SURVIVAL AND ACTIVITY OF THE OYSTER DRILL, *UROSALPINX CINEREA* (SAY), UNDER CONDITIONS OF FLUCTUATING SALINITY

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

Arthur Zachary

1970

APPROVAL SHEET

This thesis is submitted in partial fulfillment

of the requirements for the degree of

Master of Arts

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Approved, June 1970

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ACKNOWLEDGMENTS

The author expresses sincere gratitude to his major professor, Mr. Dexter S. Haven, for his suggestion of the thesis topic and his guidance and assistance. The author wishes to thank Mr. James Whitcomb of the Applied Science Department of the Virginia Institute of Marine Science for providing oyster drills and for his aid in reviewing related literature. Sincere appreciation is extended to my wife, Ingrid, for her aid in preparation of this manuscript. Dr. William J. Hargis, Jr., Dr. Morris L. Brehmer, and Dr. Marvin L. Wass are gratefully acknowledged for their criticism of the manuscript. Special thanks are extended to Mr. Clarence Richards of VIMS for his aid in establishing predictor equations on the analog computer for salinity fluctuations used in the study. Appreciation is also extended to Mr. Evon P. Ruzecki for his aid in relating field and laboratory salinity conditions.

The author wishes to thank Mrs. Barbara Kerby for typing the final manuscript and Mrs. Jane Davis for her aid with graphic presentations.

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ABSTRACT

The effects of fluctuating and constant salinities on the activity and survival of Urosalpinx cinerea from the James River, Virginia, were evaluated. Peristaltic pumps were used to establish regular salinity fluctuations in a constant volume system at summer temperatures. In fluctuating salinities the lower extremes and their duration had the greatest effect on mortality and after a ten-day mortality-free period at the start of exposure drills began to die. The upper extremes may have delayed but did not reduce mortality and the mean salinity did not relate to mortality. In contrast, most drills unable to survive exposure to a constant salinity died in the first two weeks of the experiment. Other experiments showed that drills surviving brief exposure to lethal constant salinities continued to survive when transferred to water at 15‰. In both types of experiments drills activity, measured by feeding and oviposition, increased as salinities were increased above lethal levels and was greatest at the highest salinities. These experiments also showed that lowered temperatures delayed but did not reduce mortality. The fluctuating salinity experiments approximated salinity conditions in the field and therefore provided a more realistic approach to tolerance studies than constant salinity.

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INTRODUCTION

Urosalpinx cinerea is one of the major predators of the oyster in both North America and Great Britain. Although many attempts have been made to discover a means of control, predation by *Urosalpinx* is still a serious problem.

The oyster drill is found in estuaries, where its upper distribution is limited by low salinity (Nelson, 1922; Galtsoff, Prytherch, and Engle, 1937; Cole, 1942; Stauber, 1943; Engle, 1953; Glancy, 1953; Carriker, 1955; Hancock, 1959). Numerous studies conducted at constant salinities (e.g., 10‰ for 15 days) have attempted to determine the lower survival salinity. Federighi (1931), working at summer temperatures, found that drills from Hampton Roads, Virginia, had a "salinity death point" at 11.7 to 12.5‰, while drills from Beaufort, North Carolina, died at 15.6 to 17.6‰. He attributed this difference in tolerance to the difference in environmental salinities to which the drills were subjected during their early development stages. Drills from Hampton Roads were taken from areas where salinities ranged from 15‰ to 20‰; those from Beaufort came from areas where salinities were over 30‰.

Effects of low salinities on James River drills have been studied in the laboratory by Wood (1964) and Haven and Whitcomb (unpublished). In their studies at summer temperatures, all the drills died at 8‰ in 7 to 23 days.

One objective of this thesis was to demonstrate that constant salinity studies may be misleading since they do not represent conditions in an estuary where salinities are constantly fluctuating with each tidal cycle. In most estuaries there is a zone at the upper end of the range of Urosalpinx where twice every 24 hours populations may be exposed to salinities which, if maintained for longer periods, would be lethal. This intermittent stress decreases in a down-river direction where salinities may be "lethal" only during very short periods.

The principal objective of this research was to study survival of *U. cinerea* under conditions of fluctuating salinity. The ranges selected for study approximated those of the natural environment and were chosen to simulate salinity ranges at, above, and below the upper limit of the distribution of *U. cinerea* in the James River, Virginia. Experiments were conducted at summer temperatures. In several instances, however, studies at constant salinities were conducted at spring and winter temperatures. The results of the author's constant and fluctuating salinity experiments are compared with studies conducted by other investigators at constant salinities.

MATERIALS AND METHODS

All *U. cinerea* in this investigation were collected on drill traps in the James River, Virginia, unless otherwise specified. The drills were trapped at Brown Shoals or at Miles Watch House (two miles upstream) during June, July, and August of 1967 and during June and July of 1968. Prior to each experiment, drills were stored at ambient summer water temperatures (24-26°C) and salinities (18-22‰) of the York River at Gloucester Point, Virginia. During storage the drills were color coded and sexed by the rapid method of Hargis (1957). Recently set oyster spat were kept in the holding tanks as food. All experiments at summer temperatures were conducted during March of 1968.

Experimental Temperatures

In some estuarine areas the lowest salinities and temperatures occur simultaneously in the spring when the drill population is inactive (Galtsoff *et al.*, 1937; Stauber, 1943; Carriker, 1954). The present constant and fluctuating studies were conducted at about 24°C so drills would be active, thus facilitating observation of mortality, attachment, feeding and oviposition. Several constant salinity transfer experiments were run at 6-7°C to demonstrate the effect of low temperatures on survival.

The apparatus used to expose drills to fluctuating salinity was similar in all experiments. Drills were placed in cylindrical Plexiglas tanks with an overflow tube at the top. Each tank contained 30 drills, 30 oyster spat, and several U. cinerea egg capsules. If the 30 original spat were consumed, 30 additional spat were added. Plastic screen placed below the water surface in each tank prevented escape of drills and kept the animals submerged. At the start of each experiment the original tank salinity was adjusted by diluting York River water with tap water. Fluctuation was accomplished by alternately pumping York River water diluted to 18.0‰ in the tanks for 6 hours and 0.0‰ water (tap water) for 6 hours. Two peristaltic pumps (Harvard Apparatus Co.) were used to maintain constant flow rates into the tanks through "Tygon" tubing. Flow rates could be varied to any desired level by changing pump speed or tube diameter. The pumps were set for alternate and opposite 6-hour on-off periods by two automatic timers (Sears, Roebuck and Co.). Each tank was set on a magnetic mixer (Precision Scientific Co.) and magnetic stirrers constantly mixed the incoming water. The surplus overflowed constantly through the discharge tube, thus maintaining a constant volume in each tank.

Flow rates from the two peristaltic pumps sufficient to give the desired cyclic salinity changes were determined empirically in preliminary experiments. Once the desired fluctuation was established (based on hourly salinity readings in the tanks), the flow rate from each pump was measured by pumping water into a graduated cylinder. Consequently, it was possible to duplicate the conditions of any experiment.

Since the peristaltic pumps were set at exact six-hour cycles, physical and biological observations could be made at predictable times corresponding to the maximum (after six-hour saltwater flow) and minimum (after six-hour freshwater flow) points of the salinity fluctuation. At least twice a day during each study at a maximum and at a minimum point in the fluctuation, salinity was measured with a hydrometer and readings were corrected to 15°C. To monitor the salinity fluctuation between regular hydrometer checks, an RSQ head was left in one of the tanks and conductivity changes were recorded on a chart (Beckman Scientific Instruments). Consequently, any irregularities between regular salinity readings were recorded.

