THESIS

DISTRIBUTION AND PRODUCTION OF MIDGES (TENDIPEDIDAE)
IN AN ALPINE LAKE

Submitted by

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WE HEREBY RECOMMEND THAT THE THESIS PREPARED UNDER

OUR SUPERVISION BY _____ Carl J. Walters _____

ENTITLED _____ Distribution and Production of Midges _____

_____ (Tendipedidae) in an Alpine Lake _____

BE ACCEPTED AS FULFILLING THIS PART OF THE REQUIREMENTS

FOR THE DEGREE OF MASTER OF SCIENCE.

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ABSTRACT

DISTRIBUTION AND PRODUCTION OF MIDGES (TENDIPEDIDAE) IN AN ALPINE LAKE

Larval populations and emergence of midges were sampled during the summer of 1966 in Emmaline Lake, Colorado. The fish population was removed from this alpine lake in 1964. Emergence was sampled using surface cone traps.

Midge emergence was extremely variable in time and space; greatest numbers emerged in early summer over broken rock and sandy shoreline areas. Weight of emerging midges was often greatest over the mud lake bottom where it bordered rocky slopes. Taxonomic diversity was high; at least 10 species of midges occurred in emergence samples. Statistically, emergence counts followed the negative binomial distribution with "k" usually in the range 0.1 to 0.2.

Larval populations in mud bottoms were not clearly correlated with emergence over mud areas. Survival of pre-emergent larvae to adulthood was low, but 20 to 50 adults emerging per m^2 in late July were apparently enough to yield larval populations of over 5000 per m^2 by late September. Larval growth and net biomass production were greatest in early summer and fall. Detectable larval mortality occurred only in late fall.

ACKNOWLEDGEMENTS

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INTRODUCTION

Alpine lakes will become increasingly important fishing areas as more accessable waters become overcrowded. Because productivity is low, and fish populations can have marked effects on their food supply, alpine lakes present special management problems. Many alpine lakes are overpopulated by brook trout (<u>Salvelinus fontinalis</u>) that provide large numbers of small fish to the angler. A high fish population may result in depletion of food organisms and long term reduction of productive capacity for fishes. It may be necessary in the future to remove stunted populations and replace them with more manageable species.

Effects of fish removal from Emmaline Lake, Colorado, were investigated by Wrenn (1965). The lake, devoid of fishes, provided an opportunity to study recovery and population dynamics of invertebrate organisms in the absence of fish predation. Studies of fish introduction and the effect of fish predation on invertebrate populations may provide estimates of yield of food organisms to fishes, if sufficient data can be obtained on these populations while fish are absent from the lake.

Objectives of the present study are: (1) to characterize spatial and temporal distribution of aquatic insect

larvae in Emmaline Lake during the second summer following fish removal, (2) to characterize the pattern and quantity of insect emergence during the summer, and (3) to estimate net biomass production of insects during summer 1966.

Aquatic insects, particularly midges (Diptera, Chironomidae), provide the bulk of autochtonously produced fish food in alpine lakes. They are taken by trout primarily as they pupate and emerge; therefore, much of the present study was directed to estimates of insect emergence as a direct measure of potential production to fishes. Insect larval populations were studied to determine their relationship to emergence.

Great variability is characteristic of emergence and bottom fauna sampling; this paper discusses some biological factors contributing to that variability.

LITERATURE REVIEW

High mountain lakes have received little detailed biological study. Pennak (1941) reviewed literature on alpine lakes prior to 1940. Basic biological and limnological studies were conducted by Reimers, et. al. (1955), Pennak (1958), Rawson (1942), Patalas (1964), Maciolek and Kennedy (1964), and others. Alpine lake communities and factors affecting them were considered by Tomasson (1956).

Studies that reveal importance of aquatic midges as fish food in alpine lakes have been made by Reimers, et. al. (1955), Reimers (1958), Robertson (1947), and locally by Nelson (1964). In these studies midges, primarily pupal stages, comprised about 70 to 90 percent of the lake-produced diet of trout species.

Studies of fish influence on invertebrate populations have indicated that not only depletion, but even complete disappearance of some invertebrate species may occur (Hrbacek and Hrbackova), 1960; Straskraba, 1965). Attempts to estimate production (biomass yield) of invertebrates to fish by comparing populations in the presence and absence of fish predation were made by Hayne and Ball (1956), Straskraba (1965), Lellak (1966), and Macan (1965). These

studies revealed the necessity of considering individual life histories of food species in interpreting changes caused by fishes.

