THE INFLUENCE OF TEMPERATURE, SALINITY AND

PHOTOPERIOD ON AGGREGATIONS OF UNDERYEARLING

CHUM SALMON, <u>ONCORHYNCHUS KETA</u> (WALBAUM)

by

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ABSTRACT

Underyearling chum fry were held in fresh water and salt water at two different temperatures and under two different photoperiods. The first tests were made after forty days acclimation. Aggregations were greater in salt- than in freshwater ($p < 0.01$). At the lower temperature the fish were more aggregated than they were at the higher temperature ($p < 0.05$). Photoperiod effects were not significantly different. The biological meaning of these results is discussed. It is concluded that, under the conditions of this experiment, chum salmon fry show true schooling (as defined by Keenleyside, 1955) only in salt water.

ACKNOWLEDGEMENTS

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INTRODUCTION

At present neither the nature nor the mechanisms of schooling in the Pacific salmon (genus <u>Oncorhynchus</u>) are satisfactorily explained. Conflicting reports on natural observations and experimental results are to be found in the literature.

Hoar (1951) showed a positive rheotactic response in chum fry under experimental conditions. It was also said that in the streams these fish were usually seen in daylight swimming into the currents at the time of migration, maintaining their position. The mechanism suggested for the nocturnal downstream migration in chum fry was a) the tendency of the fish to rise to the surface as light decreased coupled with b) a failure in the rheotactic response. Activity was said to increase at night. This is emphasized in Hoar (1953)

" ... juvenile seaward-moving salmon are active and vigorous, but, at the same time, carried seaward by the currents." (op. cit. p. 439).

Neave (1955) observed the behaviour of pink salmon fry in nature. (He claimed that there was no evidence to suggest that chum behaviour was essentially different). Pink fry showed "negative rheotaxis" during their downstream migration. They were moving singly and at night. Few fry were seen during the day. In slack (tidal) water the migrants were swimming randomly and were more uniformly distributed than in the stream. The positive rheotaxis of fry was a post-migratory behaviour in captive fish.

Hoar (1956) pointed out that his observations of chum and pink salmon in experimental tanks showed that these fish preferred

light and showed positive rheotaxis. Chum salmon captured at night and released during the day would hold positions in the current but would have moved away by the next morning. Experimental observations showed that chum schools were somewhat loose. In circular aquaria the rapidly swimming chums formed a file-like formation. Hoar (pers. comm.) considers that the chum salmon is less strongly schooled than the pink. Comparing his experimental results with Neave's (1955) field observations, Hoar, referring to pink and chum fry, said

"Not only is the behaviour of schooling fry ... different from that of nocturnal migrating individuals which have never schooled, but definite directions of swimming are probably established ... independently of rheotactic responses .... after the fry have schooled they no longer seek the protection of the gravel and stones but rely on the protection of the school and its associated advantages". (Hoar, 1956, p. 323).

Further experiments (Hoar et al, 1957) showed that chums preferred lighted areas when given a choice between those and dark ones. These authors recorded that chum fry when scared will hide under stones, whereas pink fry will scatter above the stones. Pink fry are less dependent on the protection of the stones once they have schooled than chums are in a similar situation.

Neave had denied that schools of pink fry could be seen in nature during the day, whereas Hoar's experiments demonstrated schools of both pinks and chums at this time. McDonald (1960), on the other hand, claimed that schooling was not observed to occur for most of the downstream migration of chum, coho, pink or sockeye fry. Individuals but not schools were observed

in the spawning streams in both daylight and darkness. McDonald admitted that some schools of chum fry were seen at the mouth of the river system in which they were spawned (Lakelse River, B. C.) and also further downstream in the quiet waters of the main river of the system (Skeena River, B. C.). The variation among chum catches at different times in the spawning-stream traps was not great enough to suggest schooling. It might be possible to combine the arguments of Hoar (1956) and McDonald here and suggest that the fry trapped in the spawning stream had not yet undergone the initial schooling reaction, whereas this had occurred in the fish seen further downstream. It is obvious that the nature of the aggregative behaviour of chum fry in fresh water has not been completely clarified by these workers.

McInerney (1961), in salinity preference studies, made notes on the group behaviour of Pacific salmon fry. His results showed an increase in the size of groups crossing the salt water/ fresh water partition of the tanks from the beginning of June until the third week in July. A decrease in group size followed until it was almost unity by the first week in September. This study was not carried out with salt-water fry, making direct comparisons with these present experiments impossible.

Houston (1959) showed that chum fry would swim more slowly in salt water than in fresh water at maximum sustained speed. These fish were only in salt water for some 36 hours. Houston's study indicated that the loss of maintained swimming speed was due to the increased demand for energy to do osmotic work in the

salt water environment.

These two papers above do not deal precisely with the subject matter of this present paper, but they do touch on some aspects to be discussed after the presentation of the results obtained.

The nature of schooling in fishes was extensively discussed by Shelbourn (1963) and it is not proposed to repeat that discussion here. A list of references from that paper appears at the end of this one, (v. Appendix D). Keenleyside's (1955) criterion for schooling was adopted in the 1963 paper and is still used in this one, i.e. "an aggregation where one fish reacts to ... other fish by staying near them".

A recent paper by Okuno (1963) records observations on 130 species of marine fishes with regard to their schooling behaviour in nature and in captivity, and contains comments on the type of "chasing behaviour" observed. This extensive work covers 76 genera, 35 families, 12 suborders and 5 orders of fishes -- from which the family Salmonidae is excluded. However, the relevant point is that Okuno found a change in schooling behaviour in some of these fish when they were transferred from the ocean to small aquaria, but not when they placed in a large tank. This problem enters into the subject matter of the thesis and will be discussed later.

The considerations of chum salmon fry behaviour which provided the problems for the present work were as follows. Firstly, McInerney (1961) showed that schooling behaviour peaked towards the end of the downstream migratory period and then

decreased to low level. If this event was meaningful it might correlate with a period of estuarine residence before the population moved into the open waters. The increase in aggression noted by McInerney would be more appropriate to residential fishes than to schooled, migrant ones.

Secondly, if this hypothetical residential behaviour is real, what are the releasers? Preliminary studies were conducted in fresh water tanks to ascertain the effects of changing the densities of fish, changing the spatial configuration of the tank, and of feeding. The results were highly variable and did not produce a change in behaviour. Repeated, similar experiments might have provided definite results but the project was abondoned in favour of a radically different test which will be described later. To provide the background for the new tests, the preliminary studies will be outlined briefly.

The hypothesis developed from the preliminary experiments is this; since external factors do not affect the schooling of large groups of fish (>20) schooling is an innate, maturation phenomenon. It will be released by factors which affect the growth rate of the fish; light, temperature and the salt water environment. Changes in the levels of these factors will change the degree of aggregation.

MATERIALS AND METHODS

This study was conducted over a period of two years on the fry of the chum salmon, Oncorhynchus keta. In the first year wild coho fry (O. kisutch) were used to provide a contrast to the chums. The chums were hatchery reared in both years.

A. Preliminary Studies

Chum fry were obtained from Smith Falls Hatchery, Cultus Lake, B. C. on April 15, 1963. They were fed three times daily with fresh-frozen brine shrimp [1] and received standard aquarium care and attention.

Coho fry were caught in the Cheakamus River, B. C. on the 11th and 15th of June, 1963. They were treated similarly to the chums.

A daily mortality record was kept for all these fish. Mortality is discussed in Appendix C.

i) Stagnant-water tests

Aerated aquaria were used for these tests. Forty chum fry were observed in an aquarium 182 cm long x 20 cm wide. A second size 60 x 30 cm was used to hold 30 chums in some tests and three chums in other tests.

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[1] Obtained from The Wardley Brine Shrimp Company, Watrous, Saskatchewan.

ii) Flowing-water tests

Observations were made on fish held in metal tanks measuring 244 x 26.5 cm. The tanks were painted with "Rustoleum"[2] non-toxic paint. During a five-minute observation the activity of the fish was recorded by counting each fish as it passed under a string stretched mid-way across the tanks. In addition, the number of "chases" and "nips" was recorded in the five minute period. Both chum and coho, in groups of various sizes, were observed in these tanks. Artificial landmarks were included in some tests. In other tests the fish were not fed for several days prior to testing.

B. 1964 Studies

i) Holding conditions

Chum fry were obtained from the Smith Falls Hatchery on 17 April, 1964. They were held in four concrete troughs with temperature and photoperiod controlled as follows:

Tank	Temperature	Photoperiod
A	9-12°C (seasonal)	8 hours
B	" "	16-17.5 hours (seasonal)
C	7°C	" "
D	7°C	8 hours

On May 21, four metal troughs painted with grey "Clorubite"[3] cement enamel were placed in the four concrete troughs and

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[2] Manufactured by The Rustoleum Corporation, Evanston, Illinois.

