

STUDIES ON THE OYSTER DRILL (*UROSALPINX CINEREA*, SAY)¹

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CONTENTS

	Page
Introduction.....	85
Natural history of <i>Urosalpinx cinerea</i> , Say.....	86
Description of the species.....	86
Range and occurrence.....	86
Salinity and distribution.....	89
Creeping and migrations.....	93
Temperature effects.....	96
Feeding habits.....	97
Breeding habits.....	101
Tropisms.....	103
Control measures.....	105
Methods for removal from infested areas.....	107
Methods for preventing distribution.....	107
Summary.....	110
Literature cited.....	111

INTRODUCTION

Although the common oyster drill (*Urosalpinx cinerea*)² feeds on many mollusks its economic importance is due to the fact that it destroys a great many oysters. At times the damage wrought has been very great. In Long Island Sound (Rowe, 1894) and in New Jersey (Nelson, 1923) the loss from this species amounts annually to over a million dollars, and recently it has been reported as causing great destruction to the oyster beds of England (Orton and Winckworth, 1928).

In spite of the above facts and although several investigators had called attention to the pressing need of more information on the subject no detailed study had ever been made of the species (Rathbun, 1892; Collins, 1890; Townsend, 1893; Hall, 1894; Moore, 1897, 1911; Churchill, 1921), and the only available data are those collected by investigators during their work on the oyster and Pope's (1910-1911) unpublished manuscript on the oyster drill in New England.

This paucity of information on the life history of the drill and its invasion of Hampton Roads, Va., brought the question to the immediate attention of the United States Bureau of Fisheries. The situation at Hampton Roads was alarming. Planters claimed to have lost as much as 90 per cent of their oysters. Since this is an important oyster producing area the continued invasion demanded some remedy and so in 1926 the author was commissioned to make a detailed study of the species. The work was carried on in a temporary laboratory at the United States Public Health Quarantine

¹ Approved for publication Jan. 16, 1931.

² The terms "drill" and "borer" have been used to describe other gastropods besides *Urosalpinx cinerea* but this report will deal only with this species. Many older reports simply use the term "drill" (Ryder, 1883; Rathbun, 1893; Hall, 1894; Rowe, 1894; Moore, 1897; 1898, 1911; Swift, 1898) and do not give the species, so that it is impossible to determine exactly to which of the many "drilling" gastropods the author is referring.

Station on Craney Island, Norfolk, Va.,³ and at the United States Fisheries Biological Station, Beaufort, N. C.

The aims of the research were to study the life history, habits, and migrations of the oyster drill and to make recommendations of measures that would either eliminate the animal or so reduce its numbers as to make it a negligible factor in the oyster industry.

Since it was impossible to make a study of the complete life history of the drill, the work was necessarily limited to the following fields: A survey was made in Hampton Roads in which salinity, temperature, pH, and character of bottom were studied; and the salinity data were corroborated by a study of the salinity death point in the laboratory. Since in a study aiming at the control of a species it is of prime importance to know the extent, direction, and periodicity of its migrations, the movements of tagged drills were studied. Other problems studied were: The effect of temperature on the activities of the animal, its feeding and breeding habits, and its tropistic behavior. Whenever possible field observations were checked by laboratory experiments under controlled conditions.

NATURAL HISTORY OF UROSALPINX CINEREA, SAY

DESCRIPTION OF THE SPECIES

The fusiform, longitudinally ribbed, and spirally striated shell of *Urosalpinx cinerea* is usually greyish yellow, light brown, or occasionally white in color. The aperture varies from light flesh to dark salmon, chocolate, or purple and possesses a comparatively short canal. The outer lip of the aperture is dentate; the operculum is semicordate with its nucleus at the outer edge or a little below the middle. In Chesapeake Bay the shells generally range between 21 to 25 millimeters in length (Federighi, 1930), and as in other gastropods (Tryon, 1880; Cooke, 1895; Dimon, 1905; Pelseneer, 1906) the females attain greater length than the males. The largest female, found in Chesapeake Bay, measured 33 millimeters in length, the largest male 29 millimeters. Aside from this rather general characteristic there is no distinguishing feature between the sexes.

The body of the animal is small; the foot scarcely covering the aperture and only very little dilated at the front angles. It is cream-colored, margined with lemon color beneath, and punctuated with light drab above. The siphon extends just beyond the canal. The head is scarcely protruded with tentacles united at the origin, and at the filamentous and contractile outer third of the tentacles are located the black eyes.

RANGE AND OCCURRENCE

Urosalpinx cinerea, the oyster drill, is commonly reported as inhabiting the marine and brackish waters of the Atlantic coast from Maine to Florida (Verrill, 1873; Tryon, 1880; Churchill, 1921). It has been collected in San Francisco Bay, carried there in the shipment of eastern oysters (Rathbun, 1892; Townsend, 1893; Dall, 1907-1909); in Bermuda (Arey and Crozier, 1919); only sparingly on the Gulf coast (Moore, 1898, 1906; Ruge, 1898); and recently (Orton, 1927; Orton and Winckworth, 1928) it has been reported from England.

The Eastern Shore of Virginia has been infested with this gastropod for many years (Uhler, 1879-80; Ryder, 1883; Henderson and Bartsch, 1915), and in 1908

³ The author wishes here to express his thanks for the help and hospitality shown him by the U. S. Public Health Service and especially to Dr. H. E. Hasseltine and Dr. C. E. Waller, also to all others who contributed in making the work possible.

BULL. U. S. B. F., 1931. (Bull. No. 4.)

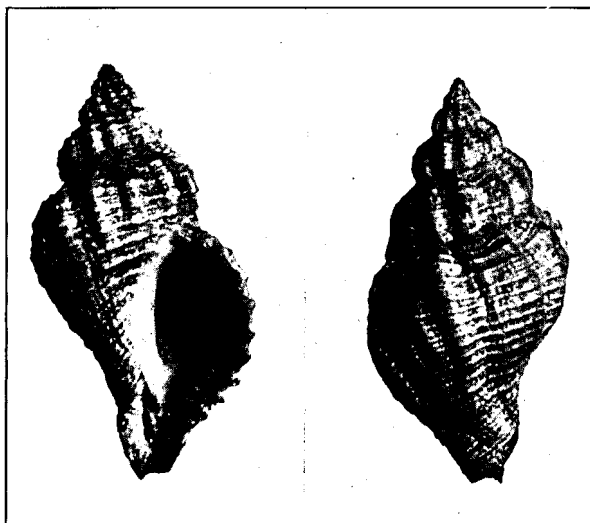


FIGURE 1.—The common oyster drill (*Urosalpinx cinerea*). Actual size, $1\frac{1}{8}$ by $\frac{3}{8}$ inches

the Virginia Fisheries Commission (Lee, 1909) wrote: "Borers are to be found only on our seaside, but in less alarming quantities than in other waters of the coast." Recently the important oyster beds of lower Chesapeake Bay have suffered from this pest to such an extent as to threaten the whole industry. This area is so large

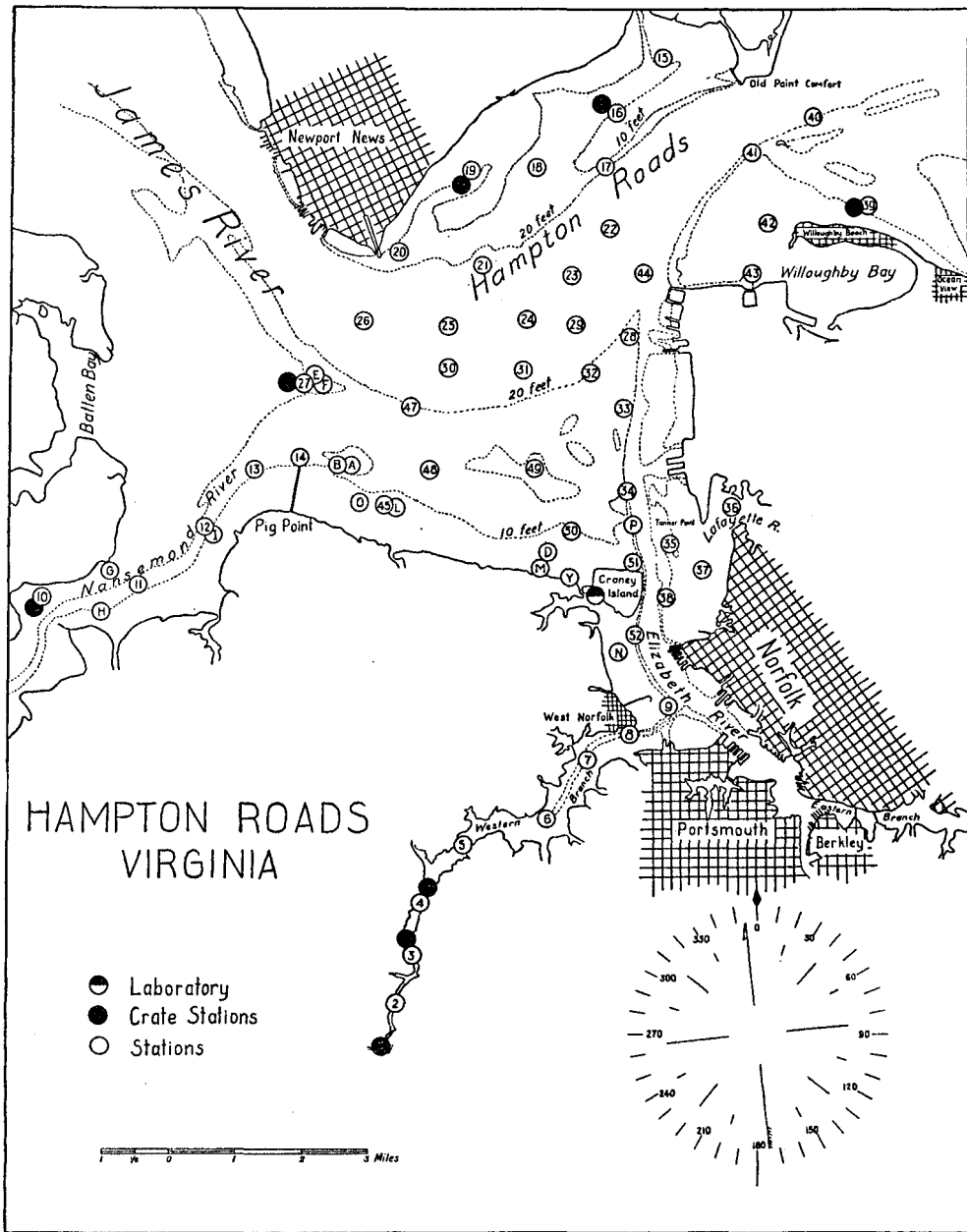


FIGURE 2.—Chart showing Hampton Roads and tributaries. Stations are indicated by circles

that it was impracticable to attempt a complete survey of the region. The survey herein reported was restricted to Hampton Roads and its tributaries. Stations as shown in Figure 2 were laid out and observations were made on the salinity, pH, character of the bottom, depth, temperature, the number of *Urosalpinx* present and,

wherever oyster beds existed, the number of perforated shells among a definite number of oysters taken at random. The study was made in June, 1927, so as to avoid the low salinities which obtain during the spring months. (See salinity chart,

