PRESSURE IN THE EARLY LIFE HISTORY 235

OF SOCKEYE SALMON

the matter of by the state of the rest of the state of th

HAROLD HENRY HARVEY

B.Sc. University of Manitoba, 1953

M.Sc. University of Manitoba, 1956

A THESIS SUBMITTED IN PARTIAL FULFILMENT OF
THE REQUIREMENTS OF THE DEGREE OF
DOCTOR OF PHILOSOPHY

in the

DEPARTMENT OF ZOOLOGY

standar degree	of DC	CTOR	OF	PHI	LOS	OPHY	7
A			2 62 G G ZI	1.775	4 99		ed o
700 %			Tron	She	1-11-	ounts:	
Sure an	at disease			September 1	4 4	THE DIE	

We accept this thesis as conforming to the

Members of the Department of Zoology

The University of British Columbia

August, 1963

ARCTIC ENVIRONMENTAL INFORMATION
AND DATA CENTER
707 A STREET
ANCHORAGE, AK 99501

investigation of this problem required methods of gas analysis a study of the limnology of the lake environment and a measure of the tolerance of fish to decompression. Ultimately the study came to include a measure of the rate at which fish equilibrate with the dissolved nitrogen of their environment.

The theoretical considerations relevant to the study of dissolved gases are summarized in Appendix A. Included in Appendix A are the tables of oxygen and nitrogen solubilities used in the calculation of per cent of air saturation.

The methods of analysis of dissolved oxygen and nitrogen in fish blood appear in Appendix B.

Limnological investigations

Site of study. Limnological investigations in relation to the smolt migration were begun in 1960 at three stations along the length of the lake. Because results were similar these were reduced to a single station in the north-central part of Cultus Lake (Fig. 1). A second was established on Sweltzer Creek, 200 yd downstream from the lake outlet. In 1960, temperature and dissolved oxygen were determined vertically at irregular intervals during the spring smolt migration. In 1961 these measurements were made every two weeks during the downstream migration and at three- to four-week intervals beyond this time. Dissolved nitrogen was measured vertically every two weeks during the smolt migration and irregularly

after that.

Measurement of temperature. The vertical temperature structure of the lake was measured to within a few feet of the bottom by means of an oceanographic bathythermograph. The bathythermograph was placed in operation at a depth of one foot below the surface and a research thermometer read concurrently at that depth. The smoked slide from the bathythermograph was located in the reading grid on the basis of the thermometer temperature. The instrument was calibrated by the Pacific Oceanographic Group, Nanaimo, B.C. prior to commencement of the study.

Measurement of dissolved gases. Water samples were collected at depths of 0, 5, 10, 15, 20, 25, 30, 40, 50 and 130 ft in one-liter limnological water bottles. The samples were transferred to 300 ml BOD bottles. Dissolved oxygen was fixed on station and the titration performed in the laboratory. Water samples were taken separately for nitrogen analyses, transferred to previously cooled BOD bottles and during transport held at temperatures below that of the coldest water sampled. In this way the possibility of gas leaving solution as a result of warming was avoided. Nitrogen analysis was conducted in the laboratory employing the modification of the Scholander method described in Appendix B. The amount of water required for nitrogen analysis was very small

and oxygen determinations were repeated once on the sample remaining.

Calculations. Oxygen and nitrogen were expressed as mg per liter (Tables III and VI, Figs. 25 and 28). Using the theoretical solubilities as prepared from the absorption coefficients, Tables IX and XI, the per cent saturation was calculated from conditions of atmospheric or surface pressure (Tables IV and VI, Figs. 26 and 29) for oxygen and nitrogen respectively.

If the fish however were to migrate vertically from temperatures at depth to surface, conditions at a rate faster than gaseous equilibration was taking place, then saturation of the fish would be expressed more correctly as percent of saturation at surface temperature and pressure. For this reason oxygen and nitrogen saturations have been expressed as such (Tables V and VI, Figs 27 and 30). Finally, no attempt has been made to calculate hypolimnion saturations to the corresponding periods of air-water equilibrium. As Hutchinson (1957) pointed out, few workers have regarded this refinement as worthwhile.

