THE EFFECT OF AGE AND ENVIRONMENTAL FACTORS ON THE VERTICAL MIGRATION AND DISTRIBUTION OF CHAOBORUS FLAVICANS (MEIGEN) LARVAE

by

Mitsuo Teraguchi

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Zoology

We accept this thesis as conforming to the required standard

THE UNIVERSITY OF BRITISH COLUMBIA

October, 1964

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Mitsuo Teraguchi

Department of Zoology

The University of British Columbia,
Vancouver 8, Canada

Date August 28, 1964

ABSTRACT

The effect of age and some environmental factors, especially light, on the vertical migration and distribution of Chaoborus flavicans larvae were studied both in the field and in the laboratory at Corbett Lake, British Columbia during the summer of 1963.

Distribution and migration of Chaoborus larvae were studied largely by frequent horizontal Clarke-Bumpus plankton tows made at 1 metre intervals from the surface almost to the maximum depth of the lake. Marked differences were noted in daytime vertical distribution and diel migration of 5 size (or age) classes of larvae. These size classes probably corresponded approximately to larval instars. Class 0 and 1 larvae inhabited the epilimnion in the daytime throughout the summer, while class 4 larvae were largely confined to the hypolimnion during the day. Class 2 and 3 larvae occupied the epi-, meta-, and hypolimnion in the daytime during June and July, but were found chiefly in the hypolimnion during August and September. Only the older larvae (class 2, 3 and 4) underwent marked diel vertical migration which consisted of 4 phases: 1) daydepth, 2) ascent from day-depth to the surface, 3) gradual descent from surface, 4) rapid descent during dawn. The ascent occurred when subsurface light was rapidly diminishing at dusk, while the descent took place during darkness and was most marked when light started to penetrate the subsurface layers during dawn. Seasonal changes in timing of ascent and descent appeared to be correlated to seasonal changes in time of disappearance of subsurface light intensity

during dusk. The rates of ascent and descent calculated from the analysis of echo traces were 13.6 and 1.1 m/hr respectively. Further analysis of the echo traces revealed that the Chaoborus scattering layer was in contact with the lake basin during daytime and descent, but not during ascent.

Results from observations of larval migration in experimental tubes housed in a dark room corroborated those of the field. Class 2 larvae having similar daytime vertical distribution (surface and 5 m) as class 0 and 1 larvae underwent virtually no diel vertical migration in the tubes, while class 2 and 3 larvae taken from the deeper layers (10-14 m) of the lake did. The diel migration consisted of the same 4 phases observed in the field, as well as a "dawn rise" phase which was particularly evident for class 3 larvae. Complete migration cycles were induced by artificially changing the natural light intensity over an experimental tube during the period of relatively constant light (0900-1900 hours); the larvae responded most markedly to changes in light intensity at the 0-1000 lux range. Experiments indicated that the diel vertical migration of Chaoborus larvae is an exogenous rhythm controlled by light.

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INTRODUCTION

The larvae of the dipteran genus Chaoborus (or Corethra) are macroplankters frequently inhabiting ponds (Miall, 1895; Krogh, 1911) and lakes (Muttkowski, 1918; Juday, 1921; Rawson, 1930; Eggleton, 1932; Berg, 1937; Miller, 1941; Deonier, 1943; Lindquist and Deonier, 1943; Davis, 1955; Dendy, 1956; Wood, 1956; Woodmanse and Grantham, 1961). They are easily recognized by their transparent bodies and black paired air sacs. Although there are several species in the genus, they have similar life histories. The larval stage lasts usually for about 6-7 weeks (sometimes as long as a year), during which time the animals undergo 4 or possibly 5 instars (Muttkowski, 1918; Deonier, 1943; MacDonald, 1956). In general the larvae feed on organisms ranging from phytoplankton to aquatic insects. Deonier (1943) has shown however that the food habits of Chaoborus astictopus differ with instars, the last 2 - 3 stadia preferring cladocerans and copepods.

The most striking aspect of the ecology of Chaoborus is a marked diel vertical migration, a characteristic of many planktonic organisms. Typically the migration cycle involves an ascent of daytime benthic larvae into the limnetic zone (to or near the lake surface) about sunset, and a descent which begins in the following early morning hours and is completed about dawn (Juday, 1921; Berg, 1937; Davis, 1955; Wood, 1956; Hamilton, 1961; Woodmanse and Grantham, 1961). Atypically it consists of an ascent of larvae, inhabiting the deep layers of the lake (but not adjacent to the bottom) during the daytime,

to the upper strata during the night and a subsequent descent to the lower strata during the early morning hours (Dendy, 1956). In both cases the migrating larvae must encounter changes in pressure, dissolved gases (especially oxygen), as well as steep temperature gradients in the summer if the lake is eutrophic.

Few studies have been made on the effects (both diel and seasonal) of age and environmental factors on the basic migration pattern of Chaoborus larvae. Several workers have shown that younger larvae remain in the limnetic zone, while the older larvae only temporarily inhabit it at night (Eggleton, 1932; Berg, 1937; MacDonald, 1956; Wood, 1956; Woodmanse and Grantham, 1961). The age and size at which this marked change in migratory behaviour occurs, or the factors responsible for its timing, have not been determined in any detail.

The purpose of this study was to examine the effect of age and several environmental factors on the vertical migration and distribution of Chaoborus larvae. Such a study may contribute additional knowledge to the phenomenon of vertical migration by planktonic organisms, a subject which has been extensively reviewed (Cushing, 1955; Hardy, 1956; Bainbridge, 1961; Raymont, 1963).

DESCRIPTION OF THE STUDY AREA

Physical and Chemical Features

Corbett Lake is located on the southern interior plateau of British Columbia at an elevation of 1068 m and about 15 km southeast of Merritt. The lake has a surface area of 24.2 hectares, a mean depth of 6.8 m and a maximum depth of 19 m. It becomes thermally stratified early in the season with usually no measurable amount of oxygen in the hypolimnion (below 8 m). The lower layers of the lake contain H_2S. Vernal and autumnal circulation do occur, but are not always complete because the lake is protected from wind action. The lake has a dissolved solid content of 336 parts per million.

The outlet stream at the south-west corner of the lake and an inlet entering the north-east end (Fig. 1) flow only during early spring.

The bottom of the littoral zone extends to a depth of about 4.5 m and is covered with "marl" and dense shoals of chara. The benthal of the limnetic region is covered with "marl" and soft black mud.

Biological Features

The lake contains only stocked populations of rainbow trout Salmo gairdneri and brook trout Salvelinus fontinalis which are occasionally subject to winterkill.

The dominant organisms inhabiting the littoral zone are the amphipod Hyallela azteca, chironomid larvae and gastropod

Gyraulus sp. (Humphreys, 1964).

Numerous plankters inhabit the limnetic zone. Daphnia pulex and Daphnia rosea are dominant cladocerans, while Diaptomus leptopus and Diaptomus nudus are the common copepods. Chaoborus flavicans, C. americanus and C. nyblaei were present in Corbett Lake with C. flavicans being by far the most abundant (about 96% of the individuals sampled).

MATERIALS AND METHODS

Part 1. Field Studies

The air and lake temperatures were measured using a Cole-Palmer (Model 8425) thermistor with a rapid responding probe. Temperature series were taken only at station 1, the deepest part of the lake.

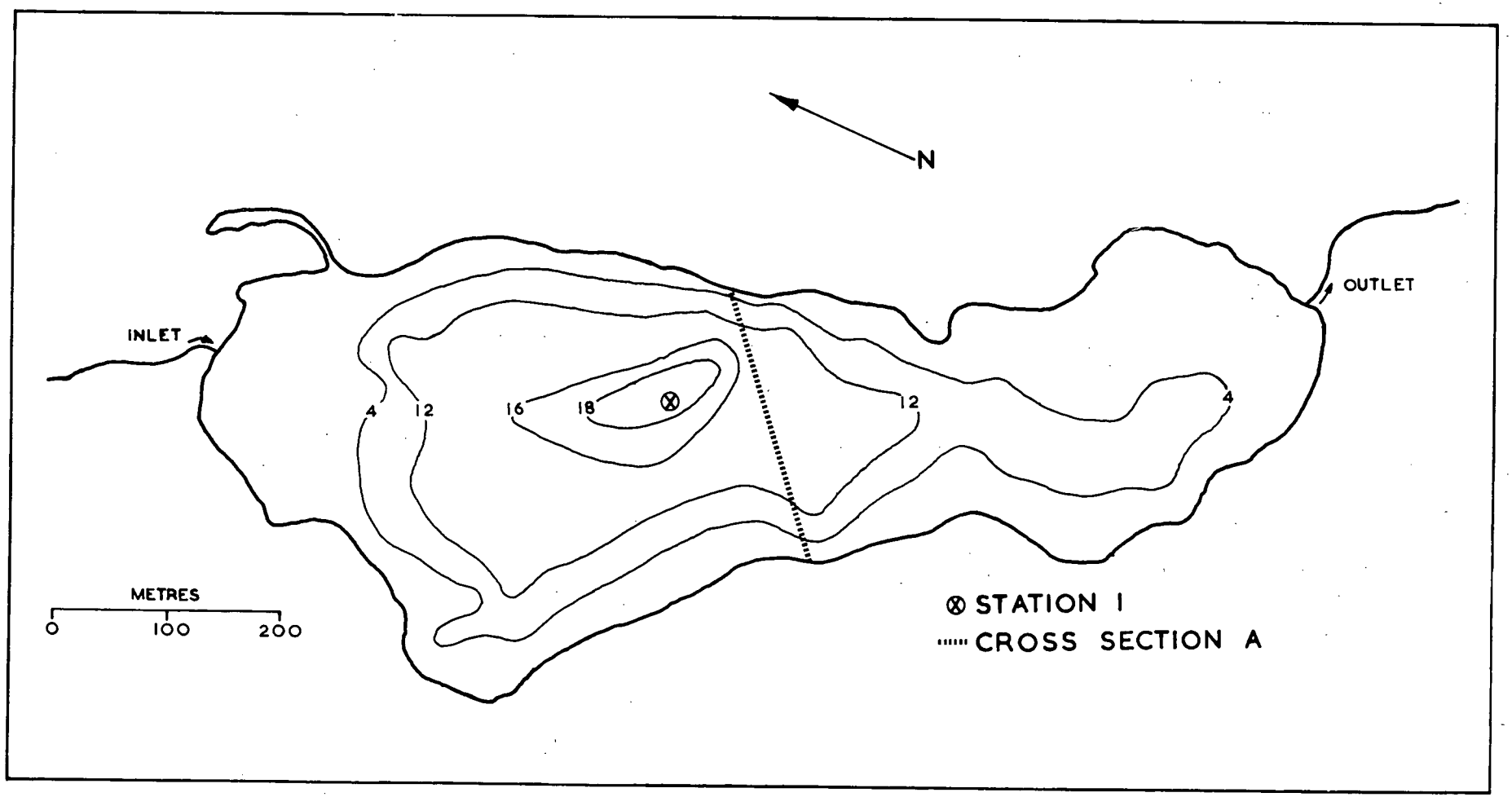
The surface and subsurface light intensities were measured at station 1 with a submarine photometer (Model 15-M-02/1-G.M. Manufacturing Co.) equipped with Weston Photronic Photoelectric "deck" and "sea" cells. Light intensities recorded in micro-ampere units were converted to foot-candles using a Photovolt (Model 200) photometer calibrated directly in foot-candles.

Cloud cover conditions, wind directions and wind velocities were recorded at each sampling period.

Water samples taken monthly with a Kemmerer bottle before or after each 24 hour sampling series were analyzed for oxygen using an unmodified Winkler Method.

A Furuno (Model F-701) 200-kc/sec Sounder was used to make echo traces. In 1962 echo traces were made at station 1

FIGURE 1. Map of Corbett Lake showing contour lines in metres, location of sampling Station 1, Cross Section A, inlet and outlet streams.


N
INLET
OUTLET
4
12
16
18
12
4
METRES
0
100
200
STATION 1
CROSS SECTION A

and Cross-section A (Fig. 1) using a gain of about 5.75 while the boat was moving at about 1.5 knots (2.9 km/hr). In 1963 traces were made only at station 1 using a gain of 6 and a boat speed of about 0.5 knots (2.8 km/hr). Traces were taken usually before and after plankton sampling at station 1 and about every 15 minutes during dawn and dusk at Cross Section A. The scattering layers on the traces have been shown by Northcote (1964) to be largely Chaoborus larvae.

A Clarke-Bumpus sampler fitted with a No. 10 (0.13 mm) nylon netting was attached to a 4 mm diameter wire towing cable. A 13.6 kgm torpedo-shaped lead weight was tied to the end of the cable.

Station 1 was the site of plankton sampling in both 1962 and 1963. The sampler was towed at each sampling depth (surface and every metre almost to the bottom) for 0.5 or 1 minute. Appropriate corrections were made for wire angle. After each tow the net was washed by splashing water on it, while the sampler bucket was cleaned by water squirted from a rubber syringe. Samples were preserved in 10% formalin solution.

Twenty-four hour sampling series were carried out in August and September, 1962 and usually once a month during the summer (June-September) in 1963. Six sampling periods (every 4 hours) were carried out during the 24 hour series in 1962, while 8 were usually maintained during each series in 1963. In the latter year sampling was carried out every 4 hours during the daytime (0800-1900 hours - Pacific Standard Time) and every 2 hours at dawn and dusk periods (0400-0600

hours and 1900-2300 hours). For both years echo traces, light, temperature and oxygen measurements were made during each sampling period.

Field calibration of the sampler was attempted in 1963 in a similar manner to that described by Clarke and Bumpus (1950). The sampler was towed for a 61 m distance at precisely 2.5 knots. Triplicate tows were made at each desired depth (surface 2, 4, 6, 8, 10 and 12 m - uncorrected depths); this was done with and without a No. 10 net attached to the sampler. As the calibration values for the sampler with and without the net were unusually high (Appendix 1), a 4.1 liters/revolution value extrapolated from the study of Yentsch and Duxsbury (1956) was used.

Although a comparable volume of water passed through the sampler (with No. 10 net attached) during triplicate tows, the triplicate samples obtained did not in all cases contain comparable numbers of Chaoborus larvae (Appendix II). The results suggested that the variability was not due to inconsistency in operation of the sampler, but rather to the larvae being clumped in nature.

Total counts were made for all samples collected in 1962 and for most of those obtained in 1963. Estimated counts using a subsampler modified from Elgmork (1959) were made for 1963 samples containing 2000-4000 larvae. The reliability of the subsampler was examined using a chi-square test for randomness (Lund et al, 1958). The subsampler gave random subsamples (Appendices III and IV). One-sixth of a sample was usually

taken for estimating total counts, while 1/2, 1/8 or 1/36 portions were taken for determining length of larvae. Total and estimated counts were made for some samples to check accuracy of estimates.

The distance (in mm) between the posterior end of the thoracic air bladders and the anterior tip of the abdominal bladders was measured in accordance with recommendations of Dr. G. G. E. Scudder. The larvae were laid on the slides on their right side so that the body between the anterior and posterior sacs was extended fully, but not stretched. Thirty to sixty larvae were placed on a standard microscope slide and covered firmly with a cover slip almost equal in dimensions to the slide before adding water.

The larvae were identified to species using the key of Cook (1956). Separation of the three species present were based on the presence and location of an antennal spine, shape of the prelabral appendage, and position of the basal mandibular tooth.

A Wisconsin plankton net having an upper ring diameter of 23 cm and fitted with No. 10 nylon net was used in 1963 to study the horizontal distribution of the Chaoborus larvae in the limnetic zone. Ten total vertical hauls were made each month (June-September) at ten randomly selected stations where the depth was about 14 m. Samples were preserved in 10% formalin solution. All larvae were counted in each sample. A test of randomness (Kutkuhn, 1958) was used to determine the type of horizontal distribution characteristic of the

larvae during the summer.

Part 2. Laboratory Studies

Experiments were carried out at Corbett Lake in a darkroom (3 x 3 x 3 m) having a wooden frame covered with black polyethylene sheets (Fig. 2A). Two plastic tubes (2 m length, 14.5 cm inside diameter and 3.2 mm thick wall) marked off in 20 cm depth intervals were placed inside on a table so that their tops (open ends) just protruded out through holes made in the roof (Fig. 2B). This arrangement made it possible to study the migration under natural and controlled light conditions.

Two shutters made from furnace vents were used to alter the light intensity over the tubes. A sheet of wax paper was placed inside each shutter to diffuse the incoming light. Usually one light shutter was fitted over the top of the tube, while the other was placed over the search unit of the photometer.

Two light recorders were used usually in each experiment. The "deck" cell of the submarine photometer (Model 15-M-02/1-G.M. Manufacturing Co.) was placed on the roof of the dark room, while the "sea" cell was used inside to record the light gradient along the plastic tube. A Photovolt (Model 514 M) photometer fitted with phototube C and neutral density filters was placed on the ground about 15 m from the dark room to obtain light readings. The light intensity recorded by the photometer at ground level was assumed to represent that at the surface of the tubes. When the surface light over the experimental tubes was changed with the shutter apparatus,

it was measured at ground level with the Photovolt photometer whose search unit was covered with the other shutter having the same degree of closure.

The thermistor described previously was used to record temperature at every 10 cm depth interval in the tube. Unfortunately it was not possible to control water temperature in the experimental tubes as the dark room was not insulated and the tops of the tubes were exposed to the outside.

The unmodified Winkler Method was used to measure the experimental oxygen conditions. Usually water samples from the surface, 100 cm depth and the bottom were analyzed.

Lake water filtered with a No. 10 net was used in all the experiments.

A dim flashlight was used to count larval distribution in the tubes at night.

One-hundred fresh larvae collected from desired depths of the lake with the Clarke-Bumpus sampler were used in every experiment.

