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Mass Mortalities

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in Scallop Mass Mortalities

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Table of Contents

ABSTRACT

Laboratory experiments with the giant scallop, Placopecten
magellanicus, show that it acclimates to temperature, the lethal
temperature becoming higher as the acclimation temperature is raised.
However, regardless of acclimation level, there is a seasonal change
in tolerance to high temperatures which may be related to the
spawning cycle. Tolerance to high temperatures was found to be least
in late summer, near spawning time. No conclusive evidence was found
to support previous suggestions that small, immature scallops are
less sensitive to high temperature than are the adults. Scallops
from the Bay of Fundy area seemed slightly less resistant to high
temperatures than were Gulf of St. Lawrence stocks.

It appears from a comparison of known hydrographic changes
in the Gulf of St. Lawrence, and the ultimate upper incipient lethal
temperature of Gulf stocks, that temperatures which are high enough
to bring about mass mortalities directly, do not occur on the scallop
beds. It is pointed out, however, that high sub-lethal temperatures
frequently produce a shock reaction in scallops which makes them more
vulnerable to predators. It is suggested that sudden mass mortalities
may be indirectly related to hydrographic conditions through this
mechanism.

ACKNOWLEDGMENTS

INTRODUCTION

Sudden mass mortalities of the Giant Scallop, Placopecten magellanicus (Gmelin) in southern Northumberland Strait have been reported from time to time in the last 25 years, (Chiasson 1949, Dickie 1951). From 25 to 80 per cent of the fishable stock have been reported as dying within a period of several days to two weeks. Observations suggested that only scallops occurring at intermediate depths (around 25 metres) were seriously affected and then only those in the southern Strait. Populations in deeper water or in the northern Strait did not seem to be similarly affected. The mortalities were observed to occur only in late summer and early fall. There was indication that small scallops (below about 60 mm) were not as seriously affected as the larger animals. From a consideration of these features of the mortalities in relation to certain hydrographic phenomena in this area Dickie (1951, and in appendix to Chiasson, 1952) advanced the hypothesis that the mortalities were the result of the exposure of scallops to lethal temperature and salinity conditions and suggested that a phenomenon described by Lauzier (1952) might be responsible for subjecting scallop beds to these conditions.

Lauzier (1952) showed that strong winds in the Strait may lead to an oscillation of the thermocline which in the summer is present at a depth of about 25 metres. In August, 1945, a survey of the nearby Magdalen shallows showed that temperatures graduated from greater than 15°C. just above the thermocline to 5°C. just below it. As temperatures increased salinites decreased from 32.4°/oo to 28°/oo.

Southerly winds tend to move warm surface waters out of the Strait producing a compensating inflow of cold water below the thermocline. With a reversal or subsidence of these winds the warm water returns perhaps even overcompensating for the initial shift, and producing a vertical oscillation of the thermocline. Oscillations like this would change the environment for scallop beds occuring at intermediate depths from a normal 8-10° down to less than 4°C. with the influx of the deep cold water and up to around 20°C. with the subsequent invasion of warm water. Internal wave disturbances of this sort generally take several days. Cold water temperatures could persist long enough for the scallops to become acclimated to temperatures below the summer normal, thus perhaps rendering them fatally less resistant to subsequent high temperatures.

Experiments to test the plausibility of this theory were carried out during summers from 1952 to 1954 by L. P. Chiasson (Annual Report of the Atlantic Biological Station for 1952, Appendix 28; 1953, Appendix 28; 1954, Appendix 21). Using techniques described by Fry (1947) he determined lethal temperatures for scallops fished from Passamaquoddy Bay. He found that in common with other species, scallop tolerated higher temperatures as the acclimation temperature was raised. However, he found that there was a definite seasonal change in resistance to high temperature, which seemed to be related to gonad development. Tolerance to high temperature was lower in July when scallop gonads are maturing rapidly than in January or March.

He failed to show differences in temperature tolerance with different sized scallops but he used only mature scallops ranging in size from 70 to 135 mm. Smaller and immature animals were not then available. He found no evidence to support the hypothesis of direct temperature death, and concluded that it was unlikely.

Despite this conclusion, the late summer mass scallop mortalities have the triple significance of occurring at the time when the thermocline is lowest, surface temperatures are highest and scallops have diverted their energies to the maturating of gonads and spawning and may be less resistant to high temperatures than in other seasons. The further fact that such sudden mass mortalities have not been observed in beds in the northern Strait, in beds much below the thermocline, or in the Bay of Fundy, where water temperatures do not reach such high values, has further increased the likelihood of some connection, direct or indirect, between the mortality and water temperatures at the time they occur. The work described here was therefore undertaken in an effort to further describe the temperature tolerance of scallops and to elucidate the relationship between hydrographic phenomena and mass mortalities. The results suggest that direct lethal affects of temperature are unlikely in the Gulf of St. Lawrence, but observations were made which indicate that high temperatures may be indirectly responsible for the sudden mass mortalities.

METHODS

(a) Stocks

Scallops from L'Etang and the Mascarene shore in Passamaquoddy Bay were used in all scallop temperature tolerance experiments previous to 1956. They were also used in the majority of tests done in 1956 and described below. They are referred to in this report as Quoddy stock. Scallops from a bed in the southern Gulf of St. Lawrence in about 17 fathoms off Toney River, Pictou County, N.S., not far from the Pictou Island bed where high mortalities were noted by Chiasson (1952), were also used. They are referred to in this report as Gulf stock. Scallops, from the Digby area of the Bay of Fundy, which varied in size more than other available stocks were used in a test to examine the relationship between size and temperature tolerance and are here called Digby stock. The size range of the various stocks used was as follows:

Quoddy stock	135-70 mm.	
Gulf stock	115-73 mm.	
Digby stock	122-90 mm.	and 68-40 mm.

(b) Acclimation Tanks and Controls

Three acclimation levels were used; 6-7°, 10-11° and 14-16°C. Scallops were acclimated in painted wooden tanks of between 80 and 100 gallons capacity at a density of not more than 1½ scallops per gallon. Compressed air was delivered through aquarium-type airstones to ensure a sufficient supply of oxygen.

Thermostatically controlled, glass-covered heaters were used to obtain high acclimation temperatures. Low acclimation temperatures were maintained by regulating the flow of sea-water into a cold room with a thermostatically controlled air temperature of 0°C. Temperatures in the acclimation tanks fluctuated less than ± 1.0°C. about the intended temperature.

Care was taken not to perform tests on stocks of animals if appreciable numbers died during acclimation. When such "abnormal" mortalities occurred the remaining stock was discarded on the grounds that it was probably no longer representative of the natural population. Such mortalities were infrequent and in all but one case traced to some fault in the temperature or oxygen regulating system.

(c) Lethal Tanks and Controls

Twelve unpainted wooden tanks measuring 25 inches by 25 inches by 6 inches were used for lethal tests. Water was first run into overhead tanks which were maintained at a constant level by allowing an excess of water to flow through them and out a "spill pipe". From each of these tanks outlets led to each of two constant level tanks in which the water was heated by glass-covered heaters. By adjusting water flow and thermostat controls in these tanks water temperatures were maintained from about 10°C. at the bottom of the tank to 60°C. at the top. Two lethal tanks were supplied with water of the desired temperature, led in with rubber tubing from the appropriate level of each constant level heating tank.

Reduced salinities were obtained by mixing flowing fresh tap water and sea-water in desired proportions in the overhead constant level tanks. To prevent salinity stratification the water was mixed thoroughly with a rotating-blade-type electric mixer.

Scallops were tested at salinties of 30°/$_{oo}$, 25°/$_{oo}$ and 20°/$_{oo}$ Salinities varied less than ± 0.3°/$_{oo}$ about the intended salinity.

(d) Procedure

Quoddy scallops were fished locally and placed in acclimation tanks at St. Andrews within two or three hours. Digby stocks were transferred from Digby by boat in circulating sea-water tanks and placed in tanks at St. Andrews within eight hours of being fished. Gulf stocks were transported by truck under damp, cold (about 2°C.) conditions and placed in tanks here about 15 hours after being fished.

The Gulf stock transfer was made twice. The first time less than 5 per cent mortality occurred despite unavoidable rough handling. The second time, however, about 20 per cent mortality occurred. The remaining 80 per cent were used in the comparison of Gulf and Quoddy stocks because of the impracticability of getting fresh stock. Lethal temperature levels were consistent with those expected from comparison with the Quoddy stocks and from the previous tests with Gulf stocks. It is therefore reasonable to suppose that for the purpose of these experiments the 80 per cent tested were still

representative of the natural population.

