THE EFFECT OF INTERTIDAL EXPOSURE ON THE SURVIVAL AND EMBRYONIC DEVELOPMENT OF PACIFIC HERRING SPAWN

by

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ABSTRACT

Eggs of Pacific herring were exposed to air for different periods of time in simulation of tidal effects on spawn deposits at varying beach heights. The maximum exposure range was 2/3 of a 24 hour day corresponding roughly to the exposure of eggs at 4 meters above mean low tide on the British Columbia coast. Egg size, spawning fish length, and egg clump size were examined as secondary factors modifying the effect of exposure. Incubation time dropped from 19 to 18 days with only two 2-hour periods of exposure per day and thereafter fell slowly. It is suggested that oxygen deprivation triggered a hatching response for the initial drop, whereas the gradual decrease was due to a higher air temperature increasing metabolism. Hatching mortality rose steadily from an unexposed 13% to 31% at maximum exposure time, with significantly higher contributions from eggs of smaller fish and smaller egg clumps. Larval length at hatching for the unexposed eggs was 7.7 mm.; lengths for all degrees of exposure were similar (7% less than for no exposure). Larval weight (body plus yolk) remained relatively constant (0.099 mg.) until the longest exposure period when it dropped to 0.087 mg. This decrease coincided with similar sharp trends in incubation time and hatching mortality, and suggests a "critical point" near the upper experimental range of exposure, above which eggs stand little chance of normal development or survival. Beach

surveys to note possible egg size stratification, although suggesting the deposition of larger eggs at the top levels, proved inconclusive, but point up the possibility that a heavy fishing pressure which reduces mean fish size might detrimentally affect potential stock recruitment via the intertidal exposure effect on the spawn.

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THE EFFECT OF INTERTIDAL EXPOSURE ON THE SURVIVAL AND EMBRYONIC DEVELOPMENT OF PACIFIC HERRING SPAWN

INTRODUCTION

The eggs of the Pacific herring (Clupea pallasii Val.) are spawned in and below the intertidal zone. Due to their adhesive nature, they become attached to certain forms of seaweed and are essentially immobile. For this reason most of them are subjected to regular periods of exposure and submergence. Such conditions cause considerable fluctuation in the environment of the eggs and may affect their survival and development. The effect of this fluctuation is ostensibly directly related to the height up the beach that the eggs are laid, and thus, the amount of time they are exposed.

Within the spawning zone a variety of egg sizes can be expected because each spawner produces a range of egg sizes (for example, for Atlantic herring, Clupea harengus, Hempel and Blaxter, 1967). In addition, every reproductive stock comprises a variety of individuals differing in length, weight, and age, and several studies (Rannak, 1958; Blaxter and Hempel, 1963) have shown that mean egg size is a function of size and maturity. The adhesiveness of herring eggs also causes the formation of clumps when exposed to sea water. Such clumps are of differing thickness and vary in egg size and number. Hence, egg size, fish size, and clump size all

have some bearing on the possible effects of environmental fluctuation resulting from exposure.

The characteristics most notably affected are incubation time, hatching mortality, and larval length and weight at hatching. In this regard, Blaxter and Hempel (1963) noted that egg size did not affect incubation time, whereas hatching mortality was found by other studies (Runnstrom, 1941; McMynn and Hoar, 1953) to be directly related to egg number. The larvae have been shown to be affected by both egg and fish sizes. For instance, Toom (1958) has demonstrated that larval size is directly related to egg size, and Cushing and Bridger (1966) have noted that larvae from first spawners are less viable than those from larger fish. In addition, it has also been shown (Nagasaki, 1958) that fecundity is directly related to spawner size.

Because fishing intensity reduced the mean size, age, and numbers of spawners of British Columbia stocks of herring (Taylor, 1963) and North Sea herring, Clupea harengus (Cushing and Bridger, 1966), then it must follow that mean egg size also decreased. There would be fewer, smaller eggs produced than in former years, and with a lesser chance of larval survival. The survival advantage accruing to a fish stock due to the presence of larger eggs and larvae has been pointed out by Marshall (1953). If environmental factors operating in the spawning zone are more detrimental to smaller eggs or the eggs from smaller fish, then there could be serious repercussions on recruitment potential,

i.e. the number of immature fish available to enter the reproductive population.

Previous work on herring egg development has been concerned with conditions for submerged eggs. This study sought to examine incubation time, hatching mortality, and larval length and weight at hatching in relation to varying degrees of exposure. The laboratory experiment was conducted and analyzed using as additional variables the effects of egg size, fish size, and clump size. A beach survey was also undertaken to note possible egg size stratification.

MATERIALS AND METHODS

The eggs used in this study were taken from spawning Pacific herring of the Lower East Coast stock (inner southern Vancouver Island region) of British Columbia, and the laboratory experiment was done at the Fisheries Research Board of Canada's Biological Station in Nanaimo, B.C.

Spawner Characteristics Analyses

Forty female spawners were used to determine if egg size was related to fish size and maturity. The first 29 were taken by beach seine and held alive in large, well-flushed holding tanks for one week prior to use. The other 11 were obtained dead from local trawlers within 6 hours of capture and used immediately. After stripping the experimental eggs, the spawners were measured for standard length (tip of snout to end of vertebral column) and three or more scales plus

both otoliths were taken for age determinations. The gonads were then removed and the spawner wet weight recorded. The fish were then tagged and preserved in 5% formalin for possible future reference.

The age of each spawner was determined by reading the scales from the areas above and below the lateral line between the rear of the gill cover and the front of the dorsal fin (Tester, 1937). These were cleaned, dyed, and mounted on a glass slide. The 11 trawl caught fish had very few scales, and hence, any scale was used. These ages were checked with the otoliths which had been cleaned and preserved in 5% formalin.

Samples of each spawners' gonads were immediately preserved in 5% formalin when removed. This succeeded in hardening and separating the eggs from each other and the ovarian tissue so that they could be easily counted. Subsequently, the gonad samples were broken up to release the eggs which were then thoroughly washed in fresh water. Five samples of 100 eggs were taken from each of two fish and put in a drying oven for 24 hours at 50° Centrigrade[1]. Several prior tests confirmed that there were no effects of position of samples in the dryer, the dryer handling capacity, the estimation of residue weight, and the length of drying time. The samples were individually removed from the oven, weighed on a Cenco electrical balance to the nearest 0.1 mg., weighed

[1] These conditions are the same as those used by Blaxter and Hempel (1963).

again as a check, and then discarded.

Exposure Laboratory Experiment

Five tanks (see Appendix A) simulated conditions at different beach levels (Figure 1) ranging from the control (0) which was continuously submerged, through 2, 4, 6, and 8 hours of exposure twice per day. These exposure times simulate a fixed tidal cycle of roughly 2 meters amplitude (not found in this area, but necessary as an experimental feature). Each tank contained forty incubators, and all were kept in a small temperature-controlled room under regulated conditions (Table 1).

From every female spawner approximately 100 eggs[2] were stripped into each of five separate incubators. In this operation, clumping of the eggs was unavoidable, but an attempt was made to produce the same clump form in all incubators. The incubators were then simultaneously placed into a glass fertilization tray containing a sperm solution and allowed to stand for 60 seconds. The sperm solution was prepared using 500 ml. of sea water and sufficient sperm from 2 or 3 males (to ensure viable sperm) to turn the water opaque. The incubators were transferred to another tray and gently flushed with fresh sea water to prevent polyspermy and remove any excess organic matter which might decay in the tanks. They were then transferred to their respective exposure tanks and kept submerged for 12 hours before the

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[2] The small size and adhesiveness of the eggs prevented counting. In fact, it was found that the mean was 132 eggs; standard deviation ± 43.

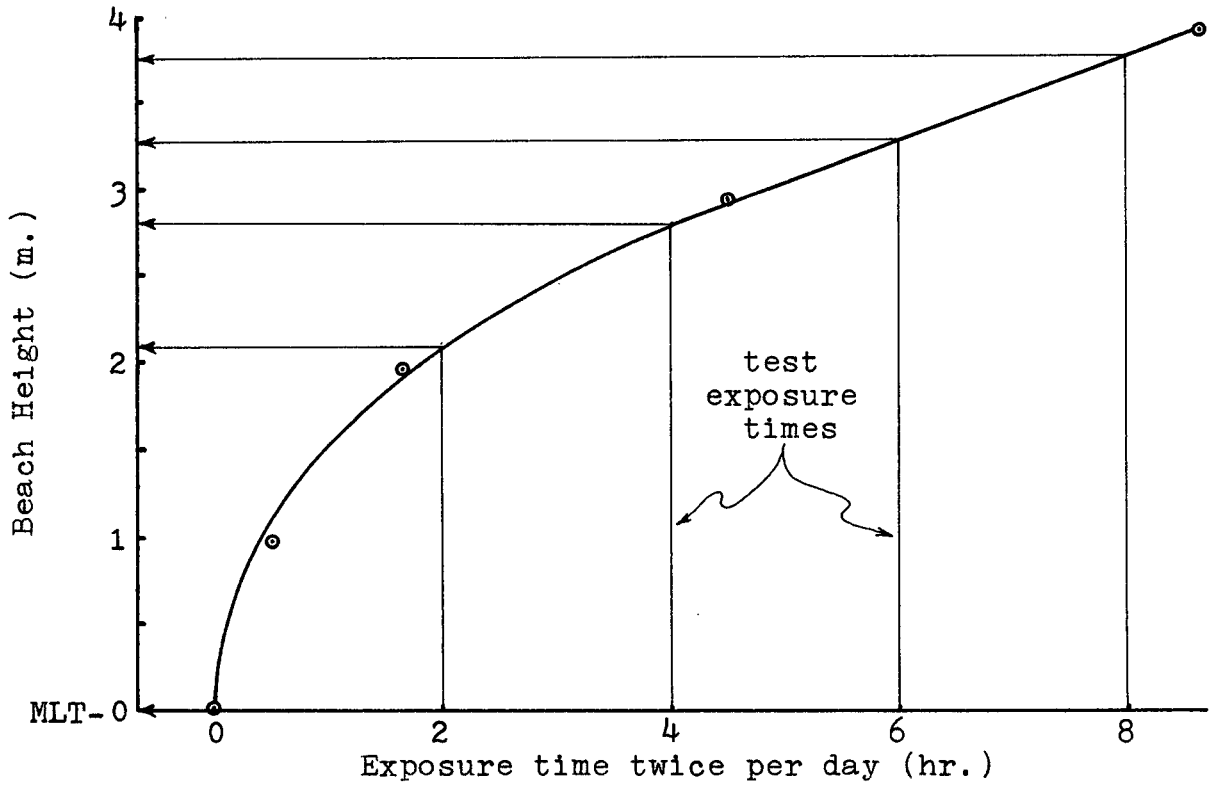

Figure 1: Relationship of beach height to exposure time. Data for Vancouver, B.C., (March, 1970) meaned from Straits Towing calendar.

Table 1: Summary of experimental conditions.

Factor	Mean	Standard Dev.(SD)
(1) Light:		
(a) Day length	13 hours	--
(b) Intensity	60 watt bulb at 75 cm. above each tank	--
(2) Air:		
(a) Temperature	11.7° C	±0.6°
(b) Relative humidity	65%	±5%
(3) Sea Water:		
(a) Temperature	7.8° C	±0.4°
(b) Oxygen	6.5 ml./l.	--
(c) Flow rate	55ml. per min. per incubator	±3 ml.
(d) Depth	5 cm.	--

experimental conditions were initiated.

The artificial environment (summarized in Table I) was similar to that recorded on the beach surveys during the experimental incubation period. An attempt was made to maintain the laboratory temperature at 12° C. A maximum-minimum thermometer checked daily gave a mean of 11.7° C; SD ± 0.6°. The mean relative humidity determined by sling psychrometer was 65%; SD ± 5%. The day length was regulated by time clock and set at thirteen hours (9 am to 10 pm) so that one exposure period was in the light and the other in darkness. The light source was a single 60-watt incandescent bulb per tank. Each bulb had a white porcelain rear reflector and was suspended 75 cm. above the level of the eggs in the center of the tank. The sea water originated from the bottom of the local bay and ran continuously through the tanks at a mean rate of 55 ml. per minute per incubator; SD ± 3 ml. When the tanks were full, all the eggs were suspended at an equal depth of 5 cm. Several oxygen determinations were carried out on the inlet and outlet waters by the Improved Winkler Method and all came to approximately 6.5 ml. per l. This would suggest that with plentiful oxygen in the inlet waters and the open circulatory system, oxygen was not a limiting factor[3]. Regular water temperature measurements yielded a mean of 7.8° C; SD ± 0.4°. This resulted in an air/water temperature differential of 4° C.

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[3] This was verified by a tank position analysis of the results using Dr. N. Gilbert's program. However, because the system was open and appropriate water sampling proved difficult, I would question the validity of these determinations, although not the conclusions drawn.

After 15 days the larvae began to hatch. Throughout the hatching period collection was done immediately prior to exposure (10 am and 10 pm) of the eggs[4]. Upon removal by large-mouth pipette, they were immobilized in a 1:50,000 solution of MS222 (Tricaine Methanesulfonate). This treatment caused the larvae to straighten out and stiffen. They were then preserved in 5% formalin. When larval emergence ceased, the incubators were cleaned out and the dead eggs counted[5]. From this data the incubation time (from fertilization to 50% hatch) and mortality were determined. At convenient times during and after the experiment the larvae were counted and the lengths (from tip of snout to end of tail) of all measurable larvae were determined by graduated microscopic eyepiece. This work took some 3 months, during which time a companion shrinkage test was run. When the measuring was completed, the test was terminated and a table of daily shrinkage correction values was computed and used to correct the mean larval length obtained for each incubator. The shrinkage was found to be only 4.2% over the entire three month measuring period. Once the larvae from each incubator had been counted and measured, they were all put into one vial. When all the incubators had been processed in this way, ten vials (incubators) at a time were taken, the larvae recounted, washed thoroughly in fresh water, and dried and weighed in

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[4] Larvae did not hatch out during the exposure periods.

[5] The dead larvae were in many stages of development.

the same manner as for the spawner egg weights[6,7].