Data from the fluctuating salinity experiments were used to derive the following equation which expresses the salinity changes produced in the experimental tanks:

$$S_f = S_i + (S_o - S_i)e^{-rt/v}$$

S_f = salinity at any time
S_i = salinity pumped in
S_o = original tank salinity at start of cycle
r = pumping rate
t = time elapsed
v = tank volume

The shape of the curves described by the equation was similar to the shape of the conductivity curves recorded by the RSQ. The computed curves were used to determine the duration of exposure to the salinities and the mean salinity for each fluctuating salinity experiment (Figure 1). Salinity curves were computed using the equation by substituting mean minimum salinity values for S_o, 9500 ml for v, actual pumping rates for r, and then solving for S_f with respect to change in time. The mean minimum and mean maximum salinities were computed by averaging daily minimum and maximum hydrometer values.

Temperature was measured with a bulb thermometer whenever salinity was determined. All experiments were conducted in an air conditioned laboratory where temperatures ranged from 22 to 26°C during the summer months; mean water temperatures ranged from 23.7 to 24.8°C in fluctuating and constant salinity experiments, unless otherwise specified.

The following biological observations were made on oyster drills introduced into the tanks:

1) number of male and female drills attached to the tank
2) number of male and female drills attached to oyster shells covered with spat
3) number of male and female drills unattached
4) number of male and female drills dead

A drill was considered dead if it failed to withdraw into its shell when poked with a blunt needle, lost its operculum, or if the odor of tissue decay was detected. Dead drills were removed as soon as detected.

Survival of James River drills at constant salinities has been investigated (Wood, 1964; Haven and Whitcomb, unpublished). Therefore, constant salinity studies by the author were not extensive and were conducted to verify previous data and to provide information on attachment, feeding, and oviposition.

One series of constant salinity studies exposed drills to 8.0, 9.2, 10.0, 12.0, and 20.0‰. These salinities spanned the critical transition from lethal to non-lethal conditions, and were similar to those used by previous investigators. The exposure period for all five salinities was 40 days.

Drills were held in cylindrical Plexiglas tanks which contained 30 oyster spat and a variable number of U. cinerea egg cases containing living embryos. A plastic screen over each tank prevented drill escapes and kept the animals submerged. Desired salinities were obtained by diluting York River water with tap water, which was changed every second day. The observations outlined for the fluctuating salinity experiments were made daily for the constant salinity experiments.

A second series of constant salinity studies were conducted to determine if a short exposure to lethal salinities (i.e., low salinities which would cause drill deaths if exposure period were longer) would continue to cause mortalities once the drills were transferred to a higher, non-lethal salinity. Three experiments similar in design were conducted at three temperatures (25°C, 17°C, and 6-7°C). Plexiglas tanks were filled with York River water diluted to 6.0, 8.0, 10.0 and 15.0‰, and 100 drills were placed in each tank. Water in all tanks was changed every second day. At varying intervals, random samples of 20 drills were removed from the tanks and placed in smaller containers filled with water at 25°C and adjusted to 15.0‰. Sub-samples were maintained for a week and mortalities were recorded. Mortality within the sub-samples was observed 24 hours after transfer to 15‰ and drills dying in this period were considered to have died during the original exposure time. Drills dying during the remainder of the week at 15‰ were considered delayed mortalities. Whenever a dead drill was observed in the large tanks (drill not included in sub-sample), it was replaced by a piece of plastic tubing. This prevented fouling and made possible the collection of representative random samples from the large tank. Pieces of tubing were counted as a dead drill when chosen in a random sub-sample. Transfer of drills held at 6-7°C to 15.0‰ water at 25°C caused surviving drills to become active, thus facilitating determination of mortality.

Prior to analysis of data a preliminary statistical study was conducted to determine if there were differences in mortality between males and females in the fluctuating and constant salinity experiments. Cumulative mortality levels for males and females in each experiment were compared after 10 days and 20 days using chi square at the 95% level. In the same manner numbers of males and females attached (all surfaces) and unattached were compared after 10 days and 20 days.

Mortality and attachment data from fluctuating and constant salinity experiments were grouped by five-day periods to facilitate analysis. In the fluctuating salinity experiments daily observations of total attachment were made at either maximum or minimum salinities and the number of observations varied (1 to 3 per day).

To prevent bias, mean number of drills attached at maximum and the mean number attached at minimum salinities were calculated for each day. From these values, mean numbers and percentages of drills attached (on all surfaces) at minimum and maximum salinities were determined for five-day periods of each experiment. Chi square was used to test for differences in total attachment at minimum and maximum salinities. All attachment percentages were computed by dividing the mean number of drills attached (shells, tank, or total) in any period by the total number of drills in the tank during that period. The percentage of spat consumed was computed by dividing the number of spat consumed by 30 (number of spat at start of each experiment).

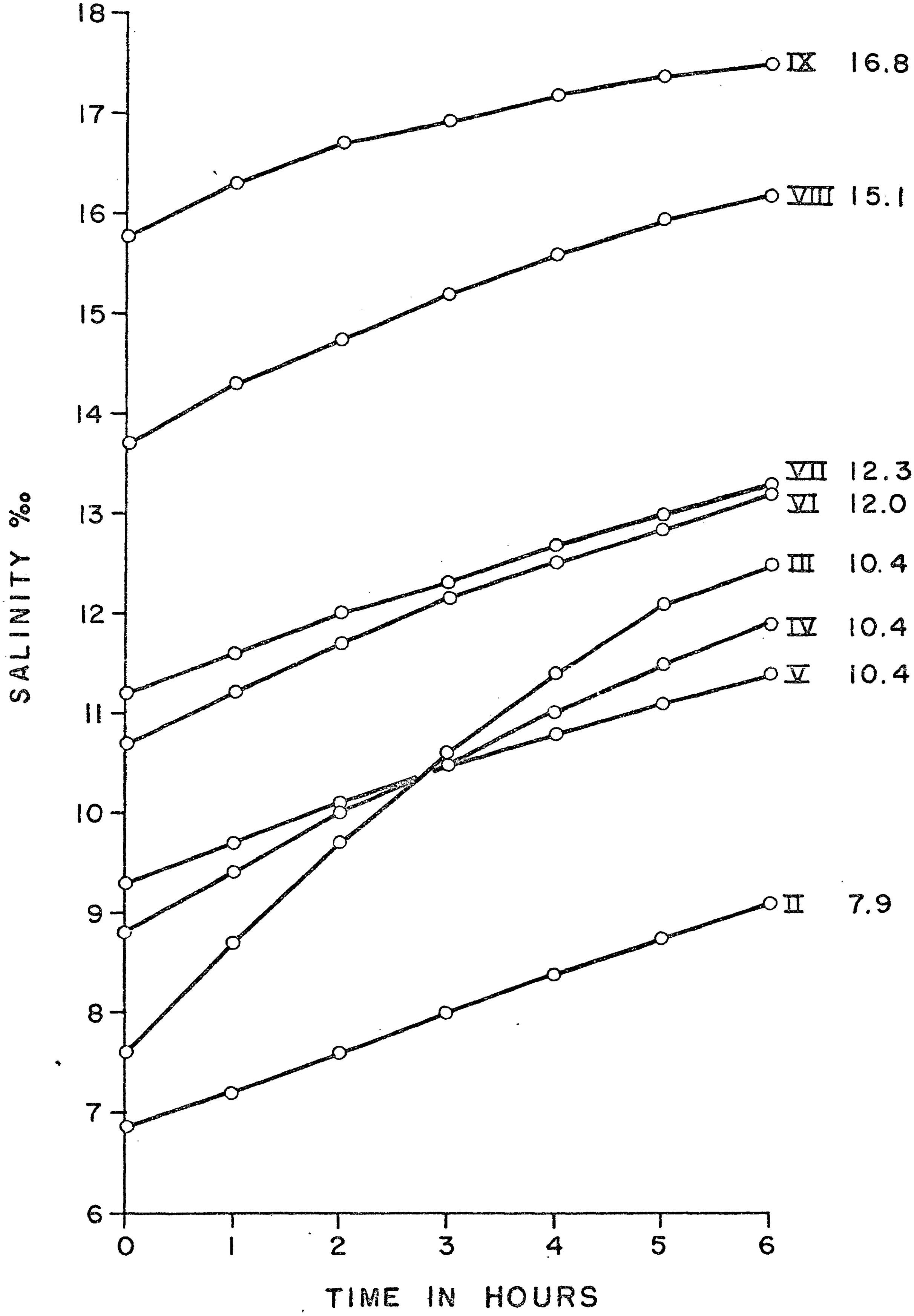
Cumulative percent mortality was determined by dividing the number of drills dying since the start of an experiment by the number of drills present at the start of the experiment. Percent mortality for five-day periods was calculated by dividing the number of drills dying during the five days by the number of drills present at the start of the five-day period.