[3] Manufactured by the General Paint Company, Vancouver, B. C.

FIGURE 1. THE 1964 TESTING TANK
(NOT TO SCALE)

PLAN

CROSS SECTION AT AA'
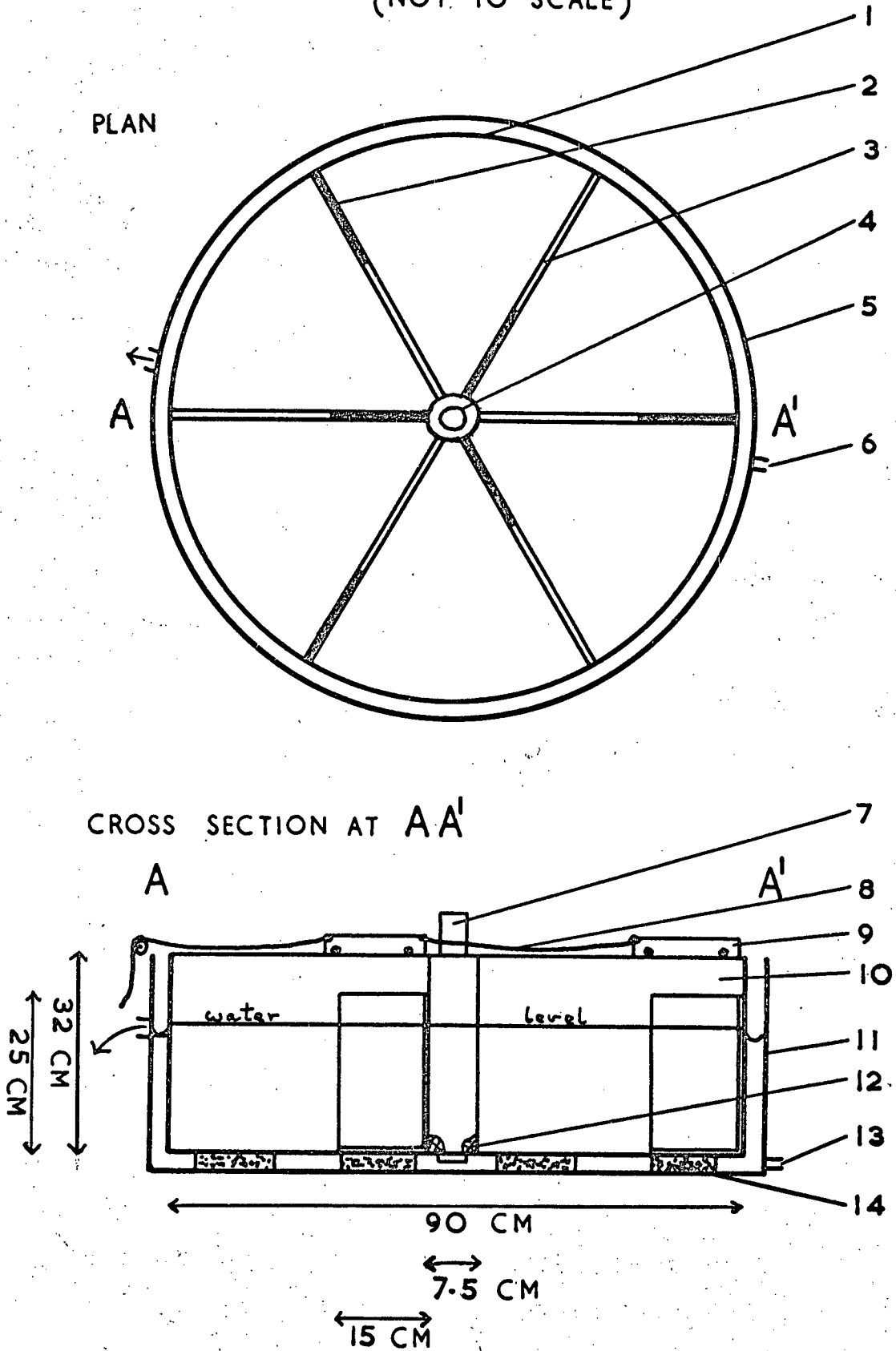
FIGURE 1. The 1964 Testing Tank

LEGEND

1	Testing Tank
2	Door
3	Double-walled Partition
4	Drain Plug
5	Cooling Tank
6	" " water inlet
7	Drain plug
8	Drawstring for opening doors
9	Door
10	Partition
11	Cooling Tank
12	Drainage Holes
13	Cooling Tank water inlet
14	Spacer

filled with salt water obtained from the Vancouver Public
Aquarium. About 1000 chum fry were placed in each tank. The
fish were tolerant to the salt water, the salinity of which
ranged from 25 to 29°/oo.

Initial mortality was high in both salt and fresh water.
The populations of these fish were stable by the middle of June.
Mortality is still low at present (14 September). An estimation
of population size and the corresponding density is given below:

Tank	Water volume	Population	Density
Fresh water	202 litres	1500	7.4 fish/litre
Salt water	67 litres	250	3.7 fish/litre

The lesser density of the salt water fish is accounted
for by the lack of flowing water. The salt water was always
slightly cloudy at the time the tanks were cleaned, in contrast
to the fresh water tanks which were always clear. Dissolved
material would limit the oxygen carrying capacity of the salt
water and thus the fish population. No pathological condition
was apparent in either the fresh water or salt water fish. The
fish were fed frozen brine shrimp and otherwise received standard
aquarium care.

ii) Testing apparatus

A sketch of a testing tank is shown in Figure 1. Four
such tanks were used, with either fresh water or salt water
as desired. All four were identical, except that the bottoms
of two tanks used for salt water were blistered in places,

leaving a "pebbled" appearance. Subsequent tests indicated that this condition did not affect the results. There was no water flowing through the tank, nor was air bubbled in. Cooling was by an outer water-bath.

Doors were slung between the six double walls. Each door opened at the center and the outside edge of the partition, alternately. This design prevented the constant-course swimming described by Hoar (1956). This behaviour may be more of a "following" reaction rather than schooling according to Keenleyside (1955) and as such was not desirable in my experiments. The doors could be opened by draw-strings, the observer remaining concealed behind a screen.

Light was provided by three vertical 40 watt gas tubes, each 30 cm in length, which were placed at the end of the double walls, alternately. Difficulties in construction prevented there being one tube per wall. This arrangement of lights enabled the observer, looking into a mirror at an angle of 45° above the tank, to see the fish well illuminated without being dazzled by reflection from the water surface or having his vision obscured by a central light. His presence never disturbed the fish.

Three tests were run each day. Six fish would be placed in the tank for a maximum of two hours during the test. They were then returned to the holding tank. The testing tanks were cleaned, drained and refilled every night. They were aerated during the night. The fish were fed in the holding tanks a half hour before any were removed for testing.

iii) Testing technique

After one hour of acclimation the doors were opened and the number of fish in each sector was recorded at 20 second intervals for a test period of ten minutes.

After the first two weeks of testing the fish were not tested until ten minutes after the doors were opened, since this movement seemed to disturb the fish for one or two minutes.

Occasionally, a fish might become "excited" by the opening of the doors and dash round the tank, disturbing the others. Such data were considered abnormal and are not included. This event occurred rarely, and generally when a particularly small fish was placed in the tank. The rarity was due to the careful selection of fish of the same size for testing. "Pinheads" or exceptionally large fish were not placed in the testing tanks after the nature of this disturbance was appreciated.

No morbid behaviour such as "bellying-up", or the "panting" due to anoxia, was ever seen in these experiments.

RESULTS

The preliminary experiments failed to reveal any orderly differences in behaviour. This seemed to be due to poor experimental design rather than to the variability in the experimental material. These observations were important as the basis for the design of the 1964 experiments. As such, they will be described below.

A. Preliminary Experiments: 1963 Observations

In the still water experiments the fry behaved differently in each of the three tanks. In the long tank the 40 fish swam constantly up and down on the first day, were less active and less strongly schooled on the second day. By the third day they were dispersed through the tank. At this time agonistic behaviour was first observed.

The 30 fry in one of the small aquaria were moving constantly round the tank in non-parallel fashion from the time they were first observed until they were removed five days later. Agonistic behaviour was observed occasionally.

In the other aquarium the 3 fry were generally quiet. Whatever activity occurred was agonistic, with nipping and chasing most apparent.

As a result of these observations the long steel tanks were set up for the rest of the summer's work, because it was realized that although the density of fish was an important factor to consider, it could be controlled easily. Space on the

other hand should in no way be limiting to density effects in these experiments.

The use of a center line as a "counting gate" was not successful because there were occasions on which the fish were observed to be actively milling at either one end of the tank or the other, but never swimming far enough up or down the tank in order to cross the line. This technique, then, would not provide an accurate measure of activity.