Egg Size Distribution Beach Surveys

A number of recent spawning sites were examined during daytime low tides. For purposes of comparison, the determination of beach height was based on the datum established by the sea level at the exact time of low tide (as indicated in the Canadian Tide and Current Tables - #5, using Point Atkinson as a reference). The sea level at this time was used as sample area M, the middle region of five beach levels sampled on each survey. The bottom sample (B) was then taken in as great a depth as practical (about 1 meter), and another sample (L-low) taken halfway between these two (about 50 cm.). The actual sample depths were determined with a graduated staff. Two further samples were taken above M -- T (top), as high as the spawn was deposited, and H (high), halfway between T and M. The heights of these were determined by clinometer and tape measure. The samples, taken in 500 ml. jars, included as many eggs and the seaweed they adhered to as possible.

Environmental conditions were also recorded at the spawning sites. Among these were the air and sea water

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6 Fixation in formalin over a three month period was shown to have negligible effects on larval weight (-0.4%) and egg weight (-0.2%) by Blaxter and Hempel (1966).

7 Larval weight in this experiment means the total weight of the body and the yolk sac.

temperature, and relative humidity as determined by sling psychrometer. These data were used as a guide for the experimental regime.

Upon returning to the lab, the age of the spawn was estimated (Outram, 1955), the samples were preserved in 5% formalin, and the beach level for each sample relative to mean low tide was calculated. Later, the eggs were separated from the seaweed by transfer to a one normal KOH solution which was then heated to 30° C. and allowed to stand for 2 hours[8]. The eggs and seaweed were then transferred to a 5% formalin solution again to harden for 24 hours before the seaweed was removed and discarded. This treatment not only loosened the eggs from the seaweed, but also from each other. The eggs were then thoroughly washed in fresh water, and ten 100-egg samples were taken from each beach level for drying and weighing as per the spawner egg weight determinations.

RESULTS

Effects of Exposure

Eggs from six of the trawl caught fish had 100% mortality in all tanks. The data from these incubators was discarded on the grounds that the eggs were probably already disintegrating when used. Data for one spawner from the beach seine group was discarded for the same reason. The net

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[8] Procedure by word-of-mouth from herring researchers at the Biological Station, Nanaimo, but slightly altered.

result was data from 33 spawners. On consideration, the experimental data was divided into three groups -- noted as small, medium, and large in the analyses (see Appendix D).

The data were initially analysed in total to note the general trend of each characteristic in relation to increased exposure time. They were then treated separately according to their groupings as noted above.

Egg size as determined from the preserved gonads was first examined for possible differences between groups. It was found of significance only in larval length and weight (see Appendix E). The second analysis examined the effects of fish length. Here hatching mortality and larval weight were shown to be affected. Since fish length and weight are so highly correlated (see Appendix C), the analysis was not repeated for weight. The effect of age was not examined as the spawners were predominantly 3-year old fish, with only a few 4 and 5-year olds. Because the egg number (clump size) was different for each incubator, a third test was run to see if this had any effect. It proved negligible for all characteristics but hatching mortality. The mean group values for these three analyses are given in Table II.

Table II: Group means and standard deviations in the analyses.

Grouping	Small	Medium	Large
(1) Egg size (mg.)	0.243±0.015	0.271±0.005	0.300±0.015
(2) Fish length (mm.)	199±5	211±4	223±6
(3) Clump Size (no.)	89±17	130±12	175±29

Another analysis was performed to determine if there was any interaction among egg size, fish length, and clump size. This was found to be non-significant in most cases for all factors and hence will not be referred to further.

These various analyses are discussed together for each of the variables examined.

Incubation Time

The relationship of incubation time to exposure time is shown in Figure 2. The control or unexposed incubators had a slightly greater than 19-day incubation period. The first exposure period (2 hours) showed an abrupt decrease of close to one full day ($p < .01$). Thereafter, there is only a gradual decrease through the remaining exposure periods, but the total decrease (from 2 to 8 hours) of 0.4 days is significant ($p = .01$-$.05$).

Hatching Mortality

As expected, the hatching mortality showed a continuous increase with increasing exposure time (Figure 3), rising from 13% in the control to 31% in the 8-hour exposure period. For the total data, this is significant ($p < .01$)[9].

Eggs from smaller fish had a higher mortality (Figure 4), but the effect was not statistically significant ($p = .05$-$.10$). Analysis of this small fish data did not indicate which egg

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[9] All hatching mortality statistical tests were done on arcsin transformation of the percentage data.

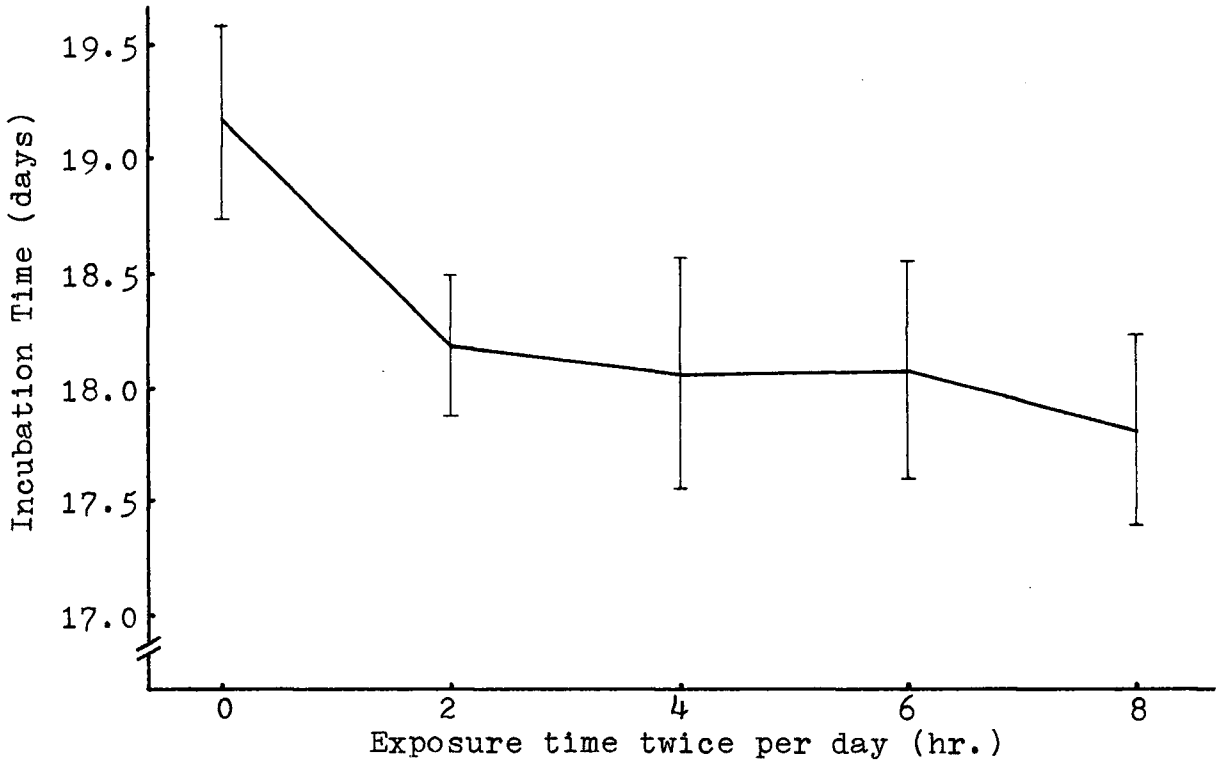

Figure 2: Relationship of incubation time to exposure time for total data.

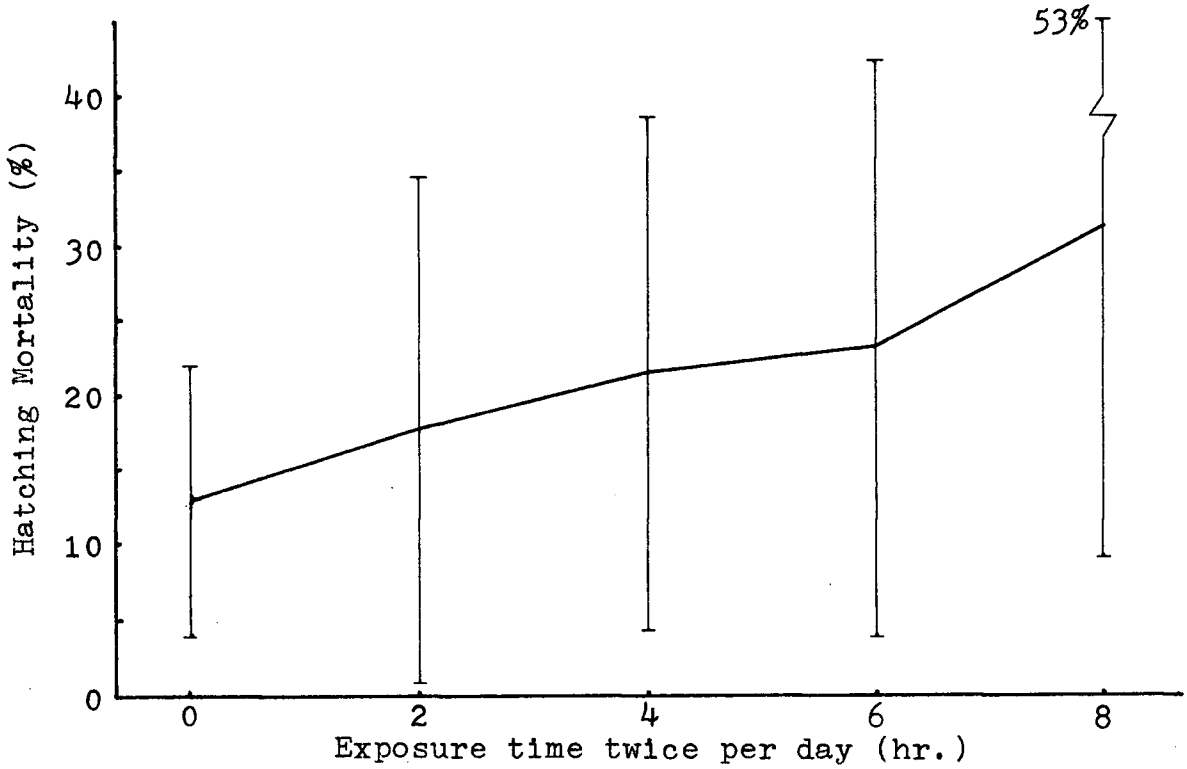

Figure 3: Relationship of hatching mortality to exposure time for total data.

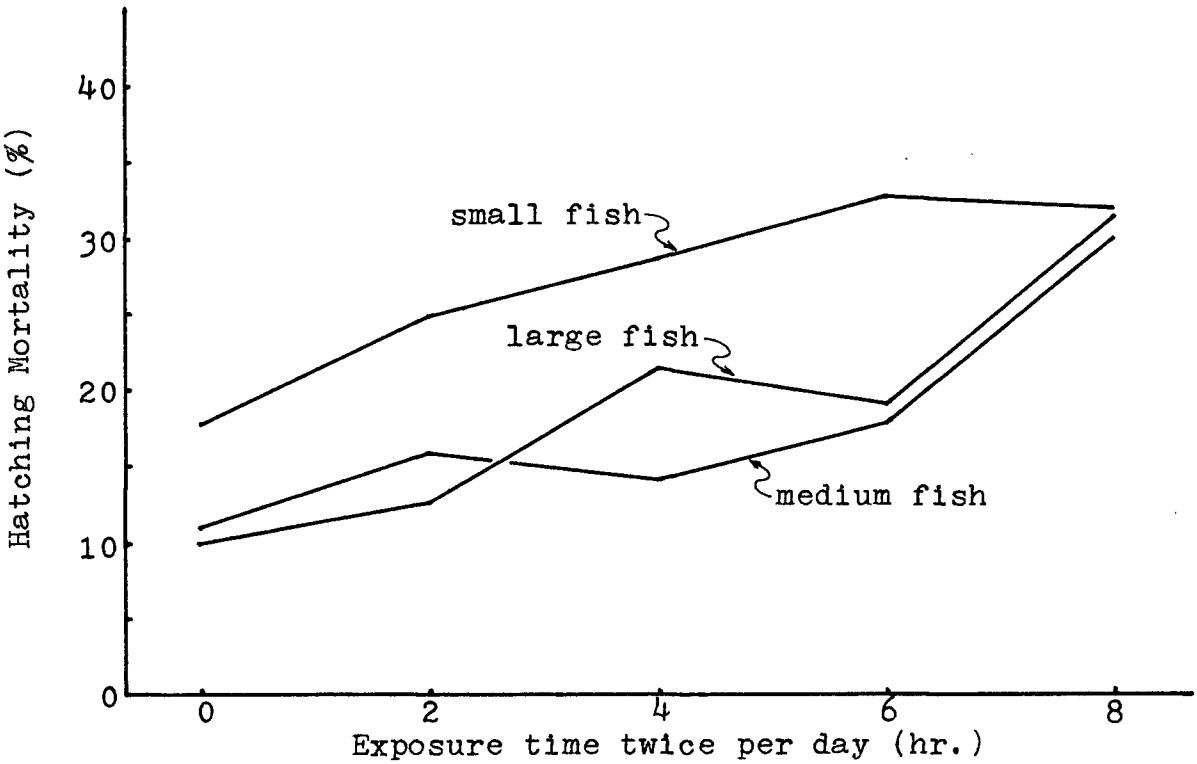

Figure 4: Fish length effects in the relationship between hatching mortality and exposure time.