Most studies have attempted to estimate midge production from larval populations, ignoring emergence or treating it as an "error" factor (Neese and Dugdale, 1959 ; Konstantinov, 1958; Hayne and Ball, 1956; Anderson and Hooper, 1956; and others). Successful attempts to study midge production over the entire life cycle, from larvae through emergence, have been made only by Jonasson (1965, 1961), who worked with Chironomus anthracinus under ideal natural conditions. A major problem in quantitative life cycle studies is that emergence of a species is not necessarily correlated spatially with the larval population; emergence may occur in entirely different areas from those occupied by the larvae (Scott and Opdyke, 1941; Borutskii, 1939).

Detailed life history data for most species are lacking. Life histories can vary greatly even among members of a single genus (Pennak, 1953; Buscemi, 1961). Species with large, mud-dwelling larvae and conspicuous adults have been studied most; examples are Chironomus anthracinus (by Jonasson, 1961, 1965), Chironomus hyperboreus (by Rempel,

1936), <u>Sergentia</u> <u>coracina</u> (by Wülker, 1961), and <u>Chironomus</u>
<u>plumosus</u> (by Hilsenhoff, 1966). Types with rock dwelling
larvae have been virtually ignored (Dusoge, 1966).

Larval populations are often difficult to sample
quantitatively. Spatial variation in numbers is great;
even different larval age classes of a single species may
inhabit different lake areas (Wülker, 1961). Causes of
variation, often not quantifiable for stratified sampling,
are water depth (Hayne and Ball, 1956; Deevey, 1941),
subtle differences in bottom type (Rawson, 1930; Tebo, 1955;
Cole and Underhill, 1965), and location of suitable breeding
areas for adults (Jonasson, 1965). Statistical studies of
this variability show some consistency; for example, Tebo
(1955), Hayne and Ball (1956), Smith (1961), and Wrenn
(1965) all found that approximately 100 samples are
necessary to estimate mean sublittoral bottom fauna within
20 percent (with 95 percent confidence).

That insect emergence alone can provide a direct
measure of midge biomass yield was first recognized by
Borutskii (1939) in Russia and by Scott and Opdyke (1941)
in America. Macan's (1965) work is a recent use of
emergence measurement when comparing lakes with and without
fish populations.

Several methods of sampling emerging insects are available (Morgan, et. al., 1963). All involve some type of trap into which pupae rising to the water surface can enter and emerge. Submerged funnels of various sorts are commonly used (Jonasson, 1954; Buscemi, 1961). In quiet waters more efficient floating tent traps can be set (Morgan, et. al., 1963; Wiltzius, 1965; Frank, 1965). Trapping efficiency depends on visibility to emerging insects of the trap used, and the time of set. Buscemi (1961), and Morgan, et. al. (1963) cautioned against set times longer than one day because catches may decompose; Macan (1965) and Mundie (1953) obtained good results with week long sets, and indicate that longer set times are acceptable in colder waters.

Due to extreme spatial variability in emergence, very large samples are required to achieve statistically precise estimates of numbers. Why is this variability so great? Mundie's (1953) work is a key to the answer. Using 27 traps along fixed transect lines in a small reservoir, he found that many species were represented in emergence, each species with characteristic habitat requirements and emergence pattern that did not always correspond to its larval habitat. Later work by Buscemi (1961), Macan (1965),

and Frank (1965) showed similar patterns in other types of lakes. Total emergence was greatest over shallows, areas of aquatic vegetation, and broken rock; it was least over profundal mud areas. That is, emergence was greatest over bottom types that present greatest surface area for larval growth.

Statistical methods have been proposed to describe extreme variability like that occurring in spatial distribution of insect emergence and larvae. Foremost are the negative binomial distribution (Bliss and Fisher, 1953, show an example for bottom fauna data), and the log-normal transformation (Cassie, 1962). Their primary assumption is that organisms are not randomly dispersed in space (Andrewartha, 1961), but are clumped because of habitat requirements, food availability, social interaction, or lack of dispersal of young from hatching points.

STUDY AREA

Emmaline Lake is at 3350 m above sea level, in a cirque near the northern boundary of Rocky Mountain National Park (S.26, T 7N., R. 74 W., 6th p. Mer.). Shoreline vegetation is of the subalpine fir-whitebark pine type. Annual snowfall is high; the lake is normally ice covered from early October to late June.

The lake is a rock basin type as defined by Pennak (1958) and was probably formed by late Pleistocene glacial scouring. Principal rock formations are granitic.