Diel vertical migration experiments were attempted in July, August and September of 1963. Each experimental 24 hour series consisted of 16 observation periods; every 2 hours during daytime and every hour during dusk and dawn. Each observation consisted of counting larval distribution for every 20 cm depth interval, measuring light intensity (if necessary), and recording water temperature. Water samples were taken at the end of each experiment. Larvae used were preserved in 10% formalin solution.

FIGURE 2A. The darkroom used to study experimentally the diel vertical migration of Chaoborus flavicans larvae.

FIGURE 2B. Cross sectional view of the darkroom showing the arrangement of the plastic tubes used to hold the Chaoburus flavicans larvae.

The importance of light in controlling vertical migration of the larvae was investigated in August and September of 1963. One tube used as a control was exposed to naturally changing light conditions, while the other was exposed to artificially changing light intensities. The experiments were carried out during the period of relatively constant light conditions (0900-1800 hours). Observations were made every 15-30 minutes. After recording the larval distribution at a given light level, the intensity was changed and measured. Temperatures were measured for both tubes before and after each experiment, while water samples were taken only after finishing the experiment. Larvae used in the experiments were preserved.

RESULTS

Part 1. Field Studies

Larval Size (or Age) Classes

Large numbers (about 2878) of larvae were identified and measured to the nearest one-tenth mm bladder-bladder length in order to determine the number and length ranges of larval size classes. The animals used were taken from samples collected in 1963 during the 1100 hour sampling period of the June, July, August and September field series. All larvae of small samples (60 larvae) were measured and identified, but only fractions of the large samples were examined. *Chaoborus flavicans* was by far the principal species (96% of the larvae sampled), so other species (*C. americanus* and *C.*

nyblaei) were not considered in the study.

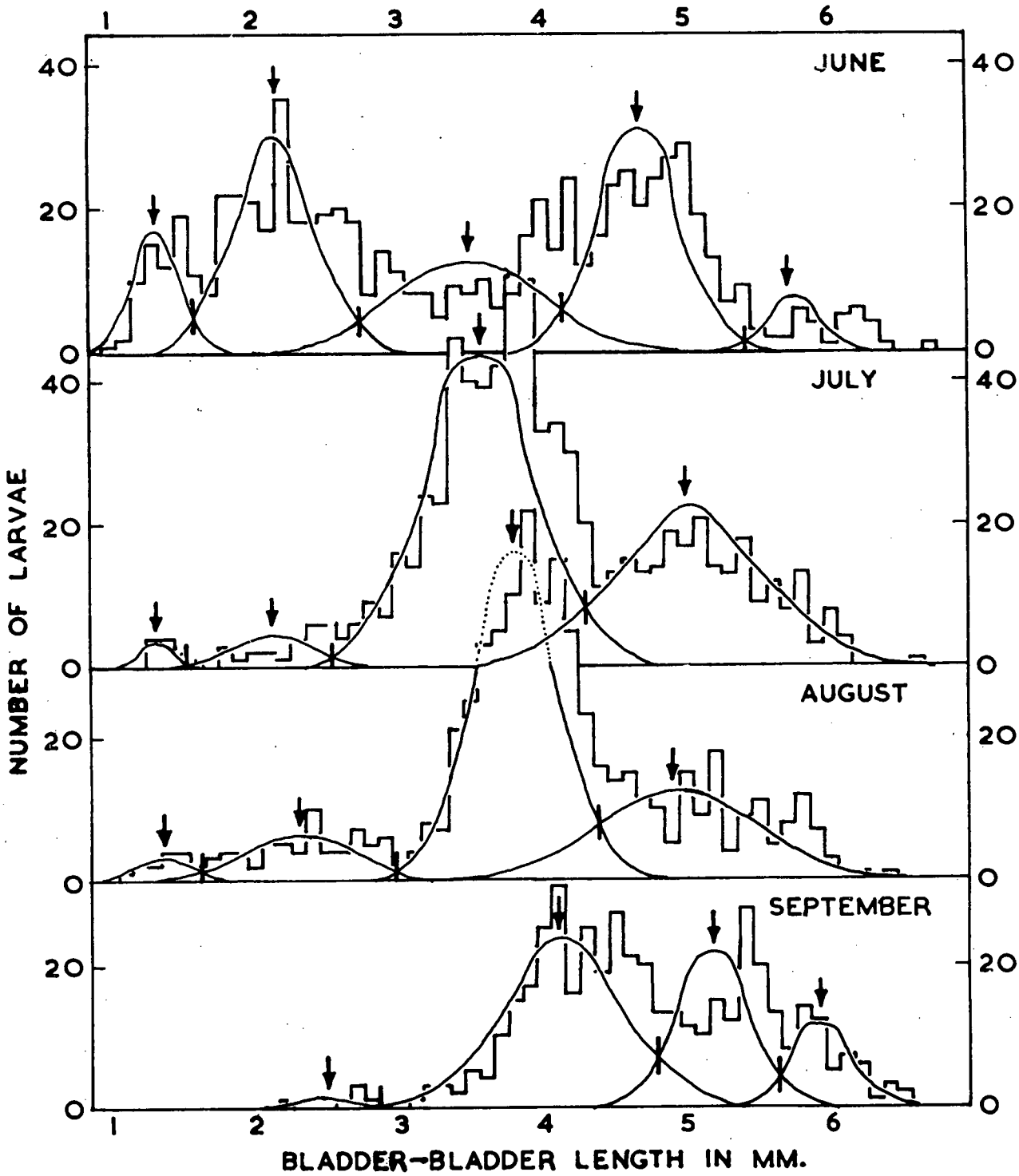
The length frequency data of each month were subjected to probit analysis (Cassie, 1954) to determine objectively the means representing size classes. These means were then used to calculate the corresponding theoretical normal curves using the method described by Snedecor (1957). The points of overlap between adjacent curves were used to determine the length ranges. It was assumed therefore that each class would contribute to and gain from the adjacent class (or classes) similar numbers of larvae. The smallest and largest lengths of each class were determined for each month and were averaged to obtain length ranges of the classes.

During the summer of 1963 there were 5 size (or age) classes as indicated by vertical arrows representing means (Fig. 3). All 5 occurred on June 17, whereas only 4 were present during the remainder of the summer. The first 4 classes were present on July 20 and August 18, while the last 4 occurred on September 21. The average bladder to bladder length ranges of class 0, 1, 2, 3, and 4 were respectively 0.87-.157, 1.58-2.77, 2.78-4.39, 4.40-6.11 and 6.12-6.51 mm.

The Validity of the Larval Size (or Age) Classes as Instars

Since an unconventional measuring method (bladder-bladder length) has been used, the question arises as to whether these size classes represent actual instars. The number and length ranges of larval instars have not been determined for C. flavicans. MacDonald (1956), using the conventional head capsule measurement, has established the existence of four

FIGURE 3. The length frequency distribution of the Chaoborus flavicans larvae collected during the 1100 hour sampling periods of the 24 hour field series of June 16-17, July 20-21, August 17-18 and September 21-22, 1963. The vertical arrows indicate means, while the vertical bars mark the points of overlap of the calculated theoretical normal curves.


JUNE
JULY
AUGUST
SEPTEMBER
NUMBER OF LARVAE
BLADDER-BLADDER LENGTH IN MM.
0
20
40
1
2
3
4
5
6

instars for two tropical species, C. anomalus and C. species B. Deonier (1943), using another recognized method (modification of the mouth parts and anal fin), has established four instars for C. astictopus of Clear Lake, California. He also mentions that the overwintering larvae of the Clear Lake gnat are significantly larger than those of the last instar; an observation similar to that made by Muttkowski (1918) for C. punctipennis of Lake Mendota, Wisconsin. It appears therefore that temperate Chaoborus larvae can develop through five instars which may be represented by five larval age (or size) groups based on the body length measurement.

As the average total length measurement of class 0 larvae (determined by bladder-bladder length measurement) is similar to that (about 1.75 mm average length) of newly hatched C. flavicans larvae measured by Berg (1937), larval class 0 must represent the first instar. Similarly the average total lengths of class 3 and 4 larvae were similar to those (10.8 and 11.2 mm mean length) of two oldest larval groups ever encountered by Berg in Esrom Lake, Denmark. As Berg states that larvae having 11.2 mm mean length overwintered, they might represent a fifth instar, thus making the fourth larval class of Corbett Lake equivalent to the fifth instar. By similar reasoning the third larval class present in Corbett Lake may be considered the fourth instar. Therefore the seasonal changes in abundance of the larval age groups may be attributed to animals undergoing instar changes.

Abundance of Larval Groups and their Daytime Vertical Distribution

The data used to determine the numbers and average ranges of the size (or age) classes were analyzed in greater detail to show the abundance and daytime vertical distribution of the larval groups on a diel and seasonal basis. Larval fragments having heads were totalled, and appropriate numbers of them were allotted to each class. All larvae encountered were assumed to be C. flavicans as the inclusion of very few of the other species would not affect the results for the major species. The abundance of larvae at each sampling depth were expressed in numbers per 100 l; the actual or estimated total counts were divided by the volume of water supposedly passed through the sampler during each tow. Confidence limits were calculated for all total estimated counts (Appendices V, VI, VII and VIII).

The relative abundance of larvae in each class changed with the progression of summer in 1963 (Fig. 4). Class 0 and 1 larvae, having their greatest abundance in June, decreased markedly in numbers until virtually none were present by September. Class 2 animals decreased slightly seasonally, while the class 3 larvae increased in abundance. The few class 4 larvae became slightly more abundant by September.

There were marked differences in the vertical distribution of larvae with respect to size during the daytime (Fig. 4). The majority of the class 0 and 1 larvae inhabited the surface to 8 m zone (the warmer, oxygenated epi- and metalimnion) during the entire summer, while the few class 4 larvae occupied

the 8 to 13 m region. Conversely the class 2 and 3 larvae underwent marked seasonal changes in daytime vertical distribution.

The class 2 animals occuppied the surface to 12 m zone on June 17 and July 20 with maximum density occurring at 3 m in June and somewhat in July (Fig. 4). In contrast most of them inhabited the 7 to 12 m region on August 18 and September 21 with greatest abundance at about 10 m on both occasions.

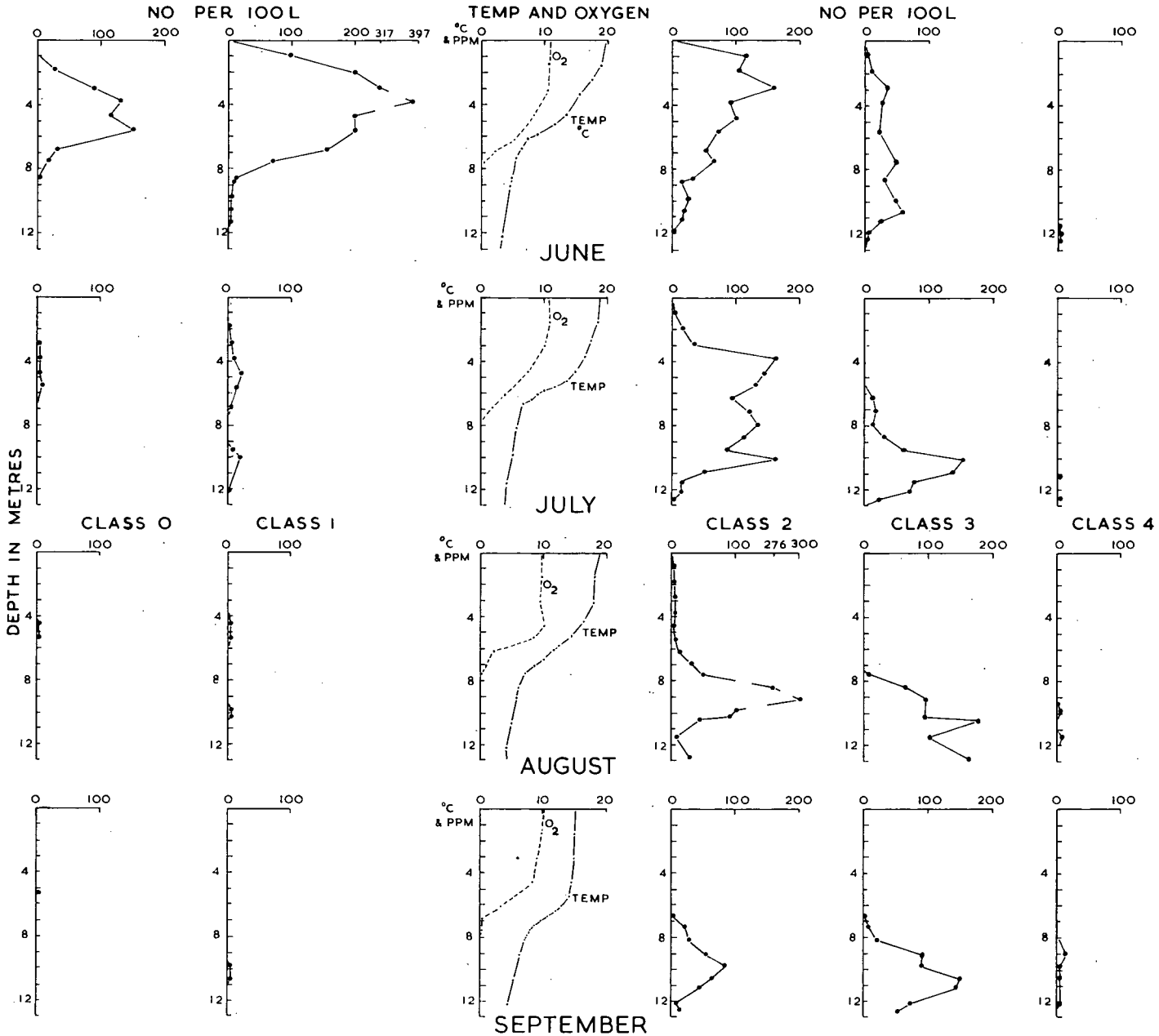
The class 3 larvae showed a trend similar to that of class 2 animals (Fig. 4). They occuppied the surface to 12 m zone on June 17 with maximum density occurring at about 11 m. In contrast most of the class 3 larvae inhabited the 7 to 13 m (or perhaps deeper) region on July 20, August 18, and September 21 with greatest abundance being at about 10.5 m.

The seasonal shift in daytime vertical distribution of class 2 and 3 larvae was not correlated to changes in light penetration. The depth at which light could no longer be measured with the submarine photometer remained at about 15-16 m during the 4 months.

Seasonal Variation in Horizontal Distribution

Because the analysis of triplicate samples taken at each of several depths in 1962 (August 12) and 1963 (June 16) revealed that the Chaoborus larvae might have a clumped horizontal distribution, a sampling design of Ricker (1938) was used during the summer of 1963 to study this aspect more extensively. Ten total vertical hauls were taken during the

FIGURE 4. The daytime vertical distribution and relative abundance of the larval classes of C. flavicans in Corbett Lake based on samples collected during the 1100 hour sampling periods of the 24 hour field series of June 16-17, July 20-21, August 17-18 and September 21-22, 1963; oxygen and temperature conditions are also shown for each period.


NO PER 100 L
TEMP AND OXYGEN
NO PER 100L
°C & PPM
O2
TEMP °C
JUNE
JULY
AUGUST
SEPTEMBER
DEPTH IN METRES
CLASS 0
CLASS 1
CLASS 2
CLASS 3
CLASS 4

late afternoon or early evening of each month (1942-1636 hours on June 16, 1835-1830 hours on July 20, 1903-1955 hours on August 17 and 1738-1836 hours on September 21). The variance over mean ratio value of 1.88 calculated with the method of Kutkuhn (1958) was used to determine whether the larvae showed a clumped (negative-binomial) or random (Poisson) distribution.

The variance over the mean ratio calculated from the sampling data revealed that the larvae had a clumped horizontal distribution on each sampling day, but the degree of clumping increased during the summer (Table 1). The results may indicate a seasonal increase in the aggregation behavior of the larvae.

Differential Migratory Behavior of the Larval Classes

Samples collected during the 1100, 2100 and 0500 hour sampling periods of the monthly 24 hour field series (June 17-18, July 20-21, August 18-19 and September 21-22) of 1963 were used to study behavior of the different larval classes. As 1100, 2000 and 0500 hour periods were chosen to represent times of daytime distribution, maximum ascent (except in September) and maximum descent respectively, any substantial migration undergone by a larval class would be detected in samples taken during these periods. The confidence limits of estimated total counts were calculated (Appendices V, VI, VII and VIII).

The younger larvae (class 0 and 1) underwent virtually

TABLE I. Comparison of the monthly total vertical hauls taken during late afternoon or early evening at randomly selected stations with No. 10 Wisconsin net at Corbett Lake in 1963.

Haul No.	June 16	July 20	August 17	September 21
1	418	251	199	167
2	422	235	205	145
3	436	271	210	214
4	480	167	108	232
5	433	220	139	124
6	447	298	234	137
7	442	297	292	95
8	356	298	156	85
9	459	294	165	111
10	447	249	155	121
Total	4340	2580	1863	1431
Mean ($\bar{x}$)	434	258	186.3	143.1
Sum of Squares	9632	16570	25240	21115
Variance (S^2)	1070	1841	2804	2347
$S^2/\bar{x}$	2.41	7.14	15.08	16.41
X^2	22.19	64.22	135.48	147.55
Probability (p)	0.01-0.005	0.005	0.005	0.005

no diel migration, while the older ones (class 2, 3 and 4) showed marked diel movements (Figs. 5 and 6). The few class 0 and 1 larvae present on August 18-19 showed practically no migration; these larvae were virtually absent in September. Although only few class 4 larvae were present, they nevertheless showed a marked diel vertical migration each month.