The hatchery-reared chum fry were observed to be more active in swimming up and down the tank than were the wild coho fry of the same year. This phenomenon is also reported by McInerney (1961). Coho were more evenly dispersed in the larger groups (20 fish), while in the smaller groups (5 fish) territorality was frequently observed (cf. Chapman 1962). Agonistic behaviour was rarer in the small groups of chums, and their schooling intensity (closeness of inter-fish distance) was not as strong as in the larger groups of these fish.

Feeding seemed to increase the activity of the fish. This was particularly true of chums which had been without food for 2 to 3 days previously. Aggressiveness increased in both species with this treatment. This was particularly true of the small groups (5 fish) of coho. There the dominant fish would remntain a territory in the area where the frozen brine shrimp was tossed in at feeding times.

Rocks of various sizes and configurations did not release territorial behaviour in either species. (It had been hoped that the rocks would form the nucleus of a territory as shown

by Kalleberg, 1958).

Since no further comment will be made on the preliminary tests, a summary of their influence on the design of the 1964 experiments will be useful.

A certain density of fish was seen to be necessary for the study of schooling in this experimental situation.

The presence of a water current was not essential to schooling.

The availability of food could affect behaviour. This was an effect on the "mood" of the fish.

Agonistic behaviour was most noticeable when the fish were of unequal sizes. This was particularly true in the small groups of chums. Thus it was considered desirable to pick fish of the same size in future experiments.

Measurements of agonistic behaviour were inaccurate because of the number and spacing of the fish. The measurement of activity was not accurate by the "center gate" technique. Both these enumerations were omitted from the 1964 tests.

Because of these considerations, the techniques for 1964 described in Materials and Methods were adopted. The following points were considered basic to the study.

Multiples of 6 fish could be used in any experiment, thus allowing density to be controlled. (6 was found to be a satisfactory number for the size of fish tested).

Fish could be maintained in separate holding tanks, thus eliminating the problems of the effects of feeding fish in an experimental tank and having food matter in the water -- as

TABLE I

Gross totals for the 1964 tests

First group, 2 June to 25 June

No. of tests[*]	Tank and salinity[**]		Group freq. x gp. size 1-3	Group freq. x gp. size 4-6	Gps. 4-6 as %	Groups 4-6 as % total for temperatures and photoperiods
12	A	f.w.	1141	1019	47.2	
18		s.w.	1720	1520	46.9	**Temperatures**
10	B	f.w.	975	825	45.8	
13		s.w.	1195	1145	48.9	high 47.2%
7	C	f.w.	739	521	41.3	low 46.3%
10		s.w.	838	962	53.4	**Photoperiods**
9	D	f.w.	846	774	47.7	long 47.4%
14		s.w.	1441	1079	42.8	short 46.2%

Second group, 30 June to 31 July

No. of tests	Tank and salinity		Group freq. x gp. size 1-3	Group freq. x gp. size 4-6	Gps. 4-6 as %	Groups 4-6 as % total for temperatures and photoperiods
26	A	f.w.	3368	1312	28.0	
24		s.w.	1906	2414	55.9	**Temperatures**
24	B	f.w.	2918	1402	32.5	
22		s.w.	1959	2001	50.5	high 41.7%
28	C	f.w.	3461	1579	31.3	low 48.9%
23		s.w.	1498	2642	63.9	**Photoperiods**
28	D	f.w.	3024	2016	40.0	long 44.5%
25		s.w.	1787	2713	60.2	short 46.1%

[*]one test consists of thirty observations over a ten minute period.

[**]for details on tank treatments A,B,C and D see Materials and Methods, p. 7.8.

discussed previously.

Selection of equal sizes of fish for testing would eliminate the disrupting effects found previously, i.e. dominance/subordinance effects would be minimized.

B. 1964 Observations

These data fall into two groups, differentiated by a slight change in experimental method (Materials and Methods p. 11). This change reduced the initial effects of opening the doors of the experimental tank, which produced "startle" behaviour for one or two minutes.

Totals of data for all the tests are presented in Table 1, which shows the frequency of group-size multiplied by the size of that particular group. Thus the totals show the number of fish participating in any one group-size. Groups of sizes 1-3 are totalled and presented as a contrast to the totals of sizes 4-6, the stronger aggregations. This 4-6 groups total is also presented as a percentage of the whole to indicate the trends in these gross data (from which the samples were taken later). The effects of salt vs. fresh water can be judged from the right-hand column of the table. The percentages for the temperature and photoperiod effects are shown beside each part of the table.

Since the first group of tests did not show any of the differences expected between salt water and fresh water fish (cf Houston, 1959) the technique was changed to that of the second group of tests. Only these latter data compare favourably

TABLE II

Chi-Square values for each

distribution pattern in the testing tank

Distribution of fish in the 6 sectors	χ^2	Schooling tendency
000006	30	Strong
000015	20	
000024	14	
000033	12	
000114	12	
000123	8	
000222	6	
001113	6	
001122	4	
011112	2	
111111	0	Weak

with the gross effects (Table I).

An analysis of variance has been performed on this second group, using a randomized blocks design. Only the results from one fresh water and one salt water testing tank were used for the analysis data. These were selected randomly from the two fresh water and two salt water tanks used in each trial. To obtain a single index of aggregation, the tests were rescored as follows.

Each of the thirty distributions of fish in the ten minute test was rescored with a chi-square value based on 1:1:1:1:1:1 as the hypothetical distribution for non-aggregated fish. These chi-square values are given in Table II. Each test of thirty chi-square values was summed and the resulting number was named the "aggregation index". This index provided the raw data for the analysis of variance and these are presented as Appendix A.

It was possible to use three replications of each holding tank (treatment) within each of four time units (blocks). The blocks covered a period of 4-5 days and their dates are as follows:

Block No.	Date
1	4 - 9 July
2	16 - 20 "
3	21 - 24 "
4	27 - 31 "

Since the total period was less than one month, it was not expected that seasonal effects would show up in such a

TABLE III

Temperature Effects

Tanks	Temperatures	Blocks				Temperatures Totals
		1	2	3	4	
A and B	9-12°C	5700	4182	4484	4628	18,994
C and D	7°C	5108	6818	4949	4578	21,453
Block totals		10808	11000	9433	9206	40,447

TABLE IV

Salinity Effects

Tanks	Salinities	Blocks				Salinities Totals
		1	2	3	4	
A,B,C,D	freshwater	3448	4986	3757	4336	16,527
A,B,C,D	salt water	7360	6014	5676	4870	23,920
Block totals		10808	11000	9433	9206	40,447

TABLE V

Photoperiod effects

Tanks	Photoperiods	Blocks				Photoperiods Totals
		1	2	3	4	
A and D	8 hrs.	5256	4919	4960	5310	20,445
B and C	16-17.5 hrs.	5552	6081	4473	3896	20,002
Block totals		10808	11000	9433	9206	40,447

Note: data is in terms of the aggregation index (v. text).

TABLE VI

Analysis of Variance for the 1964 Data

(Model I, blocks as fixed effects)

Source of error	Sums of squares	Degrees of freedom	Mean square	$F_{calc.}$	$F_{.05}$	$F_{.01}$
Temperatures	62,986	1	62,986	6.91*	3.99	7.05
Salinities	569,338	1	569,338	62.51**	"	"
Photoperiods	2,044	1	2,044	<1 NS	"	"
Blocks	106,425	3	35,475	3.89*	2.75	4.11
T x S	12,101	1	12,101	1.33 NS	3.99	7.05
T x P	1,087	1	1,087	<1 NS	"	"
T x B	250,277	3	83,426	9.16**	2.75	4.11
S x P	3,186	1	3,186	4 NS	3.99	7.05
S x B	277,699	3	92,566	10.16**	2.75	4.11
P x B	151,084	3	50,361	5.53**	"	"
T x S x P	25,299	1	25,299	2.78 NS	3.99	7.05
T x S x B	9,384	3	3,128	<1 NS	2.75	4.11
T x P x B	80,415	3	26,805	2.94*	"	"
S x P x B	72,635	3	24,212	2.66 NS	"	"
T x S x P x B	122,976	3	40,992	4.49**	"	"
Residual	582,923	64	9,108			
Total	2,329,859	95				

relatively short period of time. The record of seasonal change
in chum fry behaviour recorded by McInerney (1961) shows little
change in less than one month. This will justify the considera-
tion of time-units as blocks in this analysis instead of assuming
that time is a fourth treatment.

The totals for the different treatments are presented
in units of the aggregation index in Tables III, IV and V (p. 19).
All possible interactions between the three different treatments
and blocks were examined in the analysis of variance which is
presented in Tables VI and VII. The Replicate Tables and the
Total of Replicates Table are presented in Appendix B. Tables
for the interaction analyses are readily compiled from Appendix
B, and are not included here.