Measurement of tolerance to pressure

During the downstream migrations of 1959 and 1960, groups of sockeye smolts, numbering 200 or 300 per sample, were tested in the pressure apparatus as described under

decrease in pressure, but the maximum mortality of 1 per cent per week is within the extreme range of the control mortalities.

It should be noted the above series of tests were conducted on smolts migrating from Cultus Lake early in the season (late March to early May). Decompression tests yielded consistently low mortalities during this period, in contrast to the increasing mortalities late in the season (late May to late June), as described below.

Conditions altering resistance to decompression

Seasonal effect. The relatively small proportion of mortalities and injuries resulting from decompression changed suddenly during the course of the season. This change coincided with a temperature of 51°F in Sweltzer Creek, occurring about mid-May and coincident with the termal stratification of Cultus Lake. Among smolts tested migrating from the lake, the mortality increased rapidly with increasing temperature as shown in Fig. 34. The smolts died inside the pressure chamber within a few minutes of being exposed to a sudden reduction in pressure below atmospheric conditions. In the fish examined, death was due to minute gas emboli most commonly lodged in the heart or ventral acrta. This phenomenon was first observed during the studies of the spring of 1959.

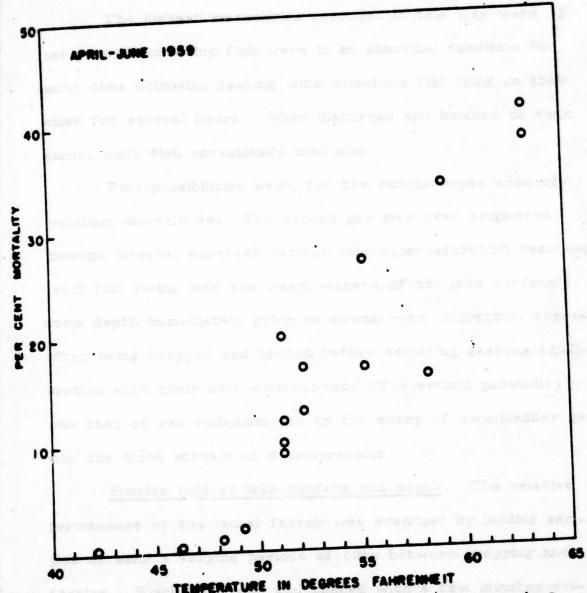


Figure 34. Mortality of sockeye smolts tested at various temperatures during the course of the migration 1959.

Similar series of tests were conducted in 1960 and 1961 yielding comparable results.

The highest mortalities recorded in this way were 35 per cent. Surviving fish were in an abnormal condition for some time following testing with numerous fish lying on their sides for several hours. When disturbed and induced to swim about, such fish occasionally died also.

Two possibilities exist for the sudden appearance of embolism mortalities. The excess gas may have originated through internal supersaturation; this supersaturation resulting from fish rising into the warm waters of the lake surface from depth immediately prior to downstream migration, thereafter being trapped and tested before achieving gaseous equilibration with their new environment. The second possibility was that of gas embolism due to the entry of swimbladder gas into the blood stream on decompression.

Smolts held at lake surface and depth. The relative permanence of the lethal factor was examined by holding samples of smolts varying periods of time between trapping and testing. Smolts trapped and tested with a few minutes evidenced a mortality of 19 per cent. The mortality declined rapidly when smolts were held in warm lake-outlet water prior to testing (Fig. 35). Mortality declined to 2 per cent within 3 days of pre-test holding.

exposure to such water. Similarly, sample of smolts exposure

The gradual loss of the lethal factor described above raised the possibility that it was due to an environmental pressure-conditioning that could be replicated experimentally. In order to test this, 400 smolts were trapped migrating from Cultus Lake in mid-June. One hundred tested immediately showed a mortality of 19 per cent. A second sample of 100 held in warm lake-surface water (Fig. 36) for 3 days evidenced a mortality of 2 per cent. Following 3 days of residence in warm surface water the remaining 200 fish were held at a depth of 40 ft in the lake for 7 days. A sample of 100 of these fish was recovered from depth and tested immediately, resulting in a mortality of 21 per cent. The fourth sample of 100 fish was held an additional 2 days in warm lake-surface water and showed an 11 per cent mortality on testing. The lethal factor thus was lost under conditions of lake-surface residence and recovered with residence at depth.