All stocks were held at acclimation temperatures for at least one day longer than the time prescribed by Chiasson for complete acclimation (one day for each 1.7° rise in temperature) before being tested.

In performing lethal tests either ten or twenty acclimated scallops were placed in each test tank. Temperatures and deaths were checked and recorded each hour during the experiment. Except in rare cases temperatures varied less than ± 0.5°C. about the intended temperature. Salinities were checked several times a day until it was established that there was little fluctuation (± 0.3°/oo) and after that salinity checks were made two or three times during each experiment.

A scallop was considered dead when the tentacles and velum failed to respond to stimulation with a glass rod or pencil. No such animals ever recovered when returned to water of normal temperature and salinity. Tests in which scallops in various stages of "heat prostration" were returned to normal conditions indicated that this criterion of death was superior to such alternatives as lack of shell movement or the drooping of the velum from the shell. The criterion was, however, difficult to apply and because several different observers were needed during the tests there were some unavoidable variations in the judgements of time of death. Comparisons showed that such differences in opinion rarely exceeded one hour and in no case was there difficulty in separating "living" from "dead" animals at the end of the experiments.

(e) Lethal Temperatures

Lethal temperatures were determined using the techniques of Brett (1944) and Fry (1947). The lethal temperature was taken as the temperature which produced 50 per cent mortality in a specified time, usually 48 hours, though determinations were also made for 24- and 120-hour periods. The approximate level of temperature required to fulfill these conditions was determined in Chiasson's preliminary experiments. At this level (between 20° and 25°C.) four test temperatures at 1°C. intervals were chosen so that within the test period little or no mortality occurred at the lowest temperature and 100 per cent mortality occurred at the highest temperature.

Unfortunately the limitations of time and facilities prevented the establishment of acclimation and test temperatures at shorter intervals than indicated. As a result, a certain amount of extrapolation was necessary in the lethal temperature graphs and their range and accuracy was thus reduced. To establish lethal temperature curves precisely it would have been useful to have 0.5°C. lethal temperature graduations.

As natural mortalities do not involve any fixed percentage of the stock, 25 and 75 per cent mortality points are considered in the report and are included in Appendix II.

RESULTS

(a) Choice of Test Duration

Fry (1947) points out that when the median survival times are plotted against the lethal temperatures on semi-logarithmic paper a straight line should result if deaths throughout the test period are the result of direct lethal effects of temperature. However, in preliminary tests on scallops, Chiasson (Annual Report of the Atlantic Biological Station for 1954, appendix 21) found a break in the slope of this line at about 48 hours. Because of this suggestion that deaths in the test tanks after 48 hours may no longer be the direct result of high temperatures, forty-eight hours was chosen at the beginning of the 1956 work as the appropriate test period. However, subsequent tests in which observations were continued longer failed to confirm Chiasson's results. Several experiments were then performed in an attempt to determine the length of time required to bring about a lethal temperature effect among scallops almost equal to that which would take place in an indefinite period of time. In the case of scallops, few mortalities occurred in the lethal tanks after about 120 hours. After this time the few deaths that were noted occurred at rates not exceeding the rate of natural mortality in the acclimation tanks and were probably not directly due to high temperature. A set of 120-hour lethal tests was therefore completed.

(b) Response to High Temperatures

When test animals were subject to a sudden temperature change such as when being transferred from a 6° acclimation temperature to a 21° test temperature, their shells opened about one half an inch within a few minutes. After this they responded only slowly to being handled, to touches on the mantle with a glass rod and not at all to moving shadows, stimuli to which normal scallops respond by quickly closing their shells. If the test temperature was sub-lethal the scallops remained in this condition for periods of from less than an hour to four or five hours, depending on the magnitude of the temperature change, before resuming normal behaviour. The reaction was interpreted as symptomatic of shock and is similar to the gaping and insensibility which nearly always occurred several hours before heat death. This reaction commonly followed immersion of the scallops in a lethal test tank if the test temperature was about 10° higher than the acclimation temperature. For animals acclimated to the lower temperatures this same reaction was elicited by exposure to temperatures several degrees below the lethal range. The significance of this reaction in nature is discussed in the conclusion.

(c) Relation of Acclimation Temperature to Temperature Tolerance

Lethal temperature determinations were carried out on Quoddy scallops acclimated to 6-7°, 10-11° and 14-16°C. The results for early August in the form of detailed mortality curves, constructed from the mortalities in the test tanks at each acclimation, are shown in Figure 1. They support Chiasson's findings that scallops acclimate to increased temperatures. The higher the temperature to which the scallops were acclimated, the higher the temperature they tolerate.

Because of this, any statement of lethal temperature is meaningless without a knowledge of the acclimation temperature.

Figure 2 combines the data from these mortality curves to show the relationship between lethal temperature, taken as the temperature that killed 50 per cent of the stock in 48 hours and the acclimation temperature. From this figure it appears that each 1.0°C. rise in acclimation temperature gave rise to about a 0.1°C. rise in lethal temperature.

(d)   48- and 120-Hour Lethal Tests

As mentioned previously a 120-hour test period approaches the length of time in which all mortalities occurring as a direct result of high temperatures will have occurred. One-hundred-and-twenty-hour tests were carried out in early August. Figure 3 shows the relationship between temperatures producing 50 per cent mortality among Quoddy scallops in 48 and 120 hours. The two lines are approximately parallel indicating comparable changes in lethal temperature with acclimation for the two observation periods used. However, temperatures producing 50 per cent mortality in 120 hours were uniformly about 0.6°C. lower than were the temperatures required to kill 50 per cent in 48 hours at corresponding acclimations.

The diagonal line in this graph is a construction line giving the locus of all points where there are identical acclimation and lethal temperatures. The point at which the 120-hour "indefinite time" lethal line intersects this diagonal is therefore the lowest point at which it is impossible for scallops to become acclimated or live for an indefinite time. Fry (1947) calls this the ultimate incipient upper lethal temperature. For Quoddy stocks in August, 1956, this temperature was 23.3°C. Similarly at the opposite end, the point at which the 120-hour lethal line intersects the ordinate may be called the minimum incipient upper lethal level. For Quoddy stocks in August 1956, if the ordinate be erected at 0°C. as in Fry's experiments with freshwater fish this would seem to be 20.8°C. However, sea-water freezes a little below zero, so that marine animals may be tested at slightly lower temperatures than freshwater animals. Scallops are known to live at temperatures as low as the freezing point of sea-water, therefore the minimum incipient upper lethal level for scallops may be read from the point where the 120-hour line intersects with an ordinate erected at the freezing point of sea-water, that is, at an acclimation temperature of about -1.5°C. If this is done in the present case the minimum incipient upper lethal temperature appears to be 20.5°C.

(e)   Salinity

(i) Effect of tap water impurities in reduced salinity tests

To obtain reduced salinites fresh tap water and sea-water were mixed in the desired proportions. Previous investigations at St. Andrews, using freshwater species have been unable to use tap water because of the toxic effect of the chloramine compound in it, however. McLeese (1950) found that it had no effect on mortality rate of lobsters when mixed with sea-water to give reduced salinity.

Accordingly a test was set up to determine whether the chloramine compound had any significant effect on reduced salinity scallop mortalities. Scallops acclimated to 8°C. and sea-water salinity (30°/oo) were used.

Twenty scallops were placed in a tank of sea-water and tap water mixed to obtain a salinity of 21°/oo at a temperature of 25°C. Twenty more animals were placed in a tank containing unchloraminated lake water and sea-water at the same salinity and temperature. The numbers and rates of deaths in the two tanks were almost identical, showing that the influence of the chloramine compound on scallop mortality was negligible.

(ii)   Lethal effects of reduced salinity

All scallops were acclimated to regular sea-water salinity which fluctuated between 29 and 30°/oo over a period of three months. Three test levels of salinity 30/°oo, 25°/oo and 20°/oo were used in combination with lethal test temperatures. Results of 48-hour experiments on Gulf stock tested in late summer are shown in Figure 4. (Also Appendix III)

It can be seen that sufficient lowering of salinity may cause a drop in temperature tolerance. That is, there was no detectable drop caused by reducing the salinity from 30°/oo to 25°/oo, although further reducing the salinity from 25°/oo to 20°/oo produced a drop of about 0.9°C. in the tolerance to high temperature. As salinities have never been observed to drop any more than 3 to 4°/oo with thermocline oscillations in Northumberland Strait and have never been observed below 26°/oo it is doubtful that lethal temperatures there are measurably lowered by reduced salinities.

