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FRESH-WATER KILL OF OYSTERS (CRASSOSTREA VIRGINICA)
IN JAMES RIVER, VIRGINIA, 1958¹

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Abstract

Fresh water invaded the upper half of James River seed area in winter and spring of 1958. Many oysters died between 1 May and 15 June. On some grounds, salinities did not become suitable until 1 July when temperature had reached 23°C. Death rates of native oysters were as high as 90 per cent.

Oysters exposed to fresh water from midwinter were "conditioned" to a low physiological state as evidenced by absence of heart beat, ciliary motion and mantle sensitivity when first opened. Oysters held in trays at one extremity of the seed area withstood fresh-water conditions similarly to oysters on natural bottom--in accordance with their previous history of exposure. Oysters in pans of fresh well water at the Laboratory endured unsuitable conditions for similar periods as those in James River.

Once broken, the "conditioned" state could not be regained at temperatures favoring activity. Apparently slow conditioning of oysters at low salinities and at low temperatures induces a state of "narcosis" which permits conservation of food supply and evasion of effects of temperature rises. This lasts only as long as closure is continuously enforced by fresh water or other factors.

Introduction

Fresh-water kills of oysters are rather commonplace in coastal waters of the Middle and South Atlantic States and the Gulf of Mexico. Troubles have been particularly frequent around the mouth of the Mississippi as evidenced by a voluminous literature (Butler 1952, Gunter 1953). In Chesapeake Bay salinities are much more stable than in the Gulf, yet waters in the upper reaches of oyster-growing estuaries frequently become too fresh in late spring for normal activities of oysters (Beaven 1946). The extensive kill of 1945 in upper Chesapeake Bay seriously reduced production in this area (Engle 1946) and recovery is not yet complete (Anonymous 1956).

Data gathered by the Virginia Fisheries Laboratory indicate that there are occasional fresh-water kills on the upper bars of

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James and York rivers but curiously there is little evidence of spring kills in the Rappahannock River where oystermen recall only the year of the Johnstown Flood (1889) as having been detrimental.

The James River has a record of occasional spring losses. For example, at Deep Water Shoal, the last upriver bar of commercial importance, a set of 7000 spat per bushel in 1947 was decimated in the spring of 1948. Box counts indicated that about one-third of the older oysters died also. Again in 1949 it appeared that nearly half the older oysters were killed by spring freshets. Summer kills are exceptional, but in 1955 unusual runoff from hurricanes in August caused at least one-third of the population to die on this uppermost bar. In each instance, losses at Horsehead Rock, the next large bar downriver, were much less. Usually fresh-water kills do not seriously affect production of seed oysters in James River. Losses in 1958, however, extended much further down river and were much greater than in any other spring since observations were begun by the Virginia Fisheries Laboratory in 1940.

Salinity and Temperature

In the last three months of 1957 Virginia had seven inches of excess rainfall. Except for a normal January, each month of 1958 from February through May had an excess of precipitation of about one inch. In the tidewater section of Virginia, excesses were larger. These estimates of excessive rainfall are based upon monthly means for a seventy-year period.

At first there was concern about the Rappahannock River which has shown a tendency in wet years to become deficient in oxygen in early May (unpublished observations). Although heavy runoff undoubtedly brought large quantities of organic matter into the Rappahannock, low temperatures into June prevented complications.

Exceptionally deep penetration of fresh water into the oyster-growing area of the James soon focused attention on this river and regular weekly or semi-weekly surveys were begun. Channel buoys were used as stations but for clarity these have been assigned numbers indicating distance in nautical miles above the mouth of the river. In fourteen salinity surveys, surface and bottom samples in the channel were obtained at many stages of tide from J16, below Wreck Shoal in the middle of the seed area, to J24 at Deep Water Shoal. This covers approximately the upper half of the seed area (Fig. 1). Pritchard (1952) has shown that the halocline in James River is located at a depth of about ten feet in late summer when fresh water inflow is at a minimum. Most oyster grounds are rather shallow, hence it is assumed that bottom salinities over the bars resembled surface salinities in the channel. Occasional samples over oyster bars indicated that this assumption is justified.