General limnological characteristics of Emmaline Lake were described by Wrenn (1965). This section will present characteristics not measured by him, and note interseasonal differences.

Morphometry and bottom types -- Depth profiles were made of the lake using a Bendix portable depth recorder, and measurements confirmed with a sounding line. The form of the depth recorder trace, along with dredge sampling and visual observation, were used to map bottom type. Lake shape and area were determined from a USGS aerial photograph by relating relative distances on the photograph to measurements (steel tape) along transect lines crossing the lake (Figure 1).

N

outlet

6 m

5

4

3

2

1

0 10 20

meters
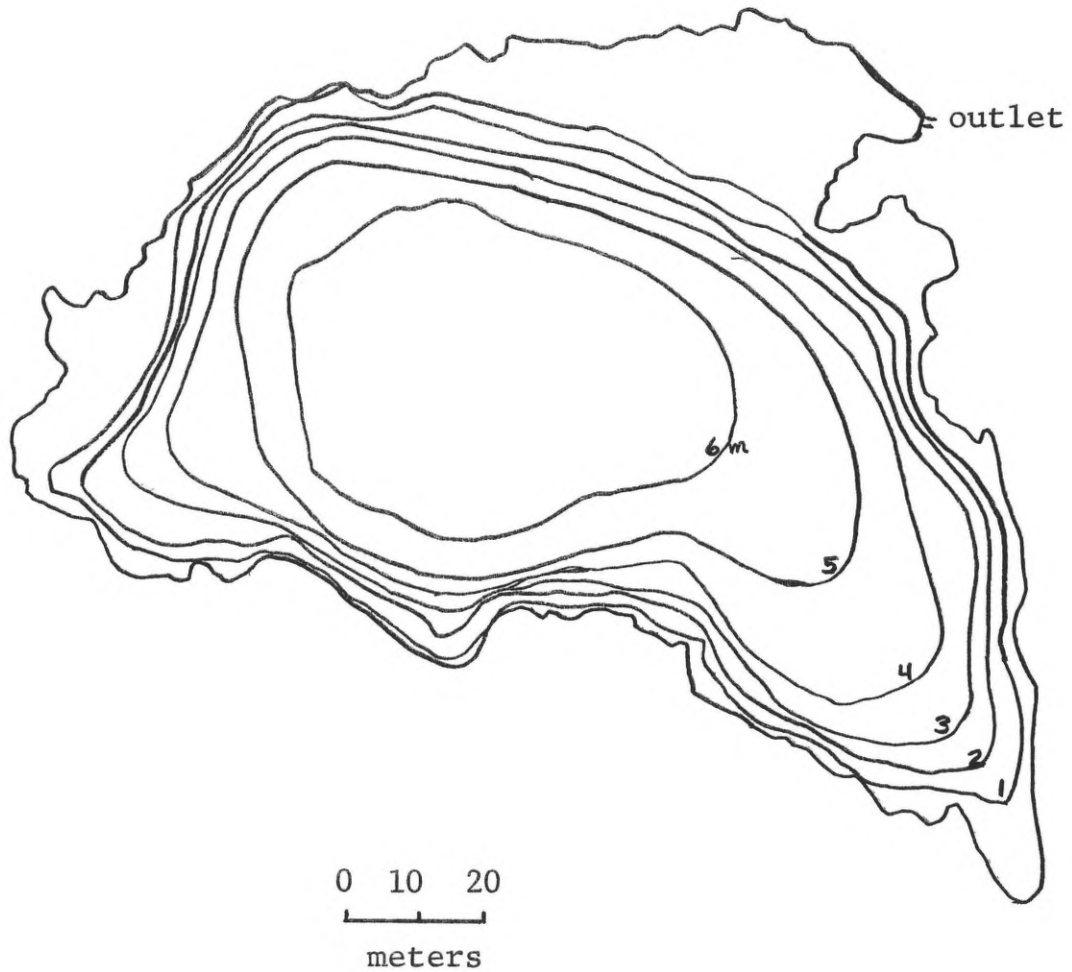
Figure 1.   Emmaline Lake, Colorado.   Depth contours at 1 m
            intervals.   Total area = 1.035 hectares

Seven bottom types were distinguished (Figure 2). Types were defined as:

(1) unbroken rock surfaces--granitic bedrock of the basin, smallest surface areas for biological activity, found only in steep shoreline areas;

(2) large boulders--bottom areas with rocks generally larger than 1/2 meter diameter; steep shoreline areas;