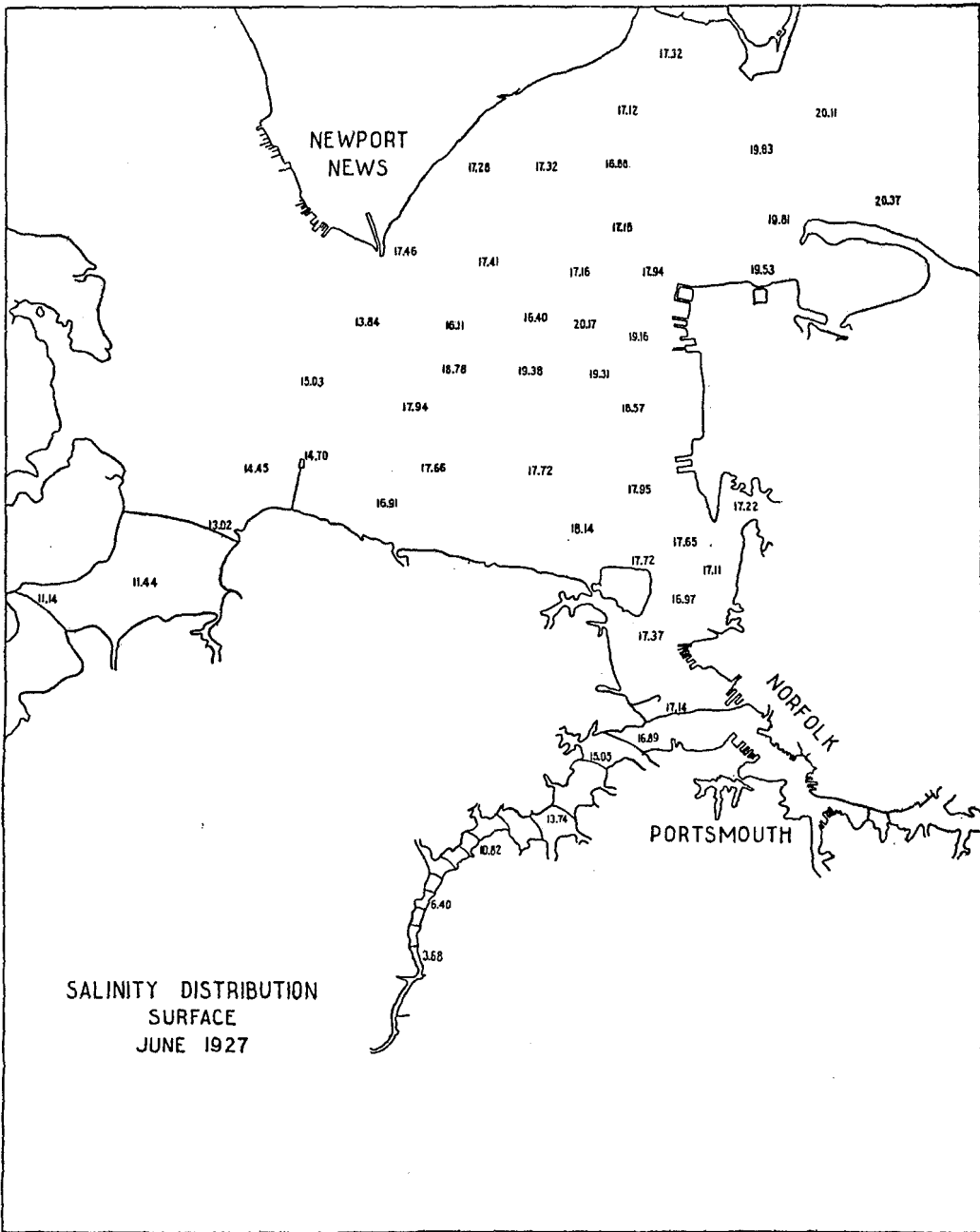


FIGURE 3.—Chart showing distribution of surface salinities over Hampton Roads for June, 1927

fig. 3.) In order to ascertain the relative number of drills over the various beds a small oyster dredge was dragged over the bottom for 5 minutes behind a slow moving motor boat. The following table shows the results of the survey:

TABLE 1.—The relation between the number of drills and various environmental factors

[Survey made at Hampton Roads during June, 1927. See fig. 2]

Station	Drills present in a unit area		Salinity in parts per mille	pH	Depth in feet	Character of bed	Station	Drills present in a unit area		Salinity in parts per mille	pH	Depth in feet	Character of bed
	Alive	Dead						Alive	Dead				
	Number	Number						Number	Number				
A-----	1	1	17.00	7.8	12	Natural.	S-----	3	2	18.00	7.8	10	Natural.
B-----	3		17.00	7.8	8	Do.	T-----	2		17.25	8.0	4	Planted.
D-----		1	18.00	7.9	7	Do.	U-----	13	3	20.00	8.4	14	Do.
E-----	8	4	15.00	8.0	10	Do.	W-----	18	2	17.00	8.2	9	Do.
F-----	8		15.50	8.1	12	Do.	X-----	13		17.00	8.0	8	Do.
G-----			11.50	8.0	5	Do.	Z-----	8	5	17.25	8.3	12	Do.
H-----			11.50	8.0	5	Do.	AA-----	3	4	19.50	8.3	7	Do.
I-----		1	13.00	8.0	2	Do.	BB-----	5	6	19.30	8.2	6	Do.
K-----			16.50	8.0	5	Planted.	16-----	17	5	17.00	8.2	10	Do.
L-----	2	1	17.00	8.0	8	Do.	18-----	14	2	17.25	8.0	9	Do.
O-----	3		17.00	8.0	8	Do.	19-----	16	4	17.25	8.1	11	Do.
P-----	2	1	17.50	7.8	12	Natural.	27-----	4	2	15.25	7.9	12	Natural.
Q-----	16	2	19.25	8.2	15	Planted.	45-----	17	1	17.00	7.8	10	Planted.
R-----	2	1	17.00	7.9	9½	Natural.							

The drill is found over the whole area of Hampton Roads, being more abundant on the planted areas than on the natural rock, a condition that is explained by the absence of any migratory habits. Salinity below 15 parts per mille, muddy bottoms, clear sands, and depths greater than 25 feet are factors unfavorable for its growth and multiplication. At Beaufort it flourishes and reproduces at average summer salinities of 35 parts per mille. In Hampton Roads the snail does not occur above the low-water mark, but in Connecticut and in North Carolina it is found on beds exposed at low water.

SALINITY AND DISTRIBUTION

Although many investigators have studied the adaptation of organisms to varying salinities, the mechanism for this adaptation, the relation between the environmental salinity and the salt content of the blood, the importance of salinity as a barrier to the multiplication and distribution of a species, and the lethal salinities for several animals (see Duval, 1925, for complete bibliography); no attempt, so far as the author knows, has been made to correlate the death-point salinity with the salinity of the environmental waters. During these studies certain data were collected on the resistance of *Urosalpinx* to low salinities. Three sets of data are available, one gives the results of a preliminary experiment made at Norfolk during the summer of 1927; the other two sets of data were collected at Beaufort, N. C. The latter are more complete and permit of more accurate analysis. The conclusions from these observations, already published elsewhere (Federighi, 1931), are given in the following paragraphs.

Moore (1911) stated that in Delaware Bay the oyster drill does not thrive at specific gravities below 1.012 to 1.013 (salinity: 15.50–17 parts per mille). In 1923 Nelson gave the minimum salinity for the survival and reproduction of this gastropod in New Jersey as 18.33 parts per mille—a figure that has recently (1928) been lowered to 15 parts per mille (private communication). At Hampton Roads, according to the author's observation made in June, 1927, the snail does not normally inhabit waters of salinities below 15 parts per mille. What the upper salinity limit may be is shown by observations made at Beaufort, N. C., where drills were found living and reproducing in areas where the summer salinities run as high as 37 parts per mille for several days (summer, 1928).

During the summer of 1927 preliminary experiments to determine the lower lethal salinity were made at Norfolk, Va., on snails collected from Hampton Roads. The animals used were taken from two localities, the June salinities of which averaged, respectively, 15 and 20 parts per mille. They were kept in the laboratory for about six weeks where the salinity was taken daily and where it never rose over 20 parts per mille. The two sets of drills were mixed and specimens for experimentation taken at random.

The procedure was as follows: Salinities between 5 and 17 parts per mille at intervals of approximately 2 parts per mille, obtained by diluting sea water with distilled water were used. The animals, 20 at each salinity, were immersed in the water and kept submerged by means of a wire screen stretched below the surface. The jars (of approximately 2 liters capacity) were kept loosely covered to prevent excessive evaporation, and the water was oxygenated twice daily by vigorous stirring. That this was sufficient is shown by the fact that drills will live in jars of sea water for several months without change of water or oxygenation. Temperature, salinity, and pH were taken daily and the condition of the animal noted. The criterion of death was whether or not the mantle would respond to a needle prick. When an animal was found that did not respond to this stimulus it was removed from the experimental jar and placed in running sea water to determine whether or not it would recover. In every case the animal would by putrefying within a few days give conclusive evidence that water of that salinity was lethal to the specimen. Death was always preceded by the animal becoming unattached, and at the lower salinities the animal swelled and protruded from the shell before dying, owing undoubtedly to the difference in osmotic pressure. The animals were kept under observation for 10 days, at the end of which time the surviving drills were returned to running sea water and their activity noted. Three different sets of observations comprise these experiments. (Table 2.)