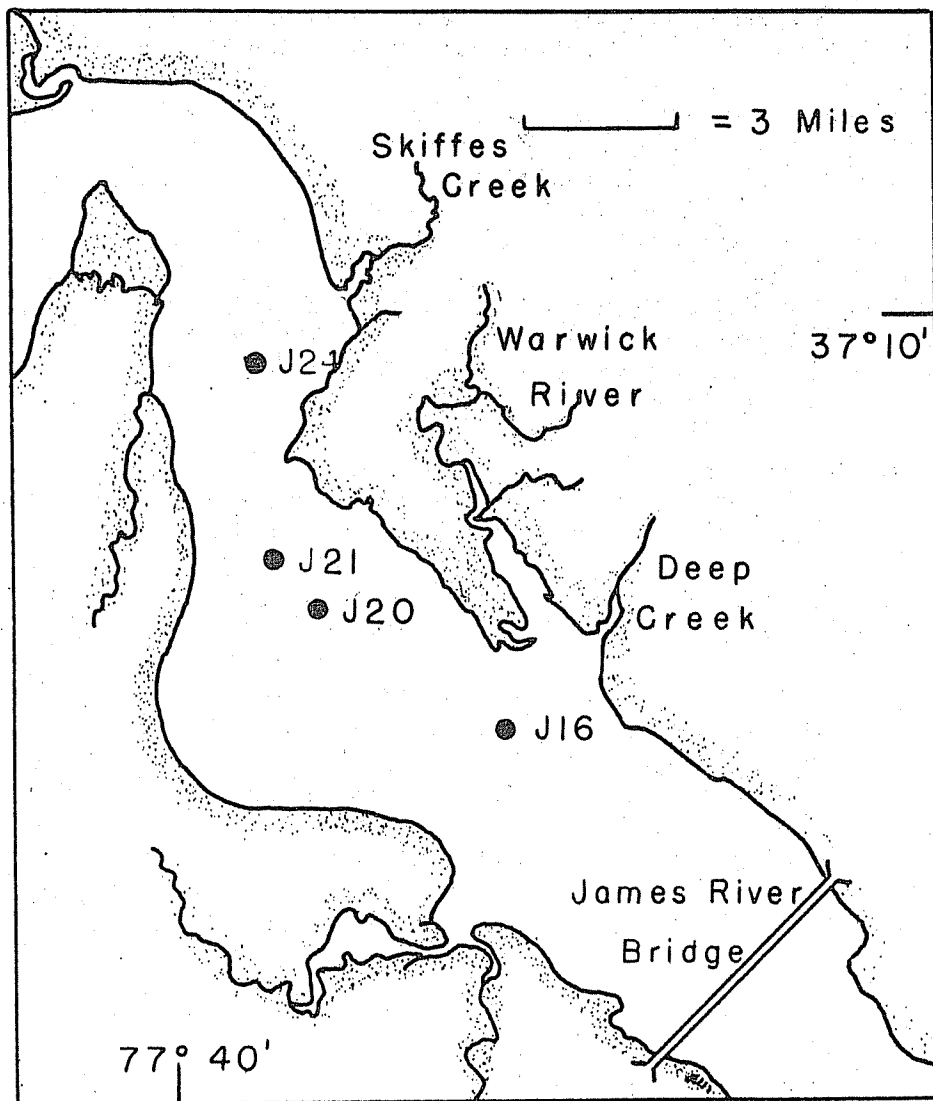


Figure 1. Map of James River seed area from bridge to J24 showing four important stations in the upper half affected by fresh water in late spring of 1958. Station numbers (J 16, J 20, etc.) correspond to the distances in nautical miles from the mouth of James River to the respective stations.

Pritchard has also shown that salinities normally decrease progressively with distance upstream in Chesapeake Bay tributaries. Surveys in the James from April to July 1958 showed a continuous horizontal gradient of salinities at surface and bottom channel stations until fresh water was reached. This regular pattern of salt distribution, which was found in numerous surveys at many stages of tide, is the basis for estimates of periods that oysters were exposed to unsatisfactory salinities.

Vertical gradients of salinity at J16 and J24, as measured by Chesapeake Bay Institute on three dates, are given in Figure 2. At first, fresh water flow stimulated salt water return flow along the bottom and produced steep vertical salinity gradients (Fig. 2, January 29, 1958), but excessive rainfall eventually pushed fresh water into the seed area at all depths.

The first survey of the James River on April 22, 1958, showed that oysters in the upper half of the seed area were already exposed to fresh water. Surface and bottom waters in the channel were fresh down to J20 and surface waters as far downriver as J16 had less than 5 ppt. It is assumed that 5 ppt is the lowest salinity at which oysters will open and pump water (Butler 1949). Nelson's (1921) figure of 11.5 ppt (density 1.009) is obviously too high for James River oysters; at Deep Water Shoal oysters often live an entire year in waters which do not reach this level. Hopkins (1936) gives 10.5 ppt as the minimum salinity at which water is pumped in *Crassostrea gigas*. Only once between April 22 and June 16 did surface salinities in the upper half of the river (above J16) exceed 5 ppt, and water salty enough for feeding did not prevail until June 16. As further evidence of penetration of fresh water into the seed area, the location of 1 and 5 ppt isohalines at the bottom of the channel is given in Table 1.