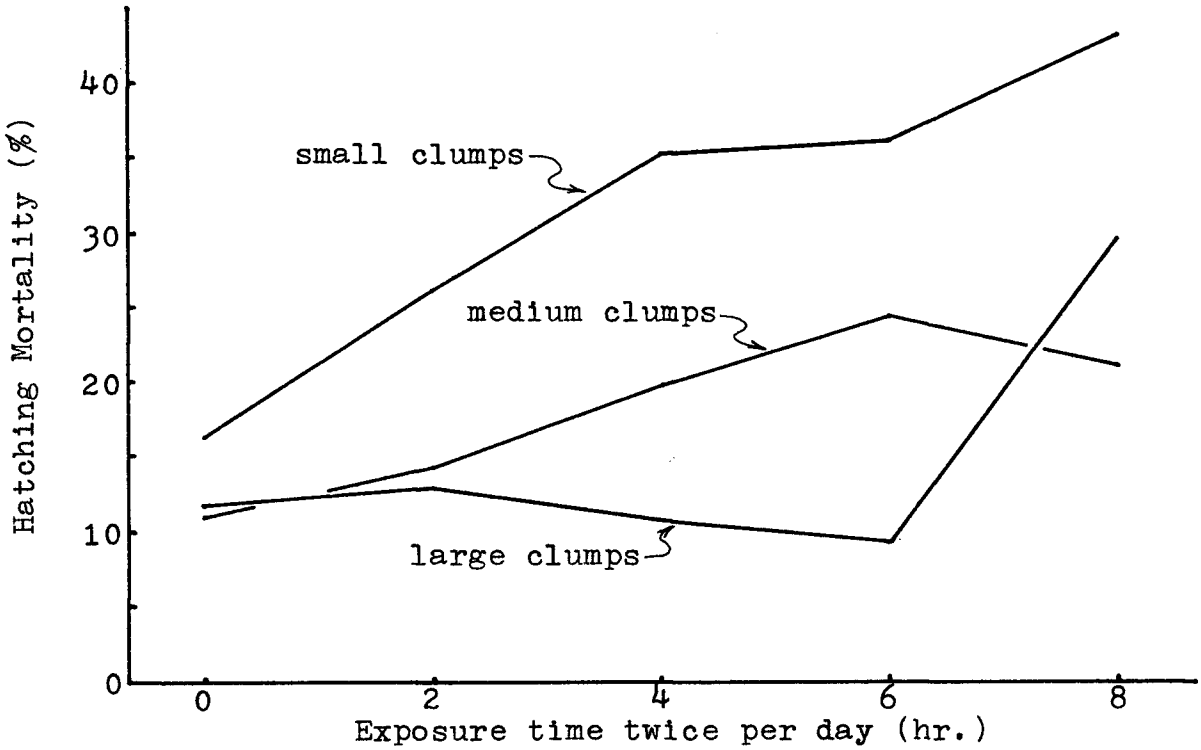

Figure 5: Clump size effects in the relationship between hatching mortality and exposure time.

sizes within the group might be suffering greater mortality. Smaller egg clumps also had a significantly higher mortality ($p < .01$ for several exposure periods) than larger egg clumps (Figure 5).

Larval Length

Larval length at hatching in relation to the exposure time (Figure 6) follows closely the pattern of incubation time. The initial drop between the control and the 2-hour exposure periods from 7.7 mm. to 7.2 mm. is significant ($p < .01$). From exposure periods of 2 to 8 hours there was no further decrease.

Larvae were shorter (Figure 7) from smaller eggs, but this difference was not significant ($p = .05$-$.10$).

Larval Weight

The relationship of larval weight to exposure time (Figure 8) follows a concave curve, rising from 0.092 mg. to a high of 0.099 mg. at the 4-hour period, and falling back to 0.087 mg. by the 8-hour period. None of the differences was statistically significant.

For egg size groups (Figure 9) there was a pronounced ($p < .01$) relationship to larval weight. Fish length had similar effects (not shown), except that they were not significant ($p = .05$-$.10$).

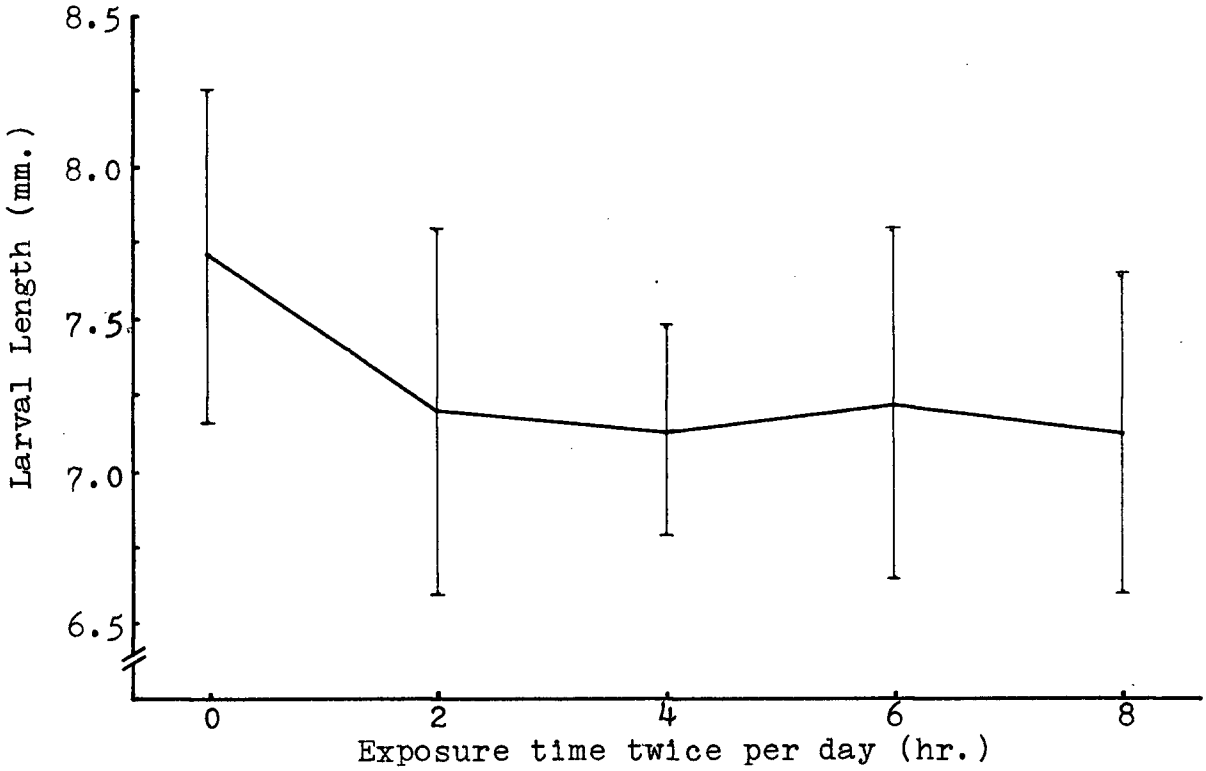

Figure 6: Relationship of larval length to exposure time for total data.

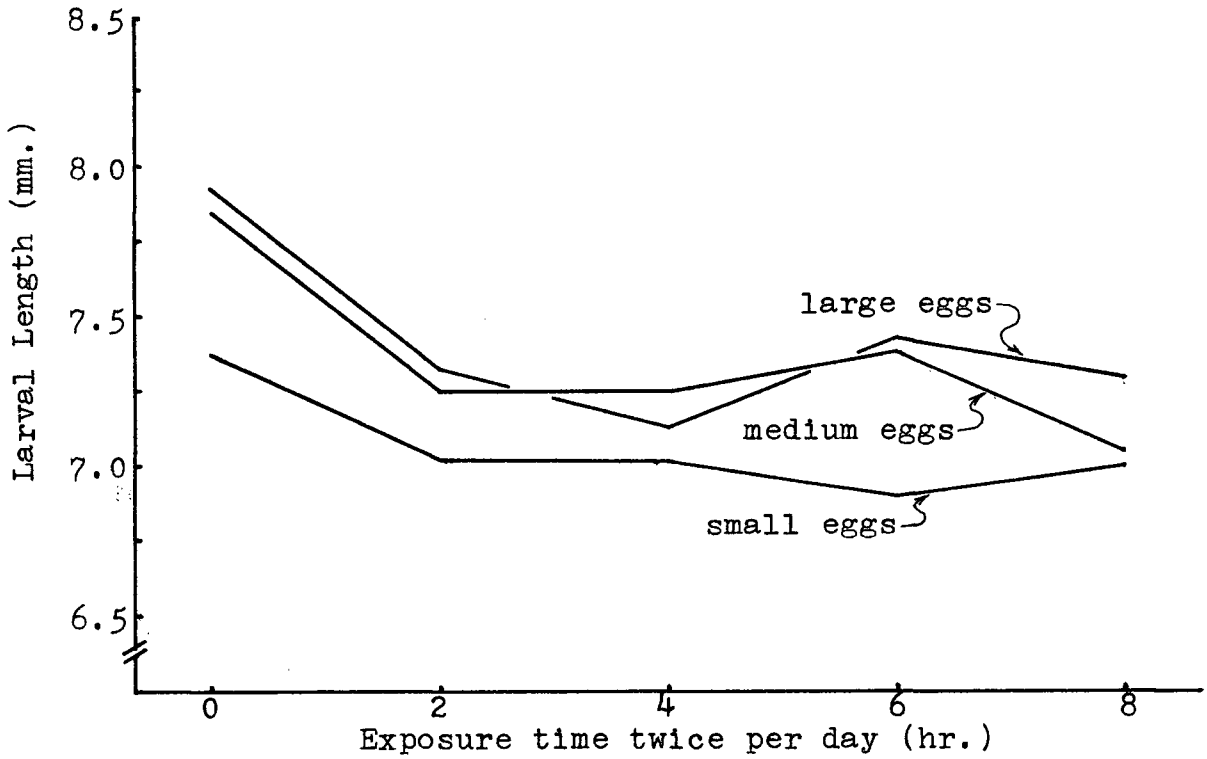

Figure 7: Egg size effects in the relationship between larval length and exposure time.

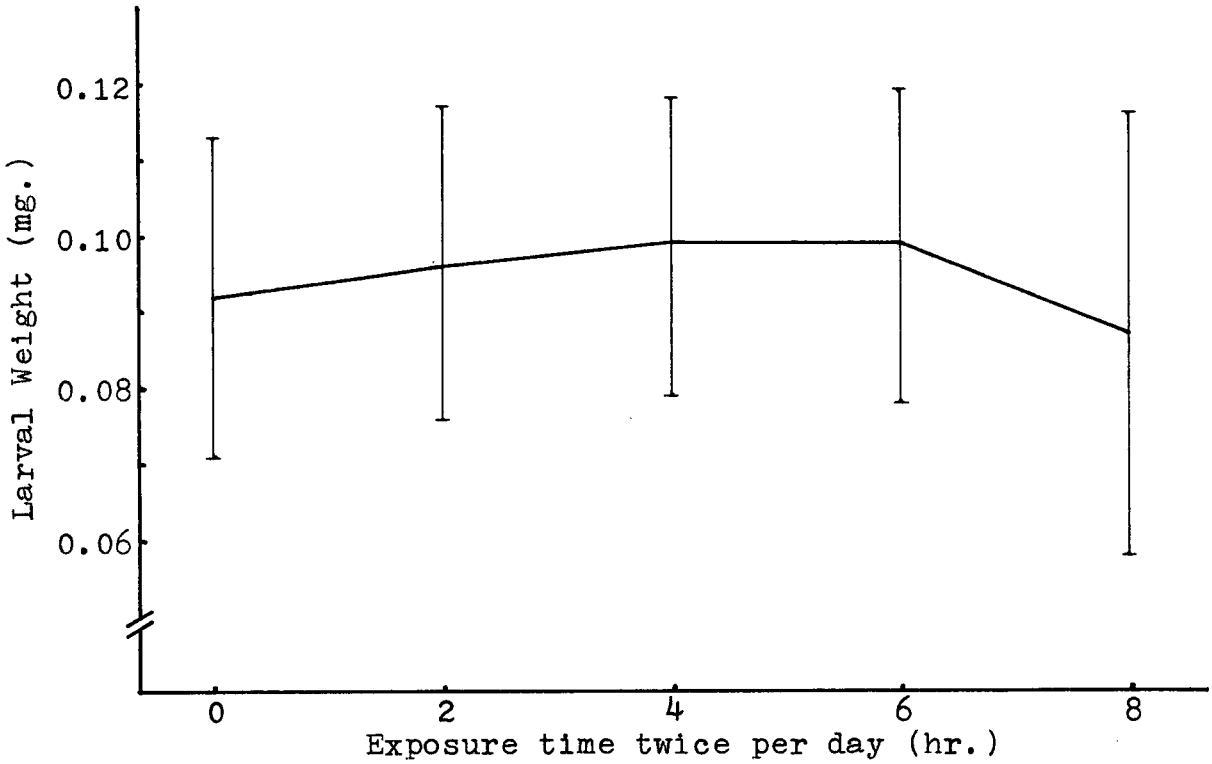

Figure 8: Relationship of larval weight to exposure time for total data.

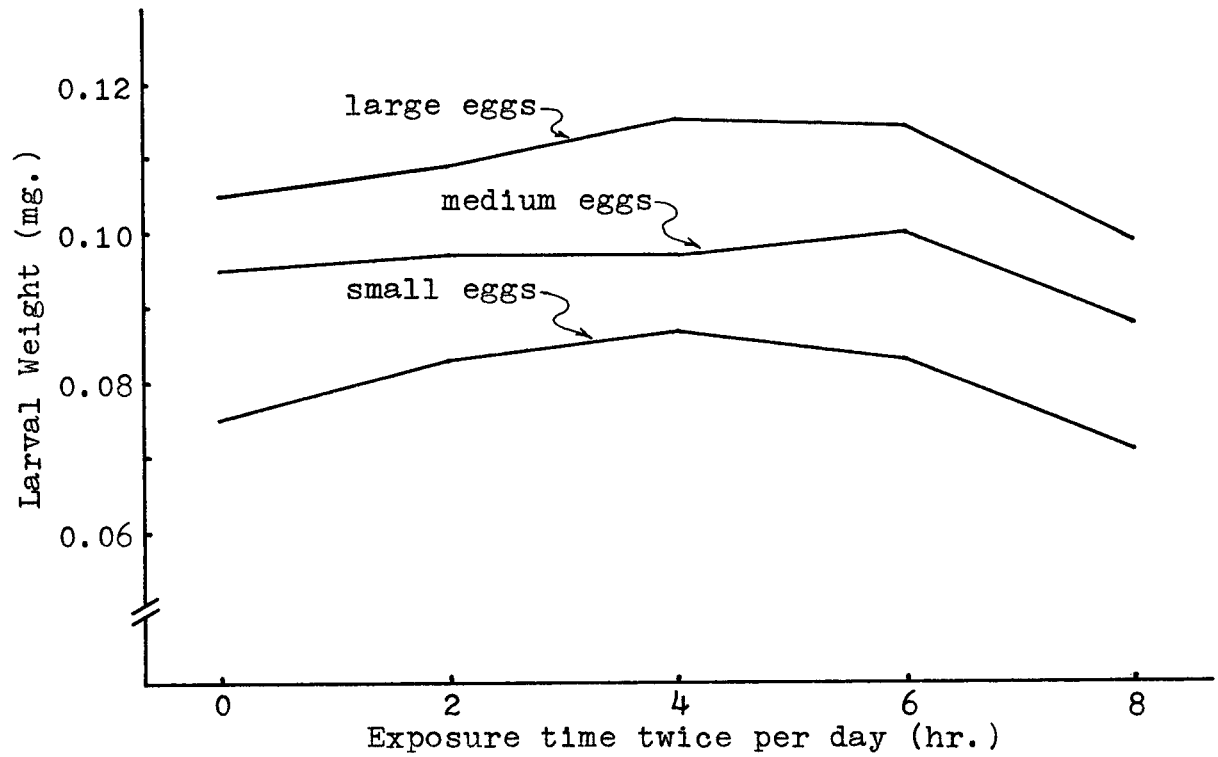

Figure 9: Egg size effects in the relationship between larval weight and exposure time.