RESULTS

With a single exception there were no significant differences in mortality between male and female drills in either the constant or fluctuating salinity experiments (Appendix, Table 1). The single exception was experiment XIII. In view of the almost consistent absence of any significant differences, mortality data for male and female drills were pooled. Chi squares tests for attachment showed significant differences between males and females for six experiments, and no significant differences in the other eight experiments (Appendix, Table 2). Since the mortality data were pooled and no definitive pattern was shown by the chi square tests for attachment, attachment data for males and females in each constant and fluctuating salinity experiment were pooled.

In most fluctuating salinity experiments the mean number of drills attached at maximum salinities appeared higher than the number attached at minimum salinities, differences were not statistically significant and attachment data for maximum and minimum salinities were pooled to compute the total number attached.

Figure 1. Calculated curves based on mean maximum and mean minimum salinities showing change in salinity during a six hour period in each fluctuating salinity experiment. Experiment numbers and mean salinity values are given for each fluctuation curve.


18
17
16
15
14
13
12
11
10
9
8
7
6
0
1
2
3
4
5
6
SALINITY ‰
TIME IN HOURS
IX 16.8
VIII 15.1
VII 12.3
VI 12.0
III 10.4
IV 10.4
V 10.4
II 7.9

In reporting and discussing data, mean values for attachment and mortality for five-day periods will be expressed as the value for the last day of the period (e.g., 13% attached by the tenth day).

Fluctuating Salinity Experiments

EXPERIMENT I: (control) Salinities fluctuated between a mean minimum of 19.2‰ and a mean maximum of 22.3‰ with a mean of 20.7‰ during this 25-day experiment (Table 1). Drills did not die and all drills were attached; between 42.0 and 71.0% on shells and the remainder attached on tank surfaces. All of the 30 original spat were consumed by the fifteenth day, and by the end of the experiment 28 of the 30 spat added on the fifteenth day were consumed. At the end of the experiment all embryos were alive and 44 egg cases were deposited during the experiment.

EXPERIMENT II: For 20 days salinities fluctuated from a mean minimum of 6.7‰ to a mean maximum of 9.1‰ with a mean of 7.9‰ (Table 2). There was an initial ten day period of low mortality in which mortality did exceed 3%. By the fifteenth day, however, 77% of the drills were dead, and by the end of twenty days all drills had died. The percent of drills attached averaged 79.4% during the first five days and then decreased steadily at 11.3% for the final five-day period. Drills did not attach to shells and spat were not consumed. Egg cases were not deposited and all embryos died by the twentieth day.

TABLE 1

Experiment I: Observations of oyster drills exposed to salinities fluctuating from a mean minimum of 19.2‰ to a mean maximum of 22.3‰ with a mean of 20.7‰.

Period in days	Number alive	Number dead	Percent dead		Number and percent attached			Percent spat consumed	State of embryos	Number of egg cases
			Period	Total	Tank	Shells	Total			
0-5	31	0	0	0	(9) 29.0	(22) 71.0	(31) 100	no ob.	living	no ob.
5-10	"	"	"	"	(14) 45.0	(17) 55.0	" "	"	"	"
10-15	"	"	"	"	(16) 52.0	(15) 48.0	" "	100*	"	"
15-20	"	"	"	"	(18) 58.0	(13) 42.0	" "	no ob.	"	"
20-25	"	"	"	"	(18) 58.0	(13) 42.0	" "	97*	"	44

* All 30 spat added on the first day were consumed by the fifteenth day; 30 more spat were then added. The 97% spat consumed on day 25 is based on the total of 60 spat.

TABLE 2

Experiment II: Observations of oyster drills exposed to salinities fluctuating from a mean minimum of 6.7‰ to a mean maximum of 9.1‰ with a mean of 7.9‰.

Period in days	Number alive	Number dead	Percent dead		Number and percent attached			Percent spat consumed	State of embryos	Number of egg cases
			Period	Total	Tank	Shells	Total			
0-5	31	0	0	0	(24.6) 79.4	(0) 0	(24.6) 79.4	no ob.	no ob.	no ob.
5-10	30	1	3	3	(17.8) 57.5	" "	(17.8) 57.5	"	"	"
10-15	7	23	74	77	(9.5) 34.1	" "	(9.5) 34.1	0	"	0
15-20	0	7	23	100	(0.4) 11.3	" "	(0.4) 11.3	"	dead	"

EXPERIMENT III: For thirty days salinities fluctuated from a mean minimum of 7.6‰ to a mean maximum of 12.5‰ with a mean of 10.4‰ (Table 3). There was an initial ten day mortality-free period; however, by the twentieth day 75% of the drills had died and all were dead after thirty days. About 68% of the drills were attached during the first ten days, but then the percent of drills attached decreased and drills were not attached during the final five days of the experiment. Although from 4.5 to 10.5% of the drills attached on shells during the first fifteen days, spat were not consumed. Egg cases were not deposited and all embryos died.

EXPERIMENT IV: For 25 days salinities fluctuated from a mean minimum of 8.8‰ to a mean maximum of 11.9‰ with a mean of 10.4‰ (Table 4). After a ten-day mortality-free period drills began to die and by the twenty-fifth day 29% were dead. The percent attached decreased slowly from 98.1% in the first five days to 79.2% in the final five days. During the experiment between 11.7 and 21.3% of the drills attached to shells and 20% of the spat were consumed. Egg cases were not deposited and all embryos were dead at the end of the study.

EXPERIMENT V: For 25 days salinities fluctuated from a mean minimum of 9.3‰ to a mean maximum of 11.4‰ with a mean of 10.4‰ (Table 5). After 25 days only 6% of the drills had died. From 81.8 to 97.3% of the drills were attached during the experiment and although no more than 11.0% were attached on shells, 17% of the spat were consumed. Egg cases were not deposited

TABLE 3

Experiment III: Observations of oyster drills exposed to salinities fluctuating from a mean minimum of 7.6‰ to a mean maximum of 12.5‰ with a mean of 10.4‰.

Period in days	Number alive	Number dead	Percent dead Period	Percent dead Total	Number and percent attached Tank	Number and percent attached Shells	Number and percent attached Total	Percent spat consumed	State of embryos	Number of egg cases
0-5	20	0	0	0	(11.4) 57.0	(2.1) 10.5	(13.5) 67.5	0	no ob.	0
5-10	"	"	"	"	(12.8) 64.0	(0.9) 4.5	(13.7) 68.5	"	"	"
10-15	13	7	35	35	(9.8) 48.8	(1.0) 5.0	(10.8) 53.8	"	"	"
15-20	5	8	40	75	(3.6) 37.7	(0.0) 0.0	(3.6) 53.8	"	"	"
20-25	1	4	20	95	(0.4) 10.1	(0.0) 0.0	(0.4) 10.1	"	"	"
25-30	0	1	5	100	(0.0) 0.0	(0.0) 0.0	(0.0) 0.0	"	dead	"

TABLE 4

Experiment IV: Observations of oyster drills exposed to salinities fluctuating from a mean minimum of 8.3‰ to a mean maximum of 11.9‰ with a mean of 10.4‰.