Table VI shows the data treated as a Model I analysis.
This model assumes that the block effects are fixed, i.e. that
they are reproducible under the same conditions of sampling.
Here the F-test uses the residual mean square as the denominator.

Of the main effects, the aggregation index is significantly
higher in salt water, at the 1% level. The index is significantly
higher at the lower temperature than at the seasonal temperature,
at the 5% level. Photoperiod effects are not significantly
different. The main effect totals are presented in Tables III,
IV and V (p. 19).

The significant blocks effect indicates that the aggrega-
tion indices summed over all three treatments differ significantly
among the four blocks. The block totals shown in the Total of
Replicates Table (Appendix B) would indicate this.
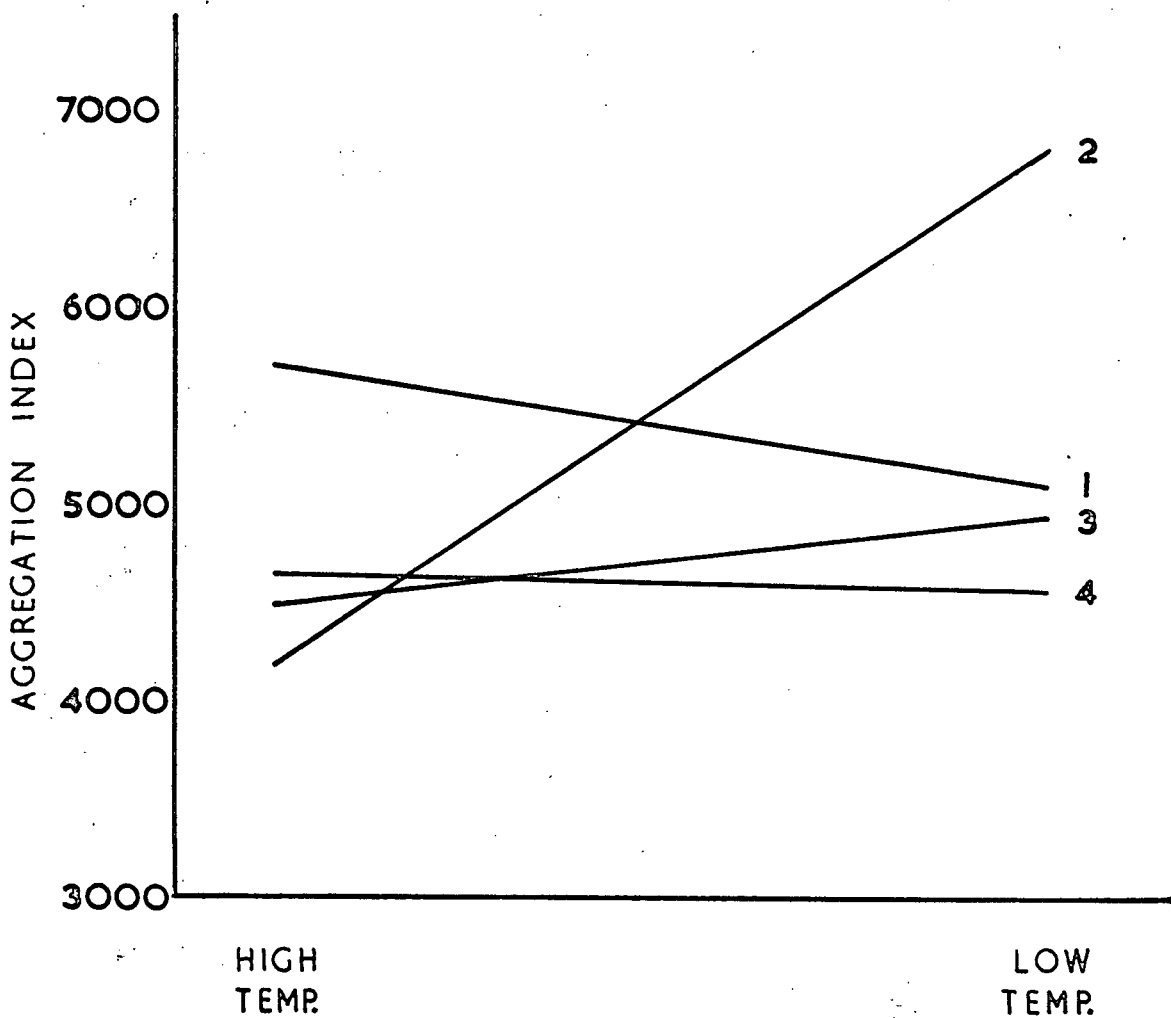
FIGURE 2. TEMPERATURE EFFECTS FOR THE FOUR BLOCKS