Beach Stratification

The beach survey done at the time of spawning (Figure 10) showed an increase in egg weight with beach height. This trend was significant ($p < .01$). By mid-incubation (Figure 11) the relationship had disappeared, becoming convexly curvilinear with no significant differences between beach levels. Time-sequenced observations consisting of an early (4 days) and a late (16 days - hatching) stage for a single egg mass was done to clarify this problem (Figure 12). However, the 16-day sample was taken lower down on the beach and hatched en route to the laboratory. The larval weights obtained were assumed to be a reflection of their former egg weights and were compared with the 4-day sample on a relative basis. No significant trends were indicated.

DISCUSSION

The spawners used in this experiment were essentially all recently mature herring. As such, the results found are only truly applicable to the spawn of these young fish. The exposure time imposed on the spawn ranged up to 2/3 of a day, and reduced incubation time, increased hatching mortality, and reduced larval length and weight. Possible explanations for some of these patterns are presented below.

Incubation time dropped markedly when the eggs were first exposed, but thereafter decreased gradually with increased exposure time. The drop with only two 2-hour exposure periods per day may be due to oxygen deprivation. In this regard,

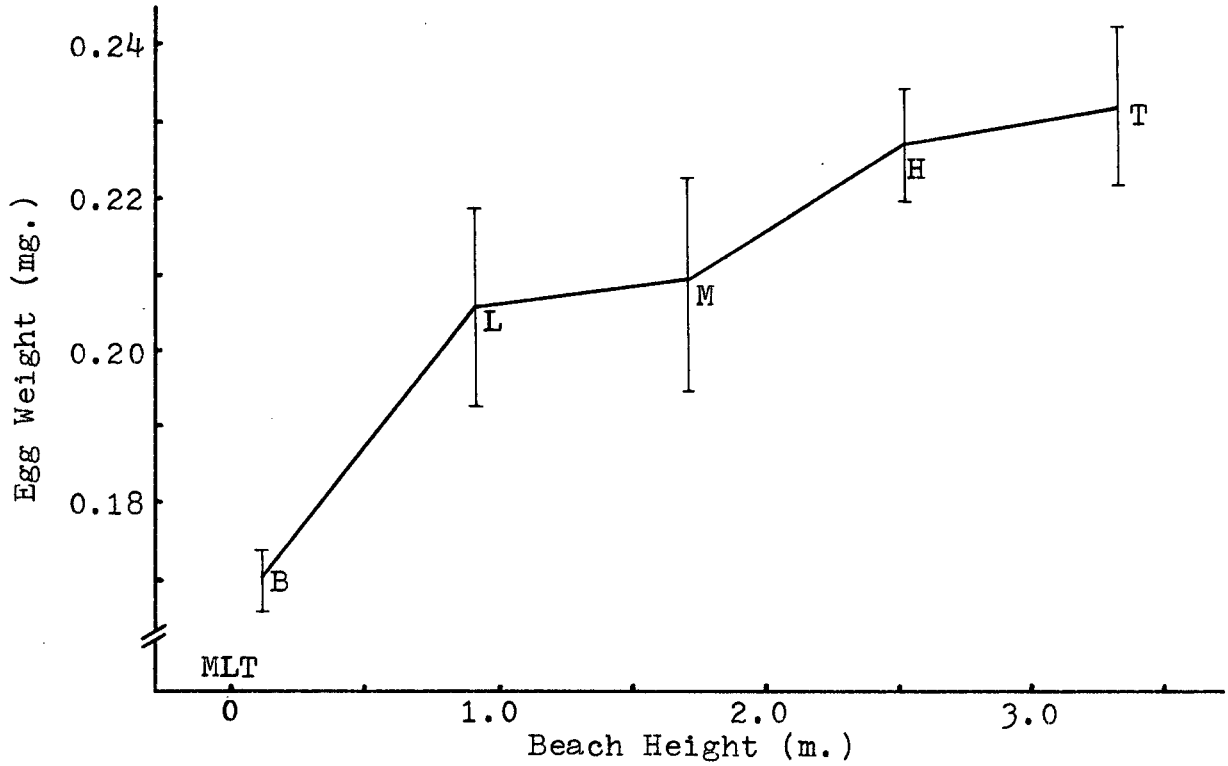

Figure 10: Relationship of egg size to beach height at spawning, Bedwell Bay, April 20, 1970.

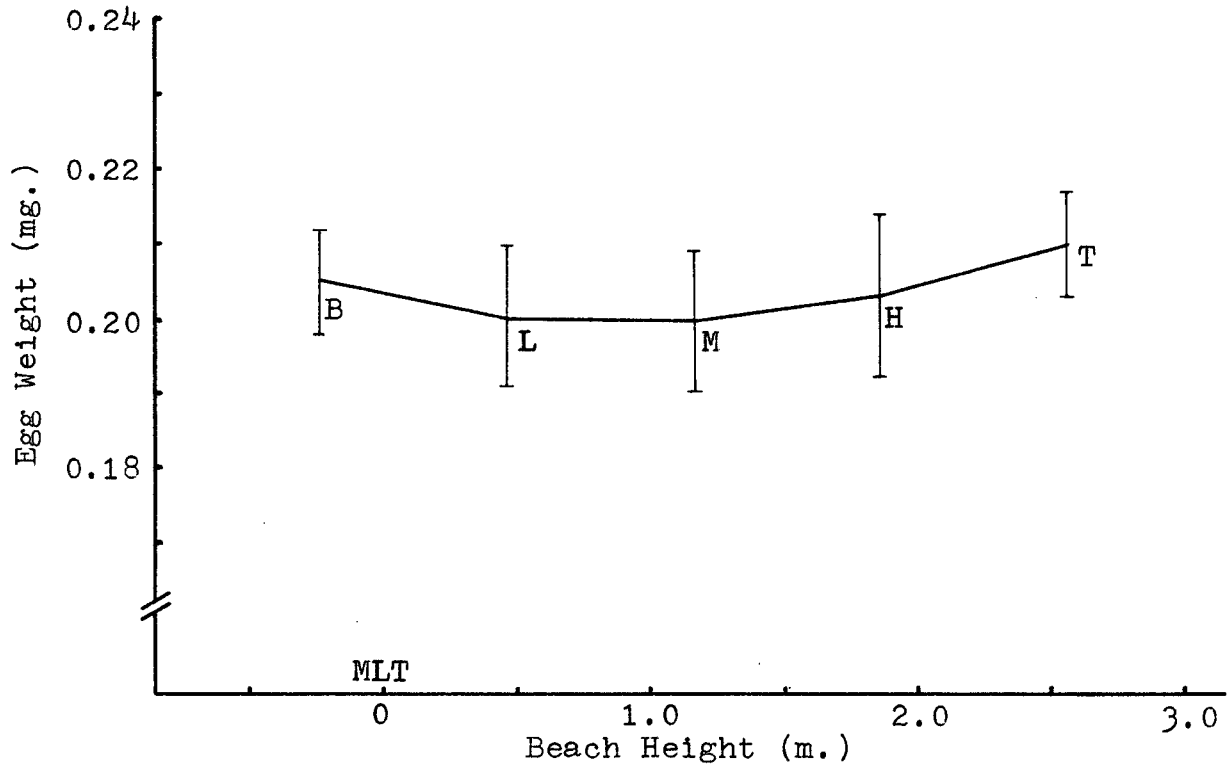

Figure 11: Relationship of egg size to beach height at mid-incubation (8 days), Nanoose Bay, March 27, 1970.

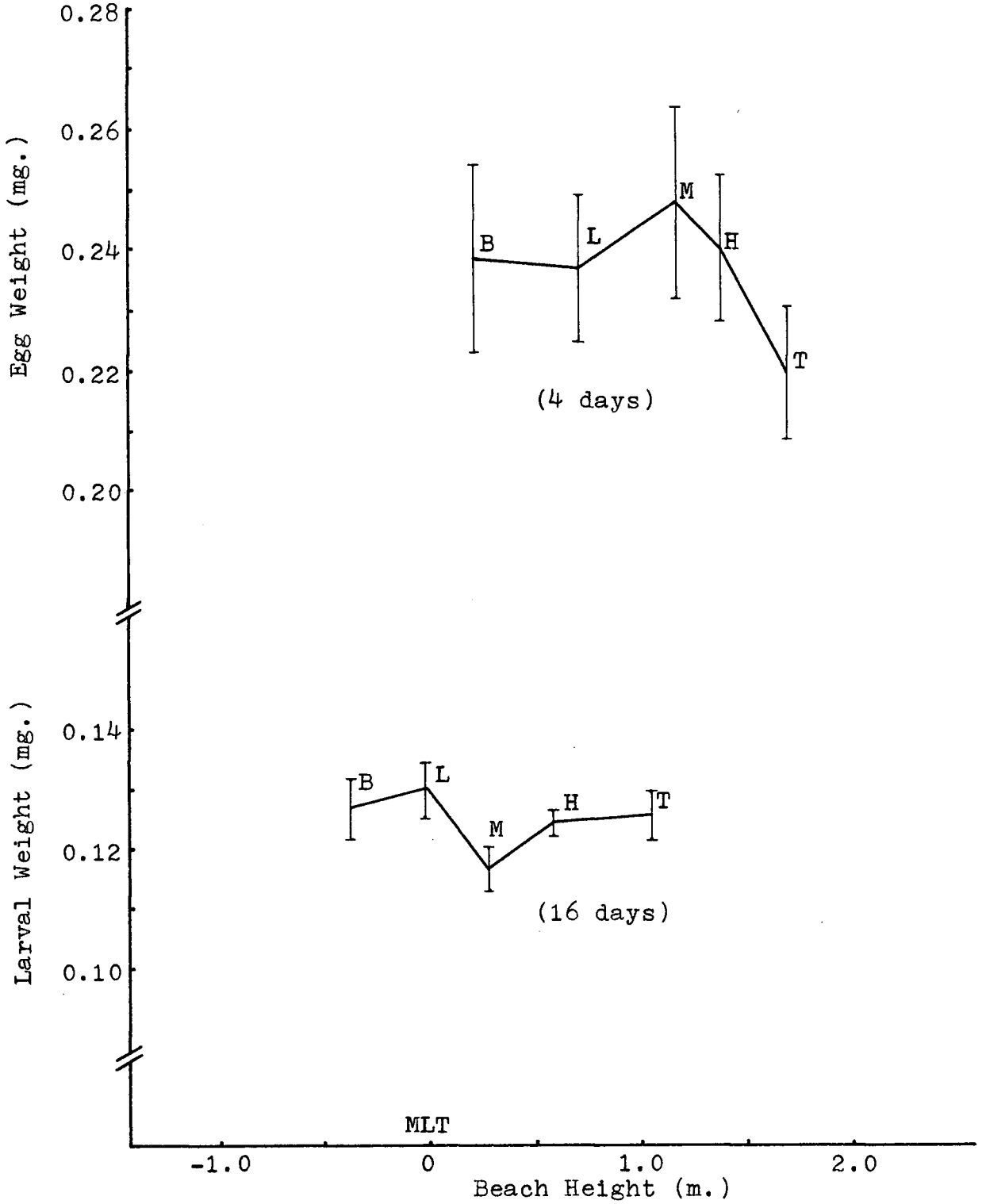

Figure 12: Relationship of egg size to beach height just after spawning (4 days) and at hatching (16 days) for the same egg mass. The latter is for larvae as the eggs hatched en route to the lab. These samples taken at Icarus Point, March 17 and 29, 1971.

Volodin (1956) noted that there was an erratic but twofold increase in oxygen requirements over the incubation period. In addition, Rannak (1958) found that hatching was initiated when eggs were transferred to lower oxygen pressures. Thus, whereas oxygen needs were satisfied in air and water when the embryos began development, just prior to hatching, when oxygen demand was much higher, the eggs may have been incapable of obtaining adequate supplies from air. A possible reason for lower oxygen availability in air would be the impairment of the egg membrane by desiccation, thereby restricting entry. As no larvae hatched out during the exposure periods, it might be that a more flaccid nature of the membrane due to desiccation prevented its rupturing until the eggs were once more submerged and their membranes taut by internal pressure. In this study, the beach survey eggs collected at 16 days were inadvertently made to hatch en route to the laboratory. As considerable living organic matter was enclosed in a very small space, the oxygen was undoubtedly depleted in a very short time, and hence, could have initiated hatching of the eggs.

The overall gradual decrease in incubation time is likely due to the higher temperature encountered in the air, promoting an increased metabolic rate. For the highest degree of exposure examined, the incubation time reached a minimum of 17.8 days. The reduction in time at this beach level was roughly 7%, over 5% of which is accounted for by the first exposure drop. This phenomenon provides a possible reason for deposition of spawn in the intertidal zone, which obviously must be of some advantage to the species survival, and that is to attune hatching to

increased air and surface water temperatures which are associated with plankton production, the source of larval sustenance. In other words, as plankton production is dependent on temperature, so also is incubation time of herring spawn (Blaxter and Hempel, 1966), and their coincidence would naturally be beneficial to the emerging larvae.