TABLE 2.—*Effects of varying salinity on Urosalpinx cinerea, from Hampton Roads, summer of 1927*

Items	Experiments		
	No. 1	No. 2	No. 3
Salinity at which drills were killed.....	10.12	12.52	11.35
Percentage of deaths after 10 days.....	90	75	90
Salinity at which drills survived.....	12.26	15.05	13.01
Percentage of survival after 10 days.....	95	90	85
Percentage of deaths in control.....	10	5	15
Average temperature for period (°C.).....	26	26	24
pH for period.....	8- 8.1	8- 8.2	7.9- 8.2

During the summer of 1928 experiments, similar to those mentioned above, were made on drills collected at Beaufort, N. C., where the summer water salinity rose as high as 37 parts per mille and remained well over 30 for the entire season. The following modifications were made in the procedure as given for the Norfolk experiments: (1) The water was oxygenated by bubbling a continuous stream of air through it; (2) instead of using the mantle as a criterion of death, the tip of the siphon was employed for this purpose. The results, which are preliminary, are given in Table 3. The pH values, which are rather high, remained with but small variations between 8.4 and 8.8. The continuous stream of air through the sea water brought about a small increase in the pH during the first 24 hours, after which it

remained constant. For this reason the animals were not introduced into the jars until the second day.

TABLE 3.—*Effects of varying salinity on Urosalpinx cinerea from Beaufort, N. C., summer, 1928*

Items	Experiments		
	No. 1a	No. 2a	No. 3a
Salinity at which 50 per cent of drills were killed.....	12.81	14.45	16.00
Percentage of deaths after 10 days.....	95	90	70
Salinity at which at least 85 per cent of drills survived.....	16.89	16.22	17.43
Percentage of survival after 10 days.....	90	85	100
Percentage of deaths in control.....	10	10	15
Average temperature for period (°C.).....	26	26	24
pH for period.....	8.4- 8.8	8.6- 8.8	8.4- 8.8

Before giving the more detailed Beaufort experiments made during the spring and summer of 1929 certain conclusions derived from the above results should be given. In order to do so a word of explanation is needed concerning lines 1 and 3 in Tables 2 and 3. Line 1 gives the experimental salinity at which at least 50 per cent of the drills died; line 3 gives the next highest salinity in the experiment at which not more than 10 to 15 per cent of the animals died. The author has arbitrarily taken the mean of the figures in lines 1 and 3 and called this the salinity death point. It is believed that the nature of the experiments and results justify such a procedure. This method gives as close an approximation to the salinity death point as can be gotten even by reducing the intervals between the salinities used.

If the results given in Tables 2 and 3 are analyzed according to the method just indicated the results obtained are these: *Urosalpinx cinerea* collected from Hampton Roads in two regions having respectively the following average summer salinities, 15 and 20 parts per mille, have a salinity death point of approximately 12.5 parts per mille. On the other hand animals collected from Beaufort where the summer salinity is well over 30 parts per mille have a higher salinity death point; that is, 15.6 parts per mille.

The discrepancy between the death-point salinity and the salinity below which drills do not occur in the field at Hampton Roads can easily be explained after a study of the variations in the salinity of this region occurring throughout the year. During March, April, and early May (1927) the salinity at Craney Island dropped below 12 parts per mille for several days, although during the summer and winter months the salinity averaged over 17 parts per mille (Federighi, 1930a). Thus, although the survey during June, 1927, showed that the drills are not found below a salinity of 15 parts per mille, this is not the minimum salinity for survival, since during the spring the salinities of these areas fall as low as 12 parts per mille—a figure sufficiently close to the experimentally determined salinity death point (12.5 parts per mille).

During the summer of 1929 detailed experiments were conducted to check the observations made in 1927 and 1928. For this purpose a total of 3,290 animals were used at salinities ranging from 8 to 35 parts per mille. Of this total number 150 drills were from Hampton Roads (Series VIII), the remainder (3,150) were collected at Beaufort. The procedure was essentially the same as that employed for the preliminary Beaufort experiments. In these studies 50 drills were placed in each jar which contained 2 gallons of sea water of the desired salinity. The water was kept

oxygenated by running a continuous stream of air through it. Each day the drills were examined, and the number of dead in each of the jars noted. In all, 8 series of experiments were run. The detailed procedure for each series is given in the following paragraphs.

In Series I, II, III, and IV the salinities used ranged from 9 to 34 parts per mille at intervals of less than 2 parts per mille. In all, these involved the use of 1,350 animals. The results may be summarized as follows: Below a salinity of 15 parts per mille over 50 per cent of the drills were killed. The optimum range seemed to be between 17 to 22 parts per mille where the number of deaths remained less than 15 per cent. Above a salinity of 23 parts per mille the number of deaths again increased to over 50 per cent. These results seemed peculiar in view of the fact that at Beaufort where these drills were collected the salinity only rarely fell below 20 parts per mille and usually remained above 30 parts per mille. This indicated that other factors besides salinity must be involved in the deaths at salinities above 23 parts per mille.

One of the factors that might contribute to the death of the drills at salinities above 23 parts per mille is the rapid reproduction of plankton and its subsequent death and putrefaction. Below 23 the low salinity might act as a retarding factor in the reproduction of the plankton. Thus it might be that the putrefaction of a large number of plankton which might obtain at the higher and more nearly normal salinities might so foul the water as to kill the drills.

In order to test this, two types of experiments were run. The first involved the use of sterile glassware, boiled sea water, and drills washed in sterile sea water. Everything was done to keep the initial plankton count to a minimum. If the putrefaction of the plankton were a contributing factor to the death of the drills at the higher salinities, we should find that with the above precautions the number of deaths at salinities above 23 parts per mille would be greatly reduced. Such indeed was the case. In Series V (see Table 4) where this was done, deaths to number of 50 per cent occurred only at salinities below 15 parts per mille. At the higher salinities the percentage of deaths only rarely exceeded 15 per cent.

Another way to test the above assumption is to change the sea water (of the proper salinity) in each jar daily. In Series VI and VII (1,200 animals) this was done, and again only salinities below 15 parts per mille were fatal. (Table 4.)

The observations made during 1929 on the drills from Hampton Roads showed that the lower limit for survival of the snail is approximately 12.5 parts per mille, a result that is similar to that one obtained during the summer of 1927. (Table 2.)

TABLE 4.—*Effects of varying salinity on Urosalpinx cinerea from Beaufort, N. C., and Hampton Roads, Va., summer of 1929*

Items	Experiment No.—			
	V	VI	VII	VIII
Salinity at which drills were killed (p. p. m.).....	15.25	16.64	16.51	10.63
Percentage of deaths after 8 days.....	94	92	76	100
Salinity at which drills survived (p. p. m.).....	18.25	18.87	19.93	12.79
Percentage of survival after 8 days.....	94	82	86	75
Percentage of deaths in control.....	2	12	12	0
Average temperature for period (° C.).....	23	23	22	25
pH for period.....	8.6	8.5	8.6	7.9

The preceding data show that the salinity death point of *Urosalpinx cinerea* is influenced to a great extent by the environmental salinity. Snails collected at the Norfolk Point localities having salinities of approximately 15 and 20 parts per mille show lethal salinities of approximately 12.5 (Table 2) and 11.7 parts per mille (Experiment No. VIII, Table 4). On the other hand snails collected at Beaufort with an environmental salinity of approximately that of sea water (over 30 parts per mille) for most of the year, show a lethal salinity of 15.6 (Table 3) and 17.6 parts per mille (Experiments V, VI, and VII, Table 4).

In this connection it is interesting to draw attention to one fact which these results bring out. The extent of adaptability, or the salinity factor of safety, becomes smaller as the animal becomes adjusted to lower salinities. Thus at Hampton Roads a drop of from 8 to 9 parts per mille (at the maximum, from 20 to 12) was fatal, while at Beaufort a decrease of over 15 parts per mille in the salinity of the waters was necessary for death (from 30 to approximately 16). The adaptation to lower salinity seems to bring about a reduction of the salinity safety factor. This lower factor of safety in an animal which has become adapted to lower salinities may become of biological importance in its distribution. For instance, heavy rains in the area drained by the Elizabeth, Nansemond, and James Rivers might reduce the salinity of the Hampton Roads region sufficiently so that *Urosalpinx cinerea* infesting oyster beds in this locality would be killed in great numbers.

CREEPING AND MIGRATIONS .

In the majority of gastropods locomotion is dependent on the formation of successive pedal waves (Parker, 1911, 1914); and according to Parker (1911, 1914) and Olmsted (1917) the pedal wave is an area lifted from the substratum in which movement takes place, the remainder of the foot being stationary. Other investigators have claimed that the wave is an area of convexity (von Uexküll, 1909; van Rijnberk, 1918-19; ten Cate, 1923). Some few gastropods have also been described as showing no pedal waves during locomotion. Parker (1911) and Crozier (1919) believe that where no cilia are present this type of locomotion is due to an "arhythmic" type of pedal waves; and Dubois and Vlès (1907) have shown that even though the pedal surface is ciliated, locomotion depends on muscular activity alone. More recently Copeland (1919, 1922) has maintained that locomotion due to cilia does obtain among gastropods (*Alectrion* and *Polynices*), a conclusion that does not seem to be altogether proven by his results. The mechanism by which the pedal wave is produced has been studied, and several theories have been brought forth; but the subject does not properly belong here. Anyone interested in it will find a complete bibliography in van Rijnberk's paper (1918-19).

In *Urosalpinx cinerea* no pedal waves can be demonstrated during locomotion. It moves by a smooth, gliding motion comparable to that of *Nassa obsoleta* (Parker, 1911; Copeland, 1919) and *Conus agassizii* (Crozier, 1919). Furthermore the pedal surface is covered with cilia whose effective stroke is backward, leading one to suppose that locomotion is due to their activity.

A study of the pedal surface both moving and at rest gave some interesting results. At rest, the animal is attached to the substratum by means of the posterior part of the foot. When movement is to take place, the anterior margin of the foot is thrust forward and attached. Until this part of the foot is in contact with the substratum no translatory movement can occur. Cessation of locomotion occurs only after the anterior margin has been lifted from the substratum. Thus there is

a close connection between locomotion and the anterior margin of the foot. On close examination of this area it was found by the author to be divided by a transverse depression forming a pair of lips at the front of the pedal surface. Anterior to this depression were seen small, irregular, transverse waves, that were too rapid to count and to examine carefully, and that never crossed the indentation. These waves had also been observed by Parker (1911) and Copeland (1919) in *Alectrion*.

The animal creeps forward at an average rate of 2.6–2.8 centimeters per minute at 26.5° C.—a relatively slow rate—and as in many gastropods reversal of progression does not occur. Adhesion depends entirely on the secretion of slime, as is shown by the absence of areas of concavity that are necessary if suction plays any part in adhesion.