Increased content of dissolved gases. The gas content and hence saturation change, corresponding to that which smolts would experience migrating from thermocline to surface, was duplicated in the pressure chamber. Groups of smolts exposed to air saturation of 100 to 110 per cent at a pressure of 2 atmos (absolute saturation 50 to 55 per cent) showed a slightly increased mortality on testing following a 24 hr exposure to such water. Similarly, sample of smolts exposed

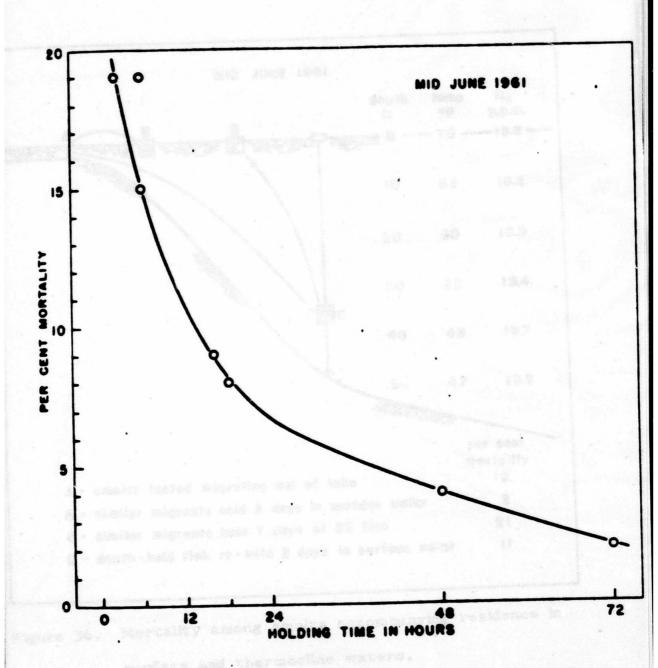


Figure 35. Decline in mortality among groups of smolts held up to 72 hours in Sweltzer Creek before testing,

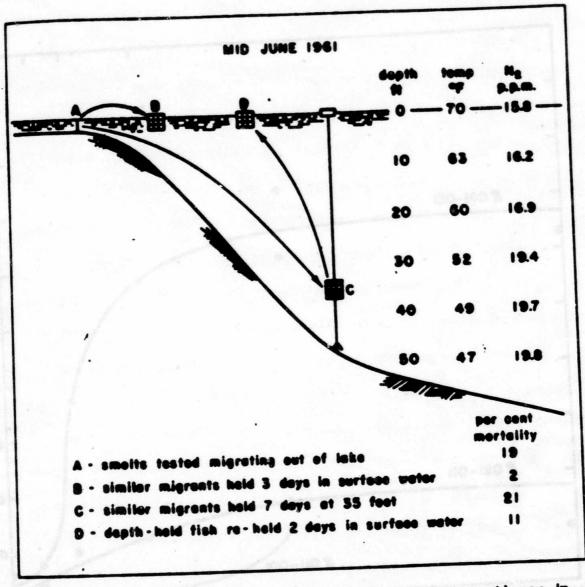


Figure 36. Mortality among smolts accompanying residence in surface and thermocline waters.

of increased air content. Gas tensions expressed .