Period in days	Number alive	Number dead	Percent dead		Number and percent attached			Percent spat consumed	State of embryos	Number of egg cases
			Period	Total	Tank	Shells	Total			
0-5	31	0	0	0	(24.7) 79.7	(5.7) 18.4	(30.4) 98.1	no ob.	no ob.	0
5-10	"	"	"	"	(22.9) 73.9	(6.6) 21.3	(29.5) 95.2	"	"	"
10-15	30	1	3	3	(23.1) 74.6	(4.5) 14.6	(27.6) 89.2	"	"	"
15-20	26	4	13	16	(18.9) 73.0	(3.5) 11.7	(22.4) 84.7	"	"	"
20-25	22	4	13	29	(15.0) 63.8	(4.0) 15.4	(19.0) 79.2	20	dead	"

TABLE 5

Experiment V: Observations of oyster drills exposed to salinities fluctuating from a mean minimum of 9.3‰ to a mean maximum of 11.4‰ with a mean of 10.4‰.

Period in days	Number alive	Number dead	Percent dead		Number and percent attached			Percent spat consumed	State of embryos	Number of egg cases
			Period	Total	Tank	Shells	Total			
0-5	31	0	0	0	(28.9) 93.4	(0.1) 0.3	(29.0) 93.7	no ob.	no ob.	0
5-10	30	1	3	3	(28.4) 96.0	(1.5) 0.5	(29.9) 96.5	"	"	"
10-15	"	0	0	3	(25.9) 86.3	(3.3) 11.0	(29.2) 97.3	"	"	"
15-20	"	"	"	"	(26.0) 86.9	(1.3) 4.3	(27.3) 91.2	"	"	"
20-25	29	1	3	6	(24.2) 80.5	(0.4) 1.3	(24.6) 81.8	17	dead	"

and all embryos were dead at the end of the experiment.

EXPERIMENT VI: For 25 days salinities fluctuated from a mean minimum of 10.7‰ to a mean maximum of 13.2‰ with a mean of 12.0‰ (Table 6). By the fifteenth day 9% of the drills were dead and after 25 days cumulative mortality reached 12%. From 89.5 and 96.4% of the drills were attached during the experiment with from 7.9 to 32.4% attached on shells and the rest on tank surfaces. Sixty-six percent of the spat were consumed, five egg cases were deposited, and embryos were alive at the end of the experiment.

EXPERIMENT VII: For 15 days salinities fluctuated from a mean minimum of 11.2‰ to a mean maximum of 13.3‰ with a mean of 12.3‰ (Table 7). By the fifteenth day 13% of the drills had died. From 91.9 to 96.6% of the drills were attached during the experiment with from 8.4 to 35.6% attached on shells and the rest on tank surfaces. Only 17% of the spat were consumed. Egg cases were not deposited, but embryos were alive on the fifteenth day.

EXPERIMENT VIII: For 20 days salinities fluctuated from a mean minimum of 13.7‰ to a mean maximum of 16.2‰ with a mean of 15.1‰ (Table 8). By the twentieth day 16% of the drills were dead. From 91.8 to 98.7% of the drills were attached during the experiment; from 26.8 to 58.8% on shells and the rest on tank surfaces. Seventy-three percent of the spat were consumed, developing embryos were alive, and 11 egg cases were deposited.

TABLE 6

Experiment VI: Observations of oyster drills exposed to salinities fluctuating from a mean minimum of 10.7‰ to a mean maximum of 13.2‰ with a mean of 12.0‰.

Period in days	Number alive	Number dead	Percent dead		Number and percent attached			Percent spat consumed	State of embryos	Number of egg cases
			Period	Total	Tank	Shells	Total			
0-5	31	0	0	0	(27.0) 66.9	(0.7) 22.6	(27.7) 89.5	no ob.	no ob.	0
5-10	30	1	3	3	(19.5) 63.5	(10.2)32.3	(29.7) 95.8	"	"	"
10-15	28	2	6	9	(18.2) 59.6	(9.7) 32.4	(27.9) 92.0	"	"	"
15-20	28	0	0	9	(21.9) 78.2	(5.1) 18.2	(27.0) 96.4	"	"	"
20-25	27	1	3	12	(23.2) 82.9	(2.2) 7.9	(25.4) 90.8	66	living	5

TABLE 7

Experiment VII: Observations of oyster drills exposed to salinities fluctuating from a mean minimum of 11.2‰ to a mean maximum of 13.3‰ with a mean of 12.3‰.

Period in days	Number alive	Number dead	Percent dead		Number and percent attached			Percent spat consumed	State of embryos	Number of egg cases
			Period	Total	Tank	Shells	Total			
0-5	29	1	3	3	(25.0) 83.5	(2.5) 8.4	(27.5) 91.9	no ob.	no ob.	0
5-10	"	0	0	"	(20.4) 70.4	(7.6) 26.2	(28.0) 96.6	"	"	"
10-15	26	3	10	13	(15.1) 56.9	(10.3) 35.6	(25.4) 92.5	17	living	"

TABLE 8

Experiment VIII: Observations of oyster drills exposed to salinities fluctuating from a mean minimum of 13.7‰ to a mean maximum of 16.2‰ with a mean of 15.1‰.

Period in days	Number alive	Number dead	Percent dead		Number and percent attached			Percent spat consumed	State of embryos	Number of egg cases
			Period	Total	Tank	Shells	Total			
0-5	31	0	0	0	(20.1 65.0	(8.3) 26.8	(28.4) 91.8	no ob.	no ob.	0
5-10	29	2	6	6	(20.2) 65.0	(8.3) 26.8	(28.5) 91.8	"	"	"
10-15	"	0	0	"	(15.9) 54.9	(12.7)43.8	(28.6) 98.7	"	"	4
15-20	26	3	10	16	(10.2) 35.2	(17.0)58.8	(27.2) 94.0	73	living	7

EXPERIMENT IX: For 15 days salinities fluctuated from a mean minimum of 15.8‰ to a mean maximum of 17.5‰ with a mean of 16.8‰ (Table 9). No mortalities occurred and all drills were attached; from 64.0 to 88.0% attached on shells, the remainder on tank surfaces. Eighty percent of the spat were consumed in the first ten days, and 90% by the fifteenth day. Eight egg cases were deposited, and the developing embryos were alive at the end of the experiment. Several of the egg cases placed in the tank at the start of the study produced living drills during the experiment.

TABLE 9

Experiment IX: Observations of oyster drills exposed to salinities fluctuating from a mean minimum of 15.8‰ to a mean maximum of 17.5‰ with a mean of 16.8‰.

Period in days	Number alive	Number dead	Percent dead		Number and percent attached			Percent spat consumed	State of embryos	Number of egg cases
			Period	Total	Tank	Shells	Total			
0-5	20	0	0	0	(2.4) 12.0	(17.6) 88.0	(20) 100.0	no ob.	no ob.	0
5-10	"	"	"	"	(6.4) 32.0	(13.6) 68.0	" "	80	"	"
10-15	"	"	"	"	(7.2) 36.0	(12.8) 64.0	" "	90	living	8

Constant Salinity Experiments

EXPERIMENT X: (control) ran for 40 days at 20.0‰ (Table 10). There were no mortalities and all drills were attached; from 30.0 to 70.0% on shells and the rest on tank surfaces. Eighty percent of the spat were consumed and embryos were alive at the end of the experiment. Thirty-three egg cases were deposited.