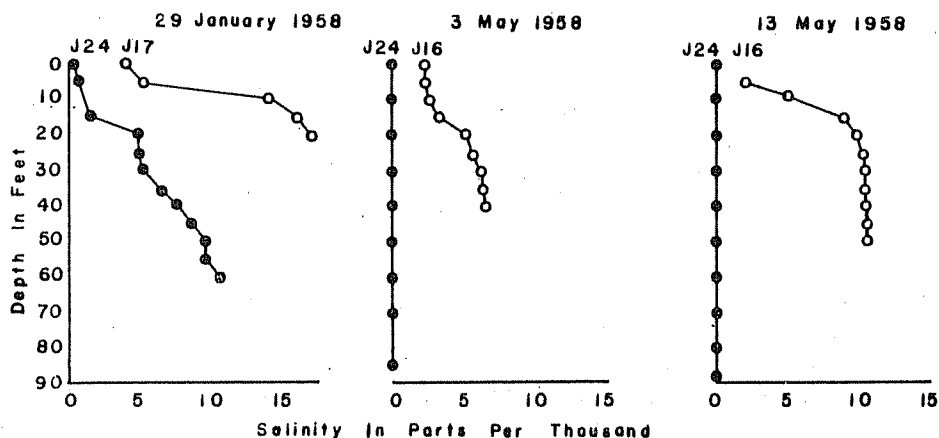


Figure 2. Salinity gradients at two stations in James River (Data from Chesapeake Bay Institute).

Table 1. Location of certain isohalines at bottom¹ of channel in James River, Virginia. Locations are given in nautical miles above mouth of river. The seed oyster area extends from J11 to J24.

Date	Tide stage	Location of isohalines on bottom	
		<1 ppt	<5 ppt
22 Apr	late flood	J20	J18
30 Apr	mid flood	J20	J18
5 May	end of flood (v. high tide)	J22	J16
9 May	late ebb	J18	J16
12 May	low slack	J19	J17
14 May	-	-	J18
19 May	late flood	J21	J18
23 May	early flood	J21	J18
26 May	mid to late ebb	J22	J20
2 Jun	late flood	J24	J19
9 Jun	mid flood	J24	J20
16 Jun	late ebb	J24	J21
23 Jun	mid flood	J24	J22

¹Only once between 22 Apr and 16 Jun did surface samples in the channel above J16 reveal salinities above 5 ppt.

With unsuitable salinities in the upper 4 to 6 miles of the channel depth, it is clear that on adjacent shallow bars water was not salty enough to permit oysters to open and pump water.

Periods of time that oysters were exposed to unsatisfactory salinities are shown in Table 2. It should be emphasized that these estimates do not include periods of low salinities prior to April 22. On January 29, 1958, surface salinities were below 5 ppt as far down-river as J17 but winter temperatures prevailed and oysters were dormant. No further hydrographic measurements were made until

Table 2. Length of exposure of oysters in nature, James River, 1958, to low salinities (based upon surface salinities in channel) and death rates derived from box and gaper counts.

Station	Days after 22 Apr at salinities of		Dates for < 5 ppt	Estimated death rate for spring (Percentages)
	<1 ppt	<5 ppt		
Wreck Shoal (J17)	0	19	30 Apr-19 May	0
Rainbow Rock (J20)	26	47	22 Apr- 9 Jun	25
Horsehead Rock (J21)	26	61	22 Apr-23 Jun	25
Deep Water Shoal (J24)	47	61	22 Apr-23 Jun	90

April 22. The long period prior to April 22 has been excluded from calculations. Not only low salinity but also low temperature prevented oyster activity during this winter period.

For each of the first three months of 1958 mean air temperatures were five or more degrees below long-range averages for Virginia. April was nearly average but May and June were one to three degrees below average. Water temperatures, which range from 16°C on April 22 to 25°C on July 1, were also lower than usual from April through June.

Running well water in pans at the Laboratory maintained a relatively uniform temperature for experimental oysters. From May 9 to June 20, temperatures seldom varied more than a degree from 20°C.

