 1960. Aspects of the ecology of the California pebble crabs (Crustacea: Xanthidae). Ecol. Monogr. 30(2):165-185.

Landers, W. S. 1954. Notes on the predation of the hard clam Venus mercenaria by the mud crab, Neopanope texana. Ecology 35(3): 422.

MacKay, D. C. G. 1943. Relative growth of the European edible crab, Cancer pagurus: II. Growth of the abdomen. Growth 7(2): 217-226.

McDermott, J. J. 1960. The predation of oysters and barnacles by crabs of the family Xanthidae. Pennsylvania Acad. Sci., Proc. 34: 199-211.

Okada, Y. K. and Y. Miyashita. 1935. Sacculinization in Eriocheir japonicus de Haan, with remarks on the occurrence of complete sex-reversal in parasitized male crabs. Kyoto Imp. Univ. Mem. Coll. Sci. Ser. B, 10:169-208.

Orton, J. H. 1936. On the rate of growth of Sacculina carcini Thompson in Carcinus maenas (Pennant). Ann. Mag. Natur. Hist., Ser. 10, 617-625.

Pearson, J. C. 1948. Fluctuations in the abundance of the blue crab in Chesapeake Bay. U. S. Fish. Wildl. Serv. Res. Rep. 14, 1-26 p.

Perez, C. 1927. Notes sur les Epicarides et les Rhizocephales des Cotes de France. I. Sur l'Eupagurus bernhardus et sur quelquequns de ses parasites. Bull. Soc. Zool. France 52:99-104.

Perez, C. 1931a. Notes sur les Epicarides et les Rhizocephales des cotes de France. VII. Peltogaster et Liriopsis. Bull. Soc. Zool. France. 56:509-512.

Perez, C. 1931b. Statistique d'infestations des Pagures par les Chlorogaster. Comp. Rend. Acad. Sci. Paris 192:1274-1276.

Prytherch, H. F. 1940. The life cycle and morphology of Nematopsis ostrearum sp. nov., a gregarine parasite of the mud crabs and oysters. J. Morphol. 66:39-65.

Rasmussen, E. 1959. Behaviour of sacculinized shore crabs (Carcinus maenas Pennant). Nature 183:479-480.

Rathbun, M. J. 1930. The cancroid crabs of America of the families Euryalidae, Portunidae, Atelecyclidae, Cancridae, and Xanthidae. U. S. Nat. Mus., Proc. 152:1-609.

Reinhard, E. G. 1942. Studies on the life history and host-parasite relationship of Peltogaster paguri. Biol. Bull. 83(3):401-415.

Reinhard, E. G. 1956. Parasitic castration of Crustacea. J. Parasitol. 5:79-107.

Reinhard, E. G. and P. G. Reischman. 1958. Variation in Loxothylacus panopaei (Gissler), a common sacculinid parasite of mud crabs, with the description of Loxothylacus perarmatus, n. sp. J. Parasitol. 44(1):93-97.

Ricker, W. E. 1958. Handbook of computation for biological statistics of fish populations. Fish. Res. Bd. Canada, Bull. 119:1-300.

Ricketts, E. F. and J. Calvin. 1962. Between Pacific tides. Stanford Univ. Press, Palo Alto. 516 p.

Ryan, E. P. 1956. Observations on the life histories and the distribution of the Xanthidae (mud crabs) of the Chesapeake Bay. Amer. Midl. Natur. 56(1):138-162.

Sprague, V., and P. E. Orr, Jr. 1955. Nematopsis ostrearum and N. prytherchi (Eugregarinina: Porosparidae) with special reference to the host-parasite relations. J. Parasitol. 41(1):89-104.

Van Engel, W. A., W. A. Dillon, D. E. Zwerner and D. Eldridge. 1966. Loxothylacus panopaei (Cirripediae, Sacculinidae), an introduced parasite on a xanthid crab in Chesapeake Bay. Crustaceana 10:111-112.

## ADDENDUM

On 24 June 1969, Mr. John A. Couch, of the Bureau of Commercial Fisheries Laboratory, Oxford, Maryland, reported an E. depressus with a L. panopaei externa from the ocean side of the eastern shore of Virginia. The specimen was taken in Chincoteague Bay in salinity of 32.3 °/oo.

VITA

Seth Jerome Daugherty

Born in New Castle, Pa., September 2, 1943. Graduated from Neshannock High School, New Castle, Pa., June 1961. Received a B.S. in Biology from the University of Notre Dame, Notre Dame, Indiana, June, 1965. Served active duty in the United States Marine Corps November, 1965 to May 1966.

Entered the Graduate program of the College of William and Mary in September 1966.