There appeared also to be a seasonal trend of progressively fewer older larvae (class 2, 3 and 4) undergoing ascent (Figs. 5 and 6). The trend was particularily evident for class 3 and 4 animals. Virtually all the class 3 larvae inhabiting the 8-13 m zone during the daytime ascended on the 2100 hour period of June 17 and July 20. About 80% of the class 3 animals moved up on the 2100 hour period of August 18, while only about 60% of the larvae ascended on this period of September 21. Similarily practically all the class 4 larvae occupying the 11 to 13 m depths during the daytime ascended during the 2100 hour period of June 17 and July 20, while fewer of these larvae moved up on the same time period of August 18 and September 19. The discrepancy in the abundance of class 2 and 3 larvae present during the 1100 and 2100 hour periods is probably due to ascent of larvae which inhabited depths below 13 m during the day time. The trend may be correlated to seasonal increase in rate of light intensity change at dusk as indicated by the isolumes plotted in Figure 9. It can be seen that the isolumes (.1, 1.0, 10 and 100 luxes) disappear on June 17 and July 20 (1920-2110 hours) at much slower rate than do those on August 18 (1920-2110 hours)

FIGURE 5. The vertical distribution of class 0, 1, 2, 3 and 4 larvae of C. flavicans in Corbett Lake during the 1100, 2100 and 0500 hour periods of the June 16-17 and July 20-21 series, 1963.

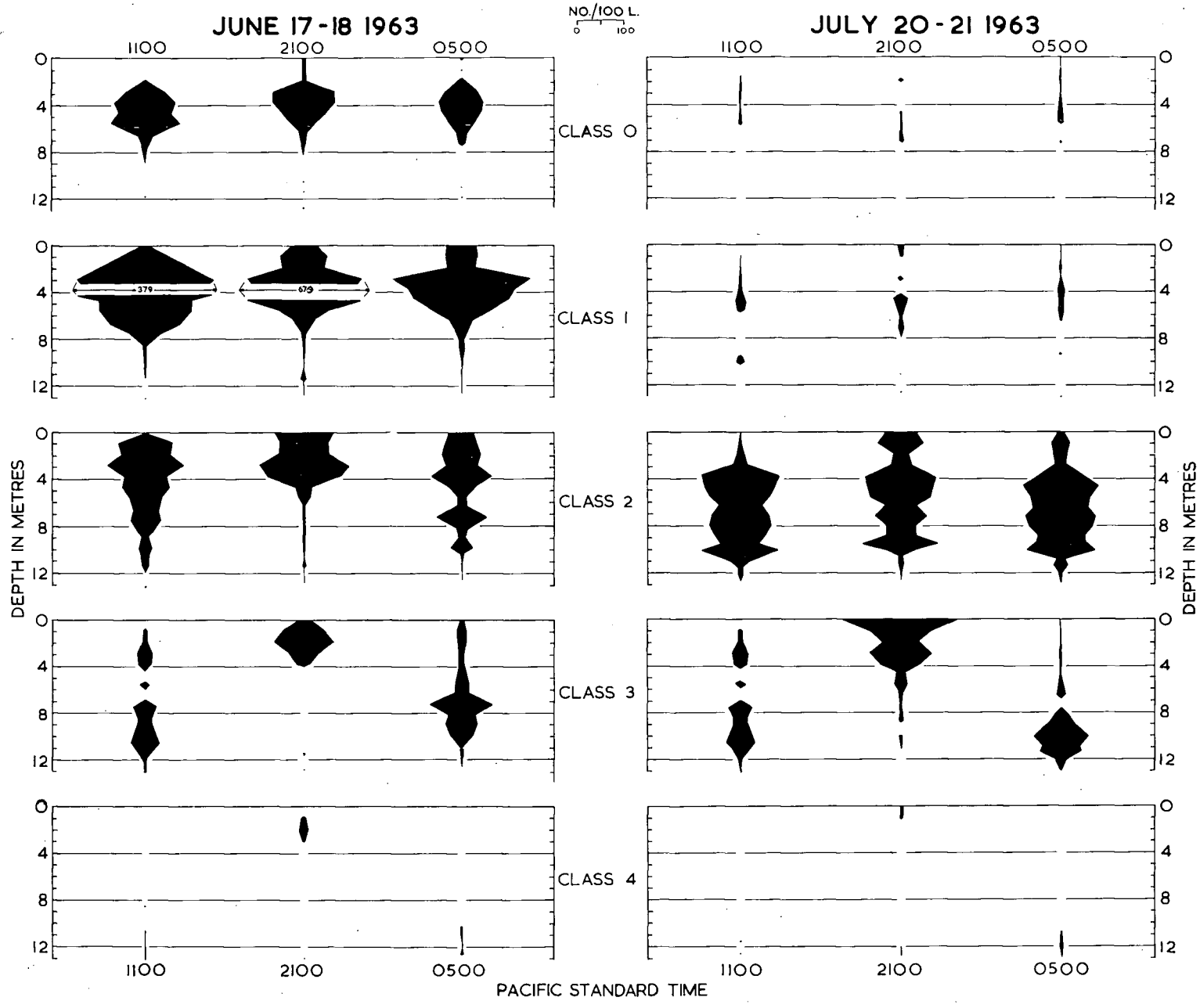
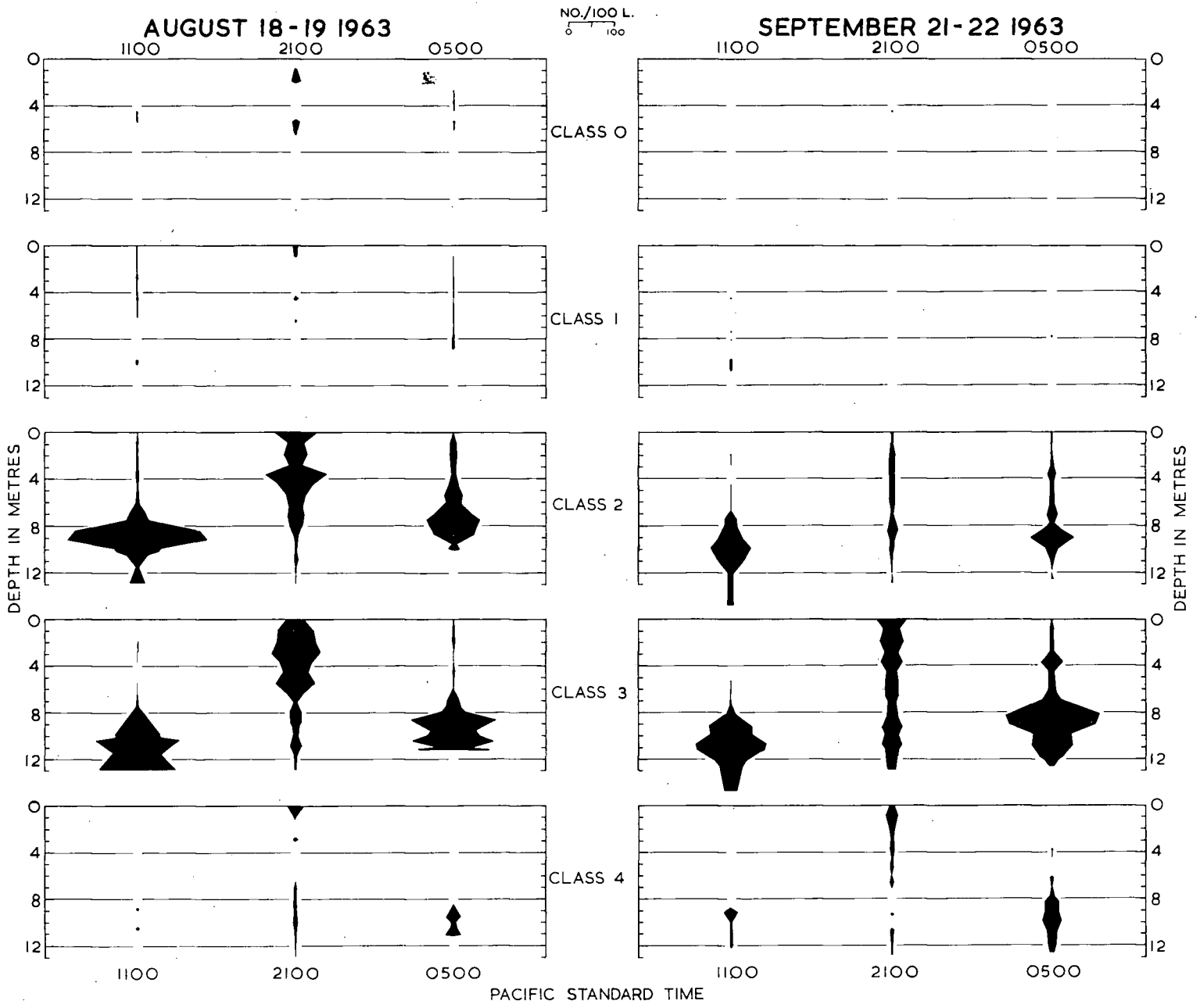

JUNE 17-18 1963
JULY 20-21 1963
NO./100 L.
0
100
1100
2100
0500
CLASS 0
CLASS 1
CLASS 2
CLASS 3
CLASS 4
379
679
0
4
8
12
DEPTH IN METRES
PACIFIC STANDARD TIME

FIGURE 6. The vertical distribution of class 0, 1, 2, 3 and 4 larvae of C. flavicans in Corbett Lake during the 1100, 2100 and 0500 hour periods of the August 17-18 and September 21-22 series, 1963.


AUGUST 18-19 1963
SEPTEMBER 21-22 1963
NO./100 L.
0
100
1100
2100
0500
CLASS 0
CLASS 1
CLASS 2
CLASS 3
CLASS 4
0
4
8
12
DEPTH IN METRES
PACIFIC STANDARD TIME

and September 21 (1520-1920 hours).

Furthermore the class 2 and 3 larvae (especially class 2) appeared to show a seasonal trend for completion of descent to occur progressively earlier (Figs. 5 and 6). About 30-40% of the class 2 larvae occupying the upper 4 metres during the 2100 hour period of June 17 and July 20 descended to lower depths by 0500 period of the following days (June 18 and July 21). In contrast about 60-70% of the class 2 animals inhabiting the upper 4 metres during the 2100 hour period of August 18 and September 21 moved down to lower layers by 0500 period of the following days. This trend may be due to darkness occurring progressively earlier.

Migration Pattern of the Older Larvae

Samples collected during the 0800, 1100, 1530, 1930, 2130, 2330, 0330 and 0510 hour sampling periods of the September 21-22 series of 1963 were used to compare the migratory pattern of the olfer larvae (Class 2, 3 and 4) on a diel basis. Samples taken during the other series (June 17-18, July 20-21 and August 18-19) were not used, as it was virtually impossible to measure and count all the larvae in the subsamples or in samples collected during the 4 series. Confidence limits were calculated for the estimated counts (Appendix VIII).

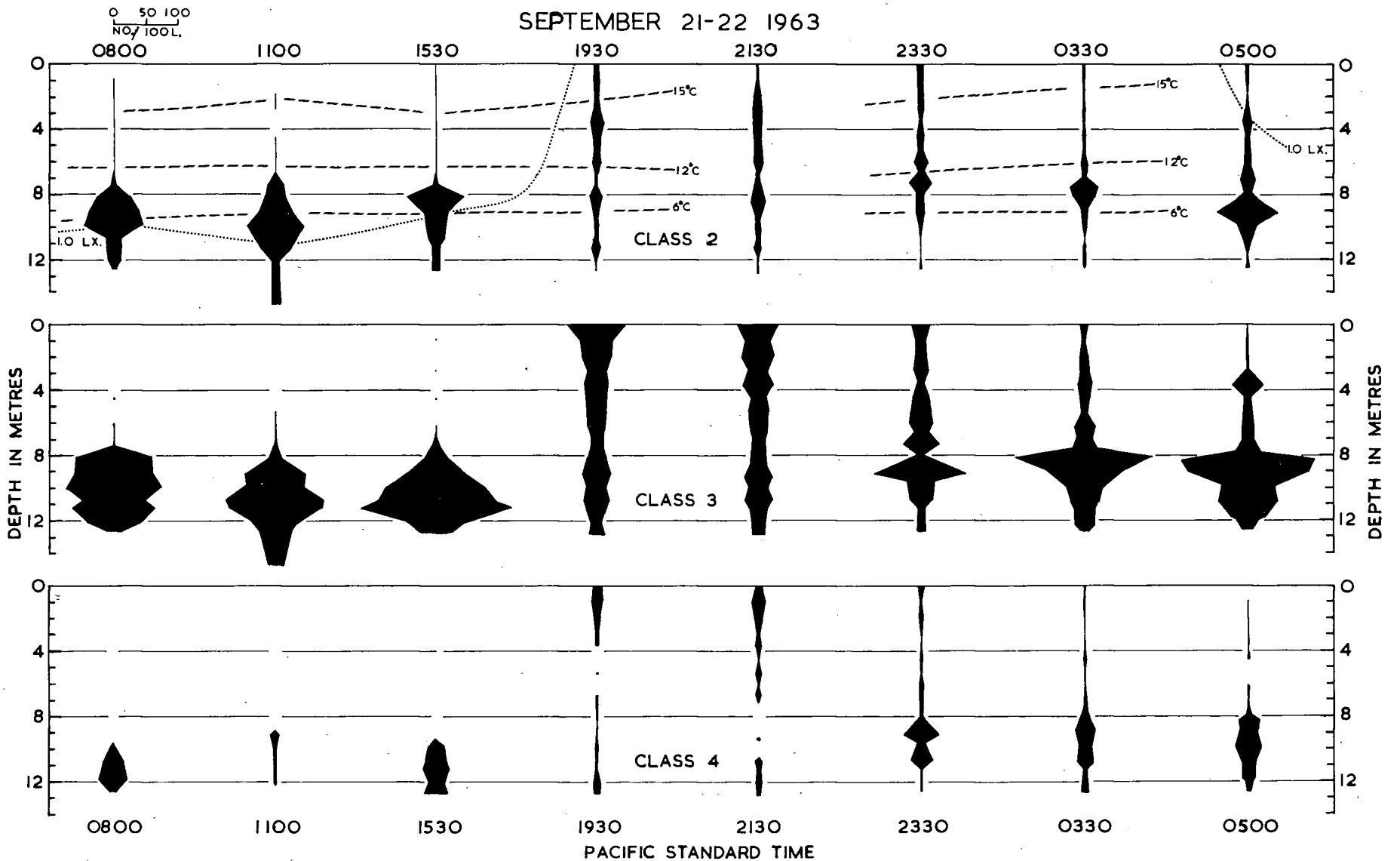
Comparison of the distribution patterns for 1930, 2130 and 2330 hours (Fig. 7) indicated that the three larval classes had approximately similar timing of ascent and descent. In

general the migratory pattern of the three larval classes appeared sufficiently similar to consider them as a single migrating group.

Furthermore the migration may be split into four phases: 1) day-depth, 2) ascent from the day-depth to the surface, 3) descent from the surface, 4) a more rapid descent during dawn (when sunlight starts to penetrate the water) (Fig. 7). In September the first phase lasted from about 0800 to slightly before 1930 hours. The second phase began about (or before) 1930 hours (dusk) and lasted until about 2130 hours. The third phase commenced at about 2130 hours and terminated at sometime before 0510 hours when sunlight started to penetrate the water; this phase occurred therefore during darkness. The fourth phase started at about 0510 hours (dawn); lack of light and distribution data after this time made it impossible to determine the termination of fourth phase. The diel vertical migration seemed therefore to be correlated with diel changes in subsurface light intensity.

Since the 3 larval classes probably behaved as a single migrating group (Fig. 7) during the entire summer, counts of larvae in samples collected during the monthly series were made in order to study seasonal changes in diel vertical migration of the class 2, 3 and 4 larvae. Changes in distribution patterns for the sampling periods during the monthly 24-hour series were attributed therefore to the movements of the older larvae (class 2, 3 and 4), as younger (class 0 and 1) larvae underwent virtually no vertical migration. Confidence limits

FIGURE 7. The diel vertical migration of class 2, 3 and 4 larvae of C. flavicans during September 12-22 series of 1963. The broken lines represent the 14.8°, 12° and 6° C isotherms; the solid lines represent the 1.0 lux isolume.