Mortality

The death rate in a wild population of oysters is always difficult to estimate unless losses are sudden and catastrophic. Counts of boxes (hinged valves) have many disadvantages (Hopkins and Menzel 1952, Gunter 1953, Hewatt and Andrews 1954). Even if sampling is representative, estimates of mortality based on box counts are minimal. In the James River, rather small seed oysters (about 1 to 2 inches) were involved and at this size boxes are easily broken apart by dredging or tonging. Counts, based upon 200 to 400 oysters, are expressed as percentages of dead (boxes and gapers) in the total number. Any dead oyster containing a fragment of meat was considered a gaper.

Occurrence of gapers is a certain sign of recent mortality but persistence of meats depends upon temperature, scavengers, and other variables. Under fresh-water conditions the usual scavengers were inactive and amphipods appeared to be the primary macroscopic feeders on gaper meats.

Percentages of dead oysters on four natural bars in the upper half of the seed area are shown in Table 3. The counts indicate no appreciable death rate from fresh water at Wreck Shoal (J17), but over 80 per cent at Deep Water Shoal (J24). A few gapers continued to appear at Rainbow and Horsehead until mid-June (Table 4) although percentage dead fails to indicate losses after May 19. The proportion of boxes and gapers on Rainbow indicates that many of these oysters probably died in mid-winter from smothering (mixed shell and mud bottom) rather than from fresh water. At Deep Water Shoal the peak occurrence of gapers was about the first of June; a few gapers were found after June 16.

Tray Studies at Deep Water Shoal

To obtain better estimates of death rates at Deep Water Shoal, three trays each containing 100 native, 100 Wreck Shoal and 50 Gloucester Point oysters were suspended from the lighthouse. Trays 1, 2 and 3 were placed at Deep Water Shoal on May 9, May 23 and June 9 respectively; and left there until after July 1. The oysters from Deep Water Shoal and Wreck Shoal had been under the influence of fresh or low-salinity waters throughout the spring, but the Gloucester Point oysters were transferred from waters of about 13 ppt. These trays were examined once or twice weekly for boxes, gapers and live oysters. The results in Table 5 show that:

1. Gloucester Point oysters were unable to withstand this sudden change of salinities; most died within two weeks.
2. Wreck Shoal oysters withstood full fresh water for at least 30 days before any appreciable number of deaths occurred. In the first group only about 25 per cent died and in the other groups very few had died by June 23; this was the approximate time when salinities at Deep Water Shoal increased to a level suitable for oyster activity.
3. Deep Water Shoal oysters began dying immediately after being placed in trays. This indicated that they had been subjected to fresh-water stress for some time prior to May 9 and much earlier and longer than oysters at Wreck Shoal.

Deaths of local oysters in trays at Deep Water Shoal continued intermittently for two months and the total death rate was approximately 90 per cent. The peak rate of death occurred about June 1

Table 3. Percentages of dead oysters (A) and total counts (B) on four natural oyster beds in James River, 1958. Total count includes live oysters, boxes and gapers.

Date	Wreck Shoal		Rainbow Rock		Horsehead Rock		Deep Water Shoal	
	A	B	A	B	A	B	A	B
22 Apr	-	-	-	-	-	-	5	304
30 Apr	2	245	-	-	17	242	10 13	251 93
5 May	3	492	27	369	11 7	114 366	11	276
9 May	9	570	-	-	11	508	9	222
12 May	4	249	16 8	230 205	10 14	402 332	10	340
19 May	4 9	360 430	- -	- -	9 22 19	364 138 437	25	373
23 May	4 5	383 247	23 -	345 -	16 -	367 -	35 27	147 251
26 May	5	338	27	212	17 17	356 255	47	359
2 Jun	6	327	22	364	17	259	62	271
9 Jun	6	458	28	333	20	359	76 78	222 151
16 Jun	4	487	15	445	22	356	70	315
23 Jun	4	337	23	222	20	246	83	181
1 Jul	5	380	27	286	20	269	86	258

Table 4. Percentages of gapers and boxes on four oyster beds in James River, 1958.