EXPERIMENT XI: ran for 20 days at 8.0‰ (Table 11). All the drills were dead after 20 days. Percent attached ranged from 11.8% in the first five days to 30.0% in the final five days. Drills did not attach on shells and spat were not consumed. Egg cases were not deposited and all embryos died.

EXPERIMENT XII: ran for 40 days at 9.2‰ (Table 12). During the first five days 52% of the drills died, by the fifteenth day 67% had died, and 81% were dead by the end of the experiment. The percent of drills attached was lowest (18.2%) during the first five days, then increased to 71.0% by the tenth day and declined to 50.0% by the fortieth day. Drills did not attach on shells and spat were not consumed. Egg cases were not deposited and all embryos died.

EXPERIMENT XIII: ran for 40 days at 10.0‰ (Table 13). Mortality reached 60% by the twentieth day but no mortalities occurred during the remainder of the experiment. The percent of drills attached was 22.0% during the first five days, then increased to 84.0% by the fifteenth day and reached 100.0% by the end of the experiment. From 0.0 to 28.0% of the drills were attached

TABLE 10

Experiment X: Observations of oyster drills exposed to a salinity of 20.0‰.

Period in days	Number alive	Number dead	Percent dead		Number and percent attached			Percent spat consumed	State of embryos	Number of egg cases
			Period	Total	Tank	Shells	Total			
0-5	20	0	0	0	(8.0) 40.0	(12.0) 60.0	(20.0) 100.0	no ob.	living	0
5-10	"	"	"	"	(7.0) 30.0	(14.0) 70.0	" "	"	"	8
10-15	"	"	"	"	(10.0) 50.0	(10.0) 50.0	" "	"	"	3
15-20	"	"	"	"	(12.0) 60.0	(8.0) 40.0	" "	"	"	6
20-40	"	"	"	"	(14.0) 70.0	(6.0) 30.0	" "	80	"	16

TABLE 11

Experiment XI: Observations of oyster drills exposed to a salinity of 8.0‰.

Period in days	Number alive	Number dead	Percent dead		Number and percent attached			Percent spat consumed	State of embryos	Number of egg cases
			Period	Total	Tank	Shells	Total			
0-5	8	3	28	28	(1.3) 11.8	(0.0) 0.0	(1.3) 11.8	no ob.	no ob.	0
5-10	5	3	27	55	(2.3) 28.8	" "	(2.3) 28.8	"	"	"
10-15	1	4	37	92	(1.0) 20.0	" "	(1.0) 20.0	"	"	"
15-20	0	1	8	100	(0.3) 30.0	" "	(0.3) 30.0	0	dead	"

TABLE 12

Experiment XII: Observations of oyster drills exposed to a salinity of 9.2‰.

Period in days	Number alive	Number dead	Percent dead Period	Percent dead Total	Number and percent attached Tank	Number and percent attached Shells	Number and percent attached Total	Percent spat consumed	State of embryos	Number of egg cases
0-5	10	11	52	52	(3.8) 18.2	(0.0) 0.0	(3.8) 18.2	no ob.	no ob.	0
5-10	10	0	0	52	(7.1) 71.0	" "	(7.1) 71.0	"	"	"
10-15	7	3	15	67	(6.5) 65.0	" "	(6.5) 65.0	"	"	"
15-20	5	2	9	76	(4.8) 68.5	" "	(4.8) 68.5	"	"	"
20-40	4	1	5	81	(2.5) 50.0	" "	(2.5) 50.0	0	dead	"

TABLE 13

Experiment XIII: Observations of oyster drills exposed to a salinity of 10.0‰.

Period in days	Number alive	Number dead	Percent dead		Number and percent attached			Percent spat consumed	State of embryos	Number of egg cases
			Period	Total	Tank	Shells	Total			
0-5	9	1	10	10	(2.2) 22.0	(0.0) 0.0	(2.2) 22.0	no ob.	no ob.	0
5-10	5	4	40	50	(3.0) 33.1	(2.5)28.0	(5.5) 61.1	"	"	"
10-15	5	0	0	50	(3.0) 60.0	(1.2)24.0	(4.2) 84.0	"	"	"
15-20	4	1	10	60	(4.2) 84.0	(0.0) 0.0	" "	"	"	"
20-40	4	0	0	60	(3.6) 90.0	(0.4)10.0	(4.0)100.0	7	dead	"

on shells and 7% of the spat were consumed. Egg cases were not deposited and all embryos died.

EXPERIMENT XIV: ran for 40 days at 12.0‰ (Table 14). Only 15% of the drills had died by the fortieth day. The percent of drills attached was lowest in the first five days (76.5%) and then rose to 100.0% by the end of the experiment. From 15.0 to 27.0% of the drills attached on shells and 13% of the spat were consumed. Embryos were alive at the end of the experiment but egg cases were not deposited.

The constant salinity transfer experiments showed that drills can survive brief exposure to low salinities and that temperature is an important factor in drill survival. The first series of experiments was conducted at 17°C with James River drills (Table 15). At 6.0‰ 32% of the drills were dead after four days and mortality reached 90% by the eighth day. At 8.0‰ mortality declined sharply and only 20% of the drills were dead after nine days. At 10.0‰ the nine-day sample showed 22% mortality but the sample on the tenth day showed only 5% dead. At 15.0‰, 10% were dead in the first day and 10% were dead in the sample on the third day (10% represented one drill dead). No delayed mortalities occurred among surviving drills transferred and maintained at 15.0‰.

Mortality was more rapid in a second study at 25°C using James River drills (Table 15). At 6.0‰ conditions were quickly lethal and all drills died in four days. At 8.0‰ after seven days, 66% of the drills were dead. The seven-day sample

TABLE 14

Experiment XIV: Observations of oyster drills exposed to a salinity of 12.0‰.

Period in days	Number alive	Number dead	Percent dead		Number and percent attached			Percent spat consumed	State of embryos	Number of egg cases
			Period	Total	Tank	Shells	Total			
0-5	20	0	0	0	(12.3) 61.5	(3.0) 15.0	(15.3) 76.5	no ob.	no ob.	0
5-10	"	"	"	"	(12.1) 60.5	(5.4) 27.0	(17.5) 87.5	"	"	"
10-15	18	2	10	10	(12.4) 62.0	(4.6) 23.0	(17.0) 85.0	"	"	"
15-20	17	1	5	15	(14.1) 78.5	(2.9) 16.0	(17.0) 94.5	"	"	"
20-40	17	0	0	15	(13.4) 82.0	(3.6) 18.0	(17.0)100.0	13	living	"

TABLE 15

Percent of dead drills in random 20-drill samples taken from indicated salinities after various exposure times. The samples minus dead drills were transferred and kept at 15.0‰ for one week. The 17 and 25°C experiments involved James River drills and the 6-7°C experiments involved York River drills.

Days of	17°C				25°C				6-7°C			
exposure	6.0‰	8.0‰	10.0‰	15.0‰	6.0‰	8.0‰	10.0‰	15.0‰	6.0‰	8.0‰	10.0‰	15.0‰
0.25	5	5										
0.5	5											
1.0	5	10	0	10	35	15	10	0	0	22	0	0
2.0			0	0	35	15	10	0				
3.0		10	5	10	95	20	5	0				
4.0	32	11			100							
5.0									22	0	11	0
7.0						66	20	7				
8.0	90											
9.0		20	22									
10.0			5						11	11	11	0
20.0									78	22	0	0

at 10.0‰ had 20% dead and after seven days at 15.0‰, 7% of the drills were dead. No delayed mortalities occurred among surviving drills transferred and kept at 15.0‰.