Microscopic study of the pedal surface showed that the whole of it is covered with cilia, and by the use of carmine it was demonstrated that their effective stroke is backward. Isolated pieces of the pedal surface showed beating cilia after 24 hours. Because the pedal surface is small, it was impossible to repeat Copeland's (1919) observations on *Alectrion* in which, by allowing the animal to creep along the surface of the water, he was able to show that the cilia beat only during locomotion.

In the study of the natural history of any animal it is important to know something about its migrations. If control measures are to be devised this question assumes even greater significance since it is so closely related to the distribution of the animal. For this reason the migrations of the drill were studied at Hampton Roads and at Beaufort. As Gowanloch (1927) found, gastropods are not easily marked. After many attempts the following methods were used: (1) Coloring the shell with a wax pencil; (2) marking with sealing wax; (3) painting with oil colors; and (4) attaching a cerise colored celluloid tag, a method that had serious objections but that yielded the best results. The tag was fastened to the outer lip of the shell with a fine silver wire. All four methods were used at Hampton Roads; at Beaufort, only the celluloid tag.

At Hampton Roads 577 marked drills were set out over bottoms of various types during the year 1927. Because of the depth of the waters those set out over sandy and muddy bottoms could not be recovered; only those planted on oyster beds were found again. For the recovery of the drills dredging was first used; but, since it was impossible to fix the location of the recovered drills and since it did not yield satisfactory returns, this method was dropped. The procedure finally adopted was as follows: A stake was planted at the desired place, around which the marked drills were set. This area was then marked off in concentric circles, 25, 50, 75, 100, 150, and 200 feet from the stake. Each circle had from four to six stations which were tonged at weekly intervals. It was then possible to know the distance and direction of migration. After the first week tonging was done at greater and more scattered distances until approximately one month from the time of planting, when collecting ceased.

TABLE 5.—Results of migrations experiments at Hampton Roads, 1927

Approximate distance traveled, in feet	Drills recovered		Approximate distance traveled, in feet	Drills recovered	
	Number	Time after planting		Number	Time after planting
0.....	2	2-4	75.....	2	2-4
25.....	9	2-4	100.....	6	2-4
50.....	8	2-4	150-200.....	1	3

The data shown in Table 5 are few because the possibility of the loss of the identification mark is great and the probability of recovery from depths in which the drill can not be seen is small. The largest loss occurred because of the inability to recover drills from areas not having oysters.

The data obtained at Hampton Roads demanded a further study of the movements of the drill at Beaufort where, owing to the shallow waters, more satisfactory results could be obtained. The oyster beds in this region are either exposed at low water or are just below the low-water mark. The method employed was similar to that used at Norfolk, except for some few minor changes. At low water a stake was driven in the desired locality, and the tagged drills planted. Each day, at low water, the locality was visited and the movements of the drills noted. Since the tags were numbered, it was possible to observe the movements of each drill day by day.

The results obtained corroborate the observations made at Hampton Roads. In every case, even after one month, the tagged drills had not moved over 10 to 15 feet from the original place of planting. This was not due to the presence of unlimited food, because in one case the drills were placed on a hard bottom about 20 feet from an oyster bed and in no case did the drills move to it.

Migration experiments at Hampton Roads and at Beaufort have shown that *Urosalpinx cinerea* does not migrate extensively. This is supported by other evidence. In the study of the distribution of the drill over Hampton Roads it was observed that contiguous oyster beds which had been left undisturbed for two years were infested by oyster drills in different quantities—an observation that was corroborated by several oystermen. The conclusion seems obvious: If any migration does take place such a condition could hardly exist, even though the presence of unlimited food might prevent any pronounced movements. The greater infestation of planted grounds over "natural rock" can not be explained except by the assumption that the drill does not migrate. An analysis of the older literature also supports this conclusion. Although this species inhabits the waters from Maine to Florida the greatest infestation obtains in Chesapeake Bay and in the waters north of it (Rathbun, 1892; Collins, 1890; Hall, 1894; Rowe, 1894; Moore, 1897; Nelson, 1922, 1923; Rich, 1924, 1925), while south of this body of water the pest is insignificant (Ryder, 1883; Dean, 1892; Ruge, 1898; Swift, 1898; Moore, 1898; Grave, 1905). Side by side with this observation is the fact that oyster culture is practiced intensely only in the northern waters; in the southern waters oyster farming is rare. Does not this indicate that oyster planting has something to do with the distribution of the snail?

How is the species distributed? In the author's opinion the agency of distribution is primarily the oysterman. Note his planting operations and the above conclusion is inevitable. The author has known a planter to move 60,000 bushels of oysters from a very badly infested area, having a salinity sufficiently low so that the drills were not doing much damage. Without screening or even forking they were transplanted to another area not so heavily infested but having a more favorable salinity. In one year the new bed was almost a total loss. Though the greatest distributor is the oysterman, there are other agencies. The crabs, especially the hermit crab, spread the animal. The drill attaches itself to the shell, feeds on the encrusting gastropods, crustaceans, etc., and is in this way carried over great distances. The young drills may be distributed by current if they become attached to floating algæ, débris, etc.

TEMPERATURE EFFECTS

Early in the study of the oyster drill it became evident that temperature had a great influence on its activities. During the winter months the animal becomes inactive, remaining attached to the substratum or lying passively on the bottom. A temporary rise in temperature causes slight creeping, but no feeding.

During the winter of 1926-27 about 100 animals were kept in the laboratory tanks and their activities studied in relation to the daily water temperature. Throughout the greater part of December and January they remained totally inactive; in February they showed slight sporadic movements. They crept up the sides of the tank—a reaction which always followed the beginning of activity. Toward the end of February and the early part of March unusually low temperatures occurred, bringing about complete immobility. On March 14, although the temperature rose above 10° C. the salinity was low so that they showed no movement. Inactivity obtained during the latter part of March and early part of April. From the middle of April until early May the animals were inactive because of a combination of low

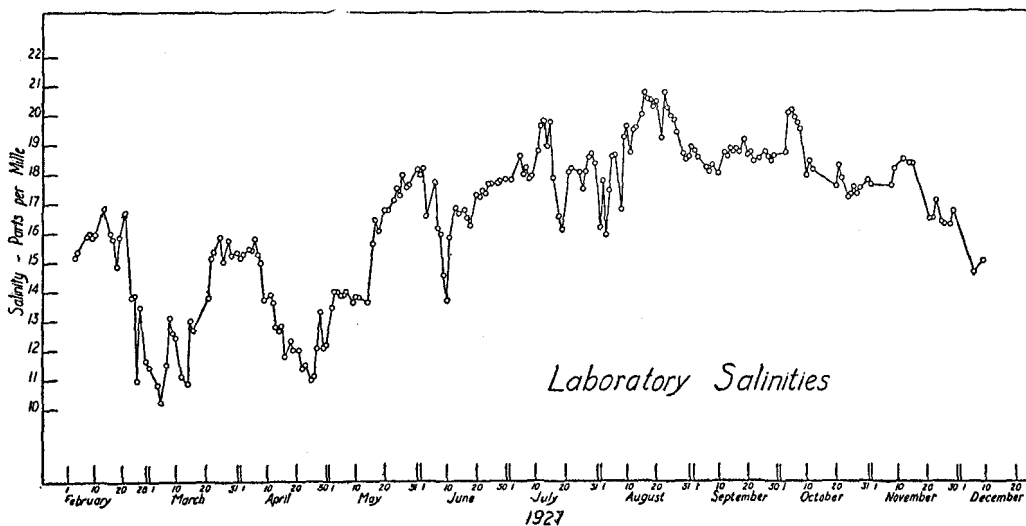


FIGURE 4.—Salinity chart for laboratory sea water at Craney Island

temperature and low salinity; then they became more and more active. These observations were corroborated by those obtained at Beaufort, where temperatures below 10° C. caused immobility.

Temperature affects not only the general activities of the animal but also feeding and spawning. At Hampton Roads during 1927 spawning first occurred in the laboratory on May 19. On May 20 the first egg cases were collected in the field. In Beaufort (1928) the first spawning occurred on March 31. In both cases the water temperature had risen over 20° C. for some time.

Feeding is greatly affected by temperature. At Hampton Roads the drills began to feed during the latter part of March (1927) when the temperature rose above 15° C. On March 23 the temperature fell to 10° C. and feeding immediately stopped, a reaction not due to salinity because on these dates the salinity was over 15.00 parts per mille. (Fig. 4.) Some feeding occurred during the middle of April, and from May 2 (17.5° C.) it continued throughout the summer. During these observations it was also noticed that drilling would be completely halted by a sudden

drop in temperature. The actively drilling animal would stop, leave its victim, and move to some other part of the aquarium. Two sets of data in support of this are available. On August 26 a sudden drop to 20.0° C. occurred (see temperature chart, fig. 5), and the drills that were actively feeding stopped and moved from the oysters. Again, on September 20, 14 drills were observed feeding on oysters. At this time the water temperature in the laboratory was approximately 27° C. On September 24 the water temperature suddenly dropped to about 20° C. and immediately feeding stopped. Again the drills left their oysters and moved away. These same results were obtained in Beaufort. At temperatures below approximately 15° C. feeding ceased, while sudden falls in temperatures during the summer months were equally effective in bringing about a cessation of the drilling activity.

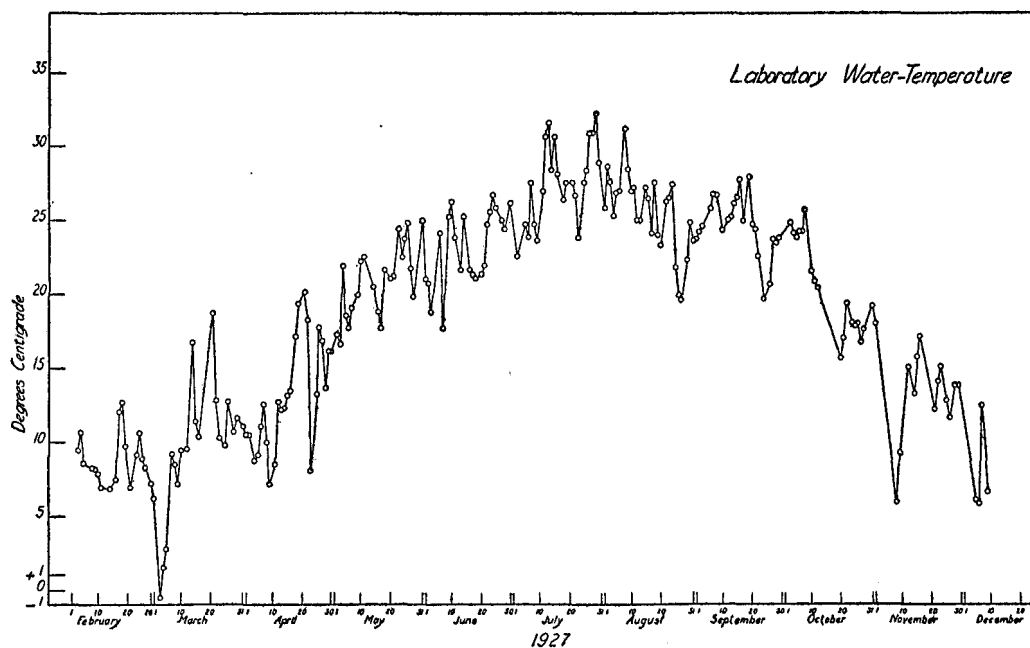


FIGURE 5.—Temperature chart for laboratory sea water at Craney Island. Observations on temperature and salinity were made between 12.30 and 1 p. m.