Date	Wreck Shoal		Rainbow Rock		Horsehead Rock		Deep Water Shoal	
	Boxes	Gapers	Boxes	Gapers	Boxes	Gapers	Boxes	Gapers
22 Apr							3	2
30 Apr	2	0			12	5	6 10	4 3
5 May	3	0	26	1	7 6	4 1	8	3
9 May	9	0			9	2	6	3
12 May	4	0	14 7	2 1	8 11	2 3	7	3
19 May	3 9	1 0			8 13	1 9	12	13
23 May	4 5	0 0	20	3	11	5	15 16	20 11
26 May	5	0	26	1	15 15	2 2	24	23
2 Jun	6	0	21	1	17	0	33	29
9 Jun	6	0	27	1	19	1	65 73	11 5
16 Jun	4	0	13	2	21	1	70	0
23 Jun	4	0	23	0	20	0	83	0
1 Jul	5	0	27	0	19	0	86	0

after what was probably continuous exposure to unsuitable salinities from January 1958. Cumulative mortality (Table 6) was calculated from death rates for periods (Table 5) using a table of exponentials. ~~Conversion to instantaneous death rates permitted adding consecutive rates before reconvertng to "annual" rates.~~ If no oysters had been lost, cumulative mortality could have been calculated more simply as the ratio of dead to original oysters.

Timing and rates of death in trays agree reasonably well with observations on natural bottom (Tables 4 & 6). From observations of gapers and boxes in trays it appeared that few oysters retained meats more than seven days after death. This is probably unusually long at 20°C, possibly because scavenger populations were disturbed also.

Laboratory Pan Studies

For comparison with bottom and tray oysters at Deep Water Shoal, several lots of about 50 oysters from James River and from Rappahannock River were held in laboratory pans with running fresh well water. Oysters for Group I (Table 7) were obtained at the same time and places as those put in trays at Deep Water Shoal. For Deep Water Shoal oysters, the timing of deaths on natural bottom, in trays, and in pans was essentially similar (Tables 3, 5, & 7). All were continuously exposed to fresh water until over 90 per cent were dead. The actual periods of exposure to unsatisfactory salinities were much longer than shown in the tables.

The first death among Wreck Shoal oysters in pans (Group I) occurred after 17 days and LD 50 (when half were dead) was 41 days (Table 7). Sixty days after being placed in fresh water, seven of these oysters were still alive. Wreck Shoal oysters of Group II, placed in pans about the time feeding began on their native ground (June 3), began dying sooner and at a faster rate than Group I oysters (LD 50, 19 days). Very few Wreck Shoal oysters died on their native beds and it was over 45 days before half of those in trays at Deep Water Shoal (Group I) had died.

On July 1 after oysters began to feed and grow at Wreck Shoal (salinity 7 ppt), the third group was placed in pans of fresh water. Deaths began on the eighth day and most oysters were dead by the fifteenth. At 25°C this approximates the picture obtained by Loosanoff with Long Island Sound oysters. Once activity had been resumed and conditioning to low salinity and low temperature had been broken, oysters apparently could not readjust to fresh water from a salinity of 7 ppt.

The Rappahannock oysters died at a rapid rate in pans. They came from a low-salinity area where damage was expected but the water over these bars did not become entirely fresh and no losses occurred. Apparently they were not "conditioned" as were oysters in James River.

Table 5. Survival of oysters in trays at Deep Water Shoal Lighthouse during fresh-water incursion, James River, 1958. Figures indicate numbers dead, total counted and percentage dead for dates examined.

Group & date placed	Dates examined	Days of exposure	Sources of oysters					
			Deep Water Shoal		Wreck Shoal		Gloucester Point	
			Dead/Total ¹	% dead	Dead/Total	% dead	Dead/Total	% dead
Tray 1, 9 May	12 May	3	8/100	8	1/100	1	1/50	2
	19 May	10	12/92	13	0/99	0	16/49	33
	23 May	14	19/80	24	0/99	0	13/33	39
	26 May	17	21/57	37	1/88	1	12/20	60
	2 Jun	24	16/37	43	1/87	1	4/8	50
	9 Jun	31	7/21	33	4/86	5	2/4	50
	16 Jun	38	3/11	27	8/78	10	1/1	-
	23 Jun	45	1/8	12	7/51	14	-	-
	1 Jul	52	4/8	50	2/44	5	-	-
Tray 2, 23 May	26 May	3	14/100	14	1/100	1	10/50	20
	2 Jun	10	29/86	34	0/99	0	24/39	62
	9 Jun	17	9/51	18	1/98	1	14/15	93
	16 Jun	24	23/40	58	3/72	4	1/1	-
	23 Jun	31	3/18	17	0/69	0	-	-
	1 Jul	38	7/15	47	1/53	2	-	-
	9 Jul	46	1/8	12	0/47	0	-	-
Tray 3, 9 Jun	16 Jun	7	8/48	17	0/100	0	49/50	98
	23 Jun	14	6/30	20	0/100	0	1/1	-
	1 Jul	21	3/30	10	1/100	1	-	-
	9 Jul	29	0/25	0	0/99	0	-	-

¹Decreases in total counts in excess of deaths were caused by losses of small oysters through the meshes of the tray. Minor counting errors or some mixing are evident in the last counts.