(f)   The Effects of Low Oxygen Saturation on Heat Tolerance

Twice during the summer, the oxygen supply in the acclimation tanks was accidentally shut off. In each case when the accident was discovered the scallops in the tanks appeared to be in a weakened condition with their shells gaping as frequently happened previous to death in the lethal tanks. The air supply to the tanks was immediately turned on and within a few hours the scallops closed their shells and appeared to have recovered completely. However, when they were used in lethal tests the next day, the results showed that they had less resistance to high temperature than usual. (Fig. 5).

Brett (1944) found that the common bullhead, Ameirus nebulosus died much faster during lethal temperature tests when it was subjected to a continuous low (though not fatally low) oxygen saturation during temperature acclimation than when there was "sufficient" oxygen. It appeared, in fact, that the bullheads' temperature tolerance failed to rise when they were exposed to insufficient oxygen before being tested. He concluded that temperature acclimation was inhibited by low oxygen concentration.

In the present case, scallops were not intolerant of high

temperature because the oxygen deficiency inhibited temperature
acclimation. In every case, sufficient time for complete temperature
acclimation had elapsed before the oxygen was turned off. It can
only be concluded that the stress of exposure to insufficient oxygen
in some way lowered the scallops temperature tolerance, reversing
the effects of acclimation rather than inhibiting its preliminary
establishment at a specific level. Insufficient oxygen probably
acted as a limiting or controlling factor which interacted with
the normal metabolic processes necessary to maintain the level
of acclimation previously reached.

Further speculation is out of place here, although such
observations suggest a multitude of questions concerning the
mechanism of acclimation. The phenomenon could not be studied further
as lowered oxygen tension is unlikely to occur on the scallop beds
and is therefore of little significance to this study of reactions
of scallops to changes in their normal environment.

(g)   Seasonal Variations in Heat Tolerance

Forty-eight-hour lethal tests on Quoddy stocks were repeated
throughout the summer. The results are summarized in Figure 6. Lines
for tests made at different seasons are approximately parallel and
indicate that at any season a given rise in acclimation temperature
produces a small but comparable rise in heat tolerance throughout
the acclimation range tested (6°-16°C.). There was, however, a
constant downward trend in tolerance to high temperatures as the
season progressed from May to August. In scallops acclimated to 11°C.,
the lethal temperature was 23.4°C. in mid-May, 23.2°C. in mid-June,
and 22.6°C. in early August.

This seasonal change in temperature tolerance may be related
to the spawning cycle in scallops. Their gonads are undergoing rapid
development from early spring to September or early October when
spawning takes place. It is known that in some species of scallops,
growth rings on the shell are formed at this season (Gutsell, 1930)
when presumably energy ordinarily used for growth is diverted to the
production of gametes. Chiasson (Annual Report of the Atlantic
Biological Station, for 1953, Appendix 28) also found a seasonal
change in tolerance to high temperature. Scallops were more resistant
in January than in March and least resistant in July.

Chiasson's lethal temperature values and this author's
are summarized in Table I. It can be seen that the two sets of
lethal levels are similar in trend but not in value. Chiasson's
results showed a consistently lower tolerance to high temperature.
This may reflect year-to-year differences in the stock as 1956 was
a relatively cold year compared with 1954 when Chiasson's work
was done. The state of the maturity of the scallop gonads in 1956
may therefore have been delayed as was the moult of lobsters along
the coast of Maine (Wilder, personal communication).

However, the writer feels that there must be some other
explanation for discrepancies of as much as 3°C. between the two
sets of results when heat tolerance seems to vary less than 2°C. in
a season. It may be that Chiasson's method of handling was responsible

for lowering the lethal temperature. For example, the adverse effects of low oxygen were not recognized at that time and insufficient oxygen in the acclimation tanks may have reduced temperature tolerance.

It must, however, be recognized that valid comparisons cannot be made between the present results and those of Chiasson's, without a knowledge of the seasonal minima, because there is otherwise no guarantee that the comparable sections of the seasonal cycles are being compared. It is advisable that temperature experiments be continued throughout late summer and fall to determine the point of seasonal minimum for a better comparison with Chiasson's results.

Brett (1944) reports finding seasonal variations in the temperature tolerance of six freshwater fish. However, the fish Brett used were not acclimated to the same temperatures before he tested them and he concluded that differences in lethal temperatures resulted simply from differences in their thermal experience immediately previous to the tests and reflected differences in the temperature to which the fish were acclimated. In the present case, scallops tested had been held in tanks in which had been acclimated to a uniform series of temperatures before each test. The seasonal differences are therefore not simply a reflection of differences in acclimation temperatures but a more complex response to previous experience in their natural environment. In the light of present results it seems likely that the stage of gonad maturity or some other related phenomenon possibly itself associated with temperature is an important factor in determining the lethal temperature at any time, and that some such additional factor may have been operating to produce a measurable part of the differences found by Brett.

(h)   Comparison of Gulf and Quoddy Stocks

(i)   Temperature tolerance differences

Gulf and Quoddy stocks have been separated geographically and have therefore constituted separate breeding stocks for an estimated 10,000 years (since the beginning of the Recent period). In this time the two populations may have developed genetic differences in temperature tolerance. Gulf scallops are subject to higher and greater fluctuations in temperature than those in the Bay of Fundy area. Consequently they might, through natural selection, have become more tolerant to high temperatures.

Because of their greater availability, Quoddy stocks were used for most lethal tests. However, the primary purpose of this work was to explore the upper temperature tolerance of Gulf scallops. After general trends of heat tolerance were established in tests with Quoddy stocks, a test for comparison with Gulf stocks was made in early August.

Comparative results are shown in Table II for both 48- and 120-hour test periods and the 120-hour observations are summarized in Figure 7. Lethal lines are parallel indicating again the similar effects of the acclimation temperature on the lethal temperature

Table I

The lethal temperature of Passamaquoddy Bay scallops at different times during the season. Underlined values are those reported by Chiasson (Annual Report of the Atlantic Biological Station, 1953) and are presented for comparison with data obtained during this study.

Acclimation 14-17° C.	Jan.	March	May	June	July	Aug.
Temp. for 50% death in 24 hrs.					_23.2_	
Temp. for 50% death in 48 hrs.				23.3	_22.6_	23.0
Temp. for 50% death in 120 hrs.				22.2*		22.3
Acclimation 10-11° C.						
Temp. for 50% death in 24 hrs.		_23.0_			_21.5_	
Temp. for 50% death in 48 hrs.		_22.6_	23.4	23.2	_20.6_	22.5
Temp. for 50% death in 120 hrs.				21.8*		21.9
Acclimation 6-7° C.						
Temp. for 50% death in 24 hrs.			23.4	22.8		
Temp. for 50% death in 48 hrs.			22.7	22.4		22.2
Temp. for 50% death in 120 hrs.				20.7*		21.5
Acclimation 2-3° C.						
Temp. for 50% death in 24 hrs.	_23.6_	_22.3_				
Temp. for 50% death in 48 hrs.	_22.3_	_21.6_				

* Oxygen supply cut off during acclimation, animals seem to be considerably less resistant to high temperature than those tested 3 days before (compare 48-hour lethals for June 14 and 18, Appendix II)

in both cases. However, Gulf stocks were more resistant to high temperature than Quoddy stocks and it required on the average 0.6° C. higher temperature to produce comparable mortality among them in 120 hours.

Table II

Lethal temperatures for Gulf and Quoddy scallops tested on August
6 to 11, 1956.

Accl. Temp.	Time to 50% mortality	Gulf Stock	Difference	Quoddy Stock
6-7°	48 hrs. 120 hrs.	22.9 22.1	- 0.8 - 0.6	22.1 21.5
10-11°	48 hrs. 120 hrs.	23.3 22.5	- 0.8 - 0.6	22.5 21.9
14-15°	48 hrs. 120 hrs.	23.7 22.9	- 0.7 - 0.6	23.0 22.3

   Seasonal temperatures in the Gulf generally reach their
peak earlier than in the Bay of Fundy and spawning usually takes
place a few weeks earlier. If seasonal differences in temperature
tolerance are related to the time of gonad maturation it might be
suspected that Gulf stocks reach their minimum temperature tolerance
earlier than the Quoddy stocks. Therefore the August difference may
be an underestimate of the difference between the two annual minima
for the two stocks. Presumably this could be observed from a
comparison not at the same season but at a time when the two are
in that state of sexual maturation when the tolerance is lowest.