(3) rubble--areas of broken, decomposed granite; stones generally of approximately 5 to 50 cm diameter; shoreline and rock-mud interface areas;

(4) sand--particle size approximately 2 to 4 mm; characteristic of inlet delta;

(5) sandy mud--sand as defined above overlain with thin silt layer;

(6) mud Type A--relatively thin layer of silt, large amount of partially decomposed organic matter, and often mixed with rubble; near rock-mud interfaces;

(7) mud Type B--thick (4 to 6 cm) silt, of relatively low organic content, generally with permanent matted overlay of blue-green algae; lake center.
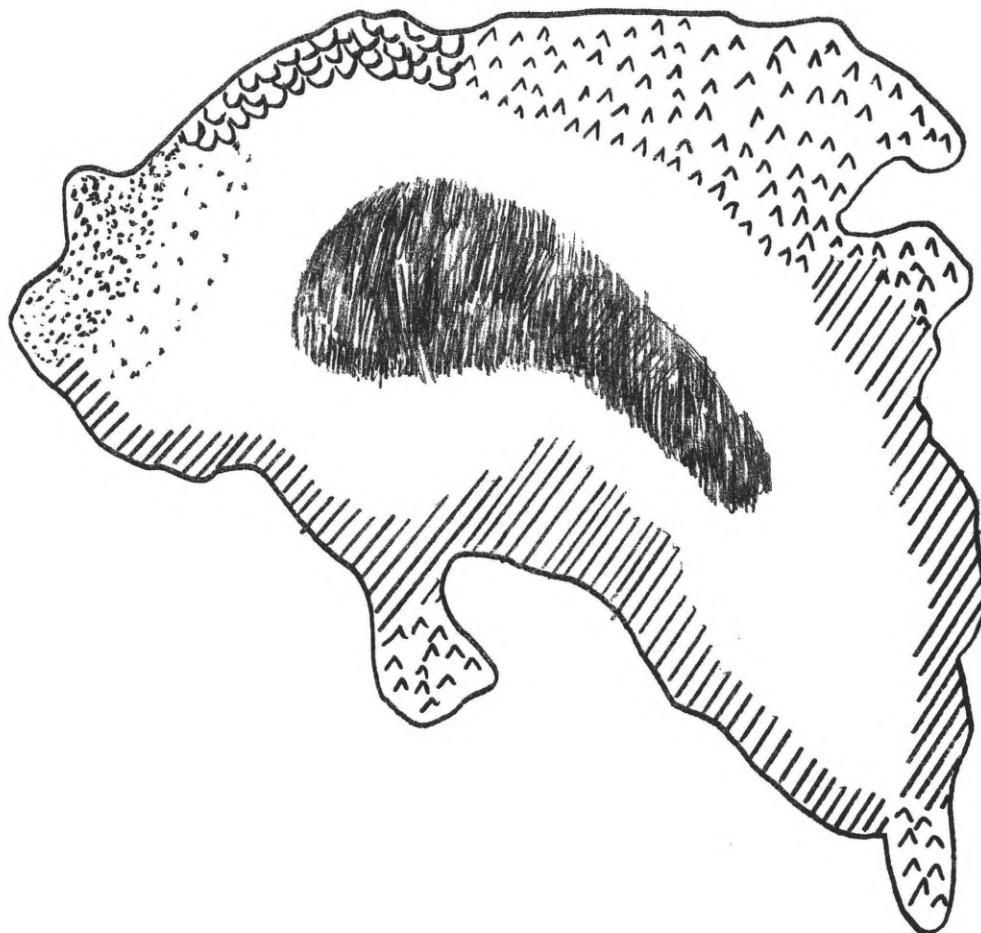
Symbol	Bottom Type	Percentage of Area
[unbroken rock symbol]	unbroken rock	5.2
[large boulders symbol]	large boulders	2.2
[rubble symbol]	rubble	8.1
[sand symbol]	sand	3.9
[sandy mud symbol]	sandy mud	4.8
[mud type A symbol]	mud type A	34.8
[mud type B symbol]	mud type B	14.9

Figure 2. Bottom types of Emmaline Lake, Colorado.

Water chemistry--Surface and bottom (6 m) temperatures
for summer 1966 are shown in Figure 3. Wrenn found similar
patterns in 1964 and 1965, but with maxima of about 18°C.

Emmaline Lake apparently became mildly stratified
during August; however, no continuous depth-temperature
series were taken. Stratification should probably be
considered abnormal for the lake: summer 1966 was
unusually calm, while strong winds and longer ice cover
are the rule.