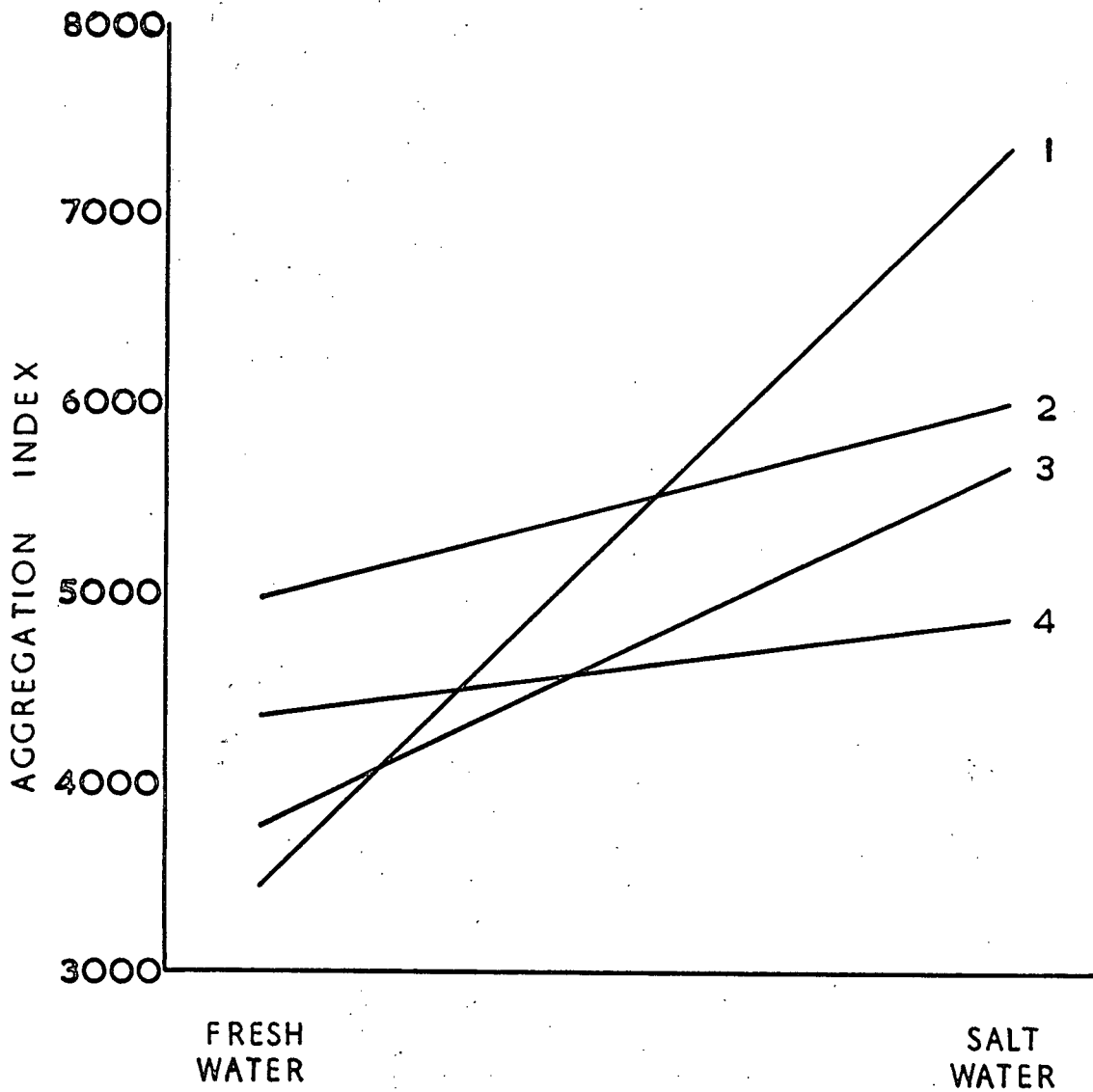# FIGURE 3. SALINITY EFFECTS FOR THE FOUR BLOCKS

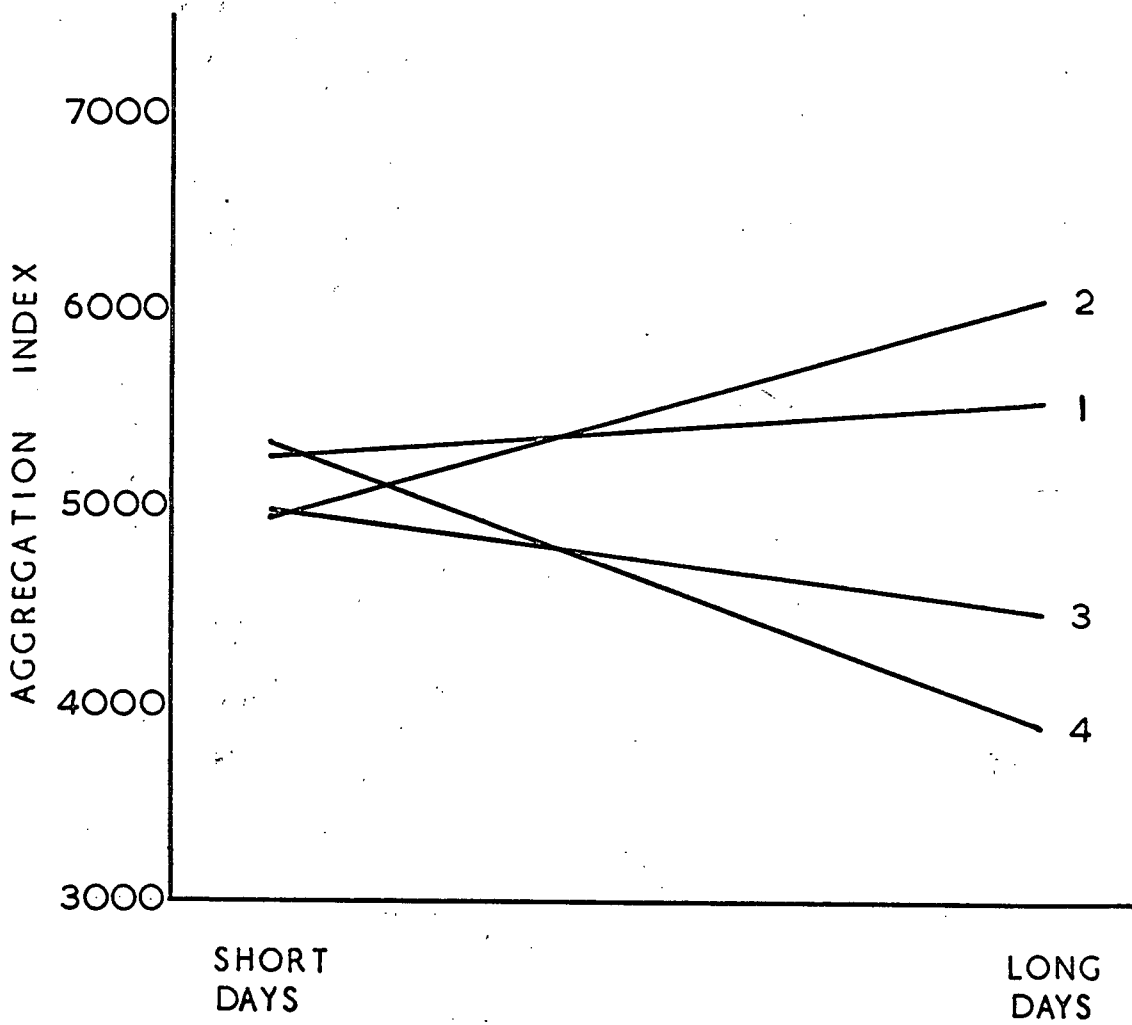# FIGURE 4. PHOTOPERIOD EFFECTS FOR THE FOUR BLOCKS

TABLE VII.

Analysis of Variance for 1964 Data

Mixed Model   (Blocks as Random Effects)

Source of error	Sums of squares	Degrees of freedom	Mean squares	$F_{calc.}$	$F_{.05}$	$F_{.01}$
Temperatures	62,986	1	62,986	<1 NS	10.13	
Salinities	569,338	1	569,338	6.15 NS	"	
Photoperiods	2,044	1	2,044	<1 NS	"	
Blocks	106,425	3	35,475	3.89*	2.75	4.11
T x S	12,101	1	12,101	3.87 NS	10.13	
T x P	1,087	1	1,087	<1 NS	"	
[1] T x B	250,277	3	83,426	9.16**	2.75	4.11
S x P	3,186	1	3,186	<1 NS	10.13	
[1] S x B	277,699	3	92,566	10.16**	2.75	4.11
[1] P x B	151,084	3	50,361	5.53**	"	"
T x S x P	25,299	1	25,299	<1 NS	10.13	
[1] T x S x B	9,384	3	3,128	<1 NS	2.75	4.11
[1] T x P x B	80,415	3	26,805	2.94*	2.75	"
[1] S x P x B	72,635	3	24,212	2.66 NS	2.75	"
[1] T x S x P x B	122,976	3	40,992	4.49**	"	"
Residual	582,923	64	9,108			
Total	2,329,859	95				

[1] Pooled error M.S. = 45,927. No change in significance

Note: in this model the F-tests are as follows –

Mean square	M.S. Tested against
Main effects	The main effect x blocks interaction
Primary interactions (excl. blocks)	Primary interactions x blocks
Main effects x blocks interactions	Residual
Secondary interactions (excl. blocks	Secondary interactions x blocks
Primary interactions x blocks interactions	Residual
Tertiary interaction	Residual

Since the primary interactions between the treatments
do not show any significance at the 5% level, each treatment
is operating independent of the others in the analysis. However,
the treatments all interact individually with blocks. This
would not be expected if the blocks effect was the same for each
of the two levels of the treatments involved. Interaction graphs
of each main effect summed over the other two then plotted for
each block are presented in Figures 2, 3 and 4 (pp. 22-24). Where
the trend lines are divergent an interaction is indicated. In
addition, an approximation of the average regression of the four
lines by eye will reflect the main effect. This is particularly
noticeable in the photoperiod effect (Figure 4) which is not
significant. The average regression line for the four blocks
would have a slope approaching the horizontal.

One other fact is apparent from these figures. It is not
possible to point out one particular block as the cause of all
the interactions. The situation is different for each main
effect.

The three-way interactions are only significant in one
instance, the T x P x B interaction. This is possibly due to
the extremely large differences in the salinity effect of Block I.
(v. Figure 3). The salinity variation may also be responsible
for the significance of the four-way interaction.

A Mixed-Model analysis is presented in Table VII. The
expected mean squares are not given, but can be deduced from
the information given with this table. Here the blocks are
considered to be random; that is subsequent testing should

TABLE VIII

Partial Analysis of Variance for the 1964 Data

Mixed model, considering blocks 1-3 as random effects

Source of error	Sums of squares	Degrees of freedom	Mean squares	$F_{calc.}$	$F_{.05}$	$F_{.01}$
Salinities	653,415	1	653,415	7.19^{NS}	18.51	
Blocks	60,874	2	30,437	2.01^{NS}	3.19	
S x B	181,714	2	90,857	6.24^{**}	3.19	5.08
Residual	699,085	48	14,564			
Total	2,125,630	71				

Note: in this model the F-tests are as follows —

Mean Square	Mean Square Tested Against
Salinities	S x B interaction
Blocks	Residual
S x B	Residual