Unfortunately, exposure of spawn also has several disadvantages. Among these are the increased hatching mortality and detrimental effects on larval length and weight.

The hatching mortality on the spawning grounds was considered by Taylor (1964) to average 37% if losses due to bird predation were not included. This may be attributed to inviability, overcrowding, and exposure to wave action and desiccation. The results of this experiment show a mortality somewhat lower than this (13 to 31%), and being dependent upon the duration of exposure. To some degree, wave action which was not an experimental feature could account for the difference. What part inviability of eggs played cannot be deduced in this study. Eggs from small fish had a higher mortality than those from larger spawners. Toom (1958) has demonstrated that less viable larvae are produced by small fish, and hence, one might suspect that they were incapable of surviving the rigors of exposure or completing hatching manipulations.

The egg density seems to have mixed effects. On the one hand large clumps might hinder fertilization, limit oxygen supplies, and promote waste product accumulation of the internal eggs. On the other hand, these same larger clumps would prevent

desiccation and mechanically protect (not applicable in this experiment) the inner eggs. It was found that the small egg clumps did in fact have a higher mortality than the larger ones. Undoubtedly though, as egg numbers get very large, the mortality will increase many times and easily surpass that of the smaller clumps. This has been shown by Runnstrom (1941). It would seem, then, that an optimum number of eggs per clump must exist for maximum survival. McMynn and Hoar (1953) have also come to this conclusion. It is possible that optimum clump size will depend on the height up the beach at which the eggs are deposited. The survivors would be from some middle layer, deep enough to be protected, but not so buried as to be smothered -- the depth of this layer depending on the degree of exposure. Whether or not clump size varies with fish size is also not known.

As for the effect of exposure on the individual egg, Hamdorf (1961), working on trout eggs, suggests that a higher mortality could stem from introducing embryos which are beyond hatching size to lower oxygen regimes. In this case, they suffocate as the oxygen available is no longer sufficient to cover their minimum needs, and the flaccid exposure membrane prevents hatching. Blaxter and Hempel (1961) have also noted the possible mortality due to accumulation of waste when eggs are exposed.

It seems probable that herring lay their eggs as high on the beach as the tide at spawning time will allow. Referring to Figure 1, this would be at or near 4 meters above mean low tide, a place where exposure is lengthy and mortality is relatively

high. This distribution is in fact borne out by Taylor (1964) and the beach samples taken in this study. It might even occur that an exceptionally high tide during a spawning would result in eggs being deposited too high on the beach and hence, subjecting them to a much more severe degree of mortality. This could account for some part of year-class fluctuation in numbers. On the other hand, laying eggs high on the beach has been shown (Tester, 1942) to contribute to year-class survival. In this case, the eggs on the lower beach and in the water died for some unknown reason, while the higher eggs survived.

As already suggested, exposure also has some effects on larval characteristics. The initial drop in larval length (7%) at first exposure is expected, as earlier hatching would certainly mean less time for larval growth or the conversion of yolk into body tissue. The lack of further decrease with additional exposure might well be due to the increasing mean temperature enhancing the metabolic rate and hence, nullifying incubation time differences. Alternatively, these results may verify Hamdorf's (1961) view that larval length is directly related to the prevailing oxygen pressure and is independent of exposure time. To some degree earlier hatching must also add to mortality during the larval stage if, as Rannak (1958) has stated, exposure prior to hatching readiness results in premature and therefore less viable larvae. This experiment indicated that the smaller eggs yielded shorter larvae. It might be that these larvae are less viable than those from

larger eggs. This would further add to their disadvantages relative to larger larvae which have lesser food requirements, faster swimming speed, and a greater degree of thermal insulation (Marshall, 1953).

Larval weight, on the other hand, (which includes yolk) might not be expected to change relative to exposure time. In fact, there is no change except at the highest degree of exposure where a decrease in weight begins. If there were any importance in the initial increase in weight with exposure, this would lend support to Hamdorf's (1961) proposal that hatching weight may actually benefit from exposure up to a point, possibly as a result of increased yolk utilization efficiency. In this experiment, the latter stage is manifest in a 12% decrease in weight with the greatest exposure. This drop may be due to inefficiency of yolk conversion into body tissue. It coincides with similar sharper trends in both incubation time and hatching mortality, and suggests that a "critical point" in exposure time is reached above which the environment is so harsh that the eggs stand little chance of contributing to year-class strength. This upper limit would seem to be near 14 hours of exposure per day, or roughly the 3.5 meter beach level during the spawning season. Eggs deposited above this level are not only subjected to a higher mortality, but also produce smaller, less viable larvae.

From this study one might infer that most spawning is high up on beaches, where the larger eggs from larger fish are better fitted to survive. In consequence, reduction in the

size of spawning fish implies a lower average rate of survival. An optimum clump size is further suggested, but its relationship to fish size or beach level is unknown. Though the older and larger fish spawn first (Rannak, 1958), since the spawning period usually lasts several days (and therefore twice as many tidal movements), the eggs of all fish may be evenly distributed over the spawning zone. The beach collection of eggs at spawning did however indicate that the larger eggs were further up the beach. Unfortunately, the other beach surveys were far less instructive, and the trends are further complicated by the increasing mortality with exposure and the differential mortality due to fish and clump sizes. Another source of confusion is the possible effects of wave action and predation by birds as noted earlier.

In any event, a heavy fishing intensity which kept the individual fish size small would imply a decreased average rate of survival at higher levels of spawning. Thus, fishing pressure has a hidden dimension in also reducing spawn survival.

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APPENDICES

APPENDIX A - Apparatus Design

The tank, fittings, and tubing were all polyethylene. For each tank, the water inflow divided into four separate compartments of ten incubators entering at the bottom rear (Figure 1A). During the exposure period it flowed across the floor under the incubators and out the bottom front control drain, exiting through the electrical valve. This valve was open only when energized and operated on a time clock. During submergence the valve was closed and the water filled the tank, flowing out the top front overflow. Emptying or filling the tank took 3 or 4 minutes.

The incubators (Figure 2A) were made from 3 mm. plexiglass tubing (2.5 cm. inside diameter) open at the top. The bottom and the four mid-level side ports (1.25 cm. diameter) were covered with Nitex #253 monofilament nylon screen. The lower 1.25 cm. separated from the top which it secured with a tight friction-grip band. The reason for this was to allow easy stripping of the eggs onto the bottom screen. This whole unit was bonded together using ethylene dichloride.

Each tank compartment was divided in half horizontally by a plexiglass plate (secured by Silicone Sealant) through which ten holes had been drilled. The incubators fitted through these holes and locked in by bayonet mount so the changing water level did not dislodge them. The water was made to flow up through the eggs and out the side ports when submerged, never reaching the top of the tube. Due to their

demersal and adhesive nature, the eggs themselves remained attached to the bottom screen and did not float freely in the upper tube.

The apparatus was run continuously for two weeks prior to the experiment for adjustment of the environmental conditions and the removal of possible leaching material which might affect the eggs.

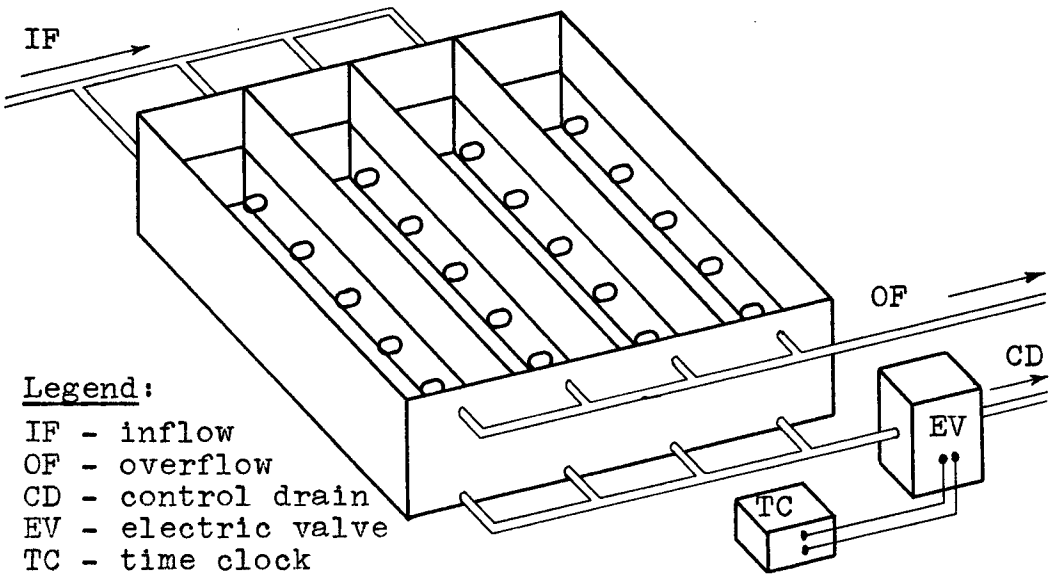

Figure 1A: Tank set-up for each exposure time.

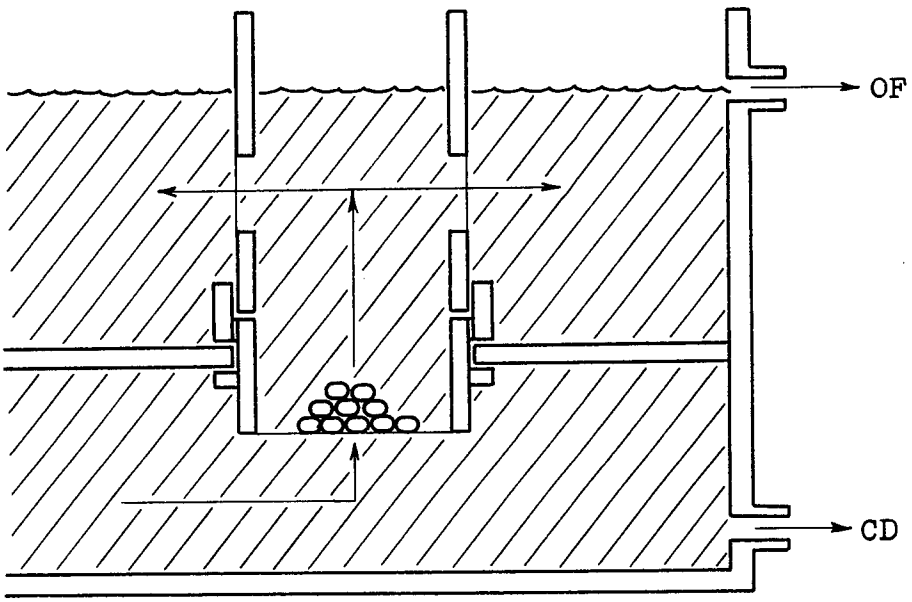

Figure 2A: Cross-section of incubator in tank.

APPENDIX B - Raw Data

The data for the spawners (Table IA) is listed according to the fish number, the order in which they were used. Numbers 14, 30 to 34, and 39 were eliminated due to 100% mortality in all incubators. Why the eggs from spawner #14 died is not known. On examination they formed a hard mass with no sign of embryonic development. It is possible they may have been infertile or were in the process of being reabsorbed when stripped. The latter is said to happen when spawners are kept for long periods in holding tanks. The other six fish were from the trawl caught batch, and all the eggs disintegrated. So as not to affect the other healthy eggs, these incubators were all removed halfway through the incubation period. Data for a total of 33 female spawners was left for analysis.

Table IIA lists the individual incubator data by exposure index. The incubator number consists of the fish number followed by the exposure index and has the same order as the spawners. The zeros mean that there was no data and were used as computer sentinels only. This lack of data is based on the following criteria:

(a) Incubation time - if less than 20 eggs hatched, the distribution seemed too disperse to pinpoint 50% hatch. Four values were rejected on this basis.

(b) Hatching mortality - any incubator with an egg number less than 45 was considered inadequate for comparison

with means based on more eggs. This level is approximately the lower boundary of the 95% range of egg number and eliminated only one value.

(c) Larval length - the mean number of larvae measured per incubator was 34; standard deviation ± 15. This number was much less than that for larval weight as many larvae were too bent or otherwise misshapen to measure accurately. If there were less than 10 measurable larvae, which again is near the lower 95% range boundary, then the data was not used. It was thought that, since each incubator had a range in larval lengths, less than 10 had too great a chance of not truly representing the mean. In this case, 11 values were discarded, the lower numbers being due to few straight larvae or a high hatching mortality. The maximum number measured per incubator was limited to 100.

(d) Larval weight - the sensitivity of the electrical balance was the deciding factor here. Thus, anything less than 15 larvae was determined inadequate to yield a fair estimate of the mean. Similar to larval length, however, fewer numbers may not have been representative. The actual mean number used was 61; standard deviation ± 14. Here also the maximum number used from each incubator was 100 larvae. Hatching mortality again played a part in this elimination which involved 11 values.

(e) Definite erratic values - there were only two rejections of this nature, and both were for larval weight. These must have been handling mistakes as the weights were

far removed from the rest of the larval weight determinations. In fact, they were actually in excess of the egg weights noted for their respective spawners.