  (ii) Physical differences

   Chiasson and Medcof (Annual Report of the Atlantic
Biological Station 1952, Appendix 29) conducted tank experiments at
St. Andrews to determine how long it is after the death of a scallop
before the two valves separate. Medcof found that the valves of
large scallops from the Bay of Fundy parted after about a month
when held in tanks at the Biological Station. It was hoped that
from this information it would be possible to determine the rate
of natural mortality (c.f. Dickie 1955) and also to estimate the
date of mass scallop mortalities by noting the date of separation
of the valves of empty shells on several occasions found in large
numbers in the Northumberland Strait by Chiasson (1952).

   However, Chiassion observing "cluckers" (empty shells
with valves cohering) on the Gulf beds concluded that in nature it
takes considerably longer. Observations of scallops from both areas
during the summer of 1956 suggest a reason for this disparity. Quoddy
scallops are often heavily infested with shell-boring worms and their
shell hinges are cracked and weak. Gulf scallops are relatively free
of these parasites and their shell hinges are much stronger and on

this account they may cohere longer after death than those of Quoddy scallops. Tank tests of Gulf stock are obviously needed before such results can be used reliably to estimate the times that mortalities occur in the Gulf.

(i)   Size Effects

Frequent references to size effects can be found in literature on temperature tolerance. They may be divided into two classes -- those that compare large and small animals, either all mature or all immature; and those that compare mature and immature animals.

In the first category work by Huntsman and Sparks (1924) Bélehrádek (1935) Fry et al (1946) Brett (1944), Hart (1952) and others suggests that there is sometimes an inverse relation between size and tolerance to high temperature although this varies from species to species and in many cases no size differences have been demonstrated. McLeese (1950, 1956) working with immature lobsters, found no size relationship. This is in accordance with the work of Chiasson on mature scallops. He found no size effect.

In the second category however, there appears to be a difference in temperature tolerance between the adults and juveniles of some species. Day (1886) found greater tolerance among fry than among adults in several species of fish. Similar observations were reported for a number of intertidal animals by Huntsman (1918) and for starfish by Smith (1940).

Mortalities on the Boughton Island bed in 1946 seem to have affected few scallops under 60 mm. in shell height. Surveys in 1950 at Richibucto and Pictou Island beds suggest that mortalities there affected scallops of all sizes equally though few scallops less than 60 mm. were prsent in samples from these beds. This suggested that small immature scallops might be more tolerant to high temperature than large. To test this hypothesis several experiments were carried out to examine the relation between size and temperature tolerance.

Unfortunately few immature scallops were available for tests during this summer's work. However, a comparison was made between two size-classes, 48-60 mm. and 78-133 mm. Undoubtedly some of the former were juveniles. But because some scallops in this smaller size range are mature and because it was not possible to estimate their numbers, the comparison cannot be regarded as critical. It may or may not be significant, therefore, that there was a small difference found in the temperature tolerance of the two size-classes. This difference was so small as to be close to the limits of error involved when using the equipment available. (Appendix I and II).

(j)   The 25 and 75 Per Cent Mortalities

Because reported natural mortalities have affected anywhere from 23 to 82 per cent of the stock, 25 and 75 as well as 50 per cent mortality lines for 120-hour tests on Gulf stock are shown in Figure 8 and are included in Appendix II. Twenty-five per cent

mortality in 120 hours requires on the average a temperature 0.2° less than 50 per cent mortality. Seventy five per cent mortality results at a temperature 0.3°C. higher than that required for 50 per cent mortality.

CONCLUSION -- TEMPERATURE AS AN INDIRECT CAUSE OF MASS MORTALITIES

The minimum incipient upper lethal temperature for Gulf scallops in August 1956 was 20.5°C. That is, water at -1.5°C. would have to rise suddenly to this value and remain there for at least 120 hours to cause 50 per cent mortality among scallops. To produce 25 per cent mortality the temperature would have to rise to 20.3°C. The lethal temperature rises 0.1° for every 1.0° rise of acclimation temperature in both cases. Lauzier (1952) reports a sudden rise from 15.5° to 21.0° in August at nearby Cheticamp, Cape Breton Island, but even this is about 1.3°C. below the temperature required for 25 per cent mortality among scallops acclimated to 15°C. It appears therefore, that unless further tests show that temperature tolerance at other seasons is lower than the minimum found in these results, or there should be distinct year-to-year differences (c.f. Chiasson's results), it is doubtful that mass mortalities can be directly attributed to effects of high temperatures. The writer has however, seen evidence that sudden, high, sub-lethal temperatures may play an indirect but important part in scallop mortalities.

It has been indicated above that a sudden temperature rise of 10°C. or more caused scallops to open their shells about one-half an inch, probably due to shock. The shells gaped for up to several hours even when the temperature was several degrees below the lethal level. Twice during the summer scallops in this condition were placed in tanks containing other animals, in one case lobsters, and in the other crabs and pollock. In both instances over half the scallops were found to have been eaten by the next day. The water in these tanks was of satisfactory temperature and salinity for scallops and they would almost certainly have lived if the other animals had not been present. It is probable that the lobsters and crabs and perhaps even the pollock, found easy access to the tender meat of scallops which were in this weakened, vulnerable condition. Ordinarily these predators do not appear to destroy "normal" scallops, probably because they cannot break or penetrate the valves.

From what is known of the hydrography of the Northumberland Strait temperature fluctuations of over 10° seem likely to occur on the scallop beds, this environmental stress may render scallops vulnerable to otherwise casual predators. These chance observations suggest a way not previously considered, in which hydrographic changes may be responsible for the Gulf scallop mortalities. It deserves further study. In all cases but one, predation has been ruled out as the cause of observed mass mortalities. It was discarded because no more than the usual number of predators were noted on the beds (Dickie, Appendix to Chiasson, 1952). However, normal numbers of predators might quite conceivably cause high, mass mortality if the scallops were suddenly made vulnerable through sudden changes in hydrographic conditions which in themselves would be insufficient to

kill scallops.

The rarity of small "cluckers" among mass mortality samples might also be explained in terms of the lethal combination of high sub-lethal temperatures and predators. Small scallops, when their shells are gaping because of shock, present a much smaller opening through which predators might gain access to their soft parts than do large scallops, and may thus be less vulnerable even though they may be no more tolerant to high temperatures.

Considerable numbers of lobsters, crabs, pollock, starfish, sea urchins and carnivorous snails, such as Neptunea decemcostata frequent scallop beds in the Northumberland Strait. Starfish and sea urchins have both been found inside the shells of partly eaten scallops on the beds (Dickie, 1951,) and Neptunea have been observed to kill large numbers of scallops held in nets at Digby (Medcof, personal communication). Predation by any one or all these species interacting with hydrographic effects on scallops could account for observed mass mortalities.

SUMMARY

As in other species, resistance to high temperature in scallops increases as the acclimation temperature increases. Within the range of acclimation temperatures used, a 1.0°C. rise in acclimation temperature results in about a 0.1°C. rise in the temperature producing 50 per cent mortality in both 48- and 120-hour tests.

Insufficient oxygen in the acclimation tanks lowers tolerance of scallops to high temperatures significantly and should be guarded against in further lethal temperature experiments.

There seems to be no relation between size and tolerance to high temperatures among scallops.

Seasonal variations in tolerance to high temperatures were observed among scallops acclimated to the same temperature. These variations seem to be related to the spawning cycle. Tolerance is low in the late summer and fall when maturation and spawning occur and when mass mortalities have been reported to occur, and high in the winter subsequent to spawning. Between May and August the temperature tolerance of Passamaquoddy Bay scallops drops about 0.8°C.

Gulf scallops have a higher tolerance to high temperatures than Passamaquoddy Bay scallops. In August the difference in upper lethal temperatures between Gulf and Bay stocks was about 0.6°C.

Gulf scallops have stronger shell hinges than Bay of Fundy scallops and undoubtedly the valves stay together after death longer than the month which is required for valves of tank-held dead Bay of Fundy scallops to separate. Further study of this might assist observers in estimating the date of occurrence of future mortalities.

The temperature beyond which Gulf scallops cannot be acclimated or live indefinitely (ultimate incipient upper lethal temperature) was 24.0°C. in early August 1956. The temperature at which 50 per cent mortality occurs when Gulf scallops are acclimated to -1.5°C. (minimum incipient upper lethal temperature: the lowest temperature which can produce 50 per cent mortality among Gulf scallops) was 20.5°C. in August 1956.