FIGURE 5. THE SALT WATER MINUS FRESH WATER TOTALS IN EACH BLOCK FOR THE FOUR HOLDING TANKS
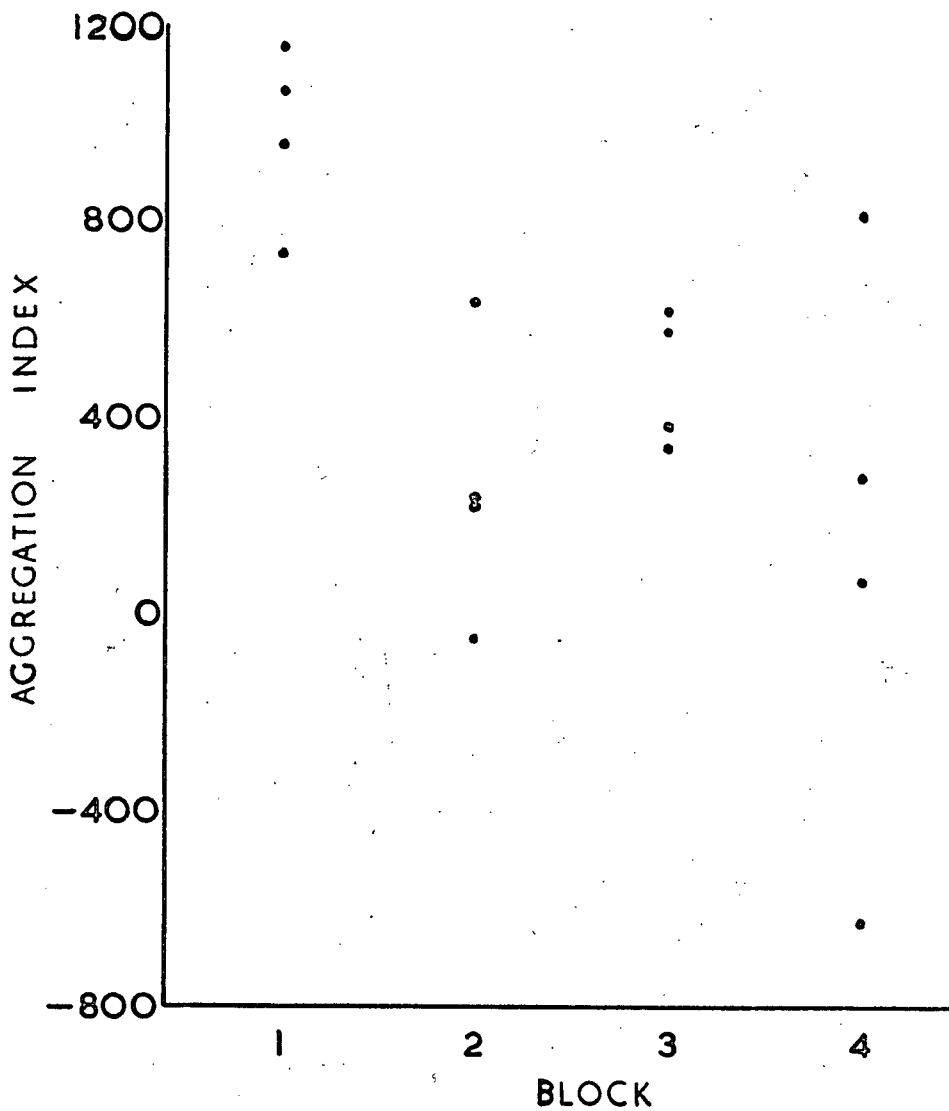
provide a random sample of block effects, not the same four
effects as was assumed in Model I, previously. As the F-test
indicates, the differences between the temperature and sal-
inity treatments in the four blocks do not show up significantly
as they did for the Model I analysis. The outcome of the other
F-tests is the same as before. Since the data in the last block
of the raw data table (v. Appendix A) showed some abnormality
for the salinity treatments in holding tanks A and B, it was
decided to retest the salinities mean square in the mixed model
for the first three blocks only. The analysis of variance is
presented in Table VIII (p. 27). No change in significance was
observed.

As a second check, the data in the mixed model were tested
with a pooled error term (Table VII). Again, no change occurred
in significance.

Finally, Figure 5 is presented in order to illustrate the
variability among blocks. Two aspects are immediately apparent;
the much greater differences between fresh and salt water aggrega-
tion indices in the first block, and the high variability in the
fourth block. This variability corresponded with some unusual
behaviour of the fish from tanks A and B (v. Appendix A) and thus
involved all three treatments. There are two points to be con-
sidered. If the data for the first block are acceptable, then
the lower differences for the other three blocks might indicate
a conditioning effect on the fish. On the other hand, field
notes indicate an unusually high noise level in the building,
during the fourth block, which disturbed the fish. This disturb-

ance <u>might</u> have been responsible for the great variability in
that block. In that case, the values shown in Figure 5 for the
first block could be considered abnormally high, while the means
of the last three blocks could all be said to show the same
block effect. The decrease in difference between salt and
fresh water response from the first block to that of the other
three is then explained as a conditioning effect. With these
considerations in mind, it is proposed to assume that the blocks
effects are fixed. The Model I analysis of variance is there-
fore preferred to the Mixed Model. Further discussion will be
made on the assumption of this interpretation.

DISCUSSION

A. The Experimental Results Compared With Those Of Some Other Workers

The experimental data show the highly significant effect of a salt water environment in increasing the aggregation of chum salmon fry. There were also differences due to temperature (lower temperature correlating with larger aggregations) which were less extreme than the salinity differences. The temperature effect is more readily acceptable since the results are summed over the two types of tank, the large and small ones. In the salinity results, the salinity effect is confounded with a difference in spatial configuration between the fresh water and the salt water holding tanks. This difference in configuration would cast some doubt on the salinity effect by prompting the following question: is the salinity effect real or is it due to the difference in tank sizes or density, or the size of the population tested? As discussed fully below, McInerney (1963) found no conditioning effect with repeated tests on coho fry and Okuno (1963) found tank size did not affect the behaviour of fishes with "stable schools". It is not considered likely that the salinities effects are due to anything other than fresh/salt water differences per se.

One of the disadvantages in using the small tanks was that fish would be re-sampled more frequently than in the more heavily populated large ones. However, McInerney (1963) demonstrated that his salinity preference phenomenon was not an artifact

due to re-sampling (i.e. conditioning). In the present exper-
iment, the fish were held in the testing tanks for a period of
two hours once every 36; they were never fed in these tanks.
The possibility of conditioning is considered to be unlikely.

Secondly, Houston (1959) claimed that the loss of the
previous maximum swimming speed in freshwater chums transferred
into salt water for a few hours was a situation the fish would
have to face all their life in such an osmotic environment.
The chums used in the present experiment were never swimming
so rapidly that the aggregations broke up because of the
inability of the fish to keep together. In fact the salt water
fish were generally more actively swimming round the tank than
were the fresh water fry. In comparison with Houston's findings,
it is considered that any impairment of the swimming ability
in the fish acclimated to salt water would not have been great
enough to produce the observed differences in the aggregation
index.

The third problem in interpreting the results of the
salinity treatment is one of density and the restriction of
movement. Okuno (1963) reported that some marine fishes were
more aggressive when placed in small tanks than they were in
the sea. There was no tendency for aggressiveness in strongly
schooled fishes when placed in the small tanks. Okuno also
reared fish in these tanks. He found again that the behaviour
of strongly schooled fishes ("fishes forming stable schools")
was not changed in the smaller tanks; the fish which formed
"unstable schools" would become more aggressive in smaller tanks

than they were in a large one. Most of the fish Okuno worked
with were larger than salmon fry. Since the tanks used in this
present experiment would be considered small by Okuno, it is
not thought that the size difference in the two types of holding
tank would affect the behaviour of fry in the testing tanks.
Certainly aggression was not higher in the salt water (smaller
tank) fish in my experiment. On the contrary, the impression was
that the fresh water fish were more aggressive.

B. The Biological Significance of the Experimental Results

i) Salinity effects

When diadromous fish are transferred between salt and
fresh water, any change in behaviour would without doubt correlate
with changes in physiology. In nature, changes in physiology
would probably precede changes in behaviour. Correlations between
the migration cycles of salmon fry and the activity of the
thyroid gland have been reported by Hoar and Bell (1950), Hoar
et al (1952), Baggerman (1960) and Eales (1963b).

Hoar (1953) pointed out that elevated temperatures and
increased thyroid activity sometimes modified reactions to
current and hastened downstream movement. He also stated

"Thyroid glands are normally quiescent in schooling
juvenile anadromous fish ... thyroid hormone is not normally
involved in any particular way during seaward movement of these
migrating species. However a prolonged stay in fresh water
produces an intense activity in the thyroid tissue. There is
evidently an increased demand for thyroid hormone in connexion
with osmotic regulation of a fish physiologically prepared
for sea water." (Hoar, 1953, p. 440).

Eales (1963b) thought that chum salmon had relatively inactive thyroids at the migration period. Activity in this gland increased when the fry were artificially retained in fresh water. Baggerman (1960) also found high thyroid activity in fry retained in fresh water. Eales (1963a) suggested that such an increased thyroid activity might be brought about by the increased metabolism of the fry coupled with the low iodine level of the fresh water.

These findings must be borne in mind when considering the salinity effect on chum aggregation. The thyroid may influence migratory behaviour but to what extent it does is uncertain.

There are two ways of interpreting the differences in aggregation between the fresh and salt water chum fry. The first is that the difference is due only to the artificial retention of the migrating fish. This would suggest a pathological condition due to "osmotic stress". The discussion by Eales (1963a) would accept this state, while Baggerman (1960) is contradictory. This "osmotic stress" was not high enough to cause the premature death of the fish in my study and will not be considered relevant.