Other chemical features (dissolved oxygen, pH,
conductivity, alkalinity, and total dissolved solids) were
the same in 1966 as described by Wrenn (1965) for the two
previous years. Oxygen-depth series taken under ice in
mid-May and late November, 1966, showed no indication of
winter oxygen depletion.

Biota--There are no higher aquatic plants in Emmaline
Lake. Phytoplankton is dominated by Desmids and, occasion-
ally, diatoms. Genera present were listed by Wrenn (1965).

Zooplankters include Daphnia rosea, Daphnia
middendorffiana, Cyclops sp., and a variety of rotifers,
dominated by a Keratella sp.
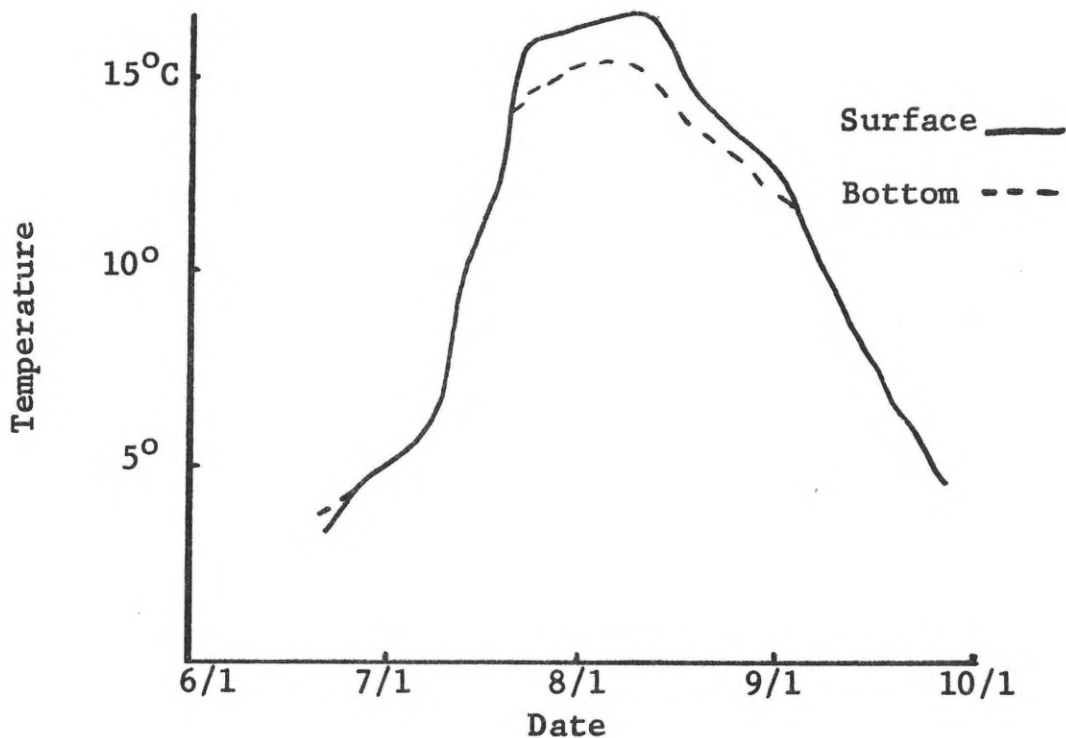
Figure 3. Water temperatures at surface and bottom,
Emmaline Lake, Colorado, summer 1966.

Benthos includes, as well as chironomids described
later, oligochaetes and presumably fingernail clams
(Pisidium sp., Pelecypoda). Clams have not been observed
since fish removal in 1964. Rocky shorelines are inhabited
by Trichoptera (Micrasema sp.) and Corixids (Hemiptera).

Plankton exhibits typical pulses, which may occur
under ice cover as well as during the summer. A phyto-
plankton bloom in May and June, 1966, was followed by

zooplankton increases in July and August. Zooplankton population remained relatively high through September. *Cyclops* *sp*. dominated the zooplankton during July and early August, was replaced by *Daphnia* *rosea* during the latter part of August, and by October *Daphnia* *middendorffiana* had become dominant. Large numbers of epphipia were produced by *D*. *rosea* during the first two weeks of September.

METHODS AND MATERIALS

Twelve two-day sampling periods spaced at one week intervals were used during summer 1966. Emergence, plankton, and water samples were taken on the first day; bottom fauna samples were taken on the second. Routine plankton samples (vertical haul) were taken using a Birge net with a 12 cm mouth size.