0 50 100
NO. / 100 L.
SEPTEMBER 21-22 1963
0800
1100
1530
1930
2130
2330
0330
0500
15°C
12°C
6°C
1.0 LX.
CLASS 2
CLASS 3
CLASS 4
DEPTH IN METRES
0
4
8
12
PACIFIC STANDARD TIME

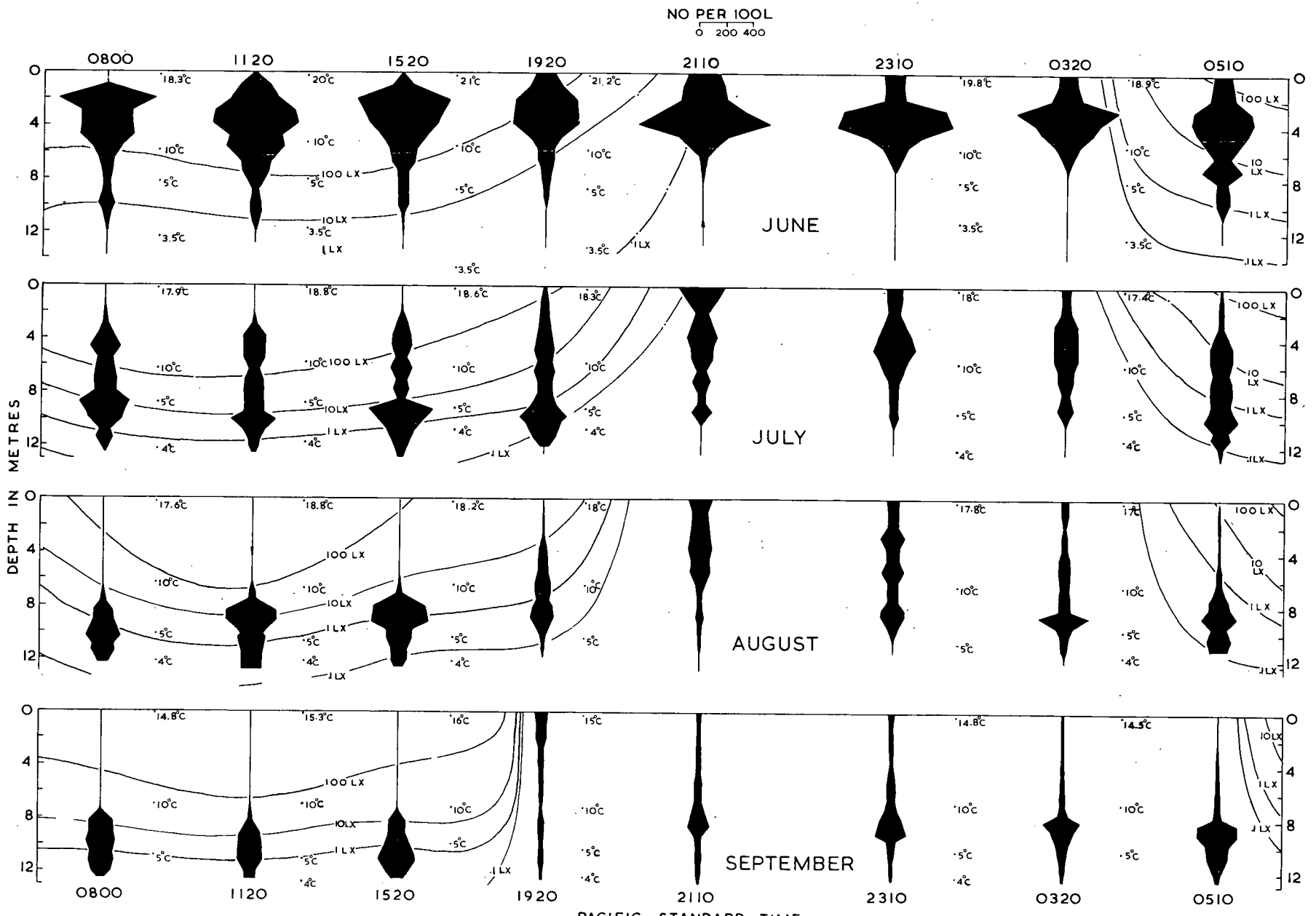
were calculated for the estimated total counts (Appendices IX, X and XI).

The diel vertical migration of the 3 larval classes showed a seasonal change apparently correlated with seasonal changes in timing of subsurface light extinction (at dusk) and of subsurface light penetration (at dawn) (Fig. 8).

The comparison of the distribution patterns of the 1520 and 1920 hour sampling periods showed that the termination of day-depth phase occurred progressively earlier (Fig. 8). The phase terminated very shortly before 1920 hours during the June 16-17 and July 20-21 series. This was inferred from the fact that the 1920 hour distribution pattern indicated very slight ascent over the previous distribution pattern. The phase ended shortly before 1920 hours during the August 18-19 series, as the 1920 hour distribution pattern showed substantial ascent over the 1520 hour pattern. The day-depth phase ended well before 1920 hours during the September 21-22 series as the 1920 hour distribution pattern may represent maximum ascent.

Comparison of the distribution patterns for 1920, 2110 and 2310 hours showed similar seasonal changes for the second phase (ascent from the day depth to the surface) of diel vertical migration (Fig. 8). The phase commenced at about 1920 hours and ended at about 2110 hours during the June, July and August series. It could not have terminated at about 2310 hours during these series as the comparison indicated the descent to be well under way by 2310 hours. In contrast

FIGURE 8. The diel vertical migration of the C. flavicans larvae in Corbett Lake curing June 16-17, July 20-21, August 17-18 and September 21-22 series, 1963. Surface temperature and 10°, 5°, 4° and 3.5° C temperature depths are shown. The 0.1, 1, 10 and 100 lux isolumes are indicated with solid lines.


NO PER 100L
0 200 400
0800
1120
1520
1920
2110
2310
0320
0510
JUNE
JULY
AUGUST
SEPTEMBER
DEPTH IN METRES
PACIFIC STANDARD TIME
0
4
8
12
100 LX
10 LX
1 LX
0.1 LX

the phase began well before 1920 hours and ended shortly after 1920 hours during the September series. The comparison of the 1920 and 2110 hour distribution patterns indicated the descent to be well under way by 2110 hours.

Comparison of the distribution patterns for 1920, 2110, 2310, 0320 and 0510 hours indicated that the third phase (descent from surface) became progressively longer and appeared correlated with changes in the duration of total darkness (Fig. 8). The phase commenced sometime at about 2110 hours and ended at about 0320 during the June, July and August series. It started shortly after 1920 hours (for reasons described previously) and ended at about 0510 hours during the September series.

The fourth phase (a rapid descent during dawn) commenced at about 0510 hours during June, July and August series and sometime after 0510 hours during September series (Fig. 8). The light conditions (time when light first penetrated the water and the depths of the 0.1, 1.0, 10, 100 lux isolumes) during the June, July and August series were similar. The time at which the light first penetrated the water during the September series was significantly later than those of the previous series.

Other Aspects of the Diel Vertical Migration

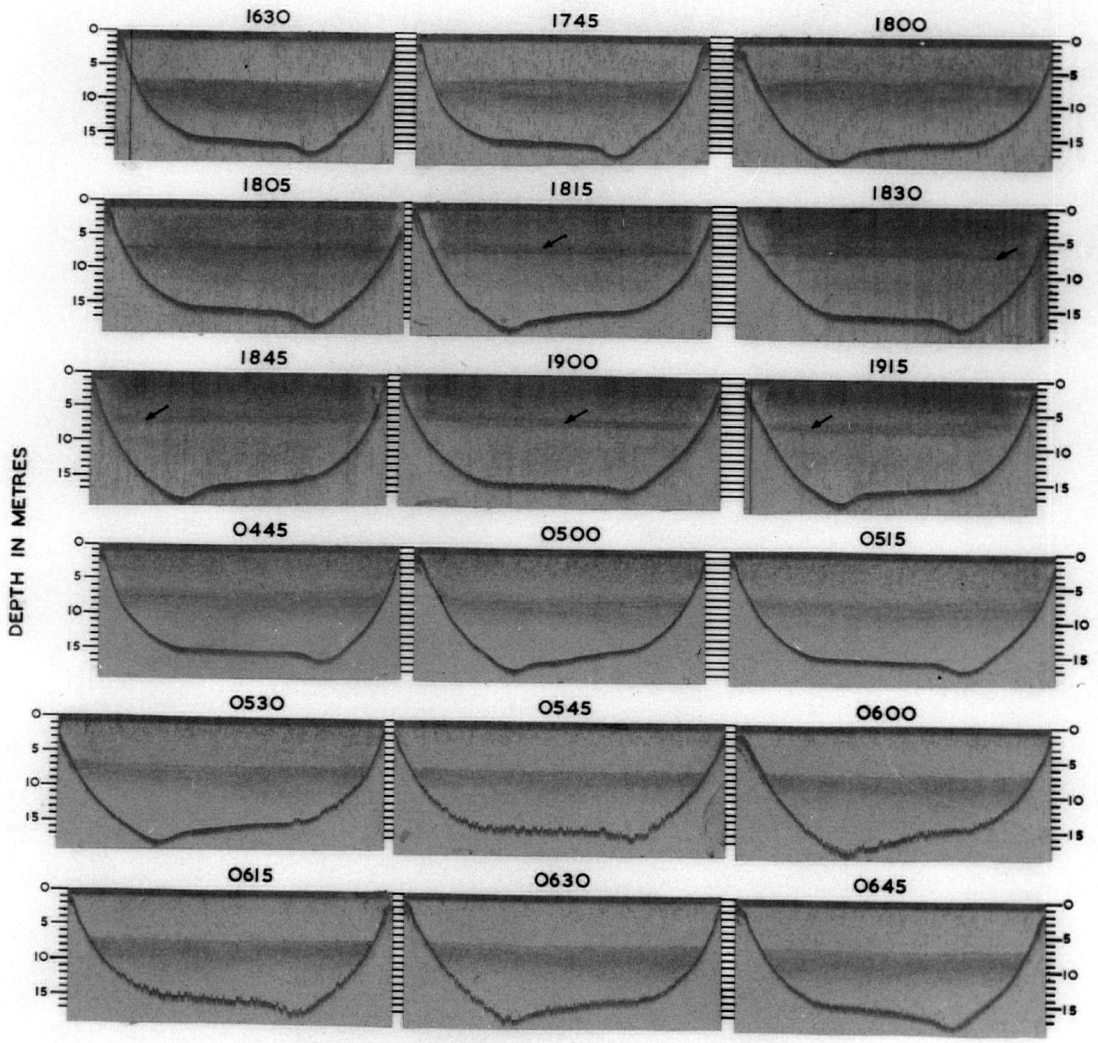
In 1962 echo traces were taken about every 15 minutes during the dusk and dawn periods of October 1-2 at Cross-section A (Fig. 1) using constant gain (volume control of

the echo sounder) and boat speed.

The traces revealed some interesting aspects on the diel vertical migration of the larval population in relation to the lake basin (Fig. 9). In the daytime (1630 and 1745 hour echo traces) the periphery of the Chaoborus scattering layer appeared to be in contact with the lake basin and was thinnest at these regions. During the ascent (1800-1915 hour traces) the layer (largely Chaoborus larvae) expanded slightly shoreward, but appeared to have little contact with the shore. The clear spots over the shore region can be seen on the 1805, 1830, 1845, 1900 and 1915 traces, and particularly well on the 1815 hour trace when background noise was minimal. In contrast the layer became more diffuse and appeared in contact with the shores during descent (0445-0645 hour traces).

The echo traces were also used to calculate the rates of ascent and descent of the larvae (Fig. 9). As the larvae occupying the bottom portion of the scattering layer appeared to ascend first (compare 1800, 1805 and 1815 hour echo traces), it was assumed that these larvae moved up to the surface and descended to the original daytime depth of 12.5 m (Fig. 10). As the ascent commenced between 1745 and 1800 hours, it was decided arbitrarily to have occurred precisely at 1750 hours. As further analysis of these and other traces suggested that the termination of ascent occurred when the "residue" layer (indicated by arrows) was thinnest (compare 1800-1915 hour echo traces), the end of ascent was decided to have occurred at 1845 hours. Since the thickening of the "residue" layer

FIGURE 9. Echo sounding traces across Corbett Lake at Cross Section A, October 1-2, 1962 (differences in length of trace caused by variation in length of run or boat speed; background noise may be ignored). The arrows indicate the "residue" layer. Time expressed in hundred hours (Pacific Standard Time).


1630
1745
1800
1805
1815
1830
1845
1900
1915
0445
0500
0515
0530
0545
0600
0615
0630
0645
DEPTH IN METRES
0
5
10
15

indicated descent, the onset of descent probably occurred at about 1900 hours (compare 1900-0645 echo traces). The descent terminated at 0745, the time at which the thickness of the scattering layer first became constant. Consequently the ascent period lasted 55 minutes (1750-1845), while the descent phase involved 705 minutes (1900-0645). Therefore the rates of ascent and descent were 13.6 and 1.1 m/hour respectively.

Part 2. Laboratory Studies

Diel Vertical Migration under Experimental Conditions

Several 24 hour laboratory experiments were carried out during the summer of 1963 to study the differential migratory behavior of the older larval classes (only class 2, 3 and 4 larvae migrated). A series was done on July 16-17 with 100 larvae (4.80 mm mean length) collected from about the 13 m depth of the lake. Two series were carried out simultaneously on August 13-14 with 100 larvae batches (3.30 mm mean length for both) taken from the surface and about the 5 m depth of the lake. On August 16-17 two 100 larvae batches (3.80 and 5.20 mm mean length) collected from 10 and 14 m depth respectively were used. Finally two series were carried out on September 13-14 with larvae batches (4.32 and 5.32 mm mean length) collected from about 10 and 14 m depths in order to replicate the results of August 16-17. (It was not possible to replicate the results of August 13-14 series in September as comparable sized larvae were not present in the lake).

The experiments were not started until the larvae appeared quiescent (lack of darting movements).

The majority of the larvae used on July 16-17, August 13-14, August 16-17 and September 13-14 belonged respectively to classes 3, 2, 2 and 3, and 2 and 3.

No experiments were conducted with the class 0 and 1 larvae, as they were too small to be observed readily in the tubes. However it was felt that the class 2 larvae taken from the surface and 5 m depth of the lake would give results since they both had a similar daytime vertical distribution in the lake.

The class 2 larvae from the surface layer of the lake (0 and 5 m) showed virtually no vertical migration in the experimental tubes (Fig. 10). The class 0 and 1 larvae underwent practically no migration in the field (Figs. 5 and 6). On the other hand class 2 larvae taken from 10 m in the lake during the daytime showed a distinct vertical migration in the tubes (Figs. 12 and 13); the class 2 animals underwent distinct vertical migration in the field (Figs. 5, 6 and 7). Similarly the class 3 larvae taken from about the 13 and 14 m in the lake on July 16, August 16 and September underwent diel vertical migration (Figs. 11, 12 and 13); the class 3 larvae also showed distinct diel vertical migration in the field (Figs. 5, 6 and 7).

The migratory pattern of the class 2 larvae in the tubes was identical to the field diel movements of the class 2, 3 and 4 larvae (Figs. 12 and 13). It consisted of the similar

FIGURE 10. Diel vertical migration of class 2 larvae (collected from the surface and 5 m depth of Corbett Lake) in adjacent experimental tubes during August 13-14, 1963. Light intensities at the surface of both tubes were identical, as were temperatures at the surface, 100 cm depth and bottom.

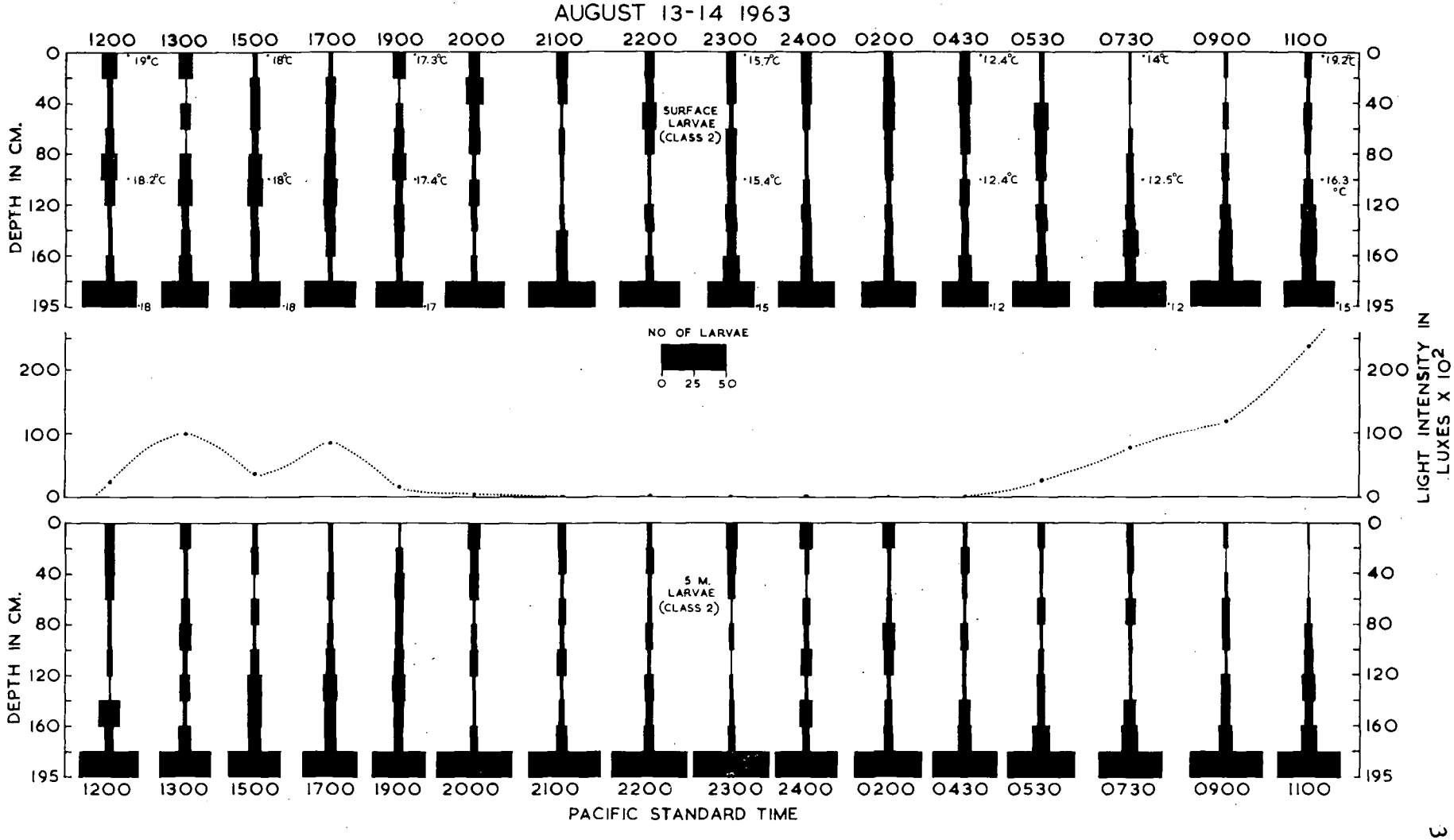

AUGUST 13-14 1963
1200 1300 1500 1700 1900 2000 2100 2200 2300 2400 0200 0430 0530 0730 0900 1100
DEPTH IN CM.
0 40 80 120 160 195
SURFACE LARVAE (CLASS 2)
19°C
18°C
17.3°C
15.7°C
12.4°C
14°C
19.2°C
18.2°C
18°C
17.4°C
15.4°C
12.4°C
12.5°C
16.3 °C
18
18
17
15
12
12
15
NO OF LARVAE
0 25 50
0 100 200
LIGHT INTENSITY IN LUXES X 10²
5 M. LARVAE (CLASS 2)
PACIFIC STANDARD TIME

FIGURE 11. Diel vertical migration of class 3 larvae in the experimental tube during July 16-17, 1963 at Corbett Lake. Surface light intensities (measured with the submarine photometer) and temperatures at surface, 100 cm depth and bottom of the tube are shown. Probable surface light intensities for 1900, 2000 and 2100 hours (if Photovolt Photometer was used) are indicated with solid dots joined with a solid line.