Table 6. Death rates of native oysters in Tray 1 at Deep Water Shoal¹. Mortality for each period, from which cumulative mortality was calculated, is given in Table 5.

Period ending	Period in days	Percentages	
		Daily death rate by periods	Cumulative mortality
9 May	0	-	-
12 May	3	2.7	8
19 May	7	1.9	20
23 May	4	6.0	39
26 May	3	12.3	61
2 Jun	7	6.1	78
9 Jun	7	4.7	85
16 Jun	7	3.9	89
23 Jun	7	1.7	91
1 Jul	8	6.2	-

¹Oysters dredged and placed in tray on May 9.

The appearance of oysters in pans of fresh water is noteworthy. There was no evidence that any oyster opened its shell until near the end of its endurance. Usually copious amounts of mucus were expelled around the edges of the shells in the later stages. Even when oysters opened their shells they were not necessarily dead; many such oysters recovered sufficiently to close tightly when placed in salt water. Odors of decay often preceded final relaxation of the muscle. Barnacles (Balanus improvisus), hooked mussels (Brachidontes recurvus), and Congerina leucophaeta died within one or two weeks of immersion in fresh water in pans--although some barnacles and mussels survived on natural cultch at Deep Water Shoal. The impression was gained from observations of tray oysters at Deep Water Shoal that introduced fouling organisms died at a more rapid rate than natives.

Conditioning and Physiological State of Oysters

In Virginia estuaries, lowest salinities for the year occur typically in April and May. It is usual for oysters in the upper seed area to encounter unsatisfactory salinity conditions as winter changes to spring. Loosanoff (1952) has shown that as temperatures rise oysters die at a more rapid rate from fresh-water exposure. Although some restriction of oyster activities in fresh water is obvious, apparently it has been assumed by most investigators of fresh-water kills that metabolic rates increase with rise in temperature even in closed oysters (Butler 1949, Gunter 1953).

Attempts to check gapers for signs of life led to the discovery that when first opened live oysters on beds in the upper James had no heart beat, no ciliary action and no visible sensitivity to probing of mantle and other tissues. This extremely low level of activity was unexpected at temperatures between 16 and 23°C. Normal oysters held out of water in cold rooms for days show some movements of heart, mantle and cilia when opened. Usually within five minutes after removing one valve, inactive oysters from the James registered feeble heart beats and some ciliary activity. The response developed whether oysters were placed in open air, fresh water, or salt water. Stauber (1940) found reduced heart beats in closed "windowed" oysters.

Partial recovery of physiological activity was rapid and usually occurred within 10 minutes after oysters were opened, but normal activity was not attained in a few hours. Usually heart beat and ciliary activity developed together but there was great variability from one oyster to another. Heart beat usually began as twitching which was observed for several minutes before ciliary action began. In some oysters, however, ciliary action was vigorous enough to clean carborundum from gill plates before heart action was observed. After heart beat had risen to 5 or 6 strokes per minute there was no further increase during several hours of observations. After several hours, changes in mantle sensitivity were barely detectable by crude probing methods. Further recovery was not followed in opened oysters but two

Table 7. Daily mortality of oysters from three sources exposed to running fresh well water at temperatures ranging from 19 to 26°C. Previous history of oysters had an important bearing on survival. Dates oysters were placed in fresh water is given with group. ID 50 is underlined in each group.

Days of exposure	Group I (9 May)			Group II (3 June)			
	Temp. (degrees C)	Deep Water Shoal	Wreck Shoal	Bowler's Rock	Temp. (degrees C)	Deep Water Shoal	Wreck Shoal
1						4	
2						4	
3					20.3	5	
4					20.0	5	
5		2		2	21.5	4	
6		2			22.5	<u>6</u>	
7					22.8	2	
8		3		1	22.1	3	
9	19.7				23.2		
10	20.3	5				1	
<hr/>							
11	21.0	1		1	23.2		
12		2		1			
13	20.0	4		4		1	2
14	20.7	3		1			
15	20.9	2		2			10
16	21.4	<u>1</u>		3			
17	20.5		1	4			
18	17.8?	2		<u>10</u>			
19	19.0	5	1	3	20.5	3	<u>15</u>
20	19.6	2		1			2
<hr/>							
21	19.8	3	2	2	20.7		1
22	20.4	4	1	5	21.0	2	8
23	21.0						
24		2				1	1
25		2	2	6			
26			1	3			
27				5	23.2	1	2
28			1	1	23.4	1	1
29	20.3			4			
30	20.0			1	24.0	0	2
<hr/>							
31	21.5		5		25.0	1	
32	22.5					2	
33	22.8					2	
34	22.1		3		25.9	1	1
35	23.2		1				

(Table 7 cont.)