The second interpretation is in ethological terms. The increasing photoperiod leads to greater activity and an ionic imbalance in chum fry, according to Eales (1963a); this results in increased thyroid activity. This is contradictory to Baggerman (1960) who would consider that the photoperiod (pituitary) effect was directly on the thyroid. Either the ionic imbalance of

Eales or the pituitary effect of Baggerman is to be considered
the stimulus releasing appetitive behaviour. The appetitive
behaviour is the increased activity, or "migration-disposition"
of Baggerman (1960). The manner in which such increased
activity results in migration is not completely shown (c.f.
Hoar (1951), Neave (1955) and Hoar (1956) in the Introduction).
The final result is the same, the entry into salt water. In
salt water either the increase expected in thyroid activity
(c.f. Eales, 1963a), the more available iodine (c.f. Baggerman,
1960) or some other factor acts to trigger the consummatory
behaviour: this is the strong aggregative behaviour of the
fry in salt water. If the change in the osmotic environment
does trigger off a change in behaviour, it could be considered
a releaser in the Lorenzian model of innate behaviour patterns
(c.f. Tinbergen, 1951).

ii) Temperature effects

If the temperature effect is correlated with thyroid
activity in migration, it can be appreciated when the period
of migration is considered. The chum fry move down into cool
Pacific waters before the temperature of the natal streams is
anywhere near the summer maximum. Temperature effects are
probably more important as "stress" factors than as directing
factors in aggregative behaviour. The alternate way of regarding
the temperature effect is to agree that it is statistically valid
but to deny that there is any biological significance. This
argument cannot be decided because the temperatures chosen were

not widely enough separated.

iii) <u>Photoperiod effects</u>

It is surprising that there is no photoperiod effect, considering the positive effects found by McInerney (1963), Baggerman (1960) and Eales (1963a). McInerney, for example, found that the cycle of salinity preference in coho fry was displaced by different photoperiods. In experiments with lake chub (<u>Couesius plumbeus</u>) Ahsan (1964) found that photoperiod was not the dominant factor in the control of the testicular cycle, but rather that temperature was.

It could be suggested that since the migration of chum salmon is relatively rapid, photoperiod might act as a trigger for the initial migratory movement and little else. Both Hoar <u>et al</u> (1957) and McDonald (1960) considered that changing light intensity was responsible for the movement of fish from the bottom of the spawning streams at night. Writing somewhat teleologically, I suggest that there is no reason to expect photoperiod to affect schooling when the more constant stimulus is the salt water in which the fry are destined to live.

CONCLUSIONS

The following principles can be derived from this study of aggregation in chum fry.

Firstly, there is an innate tendency for the fry to school in salt water. The stimulus, appetitive behaviour and consummatory behaviour are described.

Secondly, the retention of chum fry in fresh water correlates with an abnormal aggressiveness and a lethal period probably occurring at a time when the preadapted thyroid and osmoregulatory systems were no longer suited to a fresh water environment. This aggressive behaviour can be considered an artifact since it occurred after the normal migratory period and has not been observed in fish held in salt water.

Thirdly, the effect of temperature suggests that these fish would be intolerant towards the higher temperatures at which the partially-resident sockeye and coho live.

Fourthly, the greater aggregation found in salt water would be appropriate to a fish which is found in definite schools in the ocean but whose downstream migration is probably of individual fish. Directing factors in the stream (especially current) might correlate with schooling in nature but would be absent from the testing apparatus. The rheotactic factor would not be operative in the ocean.

Finally, the biological advantage of schooling in a species of anadromous fish during its oceanic existence is that a mechanism exists to ensure the return of the adult population to the natal stream. Given a normal distribution of "homing ability" in the

school, the homing success will depend on the mean ability of the whole migrant population. If the return journey to the stream was left to the erratic wanderings of each individual fish, some would be expected to home more accurately than most. Others, however, would be completely lost. The advantages of schooling in these homing fish would seem to support the philosophical proposition that the whole is greater than the sum of its parts (c.f. Brock and Riffenburgh, 1960).

The situation is entirely different in the spawning streams. Here there is no disadvantage to not being schooled. Increasing temperature and photoperiod trigger the migration of these fish by causing them to swim out of the gravel and into the current. The constant seaward flow of the river will ensure that the migration is accomplished.

In conclusion I would like to point to two aspects of this study which remain to be clarified. The first is the question of spatial configuration. Is it possible that the behaviour of the salt water fish was altered by their confinement to the small tanks? These tests should be repeated with the fish in similar tanks in order to prove conclusively the salinities treatment effect. On the basis of the present study it is claimed that the positive effects of salinity and temperature are real, just as is the failure of the photoperiod treatment to show significance.

The last point is that since seasonal differences are likely to occur, the experiment should be started with the fry as young as possible. The study could then be conducted from an ontogenetic viewpoint (c.f. Shaw, 1960, 1961). This would

provide a fuller picture of the schooling phenomenon in these small fish. The apparatus is considered both useful and suitable for this purpose.

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APPENDIX A

Raw Data for Analysis of Variance

Dates in July	Block No.	Salinities	Holding tanks*(P.p. and temp. treatments)			
			A	B	C	D
4	1	Fresh water	----	444	278	224
6			372	298	142	----
7			196	298	----	400
9			298	----	204	294
16	2		318 [1]	232	306	----
17			274	292	----	370
18			264	----	554	388
20			----	624	740	624
21	3		372	218	563	----
22			408	312	----	416
23			264	----	156	250
24			----	212	296	290
27	4		278	512	250	----
28			294	366	----	466
29			----	----	240	274
30			372	400	354	----
31			----	----	----	530
4	1	Salt water	----	742	542	546
6			480	672	666	----
7			608	784	----	564
9			508	----	482	766
16	2		425 [1]	212	782	----
17			274	445	----	640
18			382	----	628	466
20			----	440	826	494
21	3		528	664	600	----
22			312	266	----	492
23			542	----	454	538
24			----	386	346	548
27	4		622	334	348	----
28			522	162	----	386
29			----	----	498	332
30			614	152	280	----
31			----	----	----	620

*Units are in terms of the aggregation index.
[1] These two data were missing but were calculated.

APPENDIX B

Replicate Tables

1st Replicate

Treatments		Blocks				Treatments
Tank	Salinity	1	2	3	4	Totals
A	f.w.	372	318*	372	278	1340
	s.w.	480	425*	528	334	1767
B	f.w.	444	232	218	512	1406
	s.w.	742	212	664	334	1952
C	f.w.	278	306	563	250	1397
	s.w.	542	782	600	348	2272
D	f.w.	224	370	416	466	1476
	s.w.	546	640	492	386	2064
Block Totals		3628	3285	3853	2908	13674

2nd Replicate

A	f.w.	196	274	408	294	1172
	s.w.	608	274	312	522	1716
B	f.w.	298	292	312	366	1268
	s.w.	672	445	266	162	1545
C	f.w.	142	554	156	240	1092
	s.w.	666	628	454	498	2246
D	f.w.	400	388	250	274	1312
	s.w.	564	466	538	332	1900
Block Totals		3546	3321	2696	2688	12251

3rd Replicate

A	f.w.	298	264	264	372	1198
	s.w.	508	382	542	614	2046
B	f.w.	298	624	212	400	1534
	s.w.	784	440	386	152	1762
C	f.w.	204	740	296	354	1594
	s.w.	482	826	346	280	1934
D	f.w.	294	624	290	530	1738
	s.w.	766	494	548	620	2428
Block Totals		3634	4394	2884	3322	14234

*Missing data v. Snedecor (1959), p. 312.

APPENDIX B (Continued)

Total of Replicates Table

| Treatments		Blocks				Treatments
Tank	Salinity	1	2	3	4	Totals
A	f.w.	866	856	1044	944	3710
	s.w.	1596	1081	1382	1758	5817
B	f.w.	1044	1148	742	1278	4208
	s.w.	2198	1097	1316	648	5259
C	f.w.	624	1600	1015	844	4083
	s.w.	1690	2236	1400	1126	6452
D	f.w.	918	1386	956	1270	4526
	s.w.	1876	1600	1578	1338	6392
Block totals		10808	11000	9433	9206	40447

APPENDIX C

Mortality of fry in the summer of 1963

These are the most accurate and most objective of the 1963 data.

The graph following shows the high mortality of the chum fry at the end of September. Coho fry retained their previously low mortality rate during this period. These data are presented because of their close agreement with Baggerman (1960). Baggerman reported that her fish were healthy until June, when mortality began to increase. By November all her chum fry were dead; her coho were kept in good condition for two years. In salinity preference tests both Baggerman and McInerney (1961) found that chum fry always preferred hypertonic sea water in contrast to fresh water. Baggerman discusses the influence of the thyroid gland and "osmotic stress" on salinity preference, concluding that the thyroid effect is more important. The cause of death in the chums was not explained.