From the above observations it seems probable that whenever the temperature falls below 10° C. *Urosalpinx cinerea* becomes inactive, and that feeding does not take place at temperatures below 15° C. Even at temperatures above 20° C. sudden drops will interrupt the drilling activity. Spawning takes place when the water temperature has reached 20° C.

FEEDING HABITS

The damage done by *Urosalpinx* has never been accurately determined for oysters beyond the spat age. Rowe (1894) estimated that in southern New England the loss was approximately \$1,000,000 yearly, and Nelson (1922, 1923) stated that in Delaware Bay the drill killed as many as 50 per cent of 2-month-old oyster spat. Galtsoff (1925) estimated that in East Haven River (Long Island Sound) 50 per cent of the young oysters had been killed by the drills. In order to get some quantitative data on the actual amount of damage done by this pest to large oysters, surveys

were made over the various oyster beds at Hampton Roads. Oysters were dredged from the desired area, culled, and the dead shells picked out. A record was kept of the total number of live oysters, the total number of dead shells, and the number of "drilled" shells. From these figures the percentage of damage was determined. The surprising fact was the unexpectedly small percentage of deaths from the drill. Table 6 gives a summary of the percentages.

TABLE 6.—Damage caused by *Urosalpinx cinerea* over Hampton Roads for June, 1927

Station	Live oysters	Dead shells	Drilled shells	Dead oysters	Oysters killed by drills in relation to live oysters
	Number	Number	Number	Per cent	Per cent
Pig Point.....	605	104	21	14.7	¹ 3.5
Crane Island Creek.....	408	75	5	15.5	1.2
Crane Island Flats.....	103	75	8	42.0	7.8
Mouth of Nansemond River ²	110	53	1	32.5	.9
East Spit ³	353	103	28	22.5	¹ 7.8
Broad Rock ⁴	72	38	1	34.5	1.4
Western branch of the Elizabeth River ²	93	32	1	25.5	1.0
Ocean View.....	709	138	32	16.5	¹ 4.5
Little Bay.....	332	113	42	25.5	¹ 12.7
Hampton Bar.....	885	290	180	25.0	¹ 20.0
Tanners Creek.....	87	31	1	26.5	1.1

¹ Planted areas.

² Drills absent.

³ Stations Nos. 27, E, and F.

⁴ Stations Nos. 33 and 34.

The significant figures are in column 6; that is, the percentage of drilled shells referred to the number of live oysters present. These figures show that the percentage of deaths due to the oyster drills is much higher on cultivated oyster grounds than on natural oyster rock, the average for planted bottoms being approximately 10 per cent, that for natural rock approximately 2 per cent. This difference is correlated with the greater number of oyster drills present on cultivated grounds. Why more drills are present on the cultivated areas undoubtedly seems to be explained by the following: (1) The distribution of the drill by man; and (2) the presence of practically unlimited amounts of food.

Although several explanations—Stimpson, 1860 (from Colton, 1908); Ingersoll, 1884 (from Colton, 1908); Schmienz, 1891 (from Flattely and Walton, 1922); Herrick, 1906; and Colton, 1908—as to how the carnivorous gastropods attack their victims have been advanced, the accepted mechanism by which food is obtained is the rasplike radula along with its cartilage and muscles, the whole organ being called the odontophore. The "filing" is done by the radula, a ribbonlike rasp, on which the teeth are fixed. As this wears out it is replaced from the radula sac, growing forward like a nail over its bed as fast as it is worn out in front. The exact method by which the radula is moved has been studied by many investigators. Two theories have been brought forward: (1) The radula moves relatively to its cartilages and its rasping action is due to its own proper motion; (2) the radula remains at rest relatively to its cartilages, and its rasping action is due to the movements of its cartilages. The former was originally advanced by Huxley (1853) a view accepted by Wegmann (1884) and Oswald (1894), later corroborated by Herrick (1906), and at present the accepted one. The latter interpretation is that of Lacaze-Duthiers (1856) and Geddes (1879). Whether or not acid is secreted to aid the drilling is still a moot question, although glands capable of secreting acid have been described in some prosobranchs (Tryon, 1880).

Urosalpinx cinerea feeds on almost all bivalves. The author has observed it feeding on the following animals: Oysters, clams, mussels, *Crepidula*, small crabs, barnacles, and even on its own kind, while other investigators report the drill as perforating scallops (Belding, 1910) and chitons (Arey and Crozier, 1919). Contrary to Colton's (1910) results with *Sycotypus* and *Fulgur*, the drill will feed on the meat of oysters, clams, fish, crabs, etc.

The drill's method of attacking an oyster is as follows: After coming upon the oyster the drill selects a valve, the choice of which depends upon many factors, moves over it, chooses a place, and attaches itself, adhering to the substratum by means of the posterior part of the foot. Its proboscis is then thrust out, the odontophore comes into play and the rasplike radula begins to drill. After the shell has been perforated the proboscis is inserted and the animal feeds.

The first question that naturally arises is this: Does the drill limit itself as to the size of the oyster attacked? Field and laboratory observations support the conclusion that it preferably feeds on the smaller and thinner shelled oysters, but that oysters of all sizes are subject to its attack. More than one drill may attack an oyster at the same time—an observation corroborated by Belding (1910) for scallops. But even if one drill succeeds in piercing the oyster shell before the other, the unsuccessful drill continues its rasping, a fact shown by several shells which had as many as four distinct perforations and by direct observations.

As in nearly all other marine mollusks the drill possesses an osphradium—an organ intimately connected with the breathing organs, being generally placed near their base. It consists of a patch of modified epithelium connected by its own nerve with one of the visceral ganglia (Cooke, 1895) and, as was shown by Copeland (1918) for *Alectrion obsoleta* and *Busycon canaliculatum*, is the organ of smell. Through it the drill is undoubtedly attracted to the food.

The selection of the valve to be drilled depends on several factors. The first, purely mechanical, is closely related to the age and size of the oyster. For instance, oysters at the spat stage or less than 1 year old are so attached to the substratum that only the upper or right valve can be attacked. Although this is not so true of larger oysters there are other limitations. Oysters lying flat on the bottom have only one valve exposed which on natural rock is usually the right, and on planted beds may be either. The second important factor in the choice of valve is one which is not at all understood. Observation made by others as well as the author (Pope, 1910, 1911; Nelson, 1923) show that the drill preferably chooses the thinnest shelled animals—a reaction that would undoubtedly bring about the selection of the right shell since that is usually the thinner unless some other response prevented this choice. The third response, which is perhaps the most important of all, is the negative geotropism of the animal. The significance of this is apparent from observations made in the laboratory at Hampton Roads and Beaufort. The essentials were these: Individual oysters of different sizes were placed in tanks so that almost the whole of the two shells were accessible to the drill. The oysters were then arranged so that different parts of the shell would be uppermost. Drills were introduced and in almost every case the hole was made on the shell lying uppermost. These results contradict the observations which showed that the thinner shell is the one chosen. The author believes that this contradiction can be explained on the assumption that the effect of gravity overcomes the response to thin shell.

In the field all these factors play an important part, and depending on the individual bed the results will be different. Two illustrations will suffice. A newly

planted bed, having only young spat, would show almost all right valves perforated. On the other hand planted beds where oysters average 2 to 3 inches in length and are more or less single the result will give about 50 per cent rights and 50 per cent lefts. This condition exists at Hampton Roads. Out of 123 drilled valves from planted areas 67 per cent were rights—a result that is sufficiently close to be significant, since it would be quite natural to find, even under ideal conditions, more rights because the drills' tendency to attack the thinner shells.

The place of perforation on the shell depends on factors not yet determined. In the examination of this response one interesting fact became apparent. For these observations the area of the shell was divided into small squares and the perforations were correlated with them. Two important results were obtained: (1) Holes occurred on either shell and on every portion of them; and (2) 73 per cent of the perforations were over or near the place of muscle attachment. The explanation for the latter is not evident, although it may be a thigmotactic reaction.

Belding (1910) states that *Urosalpinx cinerea* requires from four to six days to drill through an adult scallop. Experiments (36 in all) made at Hampton Roads show that the average rate in oyster shells drilling is approximately 0.4 millimeter per day. Several factors such as hardness of shell, size of drill, and temperature modify this average.

A study of the reactions of the oyster after perforation gave some insight into the method by which the drill kills it. The first experiments made at Beaufort were as follows: The snail was permitted to drill through the shell of an oyster and then removed and the oyster observed. In every case the oyster eventually died from the perforation, proof that some toxic substance had been injected into it, since oysters which had been perforated with a common machinist's twist-drill continued to live indefinitely. However, there were a few exceptions. If the hole was made by *Urosalpinx* so that only the edge of the mantle was perforated, immediate removal of the drill saved the oyster from death. On the other hand if its perforation was over the adductor muscle, the pericardial cavity, or the visceral mass, the oyster opened almost immediately, while if it occurred at the periphery it might be several days before the adductor muscle relaxed. After the oyster opens, crabs and other scavengers indulge in the feast, hastening the removal of the oyster, and causing the drill to attack new ones. From data collected at Beaufort one drill can kill from 30 to 200 oysters in a season depending on their size.

The drill like some other carnivorous gastropods feeds not only on live oysters, scallops, clams, etc., in the shell, but also on the meat taken from the shell—a fact significant for any method of control that plans to use the meats of these animals and of fishes as baits. Field and laboratory experiments were made in a study of this reaction, but only the latter gave usable results. The difficulty in the field was this: Owing to scavengers and putrefaction the bait did not last long enough to allow the drills to react to it, and although various types of cages were used to eliminate the scavengers it was impossible to keep the bait for longer than 12 hours (during the summer months, which is the time most favorable for trapping, because the drills are then most active), which was of insufficient duration.