Days of exposure	Group I (9 May)			Group II (3 June)			
	Temp. (degrees C)	Deep Water Shoal	Wreck Shoal	Bowler's Rock	Temp. (degrees C)	Deep Water Shoal	Wreck Shoal
36	23.2				25.6	1	1
37			1			2	
38			3				2
39							
40							
41	20.5 20.7 21.0		3		25.0	1	
42		2					
43							
44				2			
45				2			
46				1			
47				4			
48							
49				1			
50							
51	23.2 23.4 24.0 25.0 25.9						
52			2				
53			3				
54							
55				1			
56							
57				2			
58							
59							
60							
61	25.6 25.0		2				
62			1				
63			1				
64							
65							
66				2			
67							
68							
69							
70							
71	75 (23 July)						
72							
73							
74							
75 (23 July)				1			

lots from Deep Water Shoal that were placed in trays at Gloucester Point showed a small percentage of gapers in the first few days and thereafter almost complete survival.

Erosion of shell occurred on the inner faces of both valves immediately anterior to muscle scars; erosion was quite irregular in distribution and amount in various oysters. This phenomenon has been studied by Dugal (1939) and Medcof (1959).

Discussion

There are 96 references to salinity in Baughman's Bibliography, which does not include papers published after 1947, and which missed Stauber's important note on heart beat in closed oysters. Despite this extensive literature, estimates of how long oysters have withstood fresh or low-salinity waters in particular situations are vague and empirical and the physiological mechanisms of closed and "dormant" oysters have been explored very little. Much vagueness in the literature stems from inability to assess the effects of occasional incursions of waters of suitable salinities during extended freshets. In most field studies, sampling was too infrequent to establish exact temperature and salinity levels and their durations. During the present study, there was little evidence of sudden salinity changes which would have permitted oysters to open and pump water. The salinity gradient in the James was persistent and regular. It is unlikely that periods of exposure to unsatisfactory water (Table 2) were broken by short incursions of water of favorable salinities. Furthermore, an exceptionally long cool spring minimized temperature changes during the period. No major complications such as oxygen depletion or disease were detected. Conditions were unusually propitious for measuring tolerance of oysters to fresh water in nature.

In Virginia, oysters are typically inactive from December 15 to March 15. Excessive rainfall in late 1957 and early 1958 had reduced salinities in the upper seed area of the James River below the 5 ppt level assumed to be necessary for oyster activity. When temperatures had risen (about April 1) to the level at which feeding usually begins, salinities were too low and oysters were forced to remain closed and inactive. If heart beat, ciliary motion, and sensitivity are accurate indicators of metabolic rate, these oysters were reduced to a very low rate of activity which was not affected by temperature rises. Some oysters survived in this inactive state until mid-June, when salinities increased to the critical level (5 ppt) at water temperatures of about 23°C. It is concluded that oysters can become specially conditioned to endure prolonged situations of unsuitable environment. Presumably, low salinity, insufficient oxygen, toxic substances and other factors which cause extended closure of shells produce similar physiological effects on oysters. When shells are closed, metabolic rate is reduced. If this occurs slowly at low temperatures, apparently oysters enter a special state of inactivity

much more intense than that caused by usual short-term closures. This intense "dormancy" permits them to escape the effects of subsequent rises in temperature. Oysters suddenly forced to close while actively feeding cannot attain this state. Since in Virginia low temperatures typically precede low salinities in spring, knowledge of this attribute is of considerable importance in judging the dangers of impending fresh-water kills.

The mechanism of conditioning appears to be a type of narcotization. Dugal (1941) and others have reported large increases in CO₂ and Ca in closed mollusks as a consequence of anaerobic metabolism. Carbonates are eroded from the inner faces of shells to buffer the lactic-acid-like end products of anaerobic metabolism. The rapid recovery of inactive conditioned oysters when opened suggests that CO₂ diffusion, and consequent precipitation of calcium, frees the tissues of inhibition. If oysters accumulated lactic acid and incurred oxygen debt, there would be slow recovery and change in pH. Dugal (1939) reported little change in pH of mantle cavity fluids in hard clams during anaerobiosis.