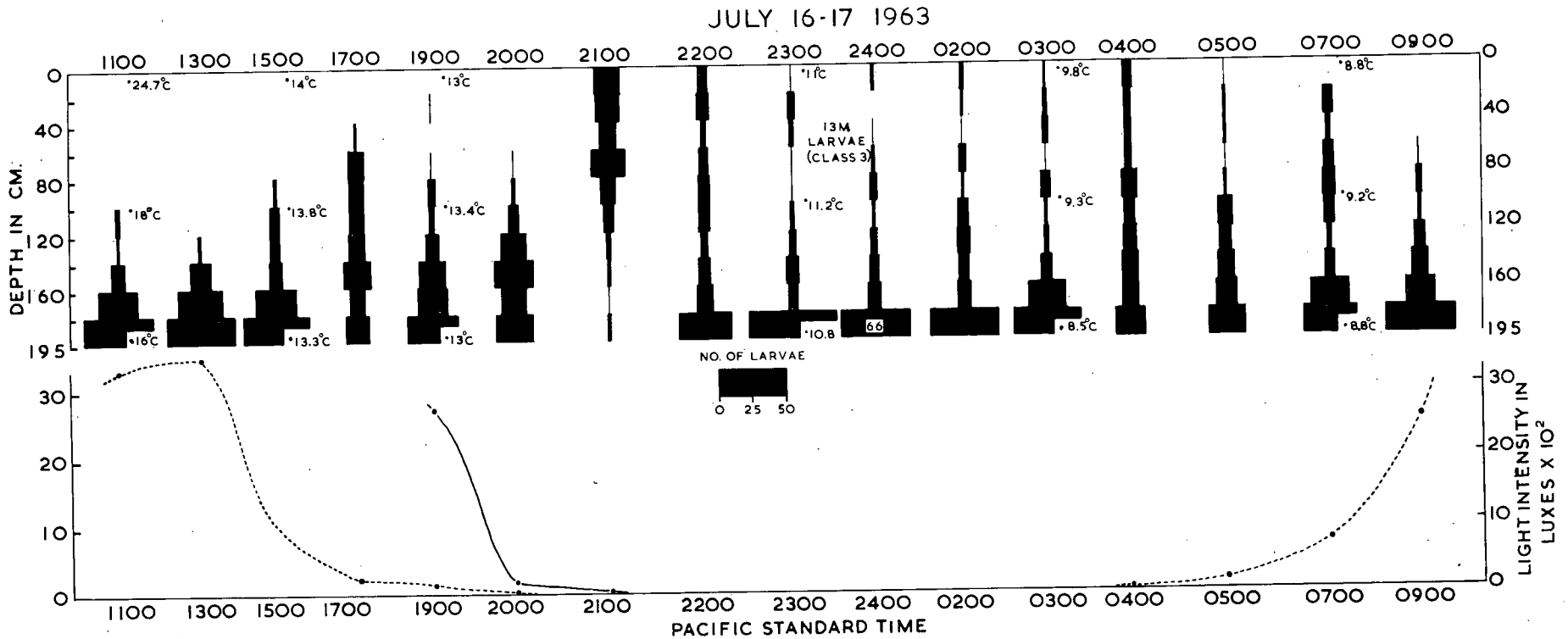

JULY 16-17 1963
1100 1300 1500 1700 1900 2000 2100 2200 2300 2400 0200 0300 0400 0500 0700 0900
DEPTH IN CM.
0 40 80 120 160 195
*24.7°C
*18°C
*16°C
*14°C
*13.8°C
*13.3°C
*13°C
*13.4°C
*13°C
*11°C
*11.2°C
*10.8
13M LARVAE (CLASS 3)
66
*9.8°C
*9.3°C
*8.5°C
*8.8°C
*9.2°C
*8.8°C
NO. OF LARVAE
0 25 50
LIGHT INTENSITY IN LUXES X 10²
0 10 20 30
PACIFIC STANDARD TIME

FIGURE 12. Diel vertical migration of class 2 and 3 larvae in adjacent experimental tubes during August 16-17, 1963. Light intensities at the surface of both tubes were identical, as were temperatures at the surface, 100 cm depth and bottom.

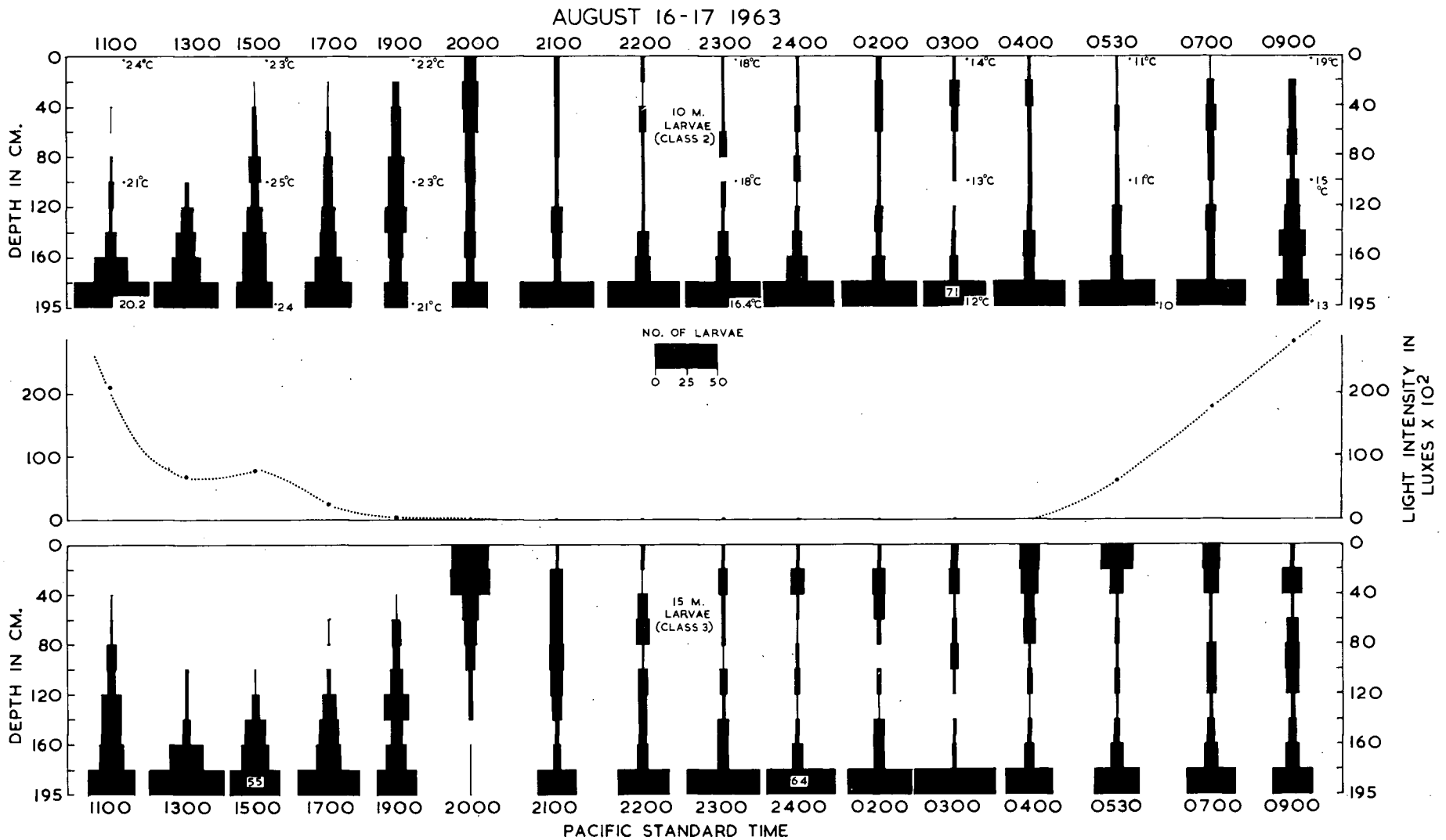
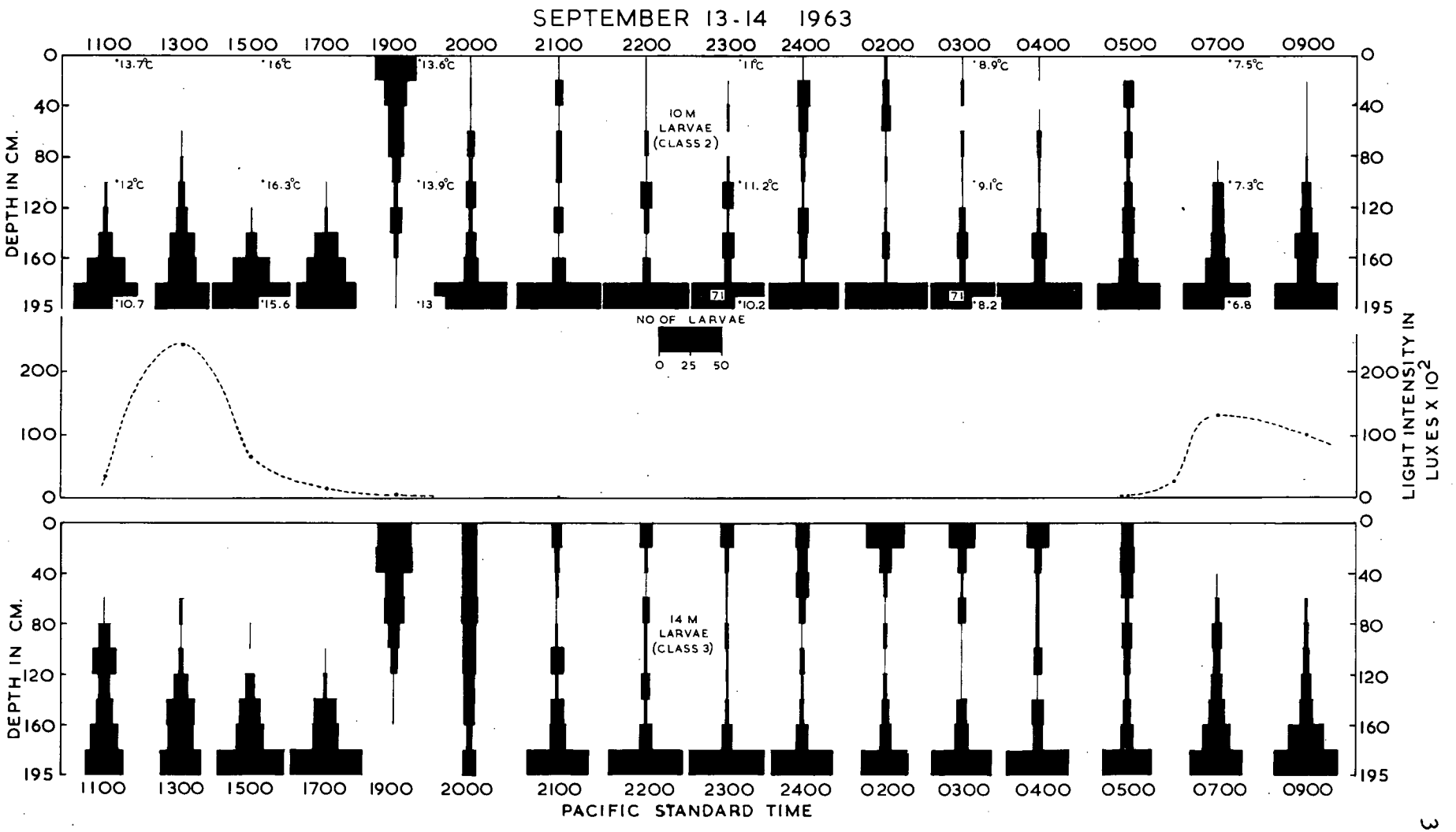

AUGUST 16-17 1963
1100 1300 1500 1700 1900 2000 2100 2200 2300 2400 0200 0300 0400 0530 0700 0900
DEPTH IN CM.
0 40 80 120 160 195
10 M. LARVAE (CLASS 2)
15 M. LARVAE (CLASS 3)
NO. OF LARVAE
0 25 50
LIGHT INTENSITY IN LUXES X 10²
0 100 200
PACIFIC STANDARD TIME

FIGURE 13. Diel vertical migration of class 2 and 3 larvae in adjacent experimental tubes during September 13-14, 1963. Light intensities at the surface of both tubes were identical, as were temperatures at the surface, 100 cm depth and bottom.


SEPTEMBER 13-14 1963
1100 1300 1500 1700 1900 2000 2100 2200 2300 2400 0200 0300 0400 0500 0700 0900
DEPTH IN CM.
0 40 80 120 160 195
13.7°C
16°C
13.6°C
11°C
8.9°C
7.5°C
10 M LARVAE (CLASS 2)
12°C
16.3°C
13.9°C
11.2°C
9.1°C
7.3°C
10.7
15.6
13
7
10.2
7
8.2
6.8
NO OF LARVAE
0 25 50
LIGHT INTENSITY IN LUXES X 10²
0 100 200
14 M LARVAE (CLASS 3)
PACIFIC STANDARD TIME

4 phases: 1) day-depth, 2) ascent from the day-depth to the surface, 3) descent from the surface after ascent, 4) a rapid descent during dawn period (Figs. 12 and 13). There may have been a morning rise at 0500 hours on September 17 (Fig. 13).

The migratory pattern of the class 3 larvae in the tubes was not identical with the field diel movements of the class 2, 3 and 4 larvae (Figs. 12 and 13). It consisted of 5 phases: 1) day-depth, 2) ascent from the day-depth to the surface, 3) descent from the surface, 4) early morning rise to the surface ("dawn rise"), 5) sharp descent during the dawn period (Figs. 11, 12 and 13). The early morning rise occurred at about 0400 hours on July 17 (Fig. 11), about 0400-0530 hours on August 17 (Fig. 12) and perhaps at about 0500 hours on September (Fig. 13).

The failure to depict the morning rise in the field may be due to the long time interval between sampling periods (every 2 or 4 hours).

In addition the migration cycles of the class 2 and 3 larvae in the experimental tubes showed a seasonal change (Figs. 11, 12 and 13), particularly in the time of maximum ascent. For the class 2 larvae maximum ascent was reached at about 2000 hours in the August 16-17 series and at about 1900 hours on September 13-14. The maximum ascent of class 3 larvae occurred at about 2100 hours in the July series (Fig. 11), 2000 hours in the August series (Fig. 12) and 1900 hours in the September series (Fig. 3).

The surface light intensity was measured during the July

series with an instrument less sensitive than that used during the August and September series. As a result the surface light intensities recorded during the 1900, 2000 and 2100 hours of the July series (Fig. 11) were corrected to intensities which probably would have been recorded with the sensitive instrument (Fig. 11). Consequently it was possible to compare the times of light extinction for the 3 series.

The seasonal variation in time of maximum ascent appeared to be correlated with changes in time of surface light extinction (Figs. 11, 12 and 13). During the July series the surface light became almost immeasurable at about 2100 hours, corresponding with the time of maximum ascent of class 3 larvae (Fig. 11). During the August series the surface light became immeasurable at about 2000 hours, corresponding with the time of maximum ascent for class 2 and 3 larvae (Fig. 12). During the September series the light intensity was virtually zero at about 1900, corresponding with the time of maximum rise for the class 2 and 3 animals (Fig. 13). A similar seasonal trend was observed in the field. The maximum ascent was estimated to have occurred at about 2110 hours during the June, July and August field series and about 1920 hours during the September field series (Fig. 8).

Role of Light on Diel Vertical Migration

Experiments to test for exogenous rhythm in the diel vertical migration of Chaoborus larvae were carried out on August 9 and September 28, 1963 with class 3 larvae collected

from the 14 m depth of the lake. During each experiment two plastic tubes were used to hold the animals; the top of one tube was exposed to natural light conditions (control tube), while that of the other was subjected to light intensities regulated by a shutter system previously described. The tubes were placed adjacent to each other in the dark room with a black plastic sheet separating them.

At the beginning and end of each experiment, the control and non-control (or experimental) animals were exposed to identical light conditions in order to evaluate whether the two batches of animals behaved similarly (Figs. 14 and 15). The responses were almost identical at the start, but somewhat different at the end of the experiments. Discrepancies between two sets of natural light readings taken near the conclusion of the experiments were probably due to time lapse between readings (Figs. 14 and 15). The temperature regimes in the control and non-control tubes were virtually identical during each experiment.

It was possible to induce complete migration cycles, including the morning rise phase (Figs. 14 and 15).

The cycle was induced at a light intensity range of 300-1000 luxes on August 9; it can be seen that non-control (or experimental) larvae responded very little to changes in light intensity at a range of 1000-15000 luxes (Fig. 14). Extremely slight changes in light intensity made the larvae ascend or descend within 300-1000 lux light range. The non-control larvae exposed previously to 1450 luxes (at 1452 hours)

FIGURE 14. The vertical movements of class 3 larvae in adjacent control (exposed to naturally changing light conditions) and non-control (exposed to artificially changing light conditions) experimental tubes on August 9, 1963. Identical temperature conditions in both tubes; identical light intensity over both tubes at the beginning and end of experiment.