It is doubtful that the mass mortalities in Northumberland Strait have been a direct result of high temperatures. However, observations of shock reaction to temperature changes suggest that it is possible that temperature fluctuations in themselves insufficient to kill scallops, may impose an environmental stress upon them sufficient to render them vulnerable to otherwise casual predators and thereby cause mass mortalities. Small scallops, when they are in a state of heat shock, are probably less vulnerable to predators than larger scallops in the same condition.

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Appendix I

Per cent of scallops dying during experiments to determine lethal temperatures (normal salinities) - summer 1956.

A. 24-hour Test Period

Month:		May 16				June 14				July 3				August 6-8			
Test Temperature:		21	22	23	24	21	22	23	24	22	23	24	25	22	23	24	25
Stock Source	Acclim. Temp.																
Quoddy	14-15					0	0	0	70								
	10-11	0	10	0	20	0	0	0	70								
	6-7	0	10	20	100	0	20	30	100								
	(May 28)	(0	0	40	100)												
Digby	14-15																
	10-11					small size				0	10	10	100				
						large "				0	0	10	100				
	6-7					small "				0	10	50	100				
						large "				10	0	50	100				
Gulf	14-15																
	10-11																
	6-7													0	0	10	100

B. 48-hour Test Period

Test Temp.		21	22	23	24	20	21	22	23	24	21	22	23	24	25	21	22	23	24	25
Quoddy	14-15					(0	0	10	60)←		(June 18) low oxygen					0	0	50	100	
							10	0	30	100										
	10-11	0	10	20	90	(0	0	20	90)←		(June 18) "					0	20	100	100	
							0	10	20	100										
	6-7	0	30	60	100	(0	20	80	100)←		(June 18) "					10	20	100	100	
							10	30		100										
Digby	14-15																			
	10-11						small size				10	60	90	100						
							large "				30	60	100	100						
	6-7						small "				10	60	100	100						
							large "				30	70	100	100						
Gulf	14-15										0	0	40	100		0	10	70	100	
	10-11					(July 17) →					(0	0	30	100		0	0	30	90	
	6-7										0	10	60	100	)	0	10	60	100	

C. 120-hour Test Period

		21	22	23	24	20	21	22	23	21	22	23	24
Quoddy	14-15	0	40	100	100								
	10-11	10	60	100	100								
	6-7												
Digby	14-15					0	10	20	100				
	10-11					0	10	60	90				
	6-7					20	70	100	100				
Gulf	14-15									20	10	100	100
	10-11									60	60	100	100
	6-7									10	90	100	100

(June 18 – low oxygen) air off →

Handwritten annotations: + 3 weeks; 40; + 1 day = 50

Appendix II

Lethal temperatures of scallops tested during the summer of 1956, derived from data presented in Appendix I. Temperatures required to kill 25, 50 and 75 per cent of test animals are all given.

A. 48- hour Lethals

Stock Source	Acclim. Temp.	May 16 — 25	50	75	June 14 — 25	50	75	July 3 — 25	50	75	Aug. 6-11 — 25	50	75
Quoddy	14-15				(22.5	22.9	23.2)←(June 18) low oxygen				22.6	23.0	23.3
					22.9	23.3	23.6						
	10-11				(22.1	22.4	22.6)←(June 18) "				22.1	22.5	22.8
					22.8	22.9	23.6						
	6-7	22.8	23.4	23.8	(21.1	21.5	21.9)←(June 18) "				21.9	22.1	22.5
		22.0	22.7	23.3	21.2	22.4	23.1						
Digby	14-15				small size			22.5	22.9	23.5			
	10-11				large "			22.3	22.7	23.2			
	6-7				small "			22.4	22.8	23.2			
					large "			22.1	22.5	23.0			
Gulf	14-15							(23.6	24.1	24.5)	23.5	23.7	24.0
	10-11				(July 17)→			22.9	23.3	23.6	22.9	23.3	23.7
	6-7							22.4	22.9	23.3)	22.4	22.9	23.3

B. 120-hour Lethals

Stock Source	Acclim. Temp.	May 16 — 25	50	75	June 14 — 25	50	75	July 3	Aug. 6-11 — 25	50	75
Quoddy	14-15				(21.7	22.2	22.6)		22.1	22.3	22.5
	10-11	21.8	22.1	22.4	21.3	21.8	22.3)←(June 18 - low oxygen)		21.7	21.9	22.2
	6-7	21.4	21.8	22.2	20.2	20.7	21.1)		21.3	21.5	21.8
Digby	14-15										
	10-11										
	6-7										
Gulf	14-15								22.6	22.9	23.2
	10-11								22.3	22.5	22.9
	6-7								21.8	22.1	22.5

Appendix III

A. Per cent of scallops dying during the period July 17-Aug. 11, 1956, in lethal temperature tests using Gulf stock in water of different salinties.

24-hour Periods

Accl. Temp.	Salinity / Test Temp.	30%				25%					20%				
		22	23	24	25	21	22	23	24	25	21	22	23	24	25
14-15												0	20	20	100
10-11							0	0	30	100		0	0	30	100
6-7		0	0	70	100		0	10	50	100	0	20	40	100	

48-hour Periods

Accl. Temp.	Salinity / Test	30%					25%					20%				
		21	22	23	24	25	21	22	23	24	25	21	22	23	24	25
14-15			0	0	40	100		0	10	40	100		0	10	50	100
10-11			0	30	100	100		0	30	100	100		10	30	100	100
6-7		0	10	60	100			0	50	90	100		0	50	100	100

B. Lethal Temperatures (July 17-Aug. 11, 1956) of Gulf stock at different salinties, derived from Appendix IIIA. (LT-50's)

Accl. Temp.	Salinity / Periods (Hours)	30%		25%		20%	
		24	48	24	48	24	48
14-15			24.2		24.1	24.4	23.0
10-11			23.4	24.2	23.4	24.2	22.4
6-7		23.9	22.8	23.6	23.0	23.0	22.0

Figure 1. Temperature mortality curves for Passamaquoddy Bay scallops in early
August 1956. The curves show the per cent of scallops acclimated to different
temperatures which, when immersed in different test temperatures, die within a period
of 48 hours. Lethal temperatures are interpolated from such graphs as the
temperature which would be expected to kill 50 per cent of the animals during
the specified test period (dashed vertical projections on abcissa).

X = 14°-15°C. acclimation temperature

• = 10°-11°C.   "   "