Whatever the mechanism, it appears that oysters properly conditioned to fresh-water at low temperatures can adjust to very low levels of metabolic activity. In closed oysters Stauber (1940) found that heart beats were reduced to about 2 or 3 per minute, apparently at high temperatures. The relevance of this finding to fresh-water kills has apparently been overlooked, for no reference to Stauber's paper was found in the literature. Since oysters possess a mechanism for reducing rates of metabolism while shells are closed, it is to be expected that this ability would be put to use under fresh-water conditions. Dugal's studies of anaerobic metabolism (1939) suggest the mechanism but no mention is made of reduction in heart beat or ciliary activity.

Apparently a low metabolic state is not easily attained in nature and probably will be difficult to induce in the laboratory. Although native oysters which had been slowly conditioned during late winter and spring survived for long periods, James River oysters of the same stock, which had lived one year in higher salinity water at Gloucester Point (13 ppt at time of transplantation), were unable to tolerate more than one or two weeks of fresh water. It seems that proper conditioning is more important than genetic factors in determining resistance of oysters to fresh water. Hopkins (1936) has observed that oysters (Crassostrea gigas) are disturbed by even slight changes to lower salinities but respond quickly to changes to higher salinities. He states that it is well known that oyster beds may be covered for weeks with almost fresh water without resulting in any considerable mortality. Loosanoff (1952) has shown that oysters conditioned gradually were able to pump and feed in lower salinities than those subjected to abrupt changes. At comparable temperatures, James River oysters which had not been conditioned lived about as long as Loosanoff's Long Island oysters, but naturally conditioned

oysters live far longer. The sudden drastic effects of fresh water during seasons of active feeding are striking in comparison with the slow mild events accompanying fresh water at the end of winter dormancy. In the Rappahannock River mortality in August 1955, following hurricanes, a sudden deluge of fresh water bathed oysters which had been feeding at salinities of 15 to 20 ppt. Most subsequent deaths occurred within a week.

Adaptation to anaerobic conditions appears to be well developed in bivalve mollusks, perhaps in conjunction with intertidal exposure, periods of fresh water, profundal habitats and other unfavorable conditions. Apparently conditioning of James River oysters under low salinity and low temperature conditions was not as simple as the accumulation of narcotizing carbonates. Once permitted waters of suitable salinity, oysters placed again in fresh water were not able to retreat to the former level of inactivity. Thereafter survival in fresh water was regulated by temperature levels much in the pattern described by Loosanoff. Oysters placed in pans of fresh water on July 1 failed to live as long as some from the same source brought in May 9.

Since the factors that induced inactivity in James River oysters are not understood, it is impossible to predict the areas or conditions under which similar tolerance to low salinities can be expected. What is the relative importance of low temperature, low salinity, and duration and intensity of accumulation of by-products of anaerobiosis? Are slow changes in temperature and salinity essential (Hopkins 1936)? Is extended inactivity limited to areas like Chesapeake Bay where winter temperatures normally inhibit oysters? Or can such a physiological state be induced in relatively warm waters of the Gulf of Mexico?

Observations in the James River in 1958 emphasize that oysters have great powers of endurance during typical spring conditions of low salinity. Apparently this ability to withstand low salinities depends upon continuous forced closure and it appears that temporary relief breaks the dormancy. Winter-long storage of Canadian oysters in air probably depends upon the same mechanisms but requires continuous low temperatures (Medcof 1959).

It has been assumed that survival under anaerobic conditions depends upon supplies of glycogen with temperature as a regulating factor. However, oysters that died in fresh water after 60 days were shrunken but not devoid of food reserves. In contrast, following the hurricane deluge of August 1955, oysters in the Rappahannock dropped from a condition index of 6.5 to 4.0 in about two weeks. This is expected under anaerobic conditions--if metabolic rate is only partially reduced--since glycolysis produces only about one-twentieth as much energy per unit of glycogen as oxidation. Conditioned oysters in the James were apparently able to reduce metabolic activity to a level which required little glycogen. Since James River oysters are

typically poor in glycogen reserves, this is important.

Oysters slowly conditioned to unsuitable environments are capable of withstanding adversities far beyond the limits tolerated by active oysters suddenly forced to close. With unlimited supplies of carbonates to buffer acid products of anaerobic metabolism, oysters are apparently able to induce some kind of self-narcotization; this conserves glycogen supply and permits long endurance of unfavorable conditions such as fresh-water exposure and cold air storage. Although typical by-products of anaerobiosis have been demonstrated in mollusks, at present the mechanisms of conditioning to low metabolic activity can be surmised only by analogies with vertebrate physiology.

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