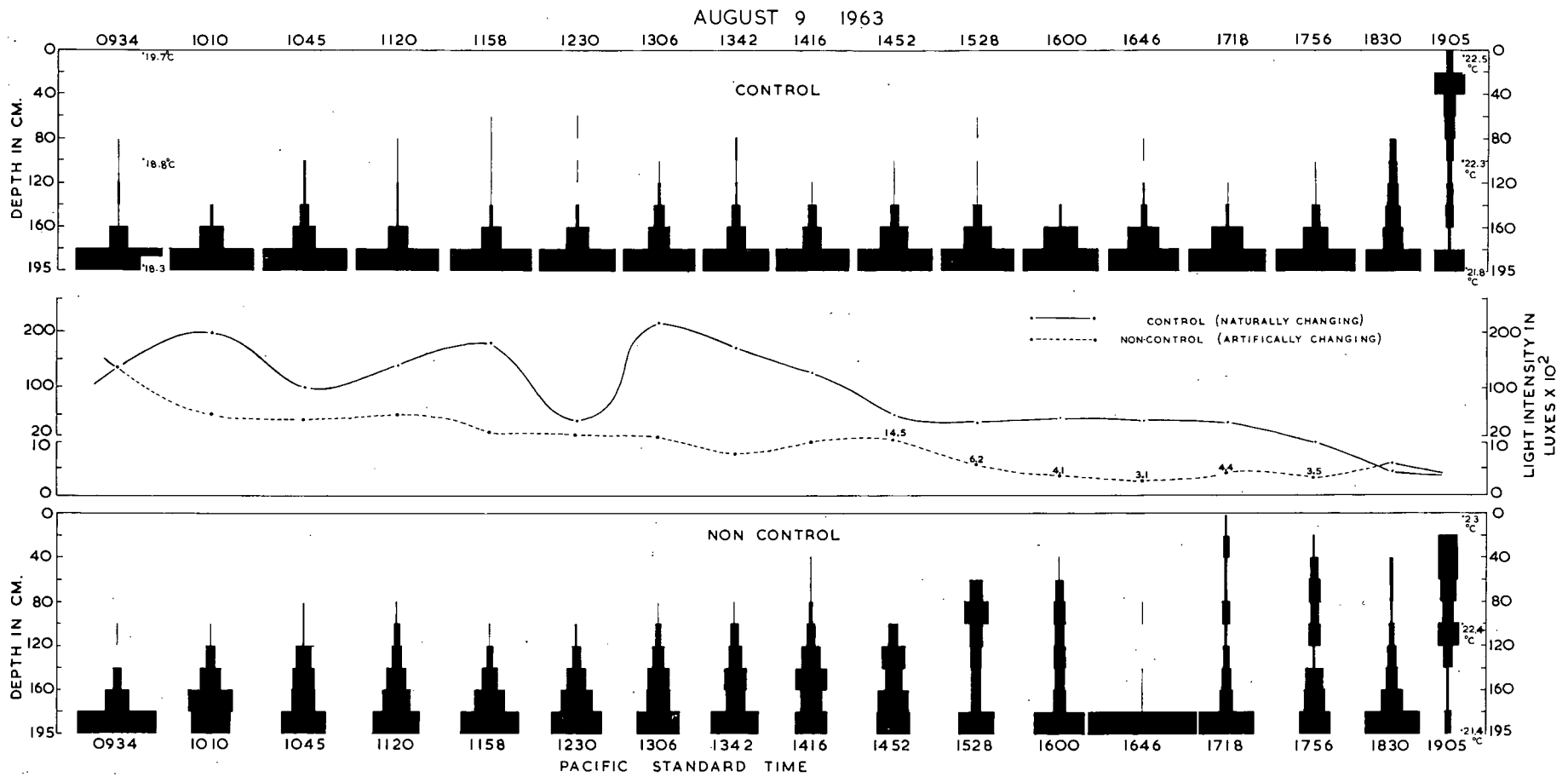
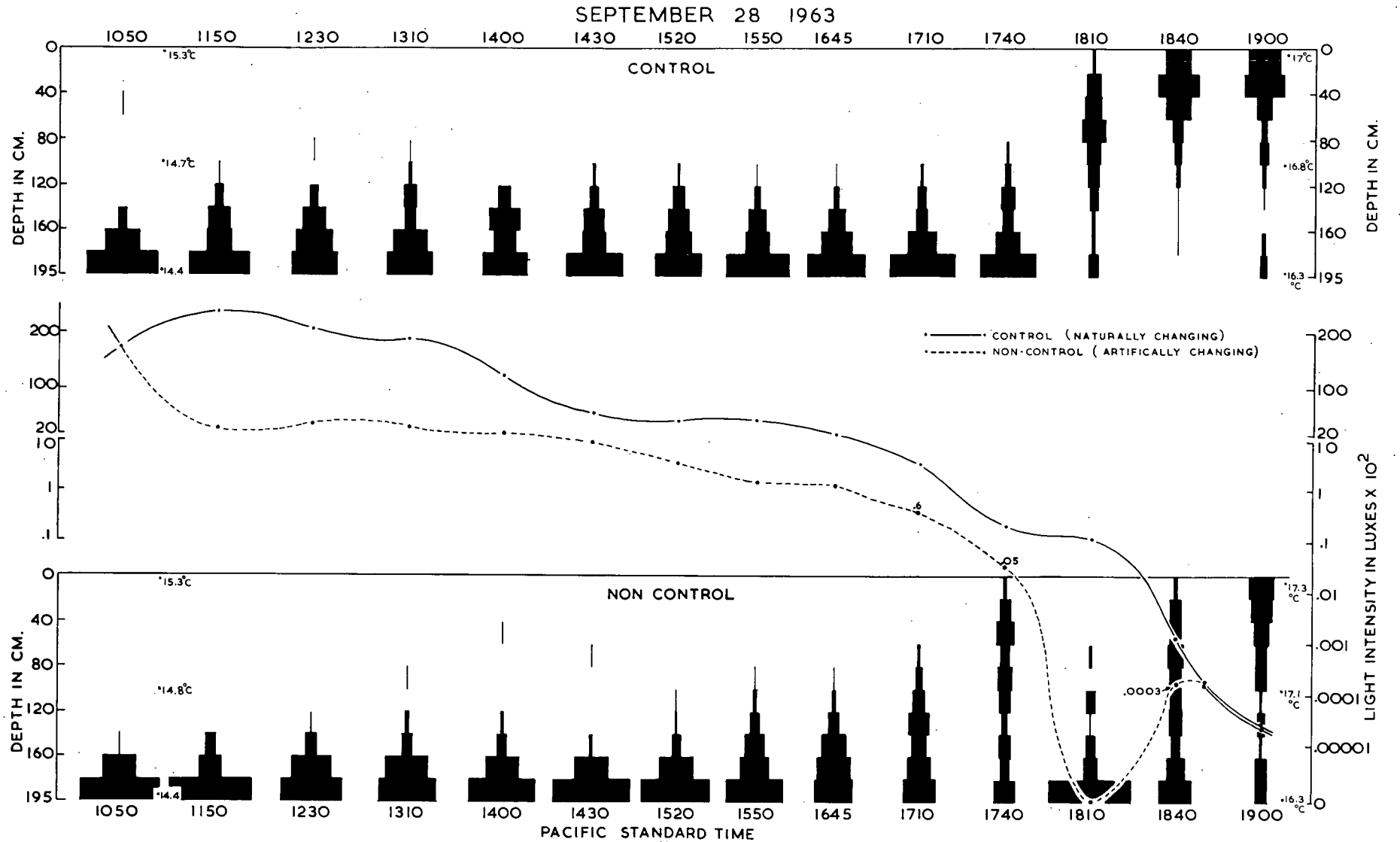

AUGUST 9 1963
0934 1010 1045 1120 1158 1230 1306 1342 1416 1452 1528 1600 1646 1718 1756 1830 1905
CONTROL
DEPTH IN CM.
19.7°C
18.8°C
18.3
22.5 °C
22.3 °C
21.8 °C
0 40 80 120 160 195
CONTROL (NATURALLY CHANGING)
NON-CONTROL (ARTIFICALLY CHANGING)
LIGHT INTENSITY IN LUXES X 10²
200 100 20 10 0
14.5
6.2
4.1
3.1
4.4
3.5
NON CONTROL
23 °C
22.4 °C
21.4 °C
PACIFIC STANDARD TIME

FIGURE 15. The vertical movements of class 3 larvae in adjacent control (exposed to naturally changing light conditions) and non-control (exposed to artificially changing light conditions) experimental tubes on September 28, 1963. Identical temperature conditions in both tubes; identical light intensity over both tubes at the beginning and end of experiment.


SEPTEMBER 28 1963
1050
1150
1230
1310
1400
1430
1520
1550
1645
1710
1740
1810
1840
1900
CONTROL
NON CONTROL
DEPTH IN CM.
0
40
80
120
160
195
*15.3°C
*14.7°C
*14.4
*17°C
*16.8°C
*16.3 °C
CONTROL (NATURALLY CHANGING)
NON-CONTROL (ARTIFICALLY CHANGING)
200
100
20
10
1
.1
.6
.5
.0003
.01
.001
.0001
.00001
*15.3°C
*14.8°C
*14.4
*17.3 °C
*17.1 °C
*16.3 °C
LIGHT INTENSITY IN LUXES X 10^2
PACIFIC STANDARD TIME

ascended markedly when exposed subsequently to 620 luxes (at 1528 hours). The experimental larvae descended only slightly when the light was lowered to 410 luxes (at 1606 hours), while they moved down markedly when light was further reduced to 310 luxes (at 1646 hours). They ascended appreciably upon exposure to 440 luxes (at 1718 hours) and moved up markedly upon subsequent exposure to 350 luxes (at 1756 hours); these results indicated that the ascent response might be greater at 350 luxes than at 440 luxes.

A migration cycle was induced at a light intensity range below 100 luxes on September 28; the non-control larvae responded very little to changes in light intensity above this range (Fig. 15). The experimental animals exposed previously to 60 luxes (at 1710 hours) ascended markedly when light intensity was reduced to 5 luxes (at 1740 hours). The larvae descended sharply in the absence of light (at 1810 hours), while they ascended upon subsequent exposure to 0.3 lux.

DISCUSSION

Seasonal Variation in Horizontal Distribution

During the summer of 1963, the larvae had a clumped horizontal distribution which increased with the progression of summer (Table 1). The significance of this result can be speculated upon by the consideration of the seasonal change in dominant size classes (or instars). There was a progressive decrease in the abundance of class 0 and 1 larvae which did not migrate and were largely confined to the epilimnion (Figs.

4, 5 and 6). These young larvae are the least structurally differentiated (for example, the muscles are poorly developed) of larvae present. In fact they may be so undeveloped structurally that they are truly planktonic with little or no control over movement and are therefore distributed within the eplimnion solely by the slight water currents in Corbett Lake. It may be expected therefore that such animals are randomly distributed. Conversely the class 2, 3 and 4 larvae will be more developed with respect to structure (greater mobility), physiology and possibly behavior. It is possible that these older larvae are clumped in distribution. Therefore the horizontal distribution of the total larval population appears least clumped in June probably owing to the modifying influence of large numbers of randomly distributed small larvae, while it is most clumped in September because there are virtually no class 0 and 1 larvae present.

The Effect of Age and Environmental Factors on Vertical Distribution

During the daytime (1100 hours) the small larvae occupied the oxygen rich epilimnion (above 8 m) of Corbett Lake, while larger and older (class 2, 3 and 4) inhabited the hypolimnion, but not the bottom mud (Fig. 4).

A nearly totally limnetic summer population of Chaoborus larvae showing this size characteristic has been observed only on rare occasions. Dendy (1956) has observed such a summer population, but did not determine whether the larvae were

vertically stratified according to size during the daytime. Hunt (1958), investigating a deep Florida lake, has found a totally limnetic population whose larvae increased in size with increase in depth. Similarly Worthington and Ricardo (1936), sampling Lake Edward in Africa, have found a strictly limnetic population whose larvae are vertically distributed with respect to size. The lakes containing such larval populations have common chemical characteristics; the lower layers of the lakes are severely depleted of oxygen and contain detectable traces of H_2S.

In most lakes containing larval populations, the larvae are vertically distributed according to size during the daytime, but with the older larvae being benthic (Muttkowski, 1918; Rawson, 1930; Eggleton, 1932; Berg, 1937; Miller, 1941; MacDonald, 1956; Wood, 1956; Woodmanse and Grantham, 1961). It is noteworthy that these lakes containing daytime benthic larvae have no H_2S in their lower layers.

It seems therefore that highly reduced mud may directly or indirectly prevent the larvae from entering the bottom of productive lakes during the daytime. The fact that larvae enter the bottom mud of Corbett Lake after fall overturn supports this speculation. In addition it may be that light detectable by the larvae does not penetrate to the bottom in such supposedly productive lakes, therefore not necessitating the animals to enter the bottom mud.

Studies done on both freshwater and marine crustacean plankters indicate similar size (or age) and depth relationships.

Gardiner (1933), working with Calanus fimarchius in the North Sea, has shown that copepodite stages 3 and 4 live in the upper layers and stages 5 and 6 in the deep waters. Langford (1938) have shown that the young stages of a freshwater cladoceran Daphnia longispina remain above the thermocline in Lake Nipissing during daytime, while the adults remain below it.

The Effect of Age and Environmental Factors on the Diel Vertical Migration

The class 0 and 1 (or first and second instar) larvae underwent practically no diel vertical migration in Corbett Lake while the class 2, 3 and 4 (or respectively third, fourth and fifth instar) larvae did (Figs. 5 and 6). The experimental results seem to corroborate the field observations; class 2 larvae taken from the upper layers (0 and 5 m) of the lake were assumed to react similarly inasmuch as class 0 and 1 larvae showed virtually no vertical movements, while class 2, 3 and 4 animals taken from the lower depths (10-14 m) made obvious migrations (Figs. 10, 11, 12 and 13).

Dendy (1956), describing the presence of totally limnetic larval population in some lakes, do not cite the existence of differential migration ability between larval groups. In contrast, others (Juday, 1921; Berg, 1937; Wood, 1956; Hamilton, 1961; Woodmanse and Grantham, 1961) have observed both benthic and limnetic distributions of larvae, but found invariably that both younger and older animals underwent a distinct vertical migration. However they fail to specify the size

ranges of the younger and older larvae. Nevertheless Berg (1937) has shown experimentally that young larvae (1.7 mm mean length) do not migrate vertically. Nicholls (1934), working with Calanus in the Clyde area, has noted that the nauplia occur above 30 m and do not undergo diel changes in distribution, while the copepodite stages 1, 2, 3 and 4 undergo vertical migration (especially stage 4). In contrast he has found the stage 5 animals to be unresponsive.

As a consequence of differential migratory behavior between larval groups of Chaoborus, the younger larvae (class 0 and 1) remained in the warmer oxygenated epilimnion throughout the entire day, whereas the older animals (class 2, 3 and 4) encountered both the epilimnion and colder deoxygenated hypolimnion during the 24 hour period (Figs. 4, 5 and 6).

These observations suggest that there may be several factors which may account for the differential migration. The smaller larvae may have a much narrower temperature and oxygen range than the older ones. However it remains to be demonstrated whether differences in physiological tolerance of these factors exist between the two sets of larvae, and whether or not these may actually affect migration. More likely the extent of physiological and morphological development of pertinent structures (muscles, sense organs and air bladder) is of greater importance. Deonier (1943), working with Chaoborus astictopus, has shown that the simple eye is present in all instars, while the compound eye appears in the third instar (comparable to class 2 of this study) and are developed fully

in the fourth instar (comparable to class 3). Therefore it may be that the compound eyes (regardless of degree of development) are a vital sense organ for vertical migration, providing that light is the controlling factor. Berg (1937) has observed the air sacs to become filled with air before the C. flavicans larvae hatch, while Akehurst (1922) has shown the air to replace fluid in the air bladders shortly after hatching. If entrance of air into the air sac is important in the hydrostatic functioning of the sac, then it would seem that the inability of smaller larvae to migrate can not be attributed directly to the structural and physiological development of this organ. Hence one must consider now the possibility of vertical migration involving strictly active body movements which implies that the degree of physiological and structural development of the body muscles is vitally important. Although the development of the body muscles in the larvae has not been examined, it may well be that the muscles of younger larvae (class 0 and 1) are not as functional as those of older larvae (class 2, 3 and 4).

Based on the September samples, there appeared to be no differential diel timing of ascent and descent between migrating larval groups (Fig. 7). Since no one has attempted to separate the migrating chaoborid larvae into age groups (or instars), the results can not be compared. It is possible that the time intervals (every 2 and 4 hours) between sampling periods are not short enough to demonstrate the existence of differential diel timing. However, since the migrating larvae do have a

similar daytime vertical distribution (indicating similar response to light conditions), it seems likely that they may have similar diel timing of ascent and descent. Fraser (1938) has found that all calyptopis stages of Euphausia superba migrate vertically and have similar timing of upward and downward migration.

The migration cycles observed in the field and laboratory differed only with respect to "dawn rise" which occurred under experimental conditions, especially for class 3 larvae (Figs. 7, 8, 10, 11, 12 and 13). Both cycles appeared to be correlated to dielly and seasonally changing light conditions, with the ascent occurring about dusk and the descent taking place during darkness and dawn. The "dawn rise" of the laboratory cycle occurred during the early morning hours.