Emergence sampling--Insect emergence was sampled using clear, conical plastic traps based on the design of Sublette and Dendy (1959). A 30° right cone with base area either 1/4 or 1/2 m^2 formed the basic trapping surface. Each cone was held open, and stretched smooth, by a wire ring glued into a fold at the base of the cone. At the apex of the cone was attached a quart jar, allowed to fill half-way with water.

Pupae entering the trap from below were funneled into the attached jar. Here, unable to swim back down because an air bubble was formed under their rudimentary wings, they emerged into the airpocket in the jar. Emergence occurred shortly (within a few hours) after pupae reached the water surface (Wiltzius, 1965).

Traps can be set at any depth without impairing effectiveness (Guyer and Hutson, 1955). In this study they

were placed with the jar just under or touching the water surface, as used by Jonasson (1954). A limitation of a subsurface set is that water less than 1/2 m deep cannot be sampled.

Traps were held in place by securing them to a series of nylon transect lines crossing the lake surface.

Two or three traps were distributed randomly along each unbroken transect segment, and one trap was placed against shore at the anchor point of each transect line (Figure 4). Trap locations were fixed throughout the summer. In all, 34 traps were used.
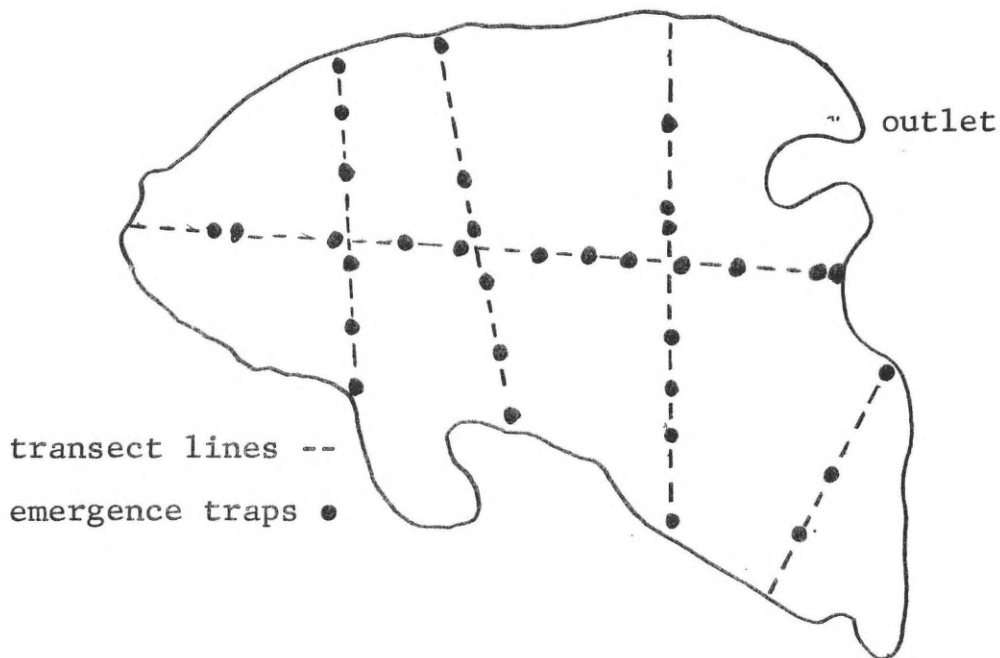
Figure 4. Location of emergence traps and transect lines, Emmaline Lake, summer 1966.

Nine were set the first sampling period, 12 the second, 24 on the third through sixth, and 34 the last six sampling periods.

Catches were removed weekly from traps. No appreciable decomposition was noticed; cold water, and subsurface sets (out of direct sunlight) inhibited decomposition.

Catches were removed from jars by pouring the contents through several layers of cheesecloth stretched over a funnel. The cheesecloth with organisms was placed in a plastic bag, and five percent formalin added.

Emergents were later counted by gross morphological type under a dissecting scope, and total blot dry weight to 0.1 mg was obtained for the sample. Blot drying was accomplished by placing insects on a paper towel as they were counted. To prevent differential drying with large samples requiring long counting time, these samples were placed on wet towels as they were being counted, then transferred to dry ones before weighing.

Bottom fauna sampling--Bottom samples were taken with a $1/4\text{ft}^2$ Ekman dredge, and screened through a 0.4 mm mesh Tyler soil seive. Organisms were removed from the screen and concentrated using the sugar flotation method of Anderson (1959). A 0.4 mm mesh screen gives quantitative recovery for all but first and some second instar midge larvae (Jonasson, 1955).