MORTALITY OF FRY IN THE SUMMER OF 1963 (GRAPH)
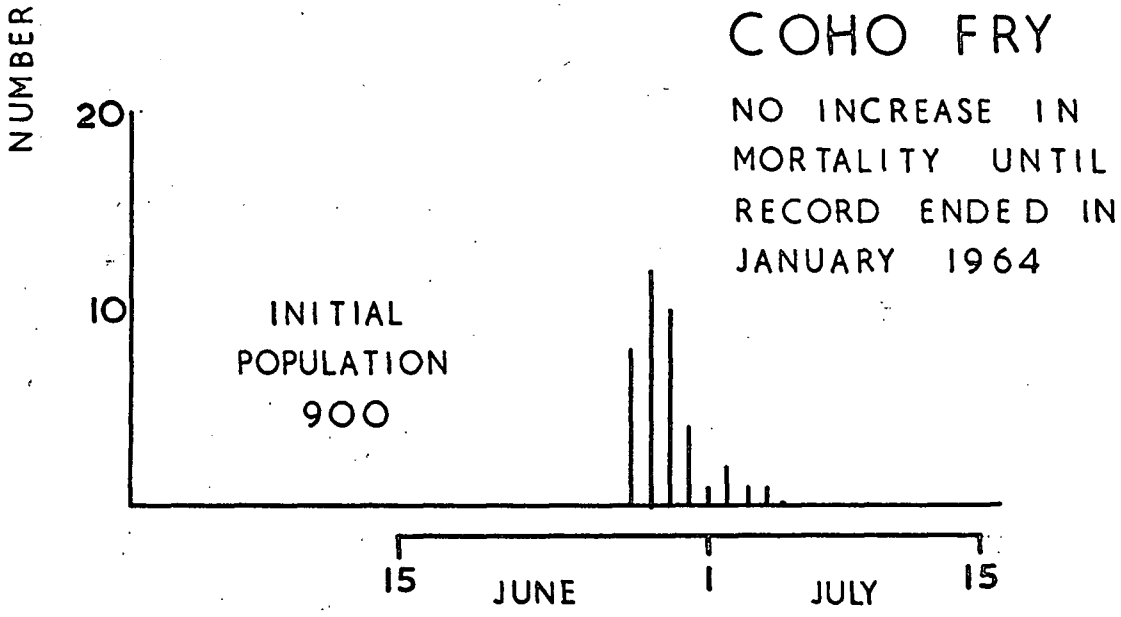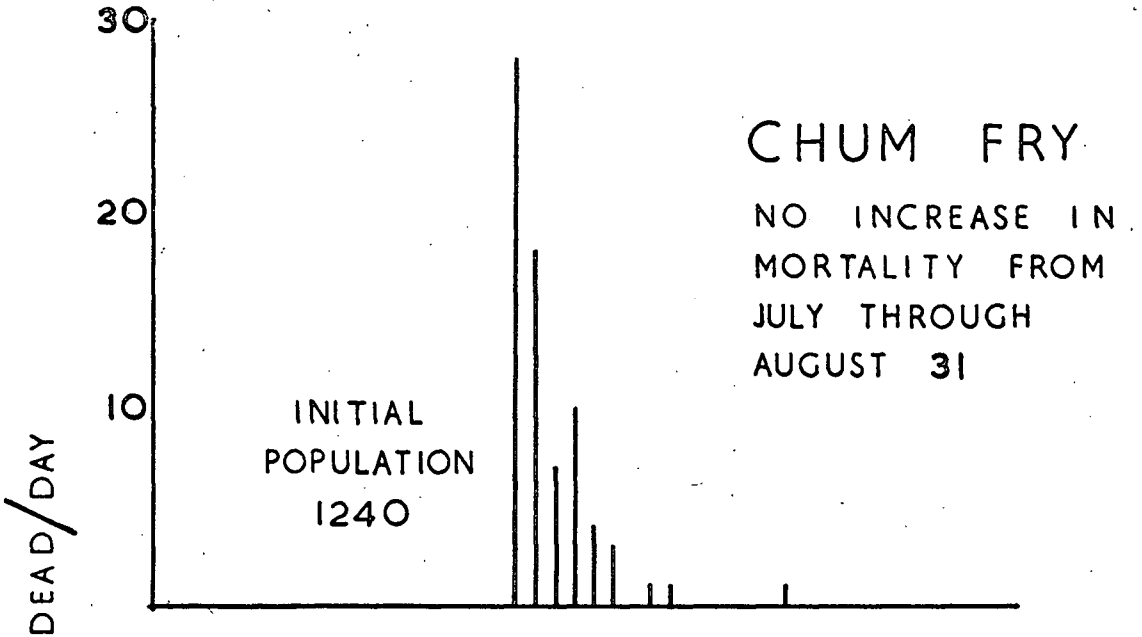
MORTALITY OF FRY IN THE SUMMER OF 1963 (GRAPH, CONTINUED)

CHUM FRY

NO INCREASE IN MORTALITY UNTIL RECORD ENDED IN JANUARY 1964
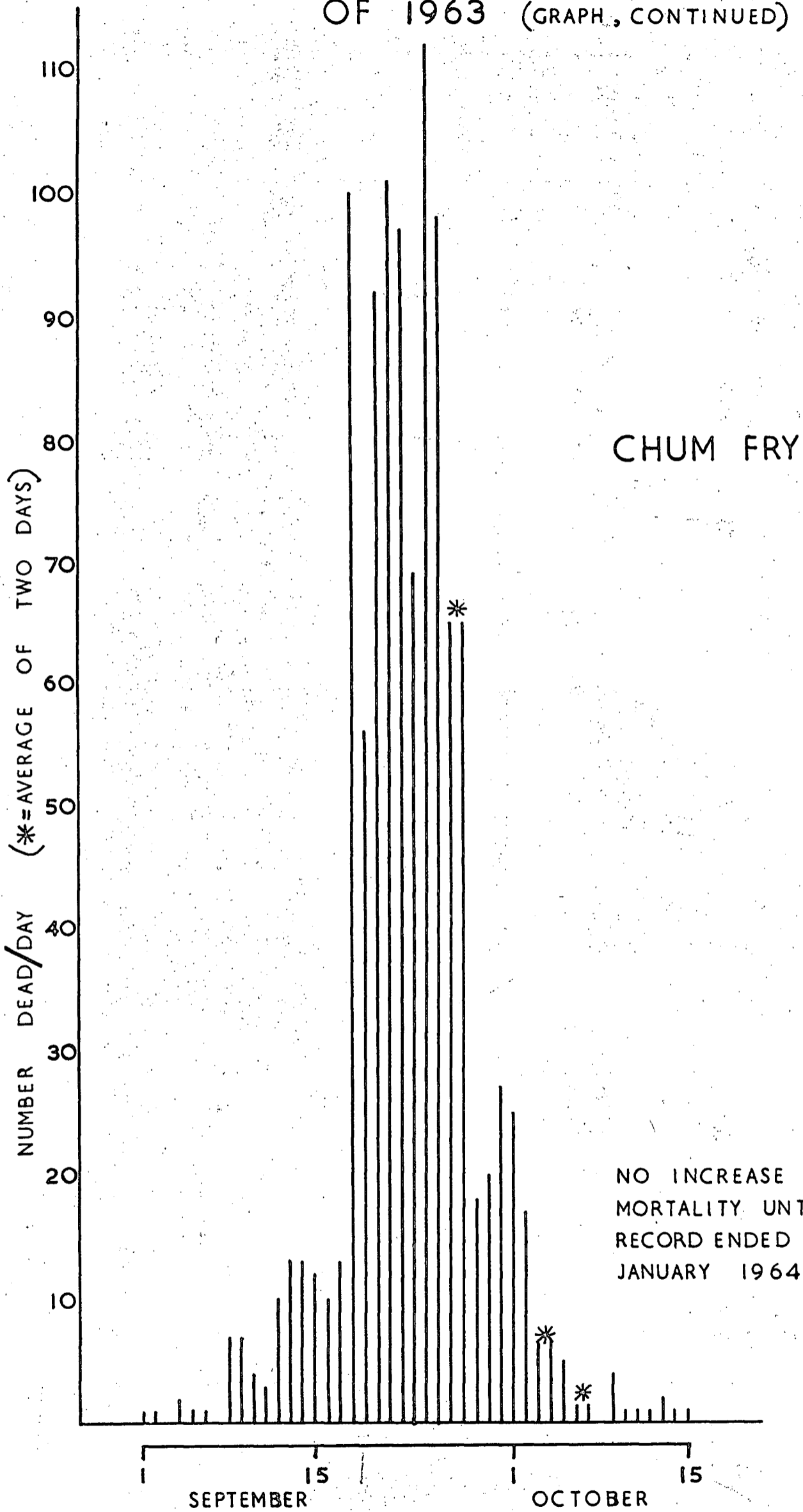
APPENDIX D

<u>References</u> <u>on</u> <u>Schooling</u> <u>Behaviour</u>

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