In the laboratory, experiments were devised to find out what meats the drill prefers and the maximum distance at which these are effective in attracting the snail. Completely satisfying results could not be obtained especially to the latter question, because the baits putrefied before the drill could get to them. The experiments were conducted in the following way: Meats of freshly killed oysters, clams, scallops, pin-

fish, spots, croakers, oyster drills, and *Crepidula* were placed at one end of a tank of aerated sea water. The water was not permitted to run in these tanks because of the effect of currents on the movements of the drills (Federighi, 1929). At varying distances tagged drills were introduced and their movements noted. Although no results were obtained as regards the greatest distance at which the drills react to the foods some data were collected on the relative efficiency of the various meats. It was found that oyster meat is preferred to any other, and mollusks are preferred to fishes. In one of the experiments there was introduced besides the various meats some oyster spat. The result was that the drills attacked these shelled oysters in preference to the more easily available meats. It is true that not all the drills went to the shelled oyster spat, but a good number did and this in spite of the fact that they had to pass by some freshly killed oyster meat to get to them.

BREEDING HABITS

In *Urosalpinx cinerea* as in other prosobranchs the sexes are separate, the males being distinguished by a large curved penis which lies at the right side of the head behind the eyes. The two sexes can also be separated by macroscopic examination of the gonads, the male glands being whitish in appearance; that of the female yellow to orange in color. The eggs are laid in small, yellow membranous, vasselike capsules attached to the substratum by a solid expanded foot. The egg case is flattened vertically with edges marked by keellike ridges and has, at the top, a small cap through which the fully grown larvæ escape. Within the capsule is a soft jellylike fluid in which the eggs are laid and which serves not only to protect them from mechanical injury but also as a source of food. At Hampton Roads during 1927 the first egg cases were collected in the field on May 20 and in the laboratory on May 19, while at Beaufort the first egg cases were gathered (during 1928) on March 21, and in the laboratory on March 30. Spawning continued throughout the summer, and during the fall it gradually decreased in intensity until at Hampton Roads spawning practically had ceased by the 1st of October.

The details of spawning, development, and hatching were studied in the laboratory. The work included observations on the following subjects: (1) Copulation; (2) behavior of the female during spawning; (3) the number of times a single female spawns during one season; (4) duration of oviposition; (5) the rate of oviposition; (6) the number of egg cases laid per female; (7) the number of eggs per egg case; (8) duration of the incubation period; and (9) the percentage of drills hatched.

Although copulation undoubtedly occurs in *Urosalpinx cinerea*, copulating drills were never collected in the field nor was copulation ever observed in the laboratory—a fact probably explainable by assuming that copulation occurs only at night. For this reason it is not known whether the drill copulates more than once a season or whether the sperm are carried over from year to year.

Because of the snail's negative geotropism the female creeps up to the higher levels to spawn. Without this response the eggs would be laid in the lower strata and be suffocated and buried in the mud. In almost all cases if oysters were present in the tank the female would climb on them to deposit the capsules in preference to the sides of the tank. While spawning the female does not feed but remains attached to the substratum and unless disturbed continues until spawning is completed. Observations in the laboratory show that each snail spawns only once during the summer, although in some cases, when the animal was disturbed while spawning, it would cease, move away, and for several days show no spawning activities. After a few

days it would resume its egg laying. In many cases the snail would return to its "original" spawning grounds. Such a response if the animal's previous history were unknown might give the impression that spawning occurred more than once during a single season.

Oviposition lasts for various lengths of time, depending on whether the animal is disturbed. Sudden drops in temperature or lifting from the substratum bring about cessation of the spawning reaction, so that it is difficult to determine accurately the duration of spawning. During 1927, at Hampton Roads, 6 animals were observed in which spawning was accomplished without any apparent interruption. In these the average time was approximately 7 days, during which time an average of 28.8 cases were laid per female. As is shown later these figures agree very closely with those obtained from an analysis of the rate of oviposition and the number of egg cases laid per female. The rate of oviposition was determined by observing 19 females that spawned 127 egg cases in 32 days, an average per female per 24 hours of 3.9 egg cases. This figure is very close to that obtained from the data on the duration of spawning in which a female spawned 28.8 egg cases in 7 days or 4.1 egg cases per female per 24 hours.

In order to determine the number of egg cases one female lays in a season, several animals were isolated and the number of egg cases laid by each one noted. These females were kept isolated throughout the whole summer in order to be sure that no further spawning took place. The data obtained from these observations support the figures previously given for the duration of oviposition. The average rate of oviposition is 3.9 egg cases per day, and the average number of egg cases laid per female is 28; thus each female, if undisturbed, would require approximately 7 days to complete her spawning.

Examination of 727 capsules collected during the summer of 1927 at Hampton Roads gave an average of 8.8 eggs per egg case. The smallest number of eggs per capsule was 3; the largest 22.

In order to determine the incubation period of the drill, freshly laid egg capsules were isolated and the time when hatching occurred noted. These experiments were necessarily performed in the laboratory. Eleven different batches of egg cases were thus isolated during May, June, July, and August. The following table (7) summarizes the results. The average incubation period obtained from these figures is approximately 40 days.

TABLE 7.—Summary of the results on the incubation period of *Urosalpinx cinerea* obtained in the laboratory at Hampton Roads during summer, 1927

Time egg case was laid	Incubation period	Minimum and maximum temperatures during incubation period ¹	Time egg case was laid	Incubation period	Minimum and maximum temperatures during incubation period ¹
	Days	° C.		Days	° C.
May 20.....	36	18.0-26.0	June 23.....	37	22.0-32.0
Do.....	38	18.0-26.0	July 9.....	44	24.0-32.0
May 23.....	38	18.0-26.0	July 12.....	42	24.0-32.0
June 20.....	39	21.0-32.0	July 15.....	40	24.0-32.0
June 22.....	43	22.0-32.0	Aug. 11.....	44	20.0-30.0
Do.....	41	22.0-32.0			

¹ See Figure 5 for daily temperatures during these periods.

Since the period of oviposition varies greatly the period of hatching is also varied, and one finds in a single group of egg cases embryos in different stages of development. This undoubtedly explains the variations in the incubation period (Table 7), since it is impossible to tell the exact age of the embryos within the capsule at the time they were isolated.

Brooks (1879) reported that some of the embryos in the capsules of *Urosalpinx cinerea* broke up, the separate cells swam about, and were drawn within the digestive cavities of other embryos. This suggested that some observations should be made on the number of larvæ hatching from the egg cases. Although the data given below are not many, they serve to indicate the magnitude of the percentage of drills hatching. Twenty-eight capsules gave rise to 144 larvæ, an average of 5.1 larvæ per capsule. Since the average number of eggs per egg case was determined as 8.8, the average percentage of eggs hatching into larvæ is about 58 per cent.

Besides these observations it seemed desirable to study the effect of salinity on the spawning of the animal, since in the transplanting of oysters, *Urosalpinx cinerea* is sometimes subjected to waters of very different salinities. The study was undertaken to show: (1) The effect of salinity upon the number of egg cases laid, and (2) the effect of salinity on the number of eggs per egg case. Between May 5 and May 26, 1927, at Hampton Roads 13 crates made of fine mesh wire and each containing 50 drills and about 1 bushel of oysters were distributed in various places of salinities varying from 4 to 20 parts per mille. Two crates were planted at each station; one at the surface, the other at the bottom. These were visited at definite intervals, egg cases collected, and the condition of spawning noted. The work was only partially successful because by July 1 the crates had all disappeared. The results shown in Table 8 are significant in that they show that the oyster drill reproduces wherever it survives. Salinity does have some effect on the number of eggs per egg case as is evident from the table. A salinity of 17 parts per mille seems the optimum salinity for the number of eggs per egg case at Hampton Roads.

TABLE 8.—Effect of salinity on the spawning of *Urosalpinx cinerea* at Hampton Roads, 1927

Average salinity	Number of egg cases counted	Average number of eggs per egg case	Approximate date of spawning	Average salinity	Number of egg cases counted	Average number of eggs per egg case	Approximate date of spawning
4.00.....	(1)	(1)	(1)	15.00.....	97	8.4	May 20
7.00.....	(1)	(1)	(1)	17.00.....	109	9.3	Do.
12.00.....	44	8.9	May 15	20.00.....	43	8.9	Do.

¹ Drills all killed.

TROPISMS

The study of the natural history of any animal must be supplemented by laboratory experiments, where conditions can be controlled and the behavior of the organism more easily analyzed and interpreted. Although it is true that conditions in the laboratory never exactly simulate the field or the natural environment, laboratory results are important in permitting one to predict what the animal will do when subjected to certain isolated stimuli. After all, the behavior in the field is only the result of several reactions working simultaneously. In the laboratory these reactions are isolated and studied individually. If inconsistencies are found between the results obtained in the laboratory and the responses in the field, one must not condemn laboratory work as the fault usually lies in insufficient data. In order to arrive at some means of controlling the oyster drill it is necessary to know something of its responses

to the stimuli to which it is normally subjected. These observations can not be made successfully in the field.

Geotropism is characteristic of many different animals. Although the theories devised to explain this response are many and varied (see Cole, 1925-26; Crozier, 1928 for complete bibliographies on the subject), there are only two hypotheses that seem to be acceptable: (1) A theory which proposes that the gravity responses depend on the otolith-apparatus (Lyon, 1905; Baunacke, 1913; Kanda, 1916, 1916b), and (2) a theory which suggests that geotropic orientation may depend on the stimulation of proprioceptors in the symmetrical parietal musculature (Cole, 1917, 1925-26; Arey and Crozier, 1919; Crozier and Federighi, 1925; Crozier, 1928). During the spring, summer, and fall—that is, when the temperature rises above 10° C. and the animals creep about actively—*Urosalpinx cinerea* exhibits a very pronounced negative geotropism. Such a reaction is important in that it is successful in keeping the egg capsules from being laid on the bottom where they would be covered with silt and the embryos killed.

That this is a geotropic response is shown by the following observations. It persists in the dark room and when the eyes are removed; and is not dependent on oxygen content because experiments have shown that animals in aerated sea water, where presumably the water is saturated as to oxygen, will give the geotropic response. If an animal is allowed to adhere to a glass plate, the plate raised vertically, and then turned as a wheel on its hub, thus changing the orientation of the animal, the snail will always turn so that the siphon points up and the shell apex down. The direction of body turning—that is, either clockwise or counterclockwise—depends on the side on which the apex is placed since in every case the apex moves down.