Bottom samples were taken in series of ten, one dredge haul per sample. Generally, one series was taken per week; two were taken on two dates, and four on another, for statistical comparisons between series.

Samples in any series were allocated to the lake surface by taking one dredge haul in each approximately rectangular area defined by emergence transect lines (Figure 4), and one on the sandy inlet delta. The sample for each area was located by dividing the area into nine subzones, and selecting one of these at random. The allocation method used permitted gross study of spatial distribution patterns of insect larvae, and approximately met a randomness criterion that every point on the bottom has equal probability of being sampled (since the areas were of approximately equal size).

Samples were preserved in five percent formalin for laboratory analysis. Larvae in each sample were separated into 2 mm length groups, counted, and a total blot dry weight to 0.1 mg for each length category was obtained.

Statistical analysis--Routine data summarization of various counts and weights was done on an IBM 1620 computer. Standard sampling estimators (Cochran, 1963), were used.

In particular, mean weight and standard deviation per individual larva for the larval size classes were calculated using ratio-regression estimators. Unless otherwise noted, logrithmic transformations were used in all count data summarization.

Comparison of total emergence from week to week was made using paired t tests; differences were those between catches for each trap on the two dates under comparison. This type of comparison was used because traps were not moved from week to week.

The negative binomial distribution was fit to emergence counts using maximum liklihood estimates for expansion coefficients ("K") (Bliss and Fisher, 1953). Calculations were performed with a CDC 6400 computer.

Only data summaries for principal organisms are presented. Raw counts and weights are on file and available at the Colorado Cooperative Fishery Unit.

INSECT EMERGENCE

Tendipedids were the only insects collected by emergence sampling in Emmaline Lake during 1966. Nymphal exuviae and adults of <u>Micrasema</u> <u>sp</u>. (Trichoptera) were occasionally observed near rocky shores, but none were taken in traps. Multiplying mean catch per m^2 for each week by total lake area and summing across weeks gave an estimated total emergence in 1966 of approximately 75,000 insects, for a total emergence weight of approximately 4,300 g.

Excessive variability in emergence sampling was caused by interactions of heterogeneity in taxonomic type, diversity in larval habitat, and time. These sources of variability, and resulting statistical trends, are analyzed in the following pages.

<u>Taxonomic</u> <u>variety</u>--Precise segregation of insects by species proved impossible. Virtually nothing is known of midge taxonomy in high mountain lakes (Pennak, 1953). From general morphological characteristics, at least 10 species of midges were present. Principal in weight and numerical abundance were:

[handwritten annotation: Trichops don't have nymphs!]

(1)   A large _Tendipes_ sp.

Adults were approximately 10 mm in length; emergence occurred throughout the summer over mud bottom areas.

(2)   A smaller _Microtendipes_ sp.

Emergence occurred in early and late summer, over gravelly interface areas between rock and mud bottoms.

(3)   A small, bright green type.

Probably at least two species were present. In early and late summer, emergence was over rock and rock-mud interfaces and in mid-summer was also over inshore mud areas.

(4)   A small, yellowish type with dark head capsule.

It may represent several species or even genera. Because of the small size, and partial destruction of key characters with the sample recovery method used, no generic identification was attempted. Emergence occurred over all areas of the lake.

Seasonal trend in emergence for these four principal types by lake area is shown in Figure 5. In general, emergence of other types was restricted to certain bottom areas and times; greatest taxonomic heterogeneity was observed over broken rock substrates (8 taxonomic types), and least over offshore mud areas (mud type B; 3 taxonomic types).

1000
100
10

one month

Broken
Rock

Solid Rock

Sand

Inshore Mud

Offshore Mud

Tendipes sp.

"Greens"

"dark headed yellows"