York River drills were used in an experiment conducted at 6-7°C (Table 15). Mortality occurred more slowly at these temperatures; therefore, longer exposure periods were used. After 20 days at 6.0‰, 78% of the drills sampled were dead. At 8.0‰, 22% of the drills were dead after only one day; however, the sample taken on the twentieth day also showed 22% dead. At 10.0‰ mortality never exceeded 11% and no mortalities occurred at 15.0‰. No delayed mortalities occurred among surviving drills transferred and kept at 15.0‰.

DISCUSSION

Mortality data from the constant salinity studies were similar to data reported by other investigators using James River drills. However, they differed from similar studies conducted with drills from other geographic areas. Analyses of these data show that in regions where environmental salinities were higher, the critical salinity levels for mortality were also higher (Table 16). These differences may reflect the fact that drills in each area may be physiologically distinct races which are affected differently by environmental factors (Stauber, 1950; Franz, 1965). Therefore, results of work in other geographic areas will not be discussed in detail except when pertinent. Emphasis will be on comparison of present data to other studies which used James River drills.

Haven and Whitcomb (unpublished) conducted studies with James River drills at 23-28°C and at 8.0‰. They reported rapid death, with all drills dead in 7 days (Table 17). Wood (1964), in experiments at 8.1‰ at 20°C, observed slower mortality with 50% dead in from 6 to 12 days and 100% dead in from 16 to 23 days. In the present studies conducted at 24°C, 55% mortality occurred in 10 days at 8.0‰ and all drills were dead after 20 days. All three studies agreed that at summer temperatures (20-28°C) 8‰ caused 100% mortality in from 7 to 23 days.

TABLE 16

Drill mortality data of constant salinity studies conducted at summer temperatures in various geographic regions by other investigators.

Region	Salinity (‰)	Method of survival determination	Time in days to reach indicated mortality	Temperature (°C)	Reference
Beaufort, North Carolina	15.6-17.6‰	LD 50	10	24-26	Federighi, 1931
Long Island Sound, Connecticut	14-16‰	LD 100	30	15.4-23.0	Engle, 1953
Delaware Bay, New Jersey	12-15‰	LD 100	7-30	summer temperatures	Sizer, 1936; Galtsoff et al., 1937; Stauber, 1943.
Hampton Roads, Virginia	11.7-12.5‰	LD 50	10	24-26	Federighi, 1931

TABLE 17

Mortality data from constant salinity experiments by researchers using James River drills.

I

Wood (1964) exposure period 33 days, temperatures 20°C

Salinity ‰	Time in days to kill 50%	Time in days to kill 100%
8.1	6-12	16-23
11.4	---	---
15.2	---	---
18.2	---	---

II

Haven and Whitcomb (unpublished) Cumulative percent mortality of drills exposed to various salinities at 23-28°C.

Salinity	Exposure time in days					
‰	3	7	11	14	17	26
8	66.7	100				
10	37.5	37.5	37.5	37.5	56.2	56.2
12			no mortality			
14			" "			
18			" "			

III

Cumulative percent mortality of drills exposed to various salinities at 24°C. (Data from Tables 10-14 in percent study).

Salinity	Exposure time in days					
‰	3	7	10	15	20	40
8.0	28	28	55	92	100	
9.2	52	52	52	67	76	81
10.0	10	20	50	50	60	60
12.0	0	0	0	10	15	15
20.0			no mortality			

TABLE 17 (continued)

IV

Federighi (1931). Cumulative percent mortality of drills exposed to various salinities at 24-26°C at Hampton Roads, Virginia.

Salinity (‰)	Exposure time of 10 days
10.12	90
11.35	90
12.52	75
13.91	15
15.05	10

In the three studies discussed in the preceeding paragraph it is suggested that for James River drills at summer temperatures, 9.0 to 10.0‰ may be the transition zone between salinities quickly lethal to all drills and salinities causing partial mortality over much longer periods. In the present studies 19% of the drills survived for 40 days at 9.2‰ and at 10.0‰, 40% survived 40 days exposure (Table 17). Haven and Whitcomb (unpublished) reported similar results at 10‰ with 43.8% surviving 26 days exposure (Table 17).

The pattern of mortality appeared characteristic at low salinities. At 9.2 and 10.0‰ there was a period of heavy mortality during the first two weeks of exposure followed by a period when few of the surviving drills died. This suggests that populations of James River Drills may be heterogeneous in respect to salinity tolerance. The heavy mortality during the first two weeks of the present studies may represent the death of drills most susceptible to 9.2 and 10.0‰. The subsequent prolonged period of relatively lower mortality may represent survival of the more salinity-tolerant individuals in the population.

Mortality in all three studies decreased sharply at salinities above 10.0‰. In the present study only 15% of the drills were dead after 40 days exposure at 12.0‰ and all drills survived 40 days exposure to 20.0‰. Similarly, Haven and Whitcomb (unpublished) reported no mortalities at salinities of 12‰ or higher during the 26 days of observation. Wood (1964) reported that at salinities of 11.4‰ or greater, mortality did not reach 50% within 33 days.

Federighi (1931) conducted constant salinity studies (at 24-26°C) using James River drills from Hampton Roads, Virginia, located about eight miles downriver from the collection site of the author. At Hampton Roads, environmental salinities are about 5‰ higher than in the vicinity of Brown Shoals. The difference in environmental salinities between the two areas was reflected in differences in the mortality data. At 10.12 and 11.35‰, 90% of the Hampton Roads drills died in ten days (Table 17). This was much higher mortality than at similar salinities in the present study.

Experiments designed primarily to determine if drills might recover from the effects of low salinity also provided data on the effects of temperature on survival. The latter aspect will be discussed first since it relates to mortality studies conducted at summer temperatures.

Most of the transfer studies were conducted at intermediate and low temperatures. The general pattern was that the lower temperatures delayed but did not prevent mortality.

After four days exposure to 6.0‰ at 25°C all James River drills in a sample were dead while 68% of drills exposed to 6.0‰ at 17°C were alive after four days. However, the eight-day sample at 6.0‰ at 17°C showed 90% dead. Similarly, exposure to 8.0‰ caused more rapid mortality at 25°C (66% dead after 7 days) than at 17°C (20% dead after 9 days). At 10.0 and 15.0‰ mortality was low at both temperatures and differences in mortality could not be distinguished (Table 15).

The transfer experiment at winter temperatures (6-7°C) involved drills from an area of the York River where environmental salinities were higher than those in the James River study ares. Therefore, drills might be expected to be less salinity tolerant and die at a higher salinity than James River drills. Even after 20 days exposure, mortality at all salinities was lower among York River drills than among the more salinity tolerant James River drills exposed to the same salinities at higher temperatures (Table 15).

In all the transfer experiments when drills surviving exposure to low salinities were transferred to 15.0‰, they continued to survive for the week they were observed. This indicates that there were no delayed mortalities associated with brief exposure to salinities that would be lethal if exposure were longer. The significance of these data with respect to drill trapping will be discussed later.

Delayed mortality at low temperatures was previously reported for Urosalpinx in Delaware Bay by Stauber (1943). Drills in Delaware Bay did not survive at 12-15‰ at summer temperatures, but at winter temperatures (8°C) Stauber found that 50% of the drills survived exposure to 8§ for 26 days. At 9‰ half the drills survived for 121 days and at 10‰, 50% of the drills survived 248 days exposure. In other experiments where drills were exposed to low salinities at successively lower mean temperatures, Stauber (1943) showed clearly that mortality delays corresponded to decreases in water temperatures (Table 18).

The complexity of the relation between fluctuating salinity and drill mortality necessitates a brief summary of the points which will be discussed in the following analysis.

1. Mortality of drills was determined by the extremes of the fluctuations. The mean of a salinity fluctuation could not be related to mortality of drills in the present experiments.
2. In experiments where heavy mortality occurred within 20 to 30 days, it appeared that the minimal salinities and the duration of exposure to them determined the magnitude of the mortality. The maximum salinities may have delayed but did not prevent mortalities.
3. Mortality patterns for drills exposed to fluctuating salinity differed from the mortality pattern in constant salinity experiments.