an per cent of saturation at atmospheric pre-

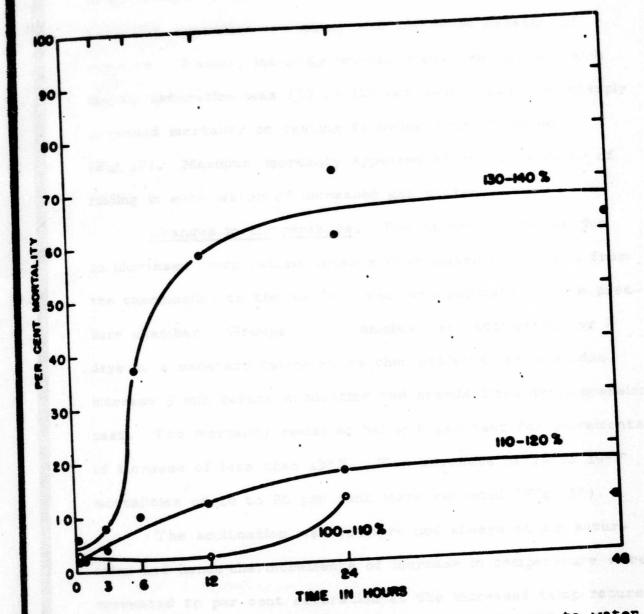


Figure 37. Mortality among smolts following exposure to water of increased air content. Gas tensions expressed as per cent of saturation at atmospheric pressure.

to air saturation of 110 to 120 per cent evidenced a gradually increasing mortality on testing with increased duration of exposure. Finally, markedly increased gas tensions in which the air saturation was 130 to 140 per cent resulted in sharply increased mortality on testing following 3 hr of exposure (Fig. 37). Maximum mortality appeared after 12 to 24 hr of holding in such water of increased gas content.

Changes in temperature. The saturation change due to increased temperature accompanying movement upward from the thermocline to the surface also was duplicated in the pressure chamber. Groups of 100 smolts were acclimated for 2 days to a constant temperature then subjected to a sudden increase 5 min before conducting the standardized decompression test. The mortality remained below 6 per cent for increments of increase of less than 13°F. For increases of 14 to 19°F mortalities of 10 to 20 per cent were recorded (Fig. 38).

The acclimation waters were not always at air saturation and hence the increments of increase in temperature were corrected to per cent saturation at the increased temperature. No clear trend is apparent (Fig. 39) between mortality on testing and temperature-induced increase in saturation.

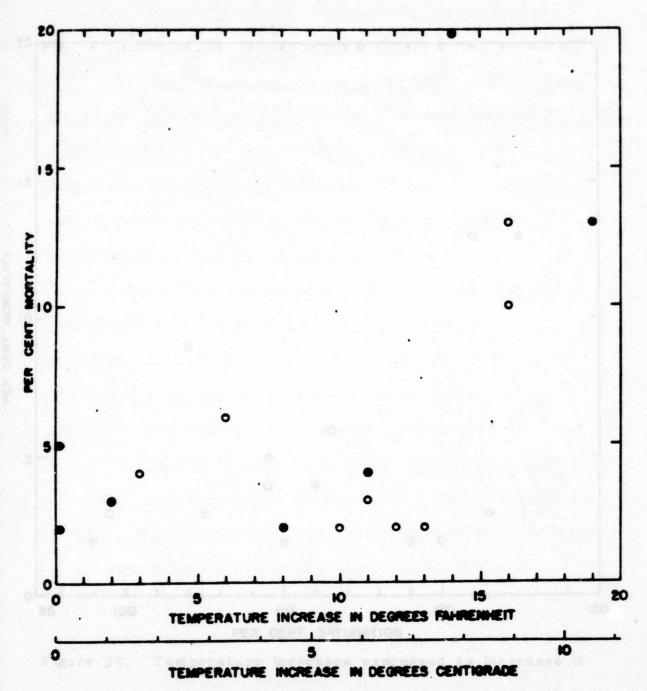


Figure 38. Mortality on decompression following sudden increase in temperature. Open circles increments above 45°F, solid circles above 55°F.