The explanation for the absence of any negative geotropism during the winter months is not altogether clear. Two hypotheses may be suggested: (1) The low temperature may bring about a reversal in the response as in lower animals (Massart, 1891; Sosnowski, 1899), or else (2) negative geotropism is dependent on the activity of the animal, an explanation that is probably the true one. This loss of geotropism is significant for any method of control which plans on trapping the drill by means of a dredge (Moore, 1897) and also for the pillar method which is described later.

The rheotropic response is found among many animals (Schulze, 1870; Verworm, 1899; Wheeler, 1899; Parker, 1903, 1904; Tullberg, 1903; Lyon, 1904; Dimon, 1905; Jordan, 1917, 1917a; Arey and Crozier, 1919, 1921), and it seems to be dependent on different sense organs in different animals. Bonnier (1896) believed that the rheotropic reaction of fishes was dependent on the lateral line organ, while Parker (1903, 1904) showed that in *Fundulus* the receptor for this response is not the lateral line organ but the skin. Tullberg (1903) believed the ear to be the organ directly concerned with the reactions of fishes to currents. According to Lyon (1904) "the primary cause of orientation in streams of some uniformity of motion is an optical reflex, a tendency on the part of the animals to follow the field of vision." Jordan (1917, 1917a) found for *Epinephelus striatus* Bloch that the end organs concerned in rheotropism are located in the integument and that these organs are the organs of touch, which also serve as the essential organs of current stimulation.

If *Urosalpinx cinerea* is placed in a water current it will orient itself so as to bring the siphon pointing upstream, the shell apex downstream, and move against the current. The response is definite and immediate. The removal of eyes and tentacles does not interfere with the normal behavior of the drill, and experiments carried on in the dark room also gave similar results. Here evidently is a rheotropic

animal that is admirably suited for quantitative study. The following is a brief account of these studies which has already been published in detail elsewhere (Federighi, 1929). Two phases of the response were studied: (1) The relationship between the rate of current and the rate of creeping, and (2) the effect of the current rate on the rate of turning.

In these experiments the animals were placed in a trough suspended in a current of water of the turbulent flow type. For the experiments on the rate of creeping the time necessary for the animal to move one-half inch was taken as a measure of the rate of creeping. The rate of turning was determined by tracing the path of orientation and recording the time necessary for its orientation, then measuring the distance thus traveled with a map measure, and finally recording the number of degrees through which the animal had passed. Knowing these, the degrees turned per centimeter of path at each current rate used was obtained. Surface current velocities of from 1.25 centimeters to 7.6 centimeters per second were used. These were determined by recording the time necessary for uniform bits of cork to travel 5 inches. Between 15 and 20 readings were taken for each velocity and these averaged. At each velocity at least 10 readings for each animal were taken on the rate of creeping or turning, and the average of these taken as the figure for that velocity. In all, 14 animals were used in the study of the effect of the rate of current on the rate of creeping and 11 for the observations on the relation between current rate and rate of turning.

A summary of these data shows that: (1) Creeping and turning are dependent on different mechanisms; (2) the rate of turning—that is, the degrees turned per centimeter of path—is a function of the current velocity, and that when plotted respectively as effect and intensity the curve obtained follows the usual effect versus intensity curve; (3) although the rate of creeping is independent of the current rate, the amount of resistance overcome—or the work done—is also a function of the current velocity; (4) creeping depends either on the ciliated pedal surface or on muscular activity, and in either case these are not affected by the flow of fluid past the animal; (5) turning depends, apparently, on the parietal musculature of the animal. The unequal tension on the two symmetrical parietal muscles, produced by the pull of the shell, which in a stream tends to straighten out so that the shell presents the least resistance to the flow of water with the foot mass as a pivot, is the stimulus which brings about orientation. After the animal has become oriented, there is no effect produced on the rate of creeping; the current acts only to keep the animal oriented.

Experiments on the behavior of the drill under the influence of light were without results, indicating that under the conditions studied, the drill is not phototropic.

Aside from any theoretical significance the tropistic behavior of the drill has a practical application. The response to currents has doubtlessly a great influence on the direction of its movements and its negative geotropism is important in the consideration of any means of control and in the success of its spawning.

CONTROL MEASURES

The preceding study of the life history, habits, and behavior was undertaken in order to devise some means to control *Urosalpinx cinerea* or at least to prevent any further invasion. At this stage the investigator feels very keenly how difficult this is. Any problem that involves the control of the number of individuals in a species already adapted to its mode of life, already having reached an equilibrium

with its surrounding environment, is confronted with tremendous difficulties. It is wise therefore at this time to take up: (1) The factors which are aiding the increase of the pest, (2) the factors which might presumably aid man in his combat with the animal, and then (3) the means by which man may control or at least prevent further infestation.

The soft body of *Urosalpinx cinerea* is covered by a hard calcareous shell well fitted to protect it from the attacks of other animals. Under adverse conditions the body retreats into the shell and the opening is effectively closed by a chitinous operculum, so that the animal can withstand unfavorable salinities and dessication for long periods of time. Besides this structural protection, it is fortunate in having no known enemies except itself.

The spawning habits of the drill insure protection to the embryo, the best supply of food for the young, and a means of distribution. The eggs, inclosed in leathery capsules, protected from the elements, and supplied with food, are laid near or preferably on a bivalve. There being no free living larval stage, the embryos remain within the egg case until completely developed and on hatching begin to feed immediately. The attachment of the capsules to oysters is of great importance. Oyster transplanting usually takes place during the summer months when the drills are spawning, so that even though the oystermen remove the adult drills when transplanting from an infested area, the egg cases still remain. A new area is infested and in a year or two the new drills cause great damage.

The size and the adhesive property of the snail are significant in successful drill control. Approximately three-fourths of an inch in length, its dull grayish-brown color blending almost perfectly with the background, the oyster drill is almost completely hidden. It adheres tenaciously to the substratum, making it difficult to remove by the ordinary methods. If this is so, what about the newly hatched drills that average from 0.8 millimeter to 1 millimeter (about $\frac{1}{16}$ inch) in length?

Perhaps the most important factor that prevents successful oyster drill control is the practice of transplanting oysters regardless of the presence of drills. Thus the oyster planter, by his careless habits, acts as a distributor of this pest, infesting new areas daily.

Against these factors that aid the increase, the distribution, and the destructiveness of the oyster drill, we can place the following: (1) The lack of any pronounced migratory habits and its inability to cross or inhabit muddy areas. (2) Temperature, since during the winter months in waters whose temperature falls below 15° C. no feeding takes place; when the temperature rises above 10° C. the animals are negatively geotropic; they move to the upper surfaces of the oysters and are more easily gathered. (3) Females are generally larger than the males; therefore in any culling process the probability is that the animals removed will be largely females; the significance of this is obvious. (4) The salinity data given above shows that the drill can not withstand salinities as low as those which the oyster can endure. Oyster spats that occur up the river in waters of low salinity are protected from the attack of this pest, and only when man moves the oyster seed down into more saline waters, or an unusually dry season occurs, does the drill become destructive.

For the control and removal of *Urosalpinx cinerea* certain methods are given in the following paragraphs. These have already been published in a preliminary report. (Federighi, 1930.)

Two problems confront the oysterman in combating this species: (1) The removal of drills from areas already infested, and (2) the prevention of the infestation of new areas.

METHODS FOR REMOVAL FROM INFESTED AREAS

(a) *The trap dredge.*—As is seen from the illustration (fig. 6) the dredge consists of a wire cage open in front and fitted with an inclined screen. The dredge is dragged over the infested oyster bed; the oysters are picked up by the blade at the edge of the dredge, moved up over the inclined plane, and the drills automatically screened, falling into the cage below while the oysters pass over and fall back onto the oyster bed. In this way the dredge can be dragged over great areas, without involving the removal of the oysters from the bottom. The dredge is quite satisfactory, provided the oyster population is not too dense.

The most effective time for dredging is the early spring when the animals have become active and are on the upper layers of the oysters, but before spawning begins. If it is done at this time the females are removed before they have spawned and so the young are eliminated. Furthermore, dredging during this season is more effective than in the winter months, since, when active, the animals creep to the top and are more easily accessible. The proper time for dredging at Hampton Roads is the latter part of March; for the Beaufort region the best time is the early part of March.

(b) *The use of small concrete pillars.*—Small concrete pillars, easily handled by one man, may be set out over the infested areas. These pillars, providing surfaces higher than the surrounding area of the oyster beds, act as traps because the animals congregate upon them, owing to their tendency to creep upward. After three or four days they are taken up, the drills removed, and the pillars set out again in new places. If the area is below low-water mark, lines and buoys can be attached to the concrete blocks, thus facilitating removal and replacement. Pillars of the size shown in the illustration have collected as many as 500 drills in three days from experimental tanks which were heavily infested. Although no field observations have been made with concrete blocks, sand-filled buckets placed on infested beds have collected a great many drills.

(c) *Dredging with an oyster dredge fitted with a small-mesh bag.*—This method is practicable only if the infested oyster bed is being dredged for oysters which are to be marketed and if the oysters are all to be taken up. The procedure is as follows: After most of the oysters have been taken up, the bed is worked with a dredge having a very small-mesh bag. In this way the drills, shells, and other débris are taken up and can later be disposed of by burning or drying in the sun. It is important that the infested bed be gone over carefully with such a dredge. After this has been done, uninfested oysters can be planted in such a locality without fear of loss from drills.

METHODS FOR PREVENTING DISTRIBUTION

The solution of the problem of the further distribution of the pest is not as difficult as that which involves the cleaning of infested areas. Because the drill is almost nonmigratory the infestation of new areas is easily controlled. The oyster planter must be careful not to plant infested oysters in noninfested areas. Before doing this it is necessary for him to remove as many of the drills as he can by use of methods described below.