O =   6°- 7°C.   "   "
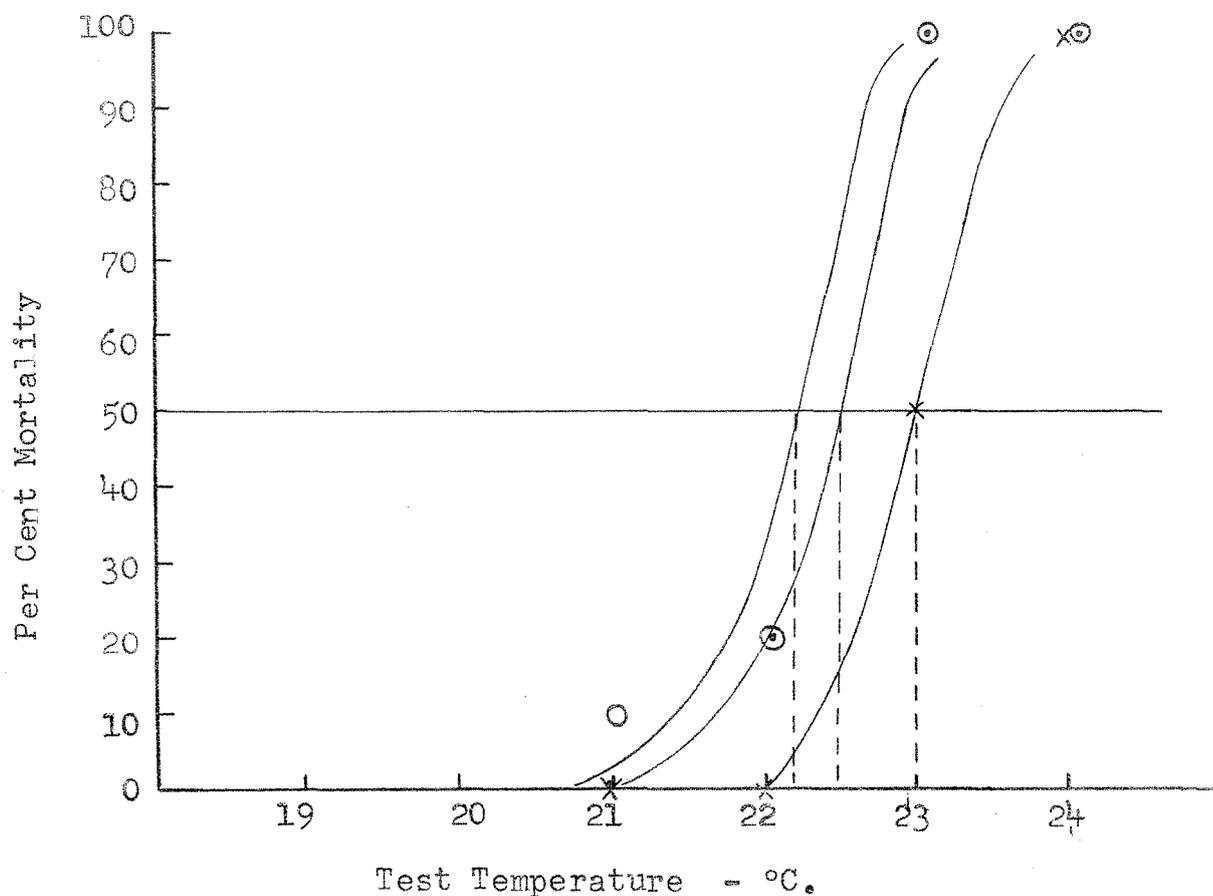
Figure 2. Relation of acclimation temperature to the 48-hour lethal temperature for Passamaquoddy Bay stock tested during August 1956. The mortality curves from which the lethal temperatures were interpolated are given in Figure 1.
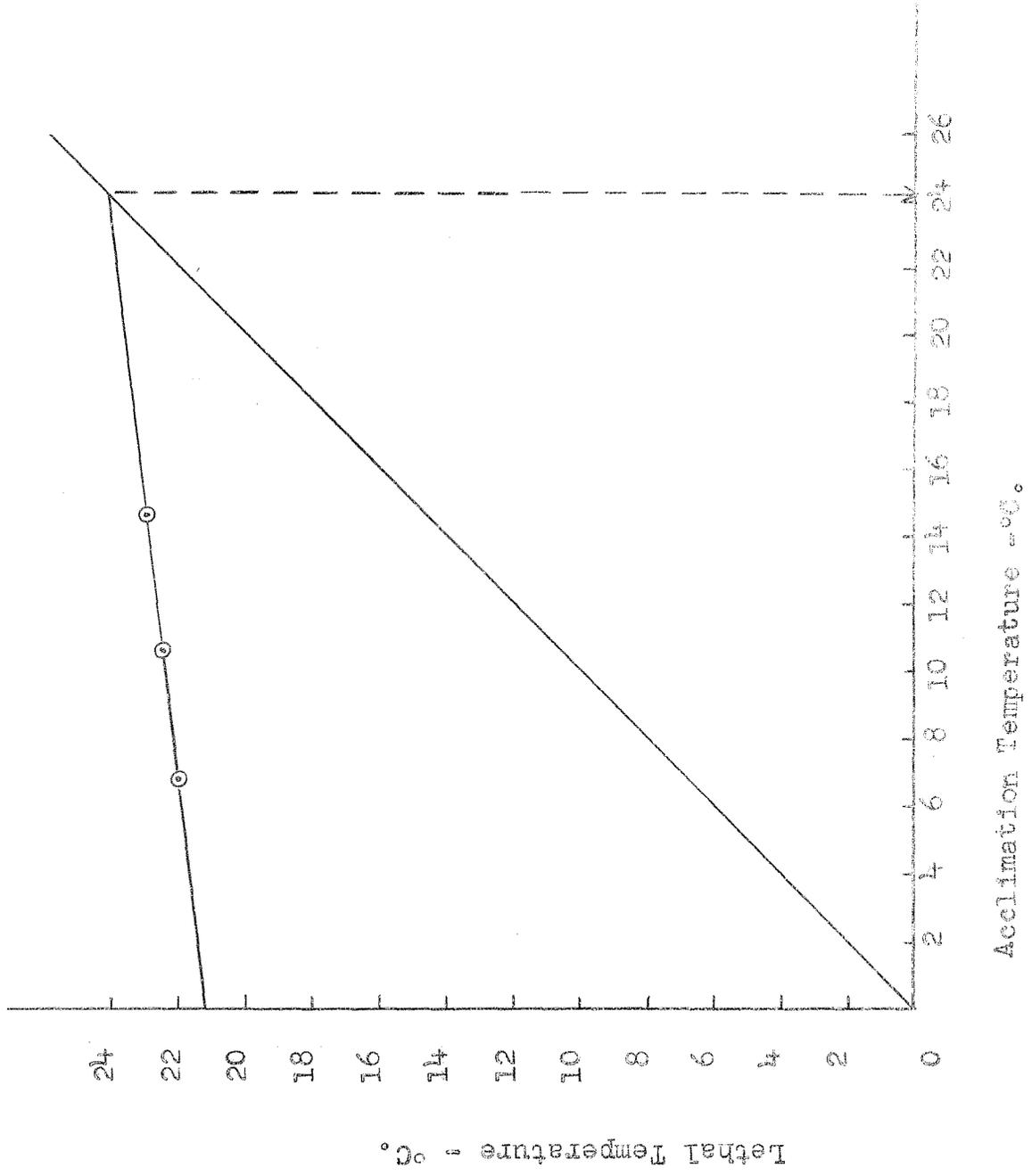
Figure 3. The relation between lethal temperatures derived from 48-hour and
120-hour observation periods. Data are for Passamaquoddy Bay scallops
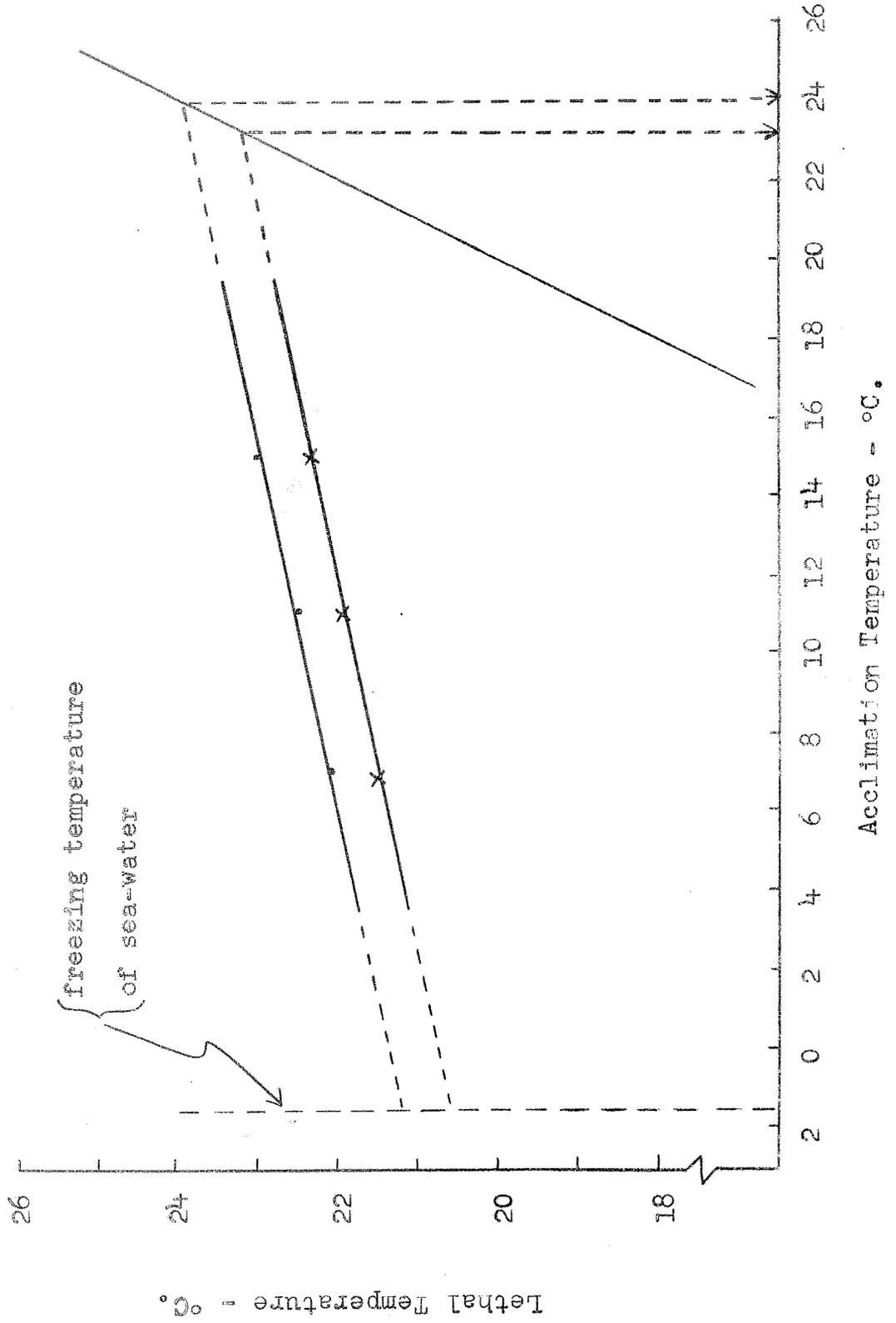tested during early August.