TABLE IA. SPAWNER DATA LIST

FISH NUMBER	LENGTH (MM.)	WEIGHT (GM.)	AGE (YR.)	EGG WEIGHT (MG.)
1	202.	86.	3.	0.2228
2	218.	105.	3.	0.2884
3	222.	102.	3.	0.2564
4	205.	84.	3.	0.2182
5	194.	72.	3.	0.2564
6	214.	92.	3.	0.2526
7	220.	110.	4.	0.2806
8	205.	81.	3.	0.2682
9	204.	83.	3.	0.2668
10	218.	98.	3.	0.2554
11	217.	110.	3.	0.2474
12	213.	97.	3.	0.2776
13	201.	79.	3.	0.2872
15	193.	67.	3.	0.2748
16	234.	134.	5.	0.2876
17	192.	67.	3.	0.2478
18	231.	127.	4.	0.3204
19	205.	85.	3.	0.2640
20	232.	128.	5.	0.2970
21	217.	110.	4.	0.2636
22	213.	103.	3.	0.2558
23	203.	76.	3.	0.2926
24	201.	79.	3.	0.2738
25	219.	107.	3.	0.3204
26	207.	87.	3.	0.2726
27	216.	97.	4.	0.3196
28	221.	100.	4.	0.2966
29	213.	86.	3.	0.2752
35	200.	74.	3.	0.2658
36	215.	88.	4.	0.3068
37	207.	77.	3.	0.2758
38	197.	76.	3.	0.2380
40	215.	98.	4.	0.2212

TABLE IIA. INCUBATOR DATA LIST

(ZERO VALUES MEAN NO DATA = COMPUTER SENTINEL ONLY)

CONTROL DATA

INCUBATOR NUMBER	INCUBATION TIME (DAYS)	HATCHING MORTALITY (PER CENT)	LARVAL LENGTH (MM.)	LARVAL WEIGHT (MG.)	NUMBER OF EGGS
10	19.15	13.3	7.31	0.000	255.
20	19.18	12.1	7.20	0.000	132.
30	18.82	3.6	7.44	0.066	166.
40	19.05	5.9	7.36	0.056	102.
50	19.76	14.5	7.17	0.068	166.
60	19.07	12.3	6.91	0.050	65.
70	19.36	17.4	7.22	0.084	92.
80	19.22	19.0	7.35	0.083	79.
90	18.71	1.8	7.11	0.066	112.
100	19.04	16.1	6.89	0.117	56.
110	18.70	3.2	7.15	0.076	216.
120	18.62	19.3	7.19	0.081	150.
130	18.95	16.2	7.30	0.085	136.
150	19.19	42.4	7.38	0.092	118.
160	20.15	23.7	7.75	0.087	156.
170	19.05	26.0	6.80	0.074	104.
180	18.48	13.6	7.98	0.105	81.
190	19.12	0.7	7.85	0.082	142.
200	18.91	3.6	7.90	0.098	138.
210	19.32	6.5	8.40	0.099	107.
220	18.66	10.3	7.85	0.093	126.
230	19.59	13.4	8.21	0.109	97.
240	18.75	6.5	7.99	0.102	155.
250	18.64	3.6	8.49	0.123	111.
260	18.76	4.3	8.33	0.106	185.
270	18.79	6.3	8.22	0.121	144.
280	19.72	7.2	8.15	0.113	166.
290	19.91	7.3	8.27	0.108	193.
350	19.50	17.4	8.28	0.114	121.
360	19.53	19.2	8.82	0.127	78.
370	19.83	21.7	8.19	0.120	106.
380	19.50	26.9	8.28	0.088	167.
400	19.15	14.6	7.96	0.072	89.

TABLE IIA (CONTINUED)

2 HOUR DATA

INCUBATOR NUMBER	INCUBATION TIME (DAYS)	HATCHING MORTALITY (PER CENT)	LARVAL LENGTH (MM.)	LARVAL WEIGHT (MG.)	NUMBER OF EGGS
12	18.00	29.2	7.07	0.054	250.
22	18.30	19.1	7.07	0.104	157.
32	18.25	18.2	6.89	0.076	137.
42	18.33	5.1	6.92	0.089	156.
52	18.33	26.7	6.64	0.090	131.
62	18.29	3.1	6.96	0.080	98.
72	18.28	20.5	7.06	0.100	127.
82	18.38	18.3	6.79	0.080	131.
92	18.04	4.0	6.87	0.070	101.
102	18.13	8.5	6.74	0.107	142.
112	18.14	1.8	6.89	0.103	170.
122	18.34	36.4	6.51	0.081	154.
132	18.06	44.3	6.45	0.083	79.
152	0.00	76.1	0.00	0.000	46.
162	18.20	31.9	6.50	0.090	94.
172	18.10	21.0	6.33	0.079	143.
182	17.61	3.7	6.90	0.098	81.
192	18.00	4.8	6.68	0.084	147.
202	18.86	8.3	7.93	0.120	156.
212	18.04	7.5	6.69	0.097	93.
222	17.99	2.7	6.82	0.085	110.
232	18.26	13.7	7.11	0.102	95.
242	18.08	13.9	6.72	0.098	101.
252	17.46	18.3	7.51	0.122	131.
262	17.57	1.4	7.98	0.131	145.
272	17.85	10.1	7.92	0.151	148.
282	17.74	0.6	8.00	0.109	168.
292	18.53	5.9	8.06	0.101	271.
352	18.25	10.4	8.07	0.114	173.
362	18.50	54.5	8.03	0.131	101.
372	18.51	16.8	8.09	0.120	113.
382	18.57	15.4	7.89	0.086	247.
402	18.47	34.3	8.14	0.067	67.

TABLE IIA (CONTINUED)

4 HOUR DATA

INCUBATOR NUMBER	INCUBATION TIME (DAYS)	HATCHING MORTALITY (PER CENT)	LARVAL LENGTH (MM.)	LARVAL WEIGHT (MG.)	NUMBER OF EGGS
14	18.19	10.0	6.96	0.077	201.
24	18.67	18.5	6.71	0.112	135.
34	18.10	8.9	6.82	0.084	157.
44	18.15	16.5	6.91	0.083	164.
54	18.30	45.7	6.79	0.075	70.
64	18.08	9.7	7.20	0.074	103.
74	18.28	31.0	7.13	0.108	113.
84	18.05	11.8	7.37	0.076	127.
94	17.65	10.3	7.24	0.067	97.
104	18.09	20.4	6.90	0.120	142.
114	18.35	7.9	6.75	0.091	140.
124	18.30	13.6	7.14	0.130	125.
134	0.00	80.8	0.00	0.000	78.
154	18.33	46.8	7.19	0.076	111.
164	18.61	32.8	7.16	0.107	122.
174	18.37	33.1	6.76	0.086	136.
184	18.23	20.1	7.34	0.131	144.
194	18.21	4.6	7.05	0.089	153.
204	0.00	0.0	0.00	0.000	35.
214	17.97	42.7	6.82	0.090	82.
224	17.58	6.1	7.07	0.091	131.
234	18.45	22.1	7.22	0.101	122.
244	18.03	17.7	6.92	0.098	96.
254	17.88	15.3	6.99	0.114	190.
264	17.41	2.0	6.82	0.100	152.
274	17.69	3.3	6.92	0.111	152.
284	17.98	17.0	7.58	0.144	176.
294	18.70	2.6	7.82	0.112	190.
354	16.79	30.1	7.53	0.112	173.
364	18.48	34.6	0.00	0.000	78.
374	17.63	21.1	7.76	0.123	90.
384	16.43	7.3	8.00	0.091	151.
404	18.44	42.3	0.00	0.000	71.

TABLE IIA (CONTINUED)

6 HOUR DATA

INCUBATOR NUMBER	INCUBATION TIME (DAYS)	HATCHING MORTALITY (PER CENT)	LARVAL LENGTH (MM.)	LARVAL WEIGHT (MG.)	NUMBER OF EGGS
16	17.93	35.7	6.94	0.063	140.
26	18.44	3.0	7.02	0.106	199.
36	17.96	14.5	6.75	0.069	131.
46	18.27	12.5	6.54	0.076	128.
56	18.21	40.0	6.35	0.112	85.
66	18.31	10.9	6.66	0.082	129.
76	18.18	11.2	6.74	0.090	116.
86	18.02	18.9	6.87	0.076	148.
96	18.06	11.1	6.40	0.088	117.
106	18.24	14.4	7.12	0.127	97.
116	18.66	34.7	6.49	0.073	118.
126	18.36	20.2	6.64	0.090	130.
136	18.02	74.2	0.00	0.000	89.
156	18.25	73.0	0.00	0.000	111.
166	18.79	39.8	7.06	0.102	123.
176	18.48	10.2	6.52	0.070	157.
186	17.98	8.8	7.34	0.124	80.
196	17.96	6.6	6.91	0.089	152.
206	18.52	24.7	7.01	0.104	170.
216	18.39	40.0	7.43	0.106	130.
226	16.76	10.9	7.33	0.088	175.
236	18.61	37.3	7.87	0.118	150.
246	18.54	20.0	7.57	0.114	180.
256	17.82	6.3	7.89	0.121	159.
266	17.69	2.4	7.79	0.107	167.
276	17.66	1.3	7.87	0.125	152.
286	17.92	13.9	8.05	0.146	187.
296	17.81	2.4	8.10	0.110	167.
356	17.69	13.1	8.07	0.113	145.
366	18.63	53.1	0.00	0.108	81.
376	17.64	26.8	8.08	0.117	112.
386	16.76	25.9	7.60	0.087	135.
406	17.64	49.5	7.48	0.077	107.

TABLE IIA (CONTINUED)

8 HOUR DATA

INCUBATOR NUMBER	INCUBATION TIME (DAYS)	HATCHING MORTALITY (PER CENT)	LARVAL LENGTH (MM.)	LARVAL WEIGHT (MG.)	NUMBER OF EGGS
18	16.86	10.3	7.95	0.046	117.
28	17.36	24.4	7.48	0.106	205.
38	17.51	58.6	7.91	0.055	70.
48	17.92	15.6	6.27	0.060	135.
58	17.58	43.4	6.71	0.000	99.
68	17.68	31.6	7.02	0.000	57.
78	17.53	3.6	6.66	0.055	111.
88	17.66	18.7	6.63	0.075	123.
98	17.54	3.4	6.77	0.045	119.
108	18.36	9.6	6.77	0.110	230.
118	17.63	29.9	6.45	0.055	177.
128	17.52	30.0	6.16	0.057	100.
138	17.37	70.8	0.00	0.000	89.
158	18.49	25.0	6.86	0.070	52.
168	17.60	35.6	6.91	0.065	101.
178	17.62	42.2	6.81	0.044	83.
188	17.65	28.8	6.93	0.102	118.
198	17.58	33.9	6.84	0.080	192.
208	17.57	36.5	6.95	0.072	178.
218	0.00	73.7	0.00	0.000	57.
228	18.27	14.2	6.76	0.110	141.
238	18.38	14.3	7.16	0.090	98.
248	18.30	16.7	7.01	0.114	114.
258	17.68	21.1	7.63	0.136	152.
268	17.70	1.8	7.49	0.102	226.
278	17.68	26.3	7.47	0.133	167.
288	17.80	26.0	7.66	0.113	192.
298	17.88	20.4	7.60	0.112	211.
358	18.59	11.6	7.14	0.115	138.
368	18.50	67.9	8.09	0.120	112.
378	18.50	48.9	8.04	0.120	92.
388	0.00	94.9	0.00	0.000	158.
408	17.67	39.8	7.38	0.090	113.

APPENDIX C - Spawner Correlations

A comparison of the various experimental spawner characteristics led to the following observations: The egg size was found to be weakly correlated to fish length (Figure 3A), fish weight (Figure 4A), and to fish age (Figure 5A). On the other hand, fish length (Figure 6A) and fish weight (Figure 7A) were more strongly related to fish age, and the relationship of fish length to fish weight (Figure 8A) was very highly correlated.

From this information, it was decided that egg size and fish length would be used as bases for analyzing the incubator data. The use of both fish weight and length would have been redundant due to their high association. Length was selected as these measurements were more exact; weight involved possible variation in moisture content and vestiges of gonads (which were removed for this determination since indeterminable amounts of eggs were already missing). The use of age was rejected because of the very narrow and skewed distribution of values. In addition, due to the poor correlation of fish length and egg size, it seemed necessary to use both these approaches to the data.

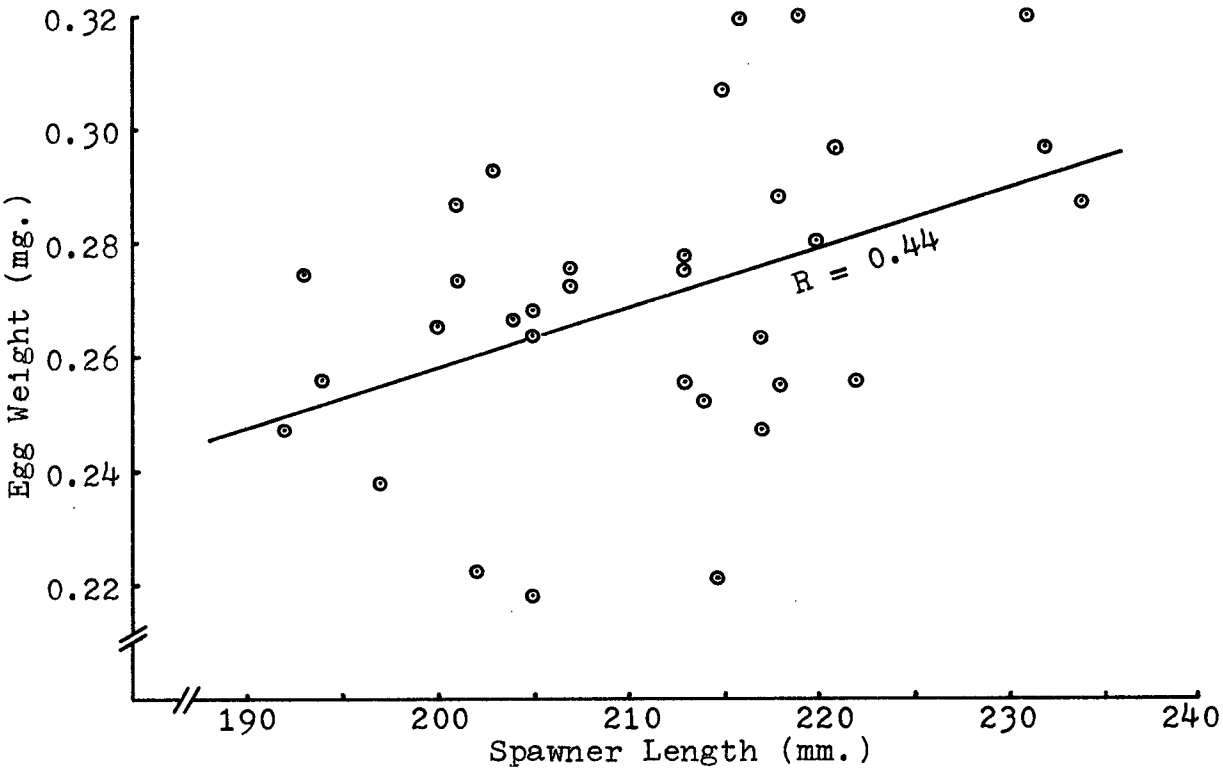

Figure 3A: Relationship of egg size to spawner length.