(a) *The use of forks.*—This method is inexpensive and simple. After the infested oysters have been put aboard the oyster boat, they are thrown overboard onto the new

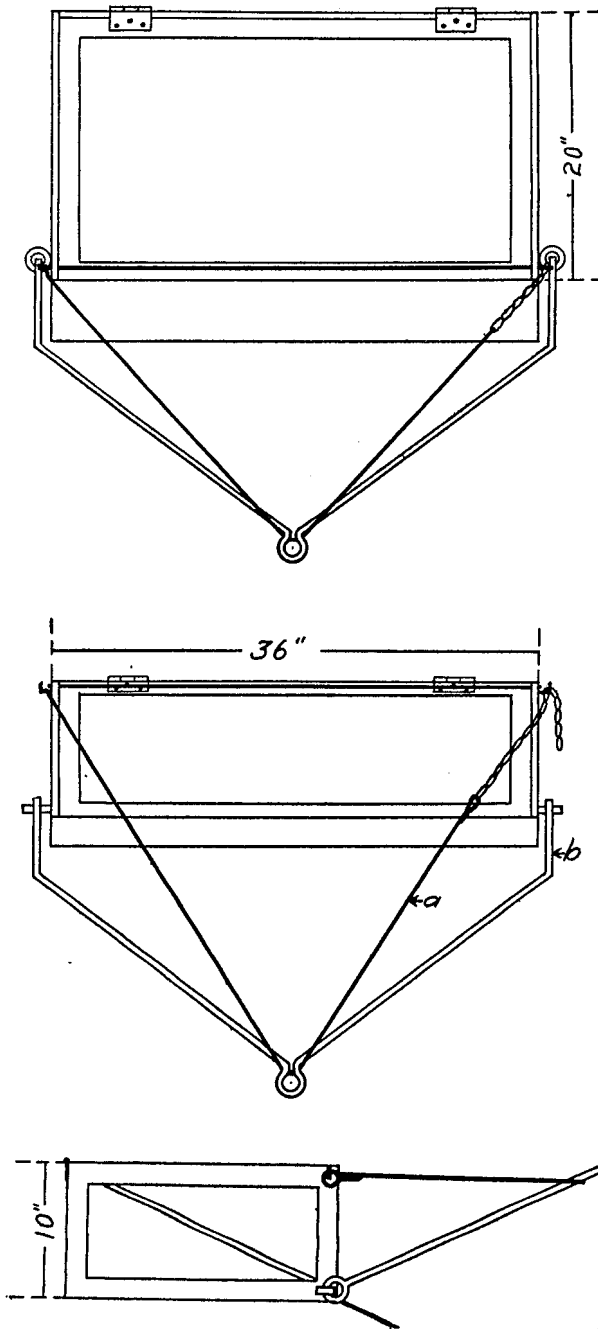


FIGURE 6.—Figure of modified drill-trap dredge. Approximate dimensions are: Length, 36 inches; width, 20 inches; height, 10 inches. Sides and back to be covered with fine hardware cloth so as to prevent the escape of the trapped drills. The lid to be covered with wire screen small enough to prevent oysters from falling into trap but large enough to allow the drills to pass through easily

bed not by shoveling but by using forks such as are employed by farmers. A forkful of oysters is taken up, and before throwing them overboard they are shaken on deck a couple of times by dropping them and taking them up again. In this way a good many of the drills are shaken off, fall on the deck, and can later be destroyed. This method involves no expensive apparatus or excessive time. The only expense is the slightly longer time required to throw the oysters overboard.

(b) *Screening*.—A little more expensive than forking, screening is a little more efficient. The method is essentially similar to that used to screen sand from gravel. The infested oysters which have been dredged and placed on deck are allowed to remain in the air for several hours. This loosens the drills from the oysters so that they can be shaken off more easily. After this exposure to the air the infested oysters are thrown against a screen, the mesh of which is sufficiently large to permit the drills to fall through but small enough so that the oysters will not. One-inch, double-weight-mesh chicken wire answers the purpose very well. There are several advantages to screening the oysters aboard, providing the boat is sufficiently large. It eliminates the expense involved in handling the oysters; and the screened oysters can be thrown overboard, using forks, immediately after they are screened, thus doing away with one more handling. The drills that fall through the screen can be destroyed by burning or by drying in the sun.

(c) *Floating*.—The effectiveness of this method depends on the fact that drills are killed in brackish water which, however, is not fresh enough to kill the oysters. This method is very efficient, and its efficacy warrants its use in heavily infested beds, even though the oysters are not to be transplanted. The procedure is this: It is first necessary to find the exact dilution of sea water which is fatal to the drills of a given locality. This is important because it has been found that drills taken from various regions can sustain different dilutions, depending on the salinity of the water in which they were grown.

After this has been determined, the infested oysters are placed in large cars and kept for about 10 days in waters of the lethal dilution. In this way the snails are killed without harming the oysters. The method has the further advantage in that it kills not only the adult animals but also the small newly hatched individuals, which in other control measures usually escape. After the drills have been destroyed, the now uninfested oysters can be planted on clean beds. For Hampton Roads the lethal dilution, or death-point salinity, is approximately 12 parts per 1,000; for Beaufort, it is slightly higher, about 14 parts per 1,000. It is important not to crowd the oysters when floating them, otherwise a great many will die.

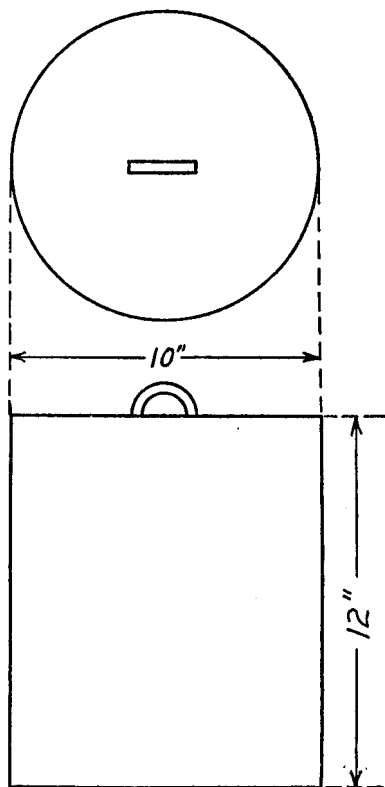


FIGURE 7.—Small, concrete pillar for the trapping of oyster drills. A hook embedded at the top facilitates handling when the pillars are to be planted below the low-water mark. To the hook can be attached a line and buoy, making the trap easy to find.

SUMMARY

The preceding studies may be summarized as follows:

1. The common oyster drill (*Urosalpinx cinerea*) is a carnivorous gastropod, about three-quarters of an inch in length, possessing a hard calcareous shell varying in color from light brown to white. The animal is small, the foot scarcely covering the aperture.

2. The snail inhabits the marine and brackish waters of the Atlantic coast from Maine to Florida, occurring also in San Francisco Bay, Bermuda, and England. At Hampton Roads it is found only below the low-water mark while in Connecticut and North Carolina it is present on beds exposed at low water. Muddy bottoms, clear sands, and depths greater than 25 feet are unfavorable for its growth and multiplication. More animals occur on planted bottoms than on natural rock.

3. Laboratory experiments at Hampton Roads and at Beaufort on the salinity death point of the drill, collected from areas having different average salinities, show that the salinity at which the animal dies (or the salinity limiting the distribution of the animal) depends upon the salinity of the environment from which the animal has been collected. In other words, the snail is capable of a large degree of adaptation to low salinities. It is important to know just how far this adaptation can be carried in order to know whether or not the setting areas will ever be threatened.

4. The exact mechanism of creeping in the oyster drill is still unknown. Either it creeps by muscular activity (arhythmic pedal waves) or through the cilia of the pedal surface. Tagging experiments, distribution observations, and an analysis of the older literature show that the animal does not migrate but that its distribution is dependent on the planting activities of man and on the migrations of other animals such as crabs to which they sometimes attach themselves.

5. Observations on the relation between temperature and the activities of the animal show that: (a) The animal becomes inactive at temperatures below 10° C.; (b) feeding does not occur until the surrounding temperature reaches 15° C.; and (c) spawning takes place only when the temperature is above 20° C.

6. Hampton Roads has not suffered as greatly from this predatory gastropod as has been reported. The percentage of deaths from drills in relation to the number of live oysters present rarely exceeds 3 per cent excepting on planted beds where it is sometimes as high as 20. Areas, where setting occurs and where beds of young oysters are found, necessarily suffer greater damage because the spat are more easily pierced and yield only a small amount of food. The mechanism of drilling is the radula, a rasplike organ which moves over its cartilages much as a belt over a pulley. *Urosalpinx* confines itself not only to drilling a great many living mollusks and crustaceans, but will also feed on the meats of these animals. Although out of a batch of oysters of all sizes the smallest and thinnest shelled are killed first, it has been shown that all oysters, no matter how large, are attacked by the drill. The choice of the valve drilled depends on many factors which are enumerated and the significance of each given in the text. The place of perforation depends on factors not yet known. In three-quarters of the valves examined, the hole occurred at or near the place of muscle attachment although any portion of the shell may be drilled. In oysters, drilling progresses at approximately 0.4 millimeter per 24 hours. The behavior of the oyster, after being drilled, depends largely upon the position of the hole. It is believed that the drill injects some fatal toxic substance into the body of the oyster.

7. Although there is no sexual shell characteristic in *Urosalpinx cinerea*, the sexes are separate. The eggs are laid in leathery, vasselike capsules attached to the

substratum by means of a solid expanded foot. Each female spawns only once a season which at Hampton Roads is from May 15 to September 30. About 28 egg cases are laid per female, and each capsule averages 9 eggs. After approximately 6 weeks, there being no free-living larval stage, the young, about 1 millimeter in length, escape from the capsules through a cap at the top of the egg case and begin to feed immediately. Approximately 60 per cent of the eggs hatch into larvæ. Studies on the relation between salinity and spawning showed that the animal will spawn at any salinity at which it will live.

8. Studies on the tropistic behavior of the snail were limited to a study of its geotropism, rheotropism, and phototropism. (a) During the months when the drill is active, it shows a very definite and marked negative geotropism which is important in its spawning reactions. Because of this, the animal climbs up to the higher levels to lay its eggs, and thus they are not covered with mud and suffocated. Experiments have shown that this is a true geotropic reaction and not one in response to oxygen content or light. (b) If the snail is placed in a current of water it will orient itself so that its siphon is pointing upstream. It will then creep in that direction. Studies on the relation between current velocity, and the rate of creeping showed that creeping is independent of current velocity. The rate of turning (orientation) is a function of the current velocity. Light does not affect the movements of the drill.

9. The oyster drill can be greatly reduced in numbers provided the oyster planter is willing to make a little effort. Because the snail is practically nonmigratory its further distribution can be checked. If an area, at present infested is cleaned of this pest, there is no reason why it should not stay so, provided the planter is careful not to reinfest it with oysters from an infested area. The oyster planter must be careful of two things: (a) He must not move oysters from an infested area to a noninfested area without first attempting to clean the infested oysters. This can be done by any of the following methods: The use of forks, screening, and floating. (b) He must avoid planting uninfested oysters on infested bottoms. The infested bottoms can be cleaned by the use of a trap dredge, the use of small concrete pillars, and the use of an oyster dredge fitted with a bag of small mesh. If these recommendations are adhered to the oyster drill pest will gradually decrease in importance.

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