• — 48-hour lethal

X — 120-hour lethal

freezing temperature
of sea-water

Acclimation Temperature – °C.

Lethal Temperature – °C.

Figure 4 The effect of reduced salinity on the relation between acclimation temperature and 48-hour lethals. Data are for Gulf stock tested during the period July 17 to August 11.
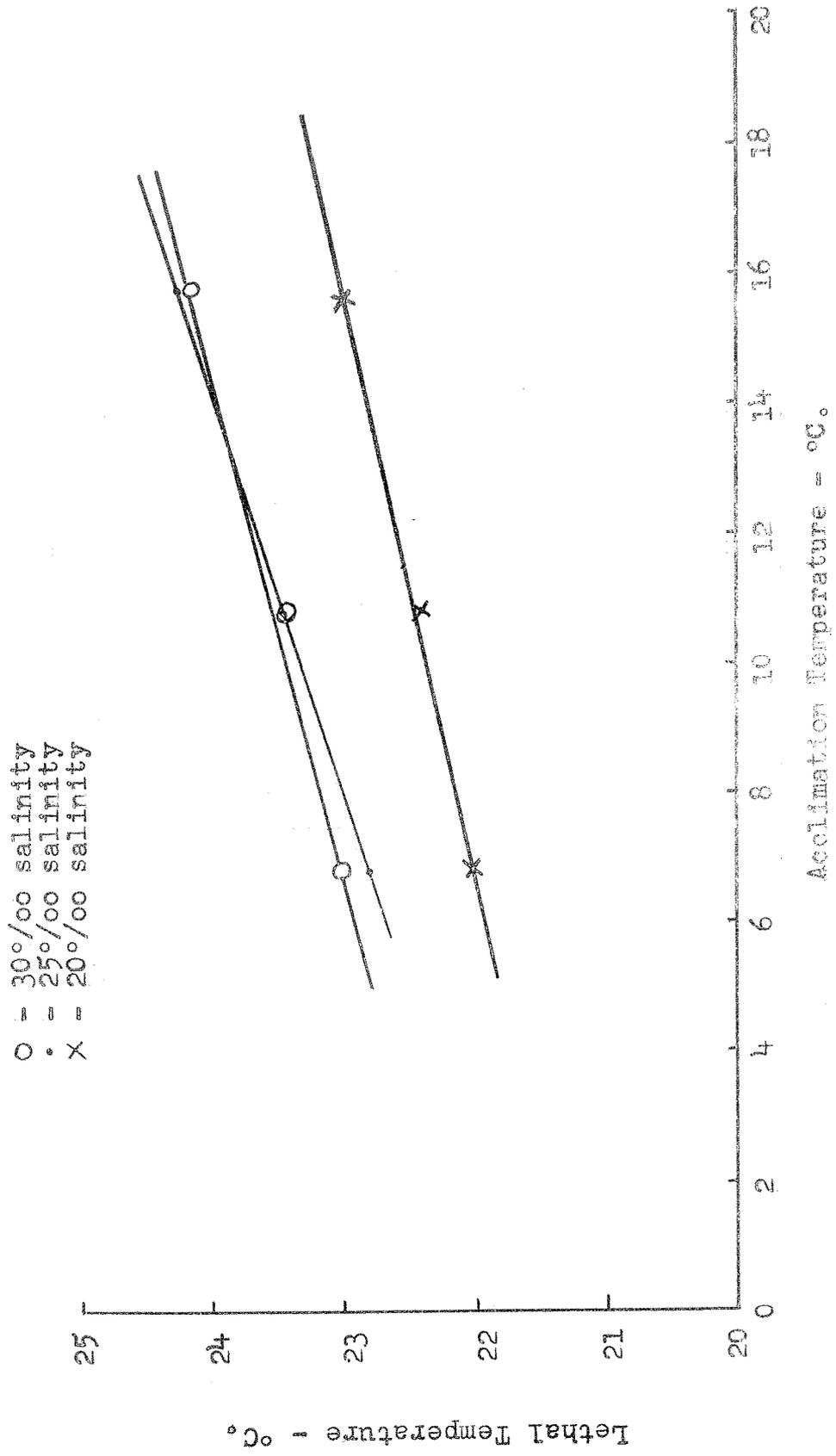
O = 30°/oo salinity
• = 25°/oo salinity
X = 20°/oo salinity

Lethal Temperature - °C.

Acclimation Temperature - °C.

Figure 5 The effect of low oxygen saturation during the latter part of the acclimation
period on the relation between acclimation temperature and 48-hour lethal
temperatures for Passamaquoddy Bay scallops.

X = Tested June 14. Water fully saturated with
O₂ during acclimation.

• = Tested June 18. Air supply accidentally turned off
subsequent to acclimation and test of June 14
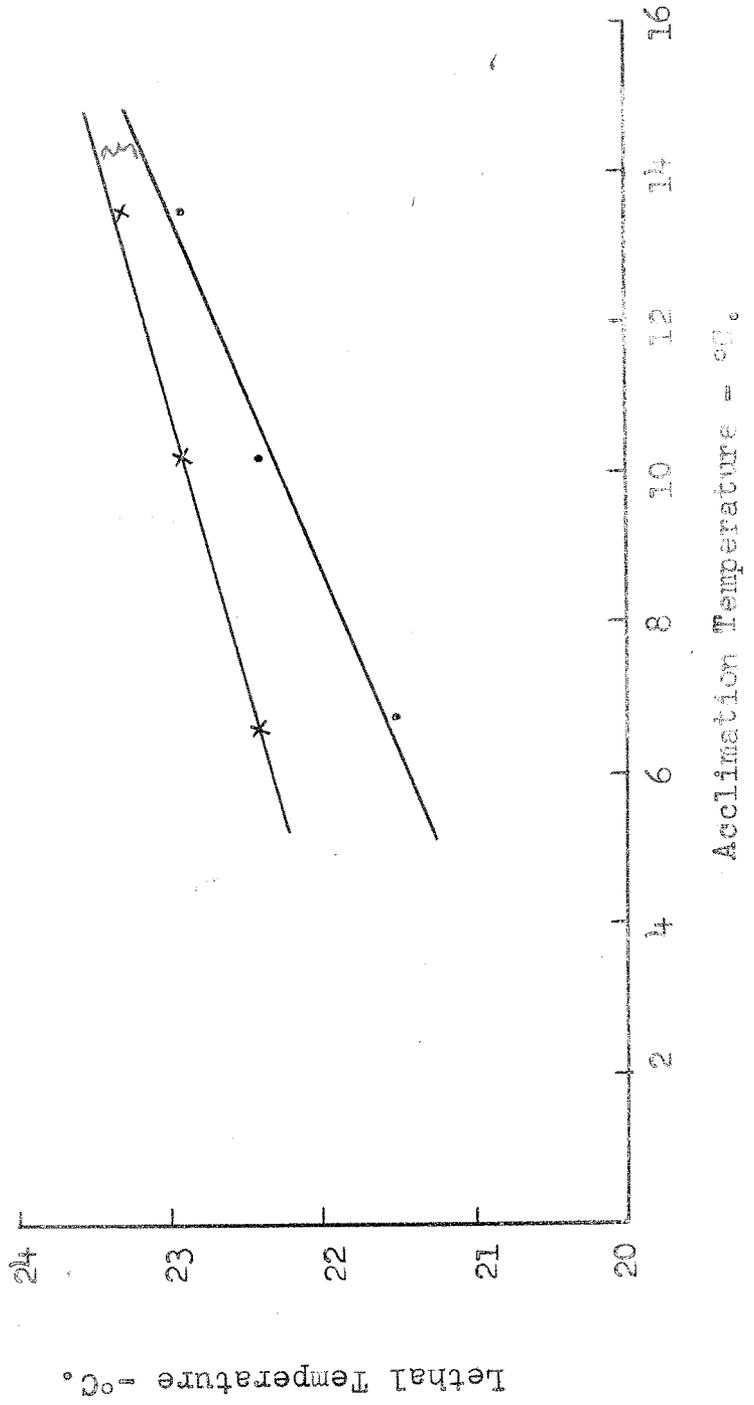and renewed for 24 hours before the June 18 test.