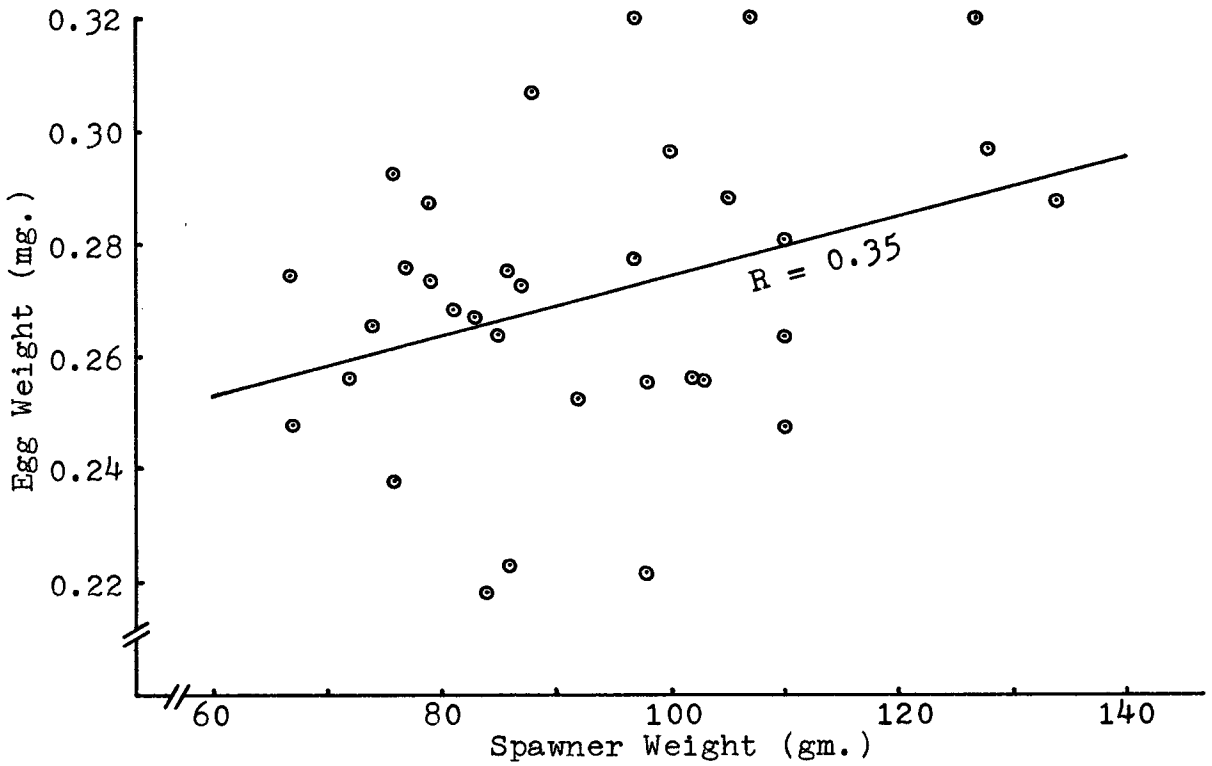

Figure 4A: Relationship of egg size to spawner weight with gonads removed.

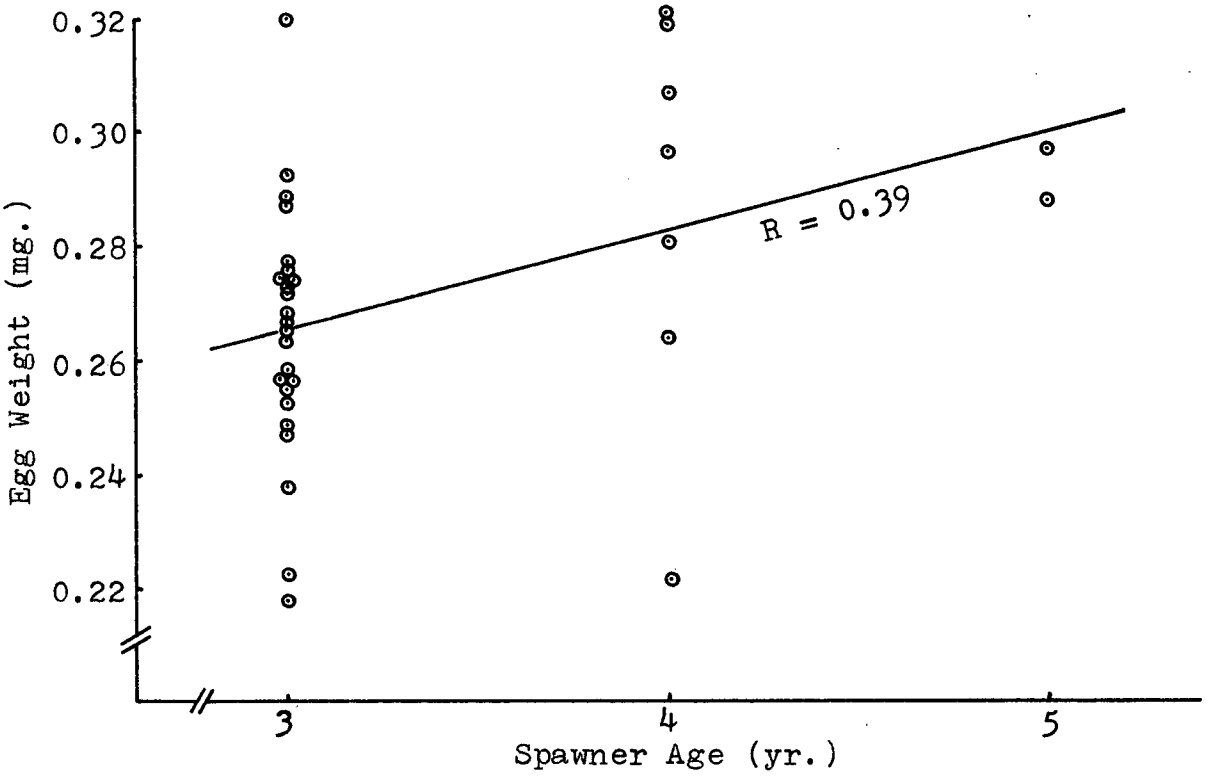

Figure 5A: Relationship of egg size to spawner age.

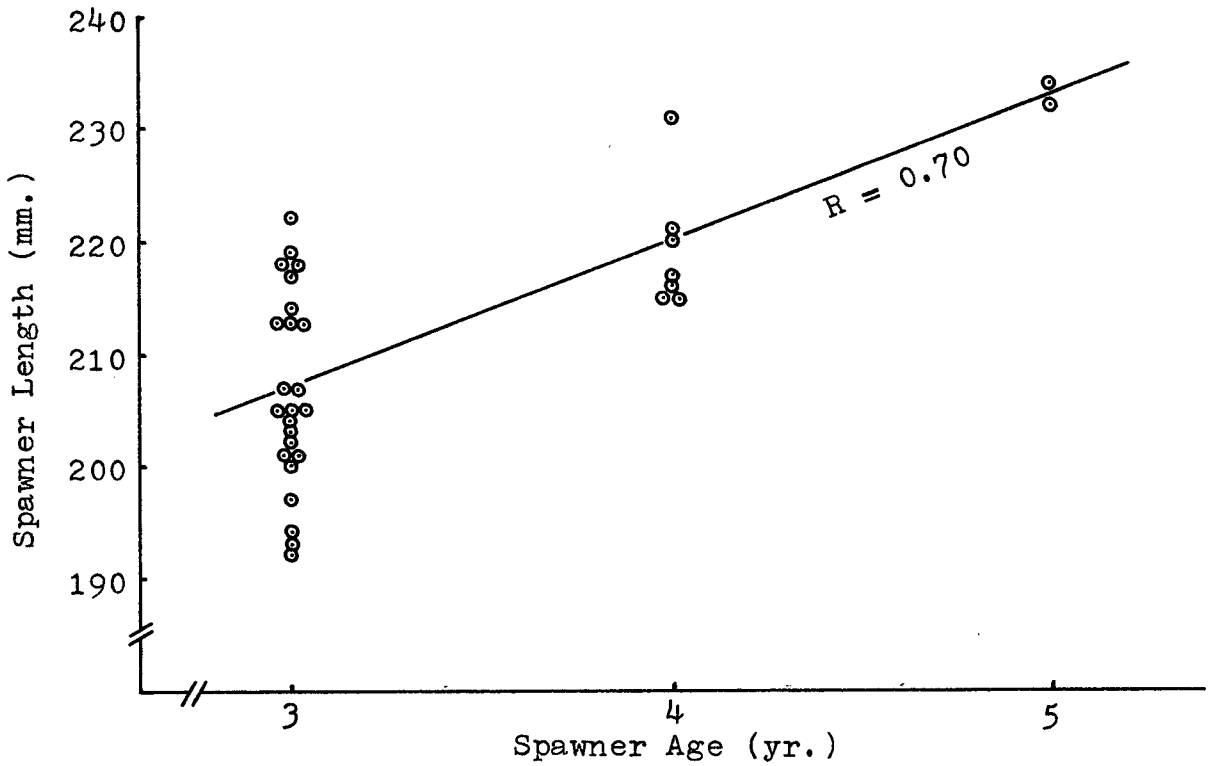

Figure 6A: Relationship of spawner length to age.

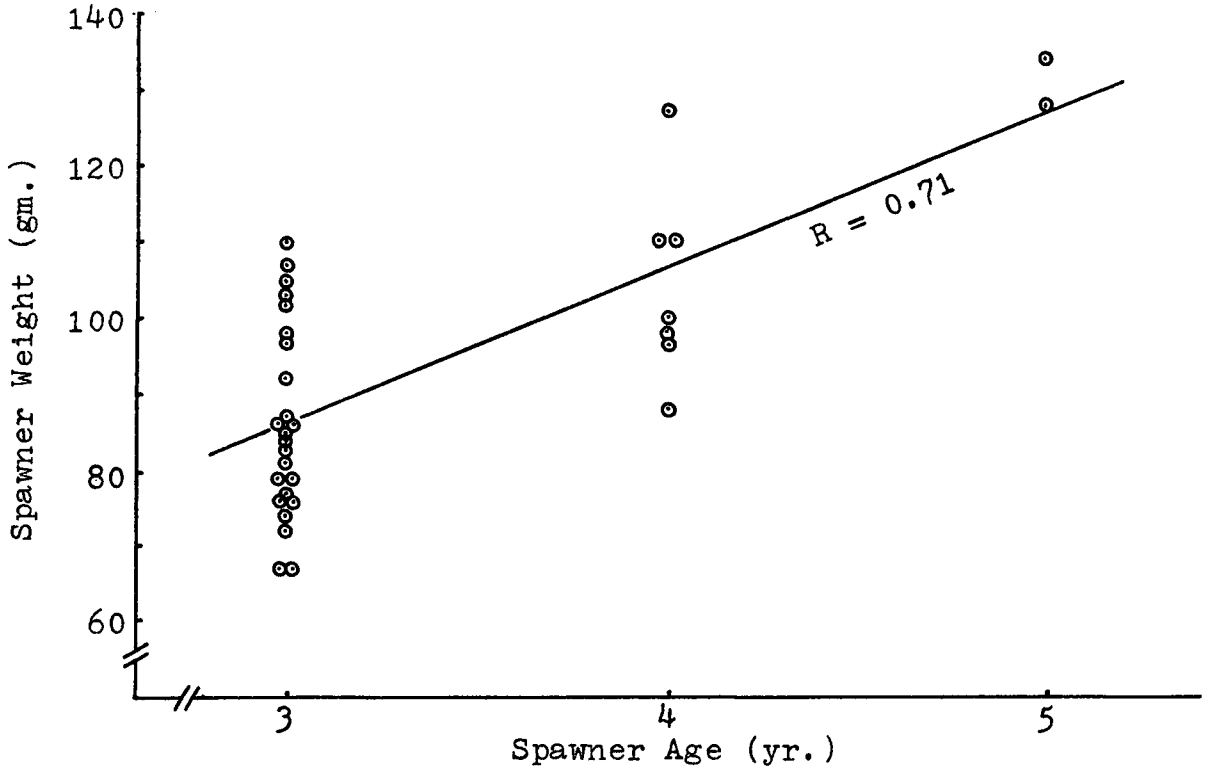

Figure 7A: Relationship of spawner weight with gonads removed to age.

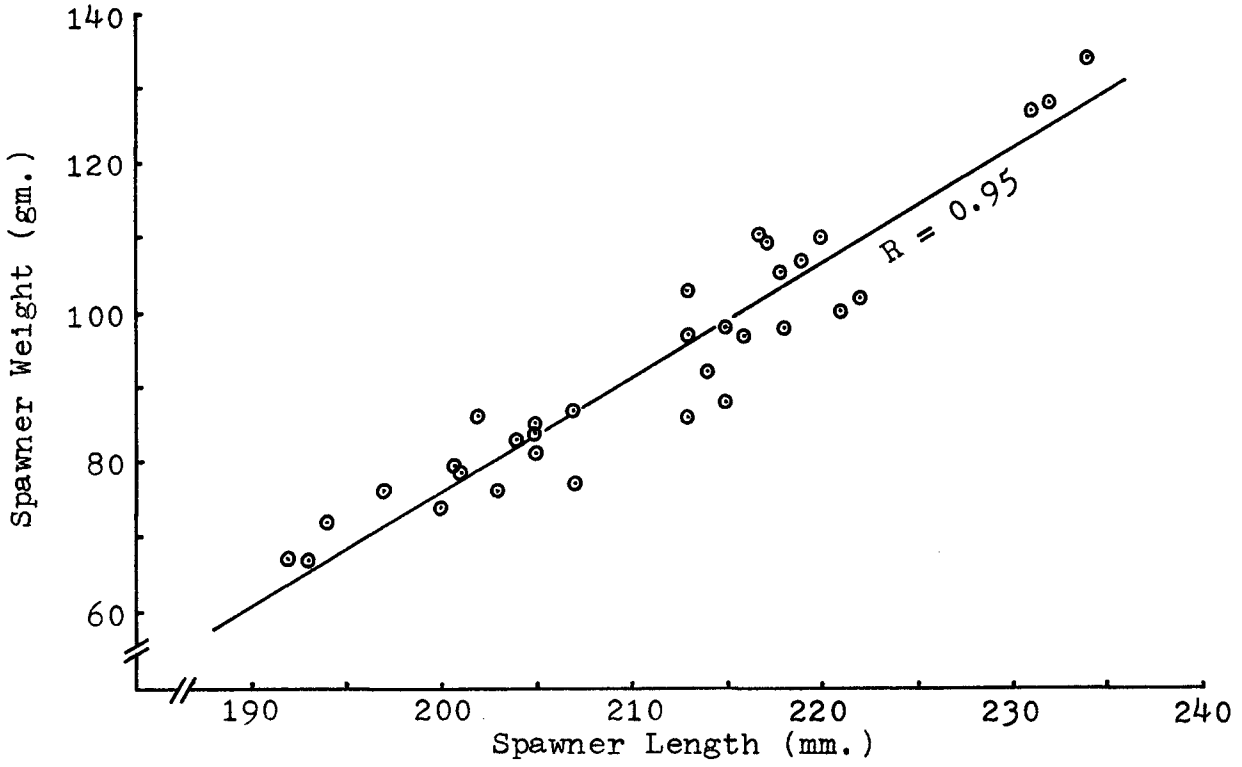

Figure 8A: Relationship of spawner weight with gonads removed to length.