The basic migration pattern observed in Corbett Lake (Figs. 7 and 8) agrees with those of the same or different species in other lakes (Juday, 1921; Eggleton, 1937; Berg, 1937; Wood, 1956; Woodmanse and Grantham, 1961). However the time of maximum ascent (consequently time of descent) of larvae in Corbett Lake does not correspond to those of larvae in other lakes. Throughout the summer the maximum ascent occurred between about 1900-2200 hours in Corbett Lake. Juday (1921) and Eggleton (1931), each working on a different lake, found the maximum rise of larvae occurring at about 2200 hours. In contrast Woodmanse and Grantham (1961), Berg (1937) and Wood (1956) studying different lakes, found the maximum upward movement to take place about 2400 hours.

The depiction of "dawn rise" in the experimental tube but not in the lake is puzzling. It may occur in Corbett Lake, but escaped detection because the time interval between sampling periods was not short enough. Failure of other workers to show a "dawn rise" in Chaoborus larvae may be due to the same reason. In addition the possibility of it occurring for a very short time adds to the difficulty of depicting it in the field.

The proportion of the older larval groups undergoing ascent and the time taken for it to complete the descent decreased as the season progressed (Fig. 8). The seasonal decline in the percentage of older larvae ascending is probably due to progressive increase in the rate of light intensity change at dusk as is indicated by the isolumes plotted in Figure 8. Perhaps the migrating population requires a slow rate of light change during the transitory dusk period for complete ascent. The migrating larvae completing descent more rapidly with the progression of summer can be attributed perhaps to increasing darkness during the late evening and early morning hours (2200-0500 hours). Experimental results indicate that the rate of descent of the larvae may be a function of rate at which absolute darkness is approached.

The fact that complete migration cycles (including "dawn rise") can be induced in the laboratory by artificially changing the natural daytime light conditions (Figs. 14 and 15) indicates that light controls the timing of diel vertical migration of Chaoborus flavicans larvae. Furthermore the experiments have

shown that the animals respond only to changes of particularly low light intensities (below 1000 lux). Harris and Wolfe (1955) have demonstrated complete laboratory migration cycles of Daphnia magna by cyclically changing the overhead light intensity using India ink suspension. However, Harris (1963) found the migration cycle of Daphnia magna to persist under constant darkness or illumination and therefore concluded the cycle to be a endogenous rhythm. In the present study on Chaoborus larvae, no such experiments have been carried out. However the larvae will remain at one depth in the experimental tube for several hours under a constant virtually dark condition; this further suggests that the larvae have an exogenous rhythm.

The diel vertical migration of the larval population in relation to the lake basin consisted of very little shoreward movement during ascent but some shoreward movement during descent. According to Siebeck (1964), an organism in the water invariably receives maximum light intensity almost vertically from above. From this it then follows that the nearly vertical ascent of the larvae is probably a function of the subsurface light penetration. "Uferflucht" (avoidance of shore) does not appear to be a pertinent factor as larvae are found in the littoral zone during daytime (Humphreys, 1964) and do more inshore during descent (indicated by echo traces). The shoreward movement during descent may be a reflection of the fact that the animals have virtually no vertical light component to orientate to and therefore are moving down in a random

fashion which brings them into the shore region.

Theoretical Interpretation of the Diel Vertical Migration

When one attempts a theoretical treatment of vertical migration of Chaoborus larvae, the effect of light on both the active swimming movement and buoyancy must be considered. Many workers have demonstrated that the air sacs are buoyancy organs (Krogh, 1911; Bardenfleth and Ege, 1916; Akehurst (1922), Damant, 1924; Holst-Christensen, 1928).

On the basis of his study, Berg (1937) speculates that the vertical migration is a strict phototactic response which he does not describe in any detail.

On the basis of results from the present study, a simple sign change (positive and negative) of phototaxis is not sufficient to explain the vertical migration. In fact it may complicate matters by formulating unrealistic larval behavior. Therefore the migration may involve an interaction of the normal larvae "seeking" an optimum light zone (low light intensity range), while having a constant positive response to gravity. The animals remain in the optimum zone through passive (buoyancy adjustment) and/or active (slight body movements) means. Passive and active movements have been observed in the laboratory. When the optimum light zone disappears at dusk, the animals may move down actively or sink as the buoyancy regulation controlled by light gradually deteriorates. At dawn the larvae may ascend actively or passively to the descending optimum zone if there is a stimulating light

gradient created between the animals and the optimum light zone to invoke responses. If there is no such light gradient, the optimum zone would reach the depth level of the slowly descending larvae, to invoke the previous interaction. The seasonal variation in the migration can be explained also by this hypothesis. Only extremely unfavourable physical and chemical conditions would offset the interactions.

Biological Significance of the Diel Vertical Migration

The biological significance can be considered best from the standpoint of the migrating larvae spending at least half of a 24 hour period in the colder deoxygenated hypolimnion before migrating into the warmer oxygenated epilimnion.

Juday (1921), observing that the larvae spend a good portion of the day in the deoxygenated hypolimnion, has suggested that the significance may involve reduced predation. He argues that most freshwater fish can not tolerate deoxygenated water more than a few hours. Predation would certainly be reduced, especially during the summer. Analysis of trout stomach indicates that the fish prey heavily on the larvae during early spring and late autumn in Corbett Lake. It is conceivable also that the fish change diets for reasons other than not being able to prey on the larvae.

As the larvae encounter daily two sets of environment, (aerobic and anaerobic) the adaptive value of diel vertical migration may involve enhancement of optimum population growth. McLaren (1963) has demonstrated empirically that vertical

migration becomes increasingly important for surface feeding zooplankters as the surface and bottom temperatures become increasingly different. The migration under such conditions enables the animals to conserve and divert more energy into growth and fecundity. Migrating larvae feed predominately in the upper layers of the lake as virtually no food organism (cladocerans and copepods) can withstand anaerobic conditions for any length of time. Temperature difference is very great between the surface and bottom in many lakes during the summer. Therefore larval growth and adult fecundity will be enhanced greatly during the summer if the larvae migrate. The larvae by spending part of the day in deoxygenated water which may have also an energy conserving effect will further enhance growth and fecundity (McLaren, 1963). Therefore larvae will be larger than it would be if they had not undergone vertical migration. Larger larvae became larger pupae which subsequently metamorphose into bigger adults with greater fecundity. Ultimately the success of any chaoborid population may depend on these energy conserving effects.

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APPENDIX I. Determination of the calibration value of the Clarke-Bumpus sampler towed at several depths for a 61 m distance at boat speed of 2.5 knots.

Towing Depth (in metres)	Corrected Depth (in metres)	Without Net: Average No. of Revolutions (3 Tows)	Without Net: Calibration Value in Liters per Revolution	With No. 10 Net: Average No. of Revolutions (3 Tows)	With No. 10 Net: Calibration Value in Liters per Revolution
Surface	-	135.3	5.7	126.0	6.2
2	1.97	133.3	5.8	125.3	6.3
4	3.80	136.0	5.6	120.0	6.6
6	5.56	137.3	5.7	124.7	6.3
8	7.42	135.3	5.7	124.7	6.3
10	9.21	136.7	5.6	126.3	6.2
12	10.87	135.7	5.7	129.6	6.1

APPENDIX II. Volume of water passed through and the number of *Chaoborus* larvae caught by the Clarke-Bumpus sampler (with no. 10 net attached) towed at several depths for a 61 m distance at a boat speed of 2.5 knots.

Corrected Depth (in m)	Sample No.	Time	No. of Larvae	No. of Larvae per 100 L
Surface	1	1252	466	93.20
	2	1256	649	119.08
	3	1301	956	189.68
1.97	1	1305	1374	267.83
	2	1314	1675	340.44
	3	1320	1278	237.98
3.80	1	1325	4235	922.66
	2	1330	4187	809.86
	3	1333	4350	870.00
5.56	1	1338	1833	360.83
	2	1345	2128	408.45
	3	1350	2067	410.2
7.42	1	1357	710	142.12
	2	1402	543	103.43
	3	1409	809	159.25
9.21	1	1415	326	63.55
	2	1429	317	60.38
	3	1434	401	77.56
10.87	1	1439	189	35.73
	2	1444	190	35.65
	3	1448	214	40.15

APPENDIX III. Comparison of the volume of water in the compartments of the subsampler using different total volumes.

Volume of Water Used (in ml.)	Compartment	Volume of Water in Each Compartment (in ml.)
about 1000	A	164
	B	164
	C	163.8
	D	164
	E	166
	F	165
about 750	A	122.2
	B	121
	C	122
	D	122
	E	122
	F	122.3
about 500	A	81
	B	80
	C	80.3
	D	81
	E	81
	F	80.8
about 250	A	40.5
	B	41
	C	41
	D	40
	E	41
	F	41

APPENDIX IV. Test of the reliability of the subsampler, using different volume of water and different number of larvae. A 0.05 significance level was used.

Approximate Volume of Water Used (in ml.)	No. of Larvae Used	Compartment	No. of Larvae in Each Compartment	X^2 Value	Type of Distribution
250	222	A	29		
		B	40	7.14	Random
		C	41		
		D	41		
		E	44		
		F	27		
500	203	A	33		
		B	40	2.69	Random
		C	36		
		D	33		
		E	27		
		F	34		
750	239	A	35		
		B	48	3.21	Random
		C	42		
		D	35 N.B. (1 larva		
		E	37 left in the		
		F	41 subsampler)		
250	599	A	104		
		B	94	1.50	Random
		C	105		
		D	93		
		E	104 N.B. (2 larvae		
		F	97 left in the subsampler)		

APPENDIX IV Continued

Approximate Volume of Water Used (in ml.)	No. of Larvae Used	Compartment	No. of Larvae in Each Compartment	X^2 Value	Type of Distribution
500	667	A	122		
		B	94	9.09	Random
		C	91		
		D	108 N.B. (4 larvae		
		E	93 left in the		
		F	125 subsampler)		
750	573	A	104		
		B	98	3.64	Random
		C	103		
		D	83		
		E	88		
		F	96		
250	1022	A	161		
		*B	154	6.96	Random
		**C	184		
		D	159 N.B. (2 larvae		
		***E	169 left in the		
		F	193 subsampler)		
250	*154 From B Compartment	A	20		
		B	29	2.57	Random
		C	25		
		D	24 N.B. (2 larvae		
		E	25 left in the		
		F	30 subsampler)		

APPENDIX IV Continued

Approximate Volume of Water Used (in ml.)	No. of Larvae Used	Compartment	No. of Larvae in Each Compartment	X^2 Value	Type of Distribution
500	**184 From C Compartment	A	29	1.15	Random
		B	29		
		C	29		
		D	29		
		E	33		
		F	35		
750	***169 From E Compartment	A	32	2.21	Random
		B	26		
		C	25		
		D	24 N.B. (2 larvae		
		E	32 left in the		
		F	27 subsampler)		
500	1143	A	191	1.98	Random
		B	181		
		C	181		
		D	201 N.B. (2 larvae		
		E	202 left in the		
		F	185 subsampler)		
750	1039	A	186	1.78	Random
		B	165		
		C	170		
		D	176		
		E	174		
		F	166		

APPENDIX V. Lower and upper confidence limits expressed in numbers per 100 l for estimated total larvae in the larval classes for samples taken during 24 hour field series of June 17-18, 1963

Time Period	Depth in Metres	Class 0	Class 1	Class 2	Class 3	Class 4
1120-1207 hours	.99		64.3	79.4	0.3	
			143.7	166.4	27.2	
	1.93	10.8	146.5	71.7	2.3	
		55.5	231.2	155.7	33.9	
	2.91	45.7	229.4	101.8	11.8	
		154.9	427.1	244.9	86.3	
	3.76	42.0	295.5	48.2	7.8	
		153.2	598.7	163.3	79.3	
	4.73	64.8	131.0	53.2		
		191.2	292.9	171.9		
	5.64	91.8	135.7	31.9	4.8	
		25.6	303.3	136.5	70.2	
	6.66	13.5	109.6	30.5		
		62.5	210.9	93.0		
	7.52	6.3	46.0	41.5	30.3	
		37.3	104.6	97.8	80.8	
	8.56	0.3	6.1	21.0	21.0	5.2
		9.3	23.0	47.7	47.7	22.2
	8.83	0.1	3.6	7.9	21.6	
		7.1	18.3	26.7	48.3	
	9.89		2.0	17.1	36.4	
			14.5	41.2	68.9	
	10.60		0.8	10.5	44.1	
			11.0	31.0	79.5	
	11.26		0.8	9.0	17.0	0.1
			11.5	29.2	41.8	7.3
	11.87	0.1		2.0	46.3	1.3
		7.0		14.6	82.4	12.8
2110-2211 hours	Surface	0.8	17.3	72.2	4.7	
		43.9	102.8	203.9	69.0	
	0.97	0.7	56.3	61.5	45.3	0.7
		41.0	172.0	181.5	153.7	41.0
	1.90	0.8	46.5	63.0	74.3	4.5
		4.2	157.5	186.0	204.0	66.0
	2.85	77.6	164.7	120.7	26.7	0.8
		213.3	345.1	279.2	123.9	43.9
	3.76	80.3	547.5	103.5	7.5	
		213.0	840.0	249.0	76.5	
	4.67	52.6	166.3	12.2		
		170.1	343.9	89.2		
	5.48	21.0	57.8	7.5		
		108.0	176.3	76.5		

APPENDIX V Continued

Time Period	Depth in Metres	Class 0	Class 1	Class 2	Class 3	Class 4
	6.24	10.6	34.9	0.3		
		31.3	67.2	9.1		
	7.52	5.0	6.4	3.1		
		15.4	17.8	12.0		
0512-0600	Surface	0.8	34.1	31.3	0.8	
hours		29.3	100.8	95.5	29.3	
	0.97		39.2	42.2	6.8	
			110.9	116.0	49.9	
	1.88	4.1	34.8	53.8	6.6	
		42.2	102.6	132.4	48.4	
	2.80	32.8	205.8	32.8	0.8	
		140.2	408.2	140.2	45.9	
	3.68	51.3	153.9	76.1	0.8	
		173.8	334.3	215.2	46.3	
	4.53	43.9	138.1	32.5	4.9	
		160.1	308.8	139.0	71.5	
	5.53	26.7	72.1	4.7	7.8	
		123.9	203.9	69.0	80.0	
	6.34	11.3	34.4	7.9	15.2	
		48.2	86.8	40.6	55.5	
	7.31	1.6	4.9	62.6	80.5	
		58.5	71.5	191.0	221.0	
	8.15		6.9	14.6	43.5	
			27.2	40.2	82.2	
	8.99		3.7	5.9	47.6	
			37.3	42.8	117.1	
	9.71		0.3	31.8	38.7	
			9.8	64.3	73.8	
	10.28		0.3	12.2	19.2	0.1
			10.0	16.3	46.2	7.8

APPENDIX VI. Lower and upper confidence limits expressed in numbers per 100 l for estimated total larvae in the larval classes for samples taken during the 24 hour field series of July 20-21, 1963.

Time Period	Depth in Metres	Class 0	Class 1	Class 2	Class 3	Class 4
1128-1223 hours	2.88	0.6	2.4	23.8	1.3	
		6.2	10.4	36.6	16.0	
	3.78	0.3	1.8	125.9		
		16.4	25.8	216.6		
	4.67	0.4	6.4	103.8		
		22.4	46.7	203.5		
	5.52	0.6	6.4	96.0		
		21.1	38.3	176.2		
	6.29			67.6	3.9	
				130.0	28.5	
	7.13			80.6	6.4	
				170.8	46.7	
	7.95			92.1	2.6	
				193.2	38.6	
	8.66			82.7	16.5	
				154.1	55.9	
	9.53		1.6	58.0	38.8	
			23.4	120.0	91.5	
	10.06		4.8	97.4	91.8	
			70.2	245.9	236.3	
	10.90			27.2	92.2	
				92.0	193.2	
	11.47			7.9	61.5	0.1
				28.8	102.4	8.2
	12.14			5.7	44.0	
				22.4	79.0	
	12.61			0.7	16.2	0.07
				6.8	32.3	3.7
2123-2211 hours	Surface		1.6	31.9	167.6	0.8
			57.5	136.5	351.2	44.7
	0.99		0.8	49.5	73.4	0.8
			44.7	167.6	207.5	44.7
	1.92	0.8		8.0	37.5	
		44.7		81.4	146.8	
	2.87		0.7	16.1	78.3	
			41.0	95.9	207.8	
	3.76			82.0	39.0	
				242.0	166.8	
	4.64	0.3	13.5	96.6	7.4	
		18.9	57.7	184.1	44.2	
	5.48		4.0	87.0	11.2	
			40.7	180.0	57.5	

APPENDIX VI Continued

Time Period	Depth in Metres	Class 0	Class 1	Class 2	Class 3	Class 4
	6.29	0.3	0.3	43.1	1.6	
		14.9	14.9	97.9	23.4	
	7.06	0.7	3.7	73.9	0.4	
		26.3	37.3	156.6	20.5	
	7.95	0.1	45.9	0.3		
		7.5	83.1	9.6		
	8.66		0.3	47.0	2.9	
			9.6	84.6	17.4	
	9.43			97.4		
				245.9		
	9.95			51.2	2.0	
				87.8	14.3	
0511-0600 hours	Surface	0.1	0.06	9.9	0.9	
		4.4	3.4	22.4	7.1	
	.99	0.2	0.08	29.3	0.08	
		5.9	4.6	52.7	4.6	
	1.92	0.3	1.3	18.4	0.3	
		9.6	13.6	44.2	9.6	
	2.87	0.06	0.1	16.3	1.7	
		3.4	4.4	31.8	8.8	
	3.78	0.3	5.9	73.7	0.3	
		9.6	34.9	141.8	9.6	
	4.64	0.8	2.4	117.3	0.4	
		28.7	35.1	221.9	22.4	
	5.48	2.4	2.4	87.0	2.4	
		35.1	35.1	180.0	35.1	
	6.49		0.1	79.8	5.9	
			4.4	165.0	42.8	
	7.19	0.4		107.6		
		20.5		203.4		
	8.02			93.8	11.2	
				189.6	57.5	
	8.75			68.0	28.2	
				147.8	86.0	
	9.33		0.4	74.6	53.6	
			24.6	166.8	135.2	
	10.07			85.4	67.1	
				226.7	198.0	
	10.78			8.3	57.3	0.2
				38.5	115.9	13.7
	11.33			16.0	93.8	0.4
				68.2	189.6	22.4
	11.99			2.6	16.3	3.3
				15.5	39.2	17.0

APPENDIX VII. Lower and upper confidence limits expressed in numbers per 100 l for estimated total larvae in the larval classes for samples taken during the 24 hour field series of August 18-19, 1963.