Figure 6   Seasonal variation in 48-hour lethal temperatures of Passamaquoddy Bay stock, acclimated at different temperatures.

O = May 16 lethal temperatures

X = June 14   "   "
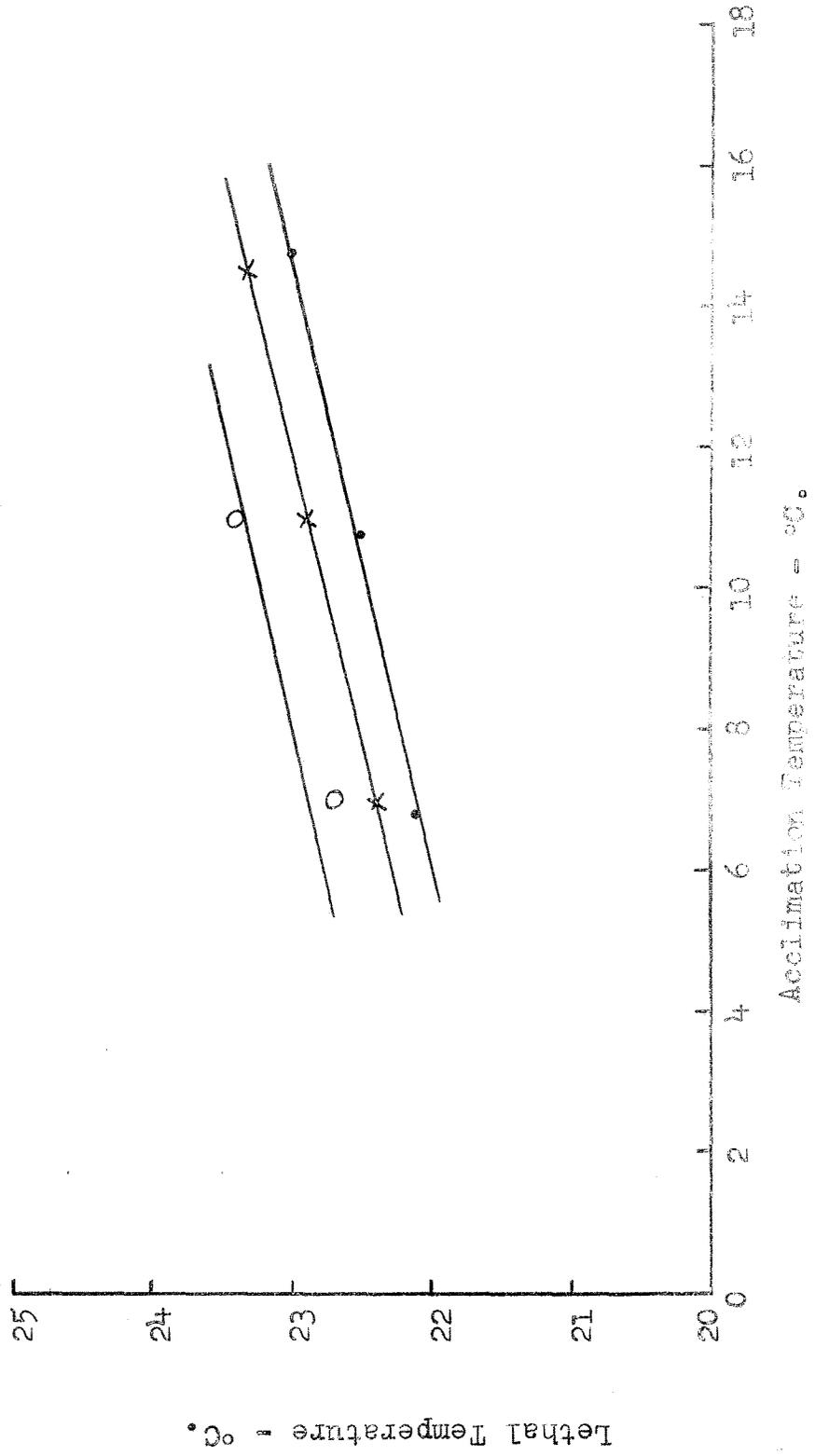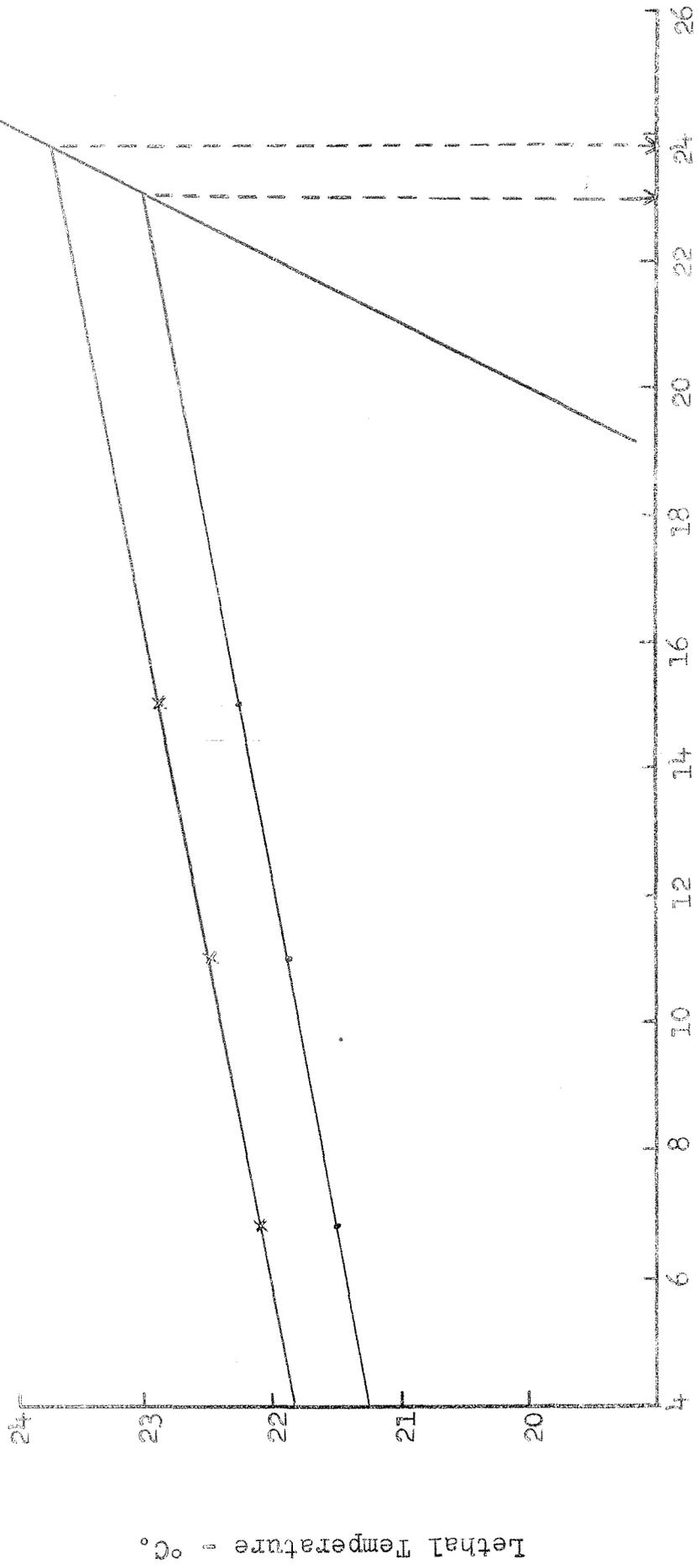
• = August 6   "   "

Figure 7   Difference in thermal tolerance by Passamaquoddy Bay and Gulf scallops, as reflected in their 120-hour lethal temperatures in early August 1956.

X = Gulf stock

• = Quoddy stock

Figure 8   The 120-lethal temperatures for Gulf stock in August, 1956 and its
relation to the temperatures required to kill 25 and 75 per cent of
the stocks.

o = 75% mortality

x = 50% mortality

. = 25% mortality