The discussion which follows is based on Tables 19 and 20 which summarize fluctuating and constant salinity experiments with respect to percent mortality at various salinities and also with respect to the number of hours drills were exposed to these salinities. Data in this discussion will be taken from these two sources unless otherwise indicated.

Salinities fluctuating from 6.7 to 9.1‰ (experiment II) were quickly lethal and all drills died by the twentieth day. Mortality was very low (3%) during the first ten days, yet all the drills died in this experiment.

TABLE 18

Effects of decreasing temperatures on survival of Delaware Bay drills in low salinities (After Stauber, 1943).

Mean water temperature for first 30 days of experiment °C	Lowest salinity in which drills survived 60 days ‰	Total number of 60 drills surviving in: 14 days	60 days
19.3	11	5	5
17.7	10	8	5
17.3	9	20	18
16.7	8	32	24
14.0	9	41	27
10.7	8	47	34

TABLE 19

Percent mortality of oyster drills exposed in the laboratory to various constant salinities for the periods indicated in hours and days.

Exposure times		Experiment numbers and salinities			
days	hours	XI 8.0‰	XII 9.2‰	XIII 10.0‰	XIV 12.0‰
5	120	28%	52%	10%	0%
10	240	55%	52%	50%	0%
15	360	92%	67%	50%	10%
20	480	100%	76%	60%	15%
40	960	-	81%	60%	15%

TABLE 20

Percent of oyster drills dead after exposure to fluctuating salinities (experiments II-IX). Elapsed time is shown in days and exposure to salinities less than indicated values is shown in hours.

Experiment & salinity range	Elapsed time in days	Salinities less than 7‰	8‰	9‰	10‰	11‰	12‰	13‰	14‰	15‰	16‰	17‰	18‰	Percent dead
Experiment II	5	12	60	114	120									0
6.7-9.1‰	10	24	120	227	240									3
X=7.9‰	15	36	180	341	360									77
	20	48	240	455	480									100
Experiment III														
7.6-12.5‰	5		7	26	46	69	87	120						0
X=10.4‰	10		14	52	92	138	174	240						0
	15		21	78	138	207	261	360						35
	20		28	104	184	276	348	480						75
	25		35	130	230	345	435	600						95
	30		42	156	276	414	522	720						100
Experiment IV														
8.8-11.9‰	5			7	40	80	120							0
X=10.4‰	10			14	80	160	240							0
	15			21	120	240	360							3
	20			28	160	320	480							16
	25			35	200	400	600							29
Experiment V														
9.3-11.4‰	5				35	94	120							0
X=10.4‰	10				70	188	240							3
	15				105	282	360							3
	20				140	376	480							3
	25				175	470	600							6
Experiment VI														
10.7-13.2‰	5					21	56	108						0
X=12.0‰	10					42	112	216						3
	15					63	168	324						9
	20					84	224	432.						9
	25					105	280	540						12

TABLE 20 (continued)

Experiment & salinity range	Elapsed time in days	Salinities less than 7‰	8‰	9‰	10‰	11‰	12‰	13‰	14‰	15‰	16‰	17‰	18‰	Percent dead
Experiment VII														
11.2-13.3‰	5						40	99						3
X=12.3‰	10						80	198						3
	15						120	297						13
Experiment VIII														
13.7-16.2‰	5								10	50	105			0
X=15.1‰	10								20	100	210			6
	15								30	150	315			6
	20								40	200	420			16
Experiment IX														
15.8-17.5‰	5										7	63		0
X=16.8‰	10										14	126		0
	15										21	189		0

Experiments III, IV, and V, each with a mean of 10.4‰, spanned the transition zone from heavy to light mortality. In experiment III with salinities fluctuating from 7.6 to 12.5‰ all drills died in 720 hours (95% dead after 600 hours). In experiments IV with salinities fluctuating from 8.8 to 11.9‰ only 29% were dead in 600 hours while in experiment V with salinities from 9.4 to 11.4‰ only 6% died in 600 hours. It is emphasized that the mean salinity gave no indication of how lethal conditions were for drills.

In the upper salinity ranges where minimum salinities increased from 10.7‰ in experiment VI to 13.7‰ in experiment VIII, mortality was low and never exceeded 16% in a 20 day period. However, the death of a few drills in each experiment suggested that conditions in this range were slowly lethal to some of the drills. When minimum salinities exceeded 15.8‰ (experiments I and IX), there were no mortalities.

Mortality had a characteristic pattern in each fluctuating salinity experiment at lower salinity ranges (experiments II-IV). Mortality was very low during the first ten days and then rose steadily until the end of the experiments. This mortality pattern was different from the one observed in constant salinity experiments at 8.0, 9.2, and 10.0‰ (experiments XI-XIII). Mortality increased steadily throughout the study as in experiment XI, or it showed rapid mortality in the first ten days followed by the relatively few mortalities for the remainder of the experiment (experiments XII and XIII).

The mortality data suggested that in fluctuating salinities it was the minimum values and their duration which killed drills and that the intermittent exposure to higher salinities (upper extreme) may have delayed but did not prevent subsequent mortalities. Evidence to support this view was seen in experiments III, IV, and V where salinity ranges were respectively, 7.6 to 12.5‰, 8.8 to 11.9‰, and 9.3 to 11.4‰. In this series the greatest mortality occurred in experiment III in spite of the fact that maximum salinities were highest in that experiment (12.5‰).

Additional comparisons indicated the importance of minimum salinities with respect to drill mortality. These were derived by comparing the length of exposure to salinities lower than certain values in fluctuating salinity experiments with the length of exposure needed to cause mortality at similar constant salinities. For example, Table 19 showed that a constant salinity of 8.0‰ (experiment XI) resulted in total mortality in 480 hours. This is contrasted to experiment II where salinities fluctuated from 6.7 to 9.1‰, conditions which caused total mortality in the same period. However, in the latter experiment salinity was below 8.0‰ for only 240 hours (Table 20). In other words, exposure to salinities from 8.0 to 6.7‰ caused total mortality in about half the time required to kill all the drills at a constant salinity of 8.0‰. Intermittent exposure to salinities as high as 9.1‰ did not seem to reduce mortality in experiment II.

In experiment XII drills were exposed to a constant salinity of 9.2‰ and only 81% of the drills died by the end of 960 hours. During a similar period in experiment III, salinities ranged from 7.6 to 12.5‰, causing total mortality in 720 hours. Salinities were below 9‰ for only 156 hours. In the latter study duration of exposure to salinities less than 9‰ was only about 1/5 the exposure time to 9.2‰ in experiment XII but mortality was greater in the fluctuating salinity experiment. This occurred because salinities less than 9‰ in experiment III included values as low as 7.6‰. Intermittent fluctuation to salinities as high as 12.5‰ in experiment III did not seem to reduce mortality.

Many additional comparisons similar to that outlined above are evident when Table 19 and 20 are compared.

Total attachment data (on all surfaces) provided further insight into the difference in the mortality patterns of constant and fluctuating salinity experiments. Failure to attach to the substrate preceded drill death; therefore, in both types of experiments total attachment was inversely related to mortality (i.e., when attachment was high, mortality was low). At the start of fluctuating salinity experiments II-IV the number and percent of drills attached was highest and as the experiments progressed the number and percent attached decreased steadily, corresponding to the steady increases in mortality (Tables 2-4). In fluctuating salinity experiments at higher salinities, few drills died and the number and percent of drills attached remained high throughout the experiments (Tables 1, 5-9). In contrast, at constant salinities the percent of drills attached increased as experiments progressed (Tables 11-14). This phenomenon occurred because as the experiments progressed removal of dead drills left only attached surviving drills. However, the actual number of drills attached remained relatively constant throughout the experiments (Tables 11-14). It is suggested that under constant salinity conditions the drills unable to survive were not attached from the start and eventually died; drills able to survive remained attached throughout the experiments.