Time Period	Depth in Metres	Class 0	Class 1	Class 2	Class 3	Class 4
1115-1204 hours	6.86			24.3		
				44.4		
	7.63			30.5	1.3	
				62.1	13.7	
	8.39			191.4	14.0	
				396.0	102.7	
	9.12			213.9	27.1	
				416.7	126.1	
	9.83		64.7	67.8	61.5	0.4
			146.9	151.7	142.1	22.4
	10.24		0.4	58.3	61.5	
			22.4	137.3	142.1	
	10.40			20.6	129.1	
				80.9	244.1	
	11.49			2.2	68.0	2.2
				32.2	147.8	32.2
	12.78			14.4	127.7	
				52.4	215.5	
2108-2200 hours	Surface		1.7	46.5	13.8	13.8
			62.0	169.7	100.8	100.8
	0.95	0.2	0.4	23.0	52.3	2.2
		12.0	15.5	61.1	104.7	21.9
	1.91	1.8		19.3	35.1	
		63.2		11.5	150.1	
	2.76			7.3	56.3	14.6
				74.6	172.0	52.7
	3.66			77.7	28.7	
				219.7	133.5	
	4.50		1.5	35.5	21.2	
			54.5	139.2	108.9	
	5.44	1.7		13.8	40.5	
		62.0		100.8	158.5	
	6.40	0.1	0.3	18.3	19.3	0.1
		7.0	9.0	43.0	44.5	7.0
	7.13			25.6	2.7	2.7
				41.5	16.0	16.0
	7.95			15.3	12.2	2.1
				39.4	34.6	15.6
	8.66			6.8	11.2	1.4
				26.7	34.1	14.8
	9.23			3.0	7.2	3.0
				17.6	26.4	17.6
	9.95		0.07	0.73	6.7	6.1
			4.1	7.5	19.0	18.1

APPENDIX VII Continued

Time Period	Depth in Metres	Class 0	Class 1	Class 2	Class 3	Class 4
	10.78			2.0	14.8	2.5
				10.5	31.3	11.6
	11.61			0.3	5.1	1.2
				3.9	13.1	6.4
0515-0600 hours	0.95		0.09	11.5	2.0	
			3.3	22.4	7.9	
	1.87		0.09	13.1	1.0	
			3.5	25.1	6.0	
	4.46	0.1	0.06	12.8	0.6	
		4.4	3.4	26.8	6.2	
	5.44	0.1	0.8	26.9	0.3	
		7.5	11.7	56.9	9.6	
	6.13	0.07	0.1	27.9	0.7	
		3.7	4.8	47.9	6.8	
	6.86		0.3	55.4	13.1	
			9.5	95.0	35.9	
	7.46			74.5	14.8	
				157.9	63.1	
	7.99		0.4	67.8	27.5	
			22.4	151.7	89.0	
	8.67		0.8	55.1	134.1	0.8
			28.7	132.5	244.7	28.7
	9.46			2.4	61.5	13.6
				35.1	142.1	63.1
	9.96			10.7	71.2	1.0
				63.9	167.8	35.1
	10.40				120.0	3.6
					254.9	52.2
	11.15				105.9	0.5
					221.8	28.2
	11.12				42.4	14.8
					109.2	63.1

APPENDIX VIII. Lower and upper confidence limits expressed in numbers per 100 l for estimated total larvae in the larval classes for samples taken during the 24 hour field series of September 21-22, 1963.

Time Period	Depth in Metres	Class 0	Class 1	Class 2	Class 3	Class 4
0758-0838 hours	8.19			118.5	75.1	
				237.6	173.7	
	9.12			47.0	81.7	
				124.7	177.4	
	9.83			41.3	86.9	0.9
				161.6	238.8	49.2
	10.65			6.4	61.5	11.2
				46.7	142.1	57.5
	11.18			7.0	85.2	17.6
				51.4	182.6	75.1
	12.14			4.4	50.5	12.3
				44.8	130.0	63.2
	12.61			3.4	17.2	5.4
				13.5	34.8	17.2
1125-1205 hours	7.37		0.05	16.4	10.7	
			2.7	29.9	21.5	
	8.19		0.1	18.4	12.3	
			7.5	44.2	34.6	
	9.12			27.2	57.1	2.6
				92.2	140.5	38.6
	9.83		0.4	38.6	47.0	0.4
			24.6	119.4	124.7	24.6
	10.65		0.4	36.9	99.7	0.4
			24.6	108.9	203.3	24.6
	11.18			23.7	99.7	0.4
				86.5	203.3	24.6
	12.14			4.1	54.1	0.3
				21.1	96.4	10.5
	12.61			6.5	38.2	
				27.8	77.2	
	14.72			8.4	19.0	0.4
				21.7	37.3	24.6
1530-1617 hours	7.37			10.6	9.3	
				26.0	24.1	
	8.19			60.6	14.9	
				145.8	69.4	
	9.12			20.2	63.1	
				68.3	135.3	
	9.83			12.3	106.7	9.7
				63.2	213.8	57.5
	10.65			7.5	133.7	13.1
				54.7	254.8	67.3
	11.18			0.9	155.3	9.1
				51.2	347.2	93.2

APPENDIX VIII Continued

Time Period	Depth in Metres	Class 0	Class 1	Class 2	Class 3	Class 4
	12.14			0.9	53.6	9.7
				31.6	135.2	57.5
	12.61			1.8	29.0	18.1
				25.8	79.6	61.3
1930-2007 hours	Surface			1.8	66.0	7.3
				18.7	118.5	31.3
	0.97			3.2	36.7	10.1
				19.2	72.9	32.6
	1.90			2.1	32.3	4.5
				15.6	64.8	21.0
	2.78			6.3	19.4	2.1
				24.5	45.8	15.6
	3.63			11.3	22.5	2.3
				34.4	52.1	17.1
	4.53			6.9	21.4	0.3
				26.9	50.3	10.5
	6.12			7.6	15.0	
				29.9	42.3	
	6.71			2.5	14.2	1.6
				11.6	30.4	9.6
	7.37			2.8	13.2	0.2
				12.8	29.9	5.9
	8.19		0.1	10.1	21.4	0.1
			8.2	32.6	50.3	8.2
	9.12			2.3	28.4	0.3
				17.1	60.9	10.5
	9.83			1.4	17.9	0.9
				14.9	45.1	12.9
	10.65			0.9	26.0	0.3
				12.9	57.4	10.5
	11.18			6.9	21.4	0.9
				26.9	50.3	12.9
	12.14			0.1	9.2	6.6
				4.8	22.1	18.1
	12.61			0.2	13.2	5.4
				5.6	29.6	17.4
2132-2216 hours	Surface			0.4	44.5	5.1
				13.2	89.1	26.3
	0.97			0.3	24.9	13.5
				10.5	55.6	38.0
	1.91			4.5	35.7	7.2
				21.0	69.4	26.2
	2.78			7.2	20.5	1.3
				26.2	47.4	13.6
	3.66			5.9	30.7	3.2
				25.0	64.4	19.2

APPENDIX VIII Continued

Time Period	Depth in Metres	Class 0	Class 1	Class 2	Class 3	Class 4
	4.50	0.1		4.1	14.5	0.3
		8.2		21.1	39.8	10.5
	5.30			5.0	21.4	3.2
				23.1	50.3	19.2
	6.06			7.5	20.4	0.3
				21.1	40.5	7.2
	6.63			4.0	19.0	4.5
				14.4	37.3	15.4
	7.09			4.4	11.9	0.08
				16.0	28.0	4.6
	8.48			13.5	15.7	
				38.0	41.6	
	9.33			3.2	27.2	0.9
				19.2	59.1	12.9
	9.95			3.2	21.4	
				19.2	50.3	
	10.65			1.5	28.4	5.0
				14.9	60.9	23.1
	11.19			5.6	20.3	2.9
				17.2	39.0	12.5
	11.99			0.1	16.6	5.0
				5.3	33.9	16.3
	12.78			1.2	11.4	2.2
				9.1	26.8	11.2
2322-0002 hours	Surface			5.9	16.8	5.0
				25.0	43.3	23.1
	0.98			4.1	11.3	0.7
				14.0	25.3	6.8
	1.90			5.0	11.9	1.6
				16.3	26.9	9.6
	2.80			5.0	16.0	0.7
				16.3	33.0	7.5
	3.60			2.9	7.2	0.4
				12.5	19.9	6.4
	4.42			4.8	16.2	0.8
				22.3	41.7	12.4
	5.30			3.9	20.1	0.3
				19.9	47.4	9.9
	6.06			13.5	27.2	4.1
				38.0	59.12	21.1
	6.63			5.0	15.7	2.3
				23.1	41.6	17.1
	7.28			18.4	34.6	5.3
				59.3	85.1	19.2

APPENDIX VIII Continued

Time Period	Depth in Metres	Class 0	Class 1	Class 2	Class 3	Class 4
	7.99			39.5	30.7	8.8
				108.6	93.8	52.3
	9.12			1.5	82.5	21.6
				55.5	218.9	111.0
	9.59			1.3	29.6	6.9
				12.9	61.0	25.3
	10.65			0.1	21.6	1.3
				7.5	49.0	13.6
	11.19			0.5	10.6	0.8
				5.0	22.0	5.7
	11.82			0.1	7.5	2.1
				3.2	16.9	8.2
	12.61			0.8	7.1	1.1
				5.7	16.8	6.4
0332-0415 hours	Surface			1.3	7.9	.05
				7.0	18.0	2.7
	.97			2.0	6.7	1.4
				8.3	16.2	7.0
	1.90			1.4	7.9	1.7
				7.0	18.0	7.7
	2.78			2.1	9.0	0.3
				8.2	19.0	3.9
	3.66			1.1	12.9	0.4
				7.8	27.7	5.9
	4.50			2.9	10.1	1.6
				12.5	24.3	9.6
	5.35			2.3	7.1	2.3
				10.3	18.9	10.5
	6.18			5.9	19.0	0.3
				25.0	46.8	10.5
	6.93			3.3	15.4	2.0
				13.0	31.8	10.1
	7.61			14.2	11.3	1.46
				30.4	26.0	14.9
	8.19			8.3	140.7	1.7
				84.4	31.4	59.6
	8.79			0.9	83.2	13.1
				33.6	183.3	67.3
	9.95			1.4	39.4	10.6
				14.1	75.2	32.4
	10.78			0.1	28.4	14.5
				8.2	60.9	39.8
	11.19			1.2	24.6	3.4
				8.6	44.9	13.5
	12.29			1.8	13.8	4.4
				10.7	30.9	16.0

APPENDIX VIII Continued

Time Period	Depth in Metres	Class 0	Class 1	Class 2	Class 3	Class 4
	12.61			.05	8.7	5.2
				2.7	19.1	13.7
0513-0555 hours	3.71			5.4	18.2	.09
				13.7	31.0	3.2
	4.53			5.4	8.0	.05
				13.9	17.8	2.6
	4.40			4.9	9.2	
				14.8	21.7	
	6.18			13.2	24.7	3.7
				36.2	53.7	19.2
	7.06			13.2	11.2	0.1
				36.2	33.0	7.5
	7.79		0.1	5.3	26.9	4.5
			7.5	22.7	56.9	21.0
	8.29			8.8	128.2	8.8
				89.6	302.0	89.6
	9.01			49.5	116.5	8.0
				167.6	274.6	81.4
	9.83			9.7	50.5	20.6
				57.5	130.0	80.8
	10.78			2.4	55.1	6.4
				35.1	132.5	46.7
	11.75			0.1	39.2	10.2
				8.2	76.4	32.6
	11.96			0.3	23.7	9.1
				10.5	53.9	30.7
	12.61			1.9	11.3	7.1
				9.6	25.3	18.9

APPENDIX IX. Lower and upper confidence limits expressed in members per 100 l for estimated total counts of larvae in samples taken during the 24 hour field series of June 16-17, 1963.

Time Period	Depth in Metres	Lower Limit	Upper Limit
0805-0922 hours	0.97	101.3	130.4
	1.90	598.6	910.3
	2.87	298.0	453.1
	3.76	263.4	495.0
	4.67	298.0	525.5
	5.60	217.1	288.6
	6.45	98.4	149.0
1120-1207 hours	.99	170.2	286.6
	1.93	281.4	429.8
	2.91	494.3	730.3
	3.76	528.7	816.4
	4.73	313.7	578.2
	5.64	339.2	587.5
	6.66	185.9	312.5
	7.52	160.7	115.2
	8.56	60.9	103.7
	8.83	43.9	79.4
	9.89	65.7	107.9
	10.60	63.8	106.3
	11.26	35.0	68.2
1522-1612 hours	0.97	132.5	196.0
	1.96	557.7	862.0
	2.87	443.3	713.1
	3.80	406.7	682.6
	4.54	285.6	512.7
	5.64	191.8	259.0
	6.34	139.1	202.6
	7.42	87.2	140.9
1922-2005 hours	Surface	127.7	187.0
	0.97	215.3	288.9
	1.92	423.6	523.4
	2.88	383.1	638.6
	3.80	396.4	655.3
	4.76	196.1	323.5
	5.68	105.6	186.1
	6.49	126.9	184.1
	7.06	94.5	143.7
2110-2211 hours	Surface	158.5	335.7
	.97	227.6	423.7
	1.90	264.8	477.0

APPENDIX IX Continued

Time Period	Depth in Metres	Lower Limit	Upper Limit
	2.85	509.8	807.8
	3.76	842.9	195.5
	4.67	297.5	511.0
	5.48	121.5	276.0
	6.24	52.9	92.0
	7.52	18.7	35.6
2310-1200 hours	Surface	114.5	166.9
	0.97	109.9	163.9
	1.91	158.8	220.3
	2.85	713.0	841.6
	3.86	767.3	1107.5
	4.76	428.5	437.4
	5.53	163.8	227.3
	6.62	58.3	97.2
0105-0153 hours	Surface	99.2	150.0
	.97	110.8	164.1
	1.92	565.2	878.3
	2.85	807.0	1163.1
	3.76	855.3	1216.1
	4.64	237.0	280.4
	5.48	130.1	188.4
	6.29	66.2	110.3
0317-0404 hours	Surface	114.7	166.2
	.96	120.3	177.4
	1.90	215.9	290.4
	2.85	587.6	889.7
	3.76	391.3	652.2
	4.64	308.8	398.7
	5.60	152.4	215.8
	6.43	108.5	158.2
0512-0600 hours	Surface	88.6	183.3
	0.97	114.3	222.7
	1.88	132.4	244.1
	2.80	340.3	582.2
	3.68	355.9	612.4
	4.53	286.9	516.8
	5.53	158.5	335.7
	6.34	97.2	176.1
	7.31	204.0	404.7
	8.99	71.0	152.2
	9.71	84.0	131.4

APPENDIX X. Lower and upper confidence limits expressed in numbers per 100 l for estimated total counts of larvae in samples taken during the 24 hour field series of July 20-21, 1963.

Time Period	Depth in Metres	Lower Limit	Upper Limit
0815-0909 hours	7.13	142.5	203.1
	7.95	132.8	188.9
	8.66	323.1	411.0
	9.53	240.8	317.7
	10.06	209.8	282.2
	10.90	74.4	115.9
1128-1223 hours	2.88	32.3	53.7
	3.78	169.8	234.1
	4.67	124.1	231.1
	5.52	120.0	204.9
	6.29	78.0	143.9
	7.13	97.0	194.4
	7.95	103.2	208.5
	8.66	109.1	186.3
	9.53	119.7	200.9
	10.06	241.9	453.4
	10.90	133.0	249.3
	11.47	74.6	122.9
	12.14	54.9	92.1
1521-1602 hours	9.33	443.4	540.8
	9.95	319.4	406.7
1920-2012 hours	9.80	324.5	412.3
	10.18	226.7	295.4
2123-2211 hours	Surface	248.2	462.2
	0.99	161.2	341.6
	1.92	67.1	198.0
	2.87	118.5	269.3
	3.76	150.2	347.3
	4.64	145.2	243.2
	5.48	1241.2	231.1
	6.29	53.7	113.9
	7.06	95.1	186.6
	7.95	49.2	87.7
	8.66	57.2	95.8
	9.43	97.4	245.9

APPENDIX X Continued

Time Period	Depth in Metres	Lower Limit	Upper Limit
2307-2354 hours	3.82	224.8	299.1
	4.70	279.8	358.8
0320-0400 hours	3.82	191.7	246.8
	4.67	182.7	250.8
0511-0600 hours	10.07	231.6	284.3

APPENDIX XI. Lower and upper confidence limits expressed in numbers per 100 l for estimated total counts of larvae in samples taken during the 24 hour field series of August 18-19, 1963.

Time Period	Depth in Metres	Lower Limit	Upper Limit
0515-0600 hours	6.13	31.3	53.2
	6.86	79.1	125.3
	7.46	102.2	196.6
	7.99	114.1	217.5
	8.67	227.5	363.2
	9.46	93.8	189.6
	9.96	102.4	214.6
	10.40	129.5	267.9
	11.12	68.6	149.0