APPENDIX D - Computations Summary

These tables summarize the means and standard deviations of all the analyses made in this study. For the experimental work, there is a separate table for each of the characteristics examined, thus incubation time may be found in Table IIIA, hatching mortality in Table IVA, and larval length and weight in Tables VA and VIA respectively. The layout is by exposure index for the total data and for the groupings of egg size, fish length, and clump size. The number of data represented by each mean is dependent upon the criteria laid out in Appendix B. Maximally, it should be 33 for the total data and 11 each for the groupings. In fact, it is found that a minimum of 28 for totals and 7 for groups exists, but with most data being close to the maximum level.

The egg weights for the beach stratification surveys (Table VIIA) are arranged by beach level and the collection time relative to the incubation stage of the spawn. The height above mean low tide that the sample was taken is also shown. The means are based on 10 subsamples per beach level throughout. It should also be pointed out that the weights for the collection done at 16 days are for larvae because the eggs hatched on the way to the laboratory for preservation, and thus can be compared to the other collections on a relative basis only.

Table IIIA: Computations for incubation time (days).

Characteristic	Exposure time twice per day (hr.)				
	0	2	4	6	8
(1) Total data	19.16 ± 0.42	18.17 ± 0.31	18.05 ± 0.50	18.07 ± 0.47	17.81 ± 0.41
(2) Egg size					
Small	19.09 ± 0.32	18.24 ± 0.19	18.01 ± 0.57	17.93 ± 0.64	17.71 ± 0.42
Medium	19.18 ± 0.44	18.17 ± 0.29	17.92 ± 0.52	18.04 ± 0.31	17.98 ± 0.44
Large	19.21 ± 0.51	18.10 ± 0.41	18.25 ± 0.34	18.23 ± 0.38	17.74 ± 0.37
(3) Fish length					
Small	19.22 ± 0.34	18.21 ± 0.18	17.86 ± 0.70	18.05 ± 0.51	17.84 ± 0.57
Medium	19.14 ± 0.45	18.22 ± 0.32	18.06 ± 0.42	17.88 ± 0.51	17.90 ± 0.36
Large	19.12 ± 0.50	18.09 ± 0.38	18.22 ± 0.27	18.26 ± 0.32	17.67 ± 0.27
(4) Clump size					
Small	19.22 ± 0.36	18.15 ± 0.26	18.10 ± 0.32	18.14 ± 0.33	17.82 ± 0.44
Medium	19.00 ± 0.29	18.09 ± 0.33	18.27 ± 0.30	18.10 ± 0.55	17.86 ± 0.51
Large	19.26 ± 0.56	18.26 ± 0.33	17.78 ± 0.67	17.96 ± 0.53	17.72 ± 0.26

Table IVA: Computations for hatching mortality (%).

Characteristic	Exposure time twice per day (hr.)				
	0	2	4	6	8
(1) Total data	13.0 ± 8.9	17.8 ± 16.8	21.5 ± 17.1	23.3 ± 19.2	31.2 ± 22.0
(2) Egg size					
Small	13.3 ± 7.9	15.1 ± 11.7	18.9 ± 14.7	23.6 ± 14.2	35.5 ± 25.3
Medium	13.4 ± 12.3	17.8 ± 21.7	18.5 ± 15.4	21.3 ± 20.4	25.8 ± 20.9
Large	12.4 ± 6.6	20.5 ± 16.9	27.5 ± 20.9	24.9 ± 23.6	32.3 ± 20.5
(3) Fish length					
Small	17.9 ± 10.9	24.8 ± 20.2	28.7 ± 22.2	32.7 ± 22.8	31.9 ± 28.6
Medium	11.1 ± 6.9	15.9 ± 17.8	14.2 ± 13.6	17.9 ± 18.3	30.0 ± 18.1
Large	10.1 ± 7.0	12.6 ± 9.7	21.5 ± 11.0	19.2 ± 13.4	31.6 ± 20.0
(4) Clump size					
Small	16.3 ± 5.3	26.1 ± 24.3	35.2 ± 21.6	36.1 ± 24.2	43.1 ± 18.7
Medium	11.0 ± 11.8	14.3 ± 8.5	19.8 ± 9.5	24.4 ± 11.7	21.0 ± 18.8
Large	11.8 ± 8.4	12.9 ± 11.3	10.7 ± 8.5	9.2 ± 7.7	29.5 ± 23.9

Table VA: Computations for larval length (mm.).

Characteristic	Exposure time twice per day (hr.)				
	0	2	4	6	8
(1) Total data	7.72 ± 0.55	7.19 ± 0.60	7.13 ± 0.34	7.22 ± 0.57	7.12 ± 0.52
(2) Egg size					
Small	7.37 ± 0.48	7.03 ± 0.53	7.02 ± 0.37	6.89 ± 0.43	7.00 ± 0.57
Medium	7.85 ± 0.50	7.25 ± 0.70	7.24 ± 0.35	7.39 ± 0.64	7.05 ± 0.54
Large	7.93 ± 0.53	7.32 ± 0.60	7.13 ± 0.27	7.43 ± 0.49	7.29 ± 0.44
(3) Fish length					
Small	7.56 ± 0.53	6.99 ± 0.57	7.20 ± 0.38	7.13 ± 0.66	7.00 ± 0.40
Medium	7.90 ± 0.56	7.46 ± 0.67	7.19 ± 0.36	7.34 ± 0.62	7.19 ± 0.64
Large	7.69 ± 0.54	7.11 ± 0.50	7.02 ± 0.28	7.17 ± 0.48	7.13 ± 0.49
(4) Clump size					
Small	7.61 ± 0.66	7.04 ± 0.59	7.13 ± 0.33	7.00 ± 0.61	7.06 ± 0.59
Medium	7.82 ± 0.50	7.05 ± 0.57	7.05 ± 0.24	7.13 ± 0.53	7.05 ± 0.56
Large	7.73 ± 0.49	7.48 ± 0.59	7.22 ± 0.43	7.46 ± 0.53	7.23 ± 0.44

Table VIA: Computations for larval weight (mg.).

Characteristic	Exposure time twice per day (hr.)				
	0	2	4	6	8
(1) Total data	0.092 ± 0.020	0.096 ± 0.020	0.099 ± 0.019	0.099 ± 0.020	0.087 ± 0.028
(2) Egg size					
Small	0.075 ± 0.019	0.083 ± 0.014	0.087 ± 0.013	0.083 ± 0.019	0.071 ± 0.027
Medium	0.095 ± 0.016	0.097 ± 0.019	0.097 ± 0.020	0.100 ± 0.014	0.088 ± 0.026
Large	0.105 ± 0.016	0.109 ± 0.019	0.115 ± 0.014	0.114 ± 0.015	0.099 ± 0.028
(3) Fish length					
Small	0.088 ± 0.016	0.085 ± 0.016	0.085 ± 0.014	0.093 ± 0.021	0.074 ± 0.029
Medium	0.092 ± 0.026	0.101 ± 0.027	0.101 ± 0.018	0.097 ± 0.016	0.098 ± 0.025
Large	0.096 ± 0.018	0.102 ± 0.012	0.110 ± 0.018	0.106 ± 0.023	0.086 ± 0.029
(4) Clump size					
Small	0.090 ± 0.026	0.091 ± 0.018	0.086 ± 0.019	0.101 ± 0.020	0.071 ± 0.025
Medium	0.097 ± 0.018	0.097 ± 0.019	0.104 ± 0.017	0.089 ± 0.018	0.084 ± 0.029
Large	0.089 ± 0.016	0.101 ± 0.024	0.101 ± 0.019	0.107 ± 0.020	0.101 ± 0.025

Table VIIA: Computations for beach stratification of egg weight (mg.), showing beach height (m.).

Time and place of sample	Sample region				
	Bottom	Low	Middle	High	Top
(1) Spawning Bedwell Bay, 20/4/70.					
Mean	0.170	0.205	0.209	0.227	0.232
Std. Dev.	0.004	0.013	0.014	0.007	0.010
Height	0.12	0.92	1.71	2.53	3.33
(2) Post-spawning (4 days) Icarus Pt., 17/3/71.					
Mean	0.239	0.237	0.248	0.240	0.220
Std. Dev.	0.015	0.012	0.016	0.012	0.011
Height	0.21	0.70	1.16	1.37	1.68
(3) Mid-incubation (8 days) Nanoose Bay, 27/3/70.					
Mean	0.205	0.200	0.200	0.203	0.210
Std. Dev.	0.007	0.009	0.009	0.011	0.007
Height	-0.24	0.46	1.16	1.86	2.56
(4) Hatching (16 days) (larvae) Icarus Pt., 29/3/71.					
Mean	0.127	0.130	0.117	0.125	0.126
Std. Dev.	0.005	0.005	0.003	0.002	0.004
Height	-0.37	-0.03	0.27	0.58	1.04

APPENDIX E - Statistical Analyses

The original number of spawners was arbitrarily set at forty (with five exposure periods) so that, with possible rejections, a good range of differences in egg and fish sizes could be obtained. One-way analyses of variance were used on the data, and the following symbols have been employed to indicate the results:

(--) not significant

(0) significant at $p = .05 - .10$

(*) significant at $p = .01 - .05$

(**) significant at $p < .01$

Due to unequal replicate numbers, Scheffé's method was used to make all possible comparisons within the experimental exposure period data. The significance of differences within the total data is shown for each characteristic examined in Table VIIIA. The significance within the individual groups was not tabulated. The between groups' significance of differences are found in Table IXA for all characteristics. Table XA shows the significance of interaction among egg size, fish length, and clump size. In these latter two tables each exposure time was examined separately using Dr. N. Gilbert's computer program. Analyses of covariance were inadvisable due to unequal sample sizes. All tests done on hatching mortality used arcsin transformation of the percentage data.

The significance of differences between beach levels for the stratification surveys are found in Table XIA. Scheffé's method was also used here.

Table VIIIA: Significance of differences within the total data.

Characteristic	Exposure period comparisons									
	0-2	2-4	4-6	6-8	0-4	2-6	4-8	0-6	2-8	0-8
(a) Incubation time	**	--	--	--	**	--	--	**	*	**
(b) Hatching mortality[1]	--	--	--	--	--	--	--	--	0	**
(c) Larval length	**	--	--	--	**	--	--	**	--	**
(d) Larval weight	--	--	--	--	--	--	--	--	--	--

[1] Used arcsin transformation.

Table IXA: Significance of differences between groups[1].

Characteristic	Exposure time twice per day (hr.)				
	0	2	4	6	8
(a) Incubation time					
(1) Egg size	--	--	--	--	--
(2) Fish length	--	--	--	--	--
(3) Clump size	--	--	0	--	--
(b) Hatching mortality[2]					
(1) Egg size	--	--	--	--	--
(2) Fish length	0	--	0	0	--
(3) Clump size	--	--	**	**	*
(c) Larval length					
(1) Egg size	0	--	--	0	--
(2) Fish length	--	--	--	--	--
(3) Clump size	--	--	--	--	--
(d) Larval weight					
(1) Egg size	**	**	*	**	--
(2) Fish length	--	0	0	--	--
(3) Clump size	--	--	--	--	--

[1] Used Dr. N. Gilbert's program.

[2] Used arcsin transformation.

Table XA: Significance of interaction[1].

Characteristic	Exposure time twice per day (hr.)				
	0	2	4	6	8
(a) Incubation time					
(1) Egg size/fish length	--	--	--	--	--
(2) Fish length/clump size	--	--	--	0	--
(3) Egg size/clump size	0	--	--	--	--
(b) Hatching mortality[2]					
(1) Egg size/fish length	--	--	--	--	0
(2) Fish length/clump size	--	--	--	0	**
(3) Egg size/clump size	--	--	--	--	--
(c) Larval length					
(1) Egg size/fish length	--	--	--	--	--
(2) Fish length/clump size	--	--	--	*	--
(3) Egg size/clump size	--	--	--	--	--
(d) Larval weight					
(1) Egg size/fish length	--	*	--	--	--
(2) Fish length/clump size	--	--	--	--	--
(3) Egg size/clump size	--	--	--	--	--

[1] Used Dr. N. Gilbert's program.

[2] Used arcsin transformation.

Table XIA: Significance of differences between beach levels.

Time and place of sample	Beach level comparisons									
	B-L	L-M	M-H	H-T	B-M	L-H	M-T	B-H	L-T	B-T
(1) Spawning Bedwell Bay, 20/4/70.	**	--	**	--	**	**	**	**	**	**
(2) Post-spawning (4 days) Icarus Pt., 17/3/71.	--	--	--	*	--	--	**	--	0	0
(3) Mid-incubation (8 days) Nanoose Bay, 27/3/70.	--	--	--	--	--	--	--	--	--	--
(4) Hatching (16 days) Icarus Pt., 29/3/71.	--	**	**	--	**	0	**	--	--	--