In observing attachment, a distinction was made between drills attached on tank surfaces and those attached on oyster shells covered with spat. It was hoped that this distinction would provide data to show that attachment to shells was an index of drill locomotion and chemoreception (i.e., the drills were able not only to attach but also to remove in response to food). If this hypothesis was correct, at low salinities the percent of drills attached on tank surfaces should have exceeded the percent attached on shells. As salinities increased, the percent of drills attached on shells should have increased and become greater than the percent on the tank (i.e., as salinities increased, more drills were able to move in response to food). Furthermore, as attachment on shells increased, the number of spat consumed should have increased.

Attachment and feeding data from constant and fluctuating salinity experiments indicated that this hypothesis was correct. In constant salinity experiments XI and XII (8.0 and 9.2‰) all drills able to attach were attached on the tank and spat were not consumed. At 10.0‰ (experiment XIII) most drills attached on the tank, but some drills did attach to shells (0-28.0%) and 7% of the spat were consumed. At 12.0‰ (experiment XIV) most drills attached on the tank but the proportion attached on shells was higher than preceding experiments and 13% of the spat were consumed. In experiment X at 20.0‰, 80% of the spat were consumed and in this experiment the percent attached on shells roughly equaled the percent attached on the tank. This was the only constant salinity experiment in which egg cases were deposited (33).

A similar pattern of increasing drill activity with increasing salinity was observed in the fluctuating salinity experiments. In experiments II and III with the lowest minimum salinities (6.7 and 7.6‰, respectively) almost all drills able to attach were attached on the tank and spat were not consumed. In experiments IV-VII where minimum salinities were increased from 8.8‰ (experiment IV) to 11.2‰ (experiment VII) some drills attached on shells; however, a greater percent were attached on the tank. In these experiments spat consumption ranged from 17 to 66%. In experiment VI where 66% of the spat were consumed, five egg cases were deposited. In experiment VIII where the minimum salinity was 13.7‰ the percent of drills attached on shells was only slightly lower than the percent on the tank and 73% of the spat were consumed. In this experiment 11 egg cases were deposited. When minimum salinities exceeded 15‰ (experiments I and IX) activity reached a maximum. Spat consumption ranged from 90 to 100% and the percent of drills attached on shells was equal to or greater than the percent attached on the tank. Many egg cases were deposited during these experiments (8-44).

It was interesting to note that in constant and fluctuating salinity experiments egg cases were deposited only at salinities where many spat were consumed (66% or greater spat consumption).

Haskin (1935) showed that in Barnegat Bay, New Jersey, drills survived where they could not deposit egg cases; Stauber (1943) reported a similar situation in Delaware Bay. In experiments IV, V, and VII where respectively, 71%, 94% and 87% of the drills survived, egg cases were not deposited. This agrees with the observations made in other areas.

Developing embryos died in fluctuating salinities where minimum values were less than 9‰ (experiments II-IV) and at constant salinities of 8.0, 9.2, and 10.0‰ (experiments XI-XIII). In all these experiments adult mortalities were high. Developing embryos survived in fluctuating salinities with minimum values greater than 10‰ (experiments X and XIV). At these higher salinities adult mortality was low. Haskin (1935) stated that drills survived in salinities in which their ova did not develop. This occurred in experiment V (9.3-11.4‰) where developing embryos died but only 7% of the adults died. Previous workers using constant salinity research have been limited to implying drill distribution in estuaries based on a single salinity (Federighi, 1931; Sizer, 1936; Galtsoff et al., 1937; Stauber, 1943; Engle, 1953; and Carriker, 1955). However, in estuaries, drills are exposed to fluctuating salinity conditions similar to those used in the present experiments. Results of the present studies clearly demonstrated that a single salinity, even the mean salinity, cannot accurately represent the effects of a range of salinities. Therefore, implication of drill distribution in the field based on the effects of a constant salinity on drills is not valid. Stauber (1943) stated that salinity extremes and their duration, not the means, are the factors limiting distribution of estuarine species. In the present work we have proven this contention for Urosalpinx and have in addition shown that the lower salinity extremes are most important in drill survival. The maximum salinities of fluctuations were of lesser importance.

In Virginia oyster drill distribution has been studied using drill traps (Andrews, 1956; McHugh, 1957a, 1957b; Griffin and Engle, 1962). Griffin and Engle (1962) interpreted the absence of drills on traps as an indication that drills had migrated downstream, died, or been immobilized. The results of the constant salinity transfer experiments showed that drills can survive brief exposure to low salinities without delayed lethal effects. When salinities are low, most drills may be unattached or immobilized and trap catches would indicate few drills present. However, if salinities were to rise again many of the "uncounted" drills might resume normal activity. Trapping data must, therefore, be collected for extended periods to prevent error due to temporary immobilization of drills.

It is realized that the present limited studies have left many questions, among them the effects of long term fluctuations of 60 to 100 days in the 10 to 15‰ range. However, it is the author's view that while fluctuating salinity studies are at times difficult to relate to animal populations, they do offer a more realistic approach to the problem of salinity tolerance than experiments at constant salinities.

SUMMARY

1. In the laboratory Urosalpinx cinerea from the James River, Virginia, were exposed to fluctuating and constant salinity conditions which spanned the transition from low lethal salinities to higher non-lethal salinities. The effects of these varied salinity conditions on drill mortality, attachment, feeding and ovipositon were recorded and compared. The results of constant salinity experiments were compared to similar studies conducted by other investigators.

2. At 24°C constant salinities of 8.0‰ killed all drills in 20 days; 19% of drills survived 40 days at 9.2‰ and at salinities of 12‰ or greater few drills died.

3. At constant salinities greatest mortality occurred in the first ten days and few drills died afterward.

4. In fluctuating salinities few mortalities occurred in the first ten days but then drills began to die.

5. The mean of a salinity fluctuation gave no indication of how lethal salinities were.

6. The lower salinities of the fluctuations had the greatest effect on mortality, and when salinities fluctuated below

8.0‰, all drills died. As minimum salinities increased, drill mortality decreased sharply.

7. The upper salinities did not reduce but did delay mortality.

8. As both constant and fluctuating salinities increased above lethal levels, drill activity increased; drills attached on the tank, then moved on to oyster shells and drilled spat. At the highest minimum salinities, when more than 65% of the spat were consumed, egg cases were deposited.

9. Transfer experiments in constant salinities showed that drills can survive brief exposure to lethal salinities without delayed lethal effects and low temperatures delay but do not reduce drill mortality.

10. Experiments in fluctuating salinities proved more realistic for salinity tolerance studies than constant salinities.

APPENDIX

TABLE 1

Chi square values for tests comparing male and female mortality in fluctuating and constant salinity experiments.

Experiment	Chi square
I	0.000
II	0.108
III	0.109
IV	0.579
V	1.350
VI	1.520
VII	0.279
VIII	1.300
IX	0.000
X	0.000
XI	0.248
XII	0.213
XIII	4.490*
XIV	0.517

TABLE 2

Chi square values for comparison of attachment data for male and female drills after 10 days and after 20 days in fluctuating and constant salinity experiments.

Experiment	Chi square	
	10 days	20 days
I	0.000	0.000
II	0.405	0.111
III	0.017	2.244
IV	1.959	8.950*
V	3.320	0.618
VI	11.620*	13.360*
VII	0.885	10.490*
VIII	5.030*	0.519
IX	1.430	1.480
X	0.000	0.000
XI	2.612	5.273*
XII	0.080	1.465
XIII	5.262*	12.054*
XIV	3.476	1.952

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