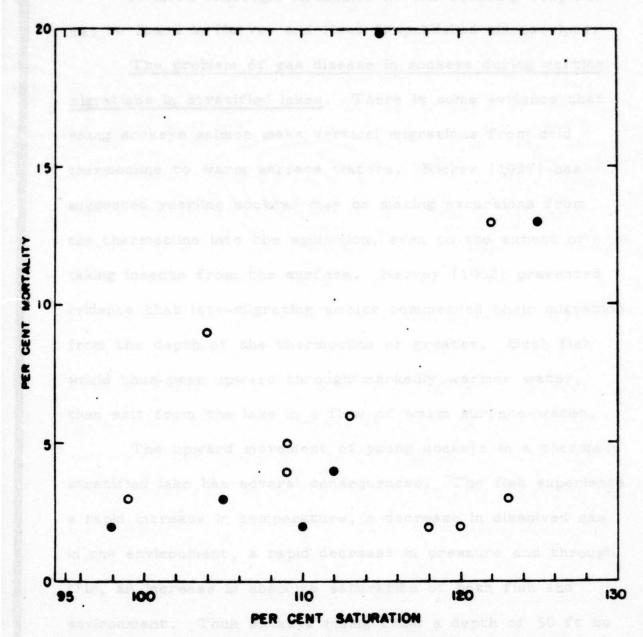


Figure 39. Temperature increases expressed as increases in per cent saturation.

A more thorough discussion of the sounding response may be found in Harvey and Hoar (unpublished manuscript).

The problem of gas disease in sockeye during vertical migrations in stratified lakes. There is some evidence that young sockeye salmon make vertical migrations from cold thermocline to warm surface waters. Ricker (1937) has suggested yearling sockeye may be making excursions from the thermocline into the epilimnion, even to the extent of taking insects from the surface. Harvey (1962) presented evidence that late-migrating smolts commenced their migration from the depth of the thermocline or greater. Such fish would thus pass upward through markedly warmer water, then exit from the lake in a flow of warm surface-water.

The upward movement of young sockeye in a thermally stratified lake has several consequences. The fish experience a rapid increase in temperature, a decrease in dissolved gas in the environment, a rapid decrease in pressure and through this, an increase in absolute saturation of both fish and environment. Thus sockeye rising from a depth of 50 ft to surface conditions in August of 1961 would experience an increase in temperature from 48 to 73°F (Fig. 24), an increase of 25 Fahrenheit degrees. Based on Brett (1952) a temperature of 73°F may be slowly lethal to sockeye. The more immediate consequences would include a sharply increased

saturation of nitrogen internally. From the nitrogen data of July, 1961, fish arriving at the surface would have an internal saturation of nitrogen approaching 136 per cent (Fig. 30). Absolute saturation would not exceed 100 per cent until the fish were within approximately 12 ft of the surface. Thereafter absolute saturation would increase rapidly (Fig. 46) toward 136 per cent. As described previously, the possible consequence of this decompression, plus saturation increase, is the "bends". This is obviated through the rapid rate of nitrogen equilibration between fish and environment (Fig. 40 and 41). This is not regarded, of course, as a unique adaptation of sockeye salmon. Rapid equilibration of dissolved nitrogen is a process of passive diffusion and thus should be common to fish in general. It does explain, however, how pelagic fishes such as sockeye are able to pass upward through a thermally-stratified body of water without developing gas disease.

The rapid clearance of dissolved nitrogen described above does not protect fish from developing gas disease in supersaturated water. Surface water saturations in excess of 100 per cent are relatively common in lakes during the spring period when water temperature is rising more quickly than gas is being lost. Ricker (1937) found surface saturations of 104 per cent during spring and Harvey (1962)

measured oxygen saturations of 110 and nitrogen of 107 per cent. Saturations as low as these are not usually lethal to adult fish (Harvey and Smith, 1961) although sockeye alevins are prone to gas disease at low levels of supersaturation (Harvey and Cooper, 1962). Foerster (1925) reported oxygen saturation as high as 127 per cent (133 per cent calculated to the theoretical solubilities, Handbook of Chemistry and Physics) for Cultus Lake in August, 1923. Such saturations would approach lethal conditions for surface dwelling fish. These high saturations in the epilimnion occurred the day following intense mixing by storm action and the oxygen values presented by Foerster are considerably higher than would be expected following air-equilibration.

A less common but more serious form of lake-surface supersaturation is that resulting from photosynthesis.

Woodbury (1941) measured oxygen saturations on the surface of Lake Waubesha (Wisconsin) ranging from 171 to 306 per cent and attributed to this the deaths of a variety of fishes. In the present study of dissolved gases in Cultus Lake, oxygen supersaturation through photosynthesis was limited to the depths of 15 to 50 ft. The absolute saturation remained below 100 per cent and hence mortalities such as described by Woodbury could not occur.