Microtendipes sp.
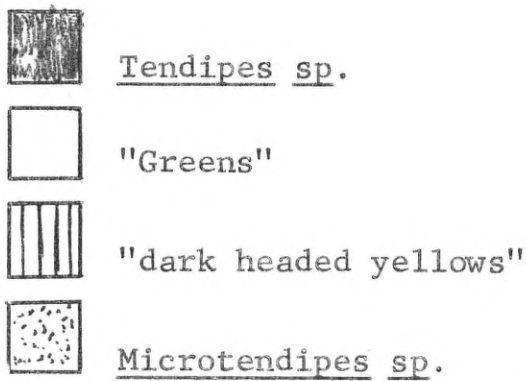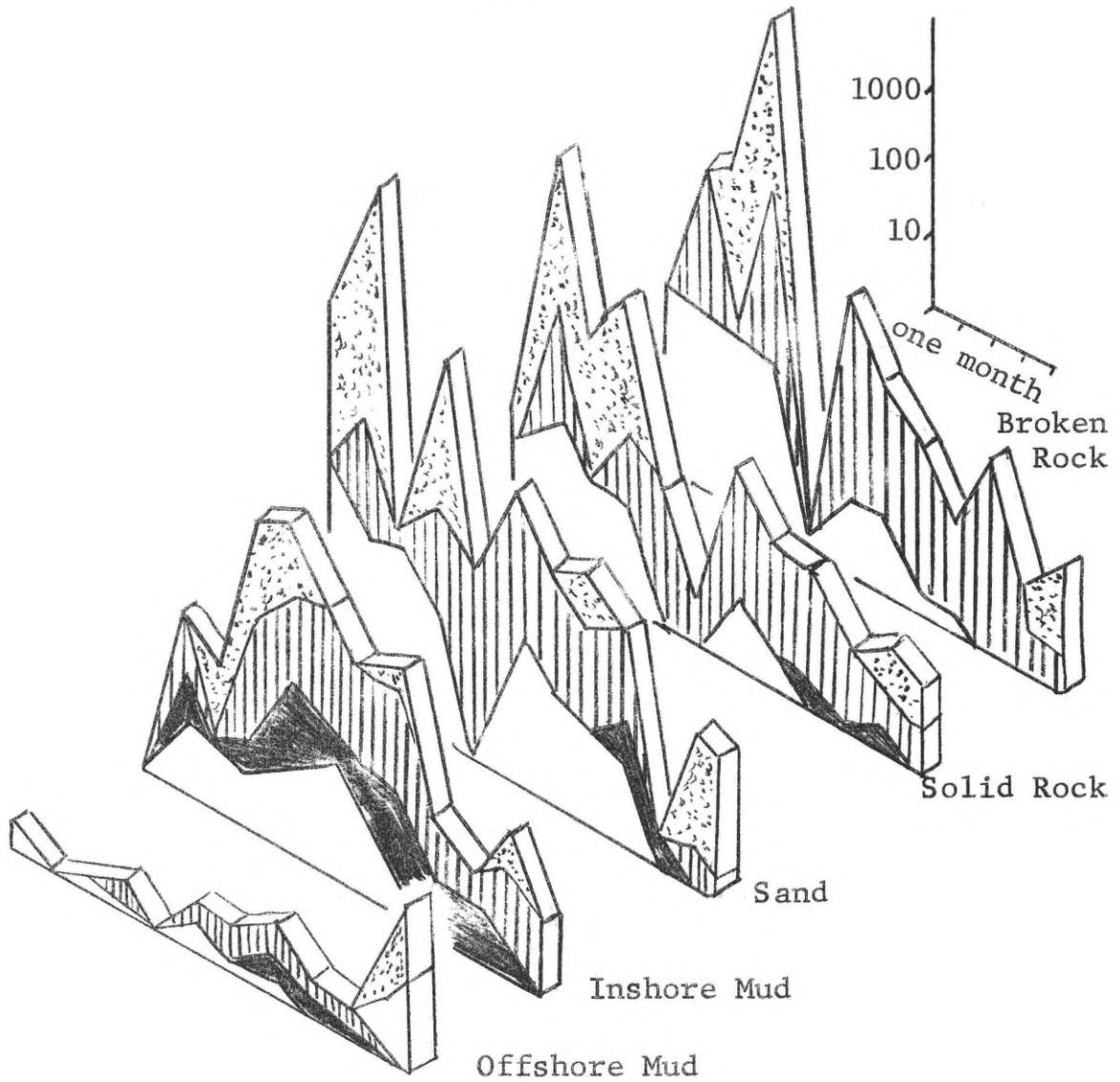
Figure 5.   Emergence by lake area and time of four
            principal midge types, Emmaline Lake, 1966.

Temporal variability--Since location of emergence traps was fixed throughout the summer, estimates of temporal variation in emergence were affected only by changes at each trap location.

Mean total number and weight of emergence over time are shown in Figure 6. The running series of paired t tests obtained by comparing catch of each trap (weight) on a given week to catch on the following week indicated significant weight changes $(P < .05)$ only during the first four weeks of summer (June 22 - July 8).

Individual taxa showed more striking temporal variation (Figure 5). If species separations were approximately accurate, at least two life cycles per year are indicated for several species.

Spatial variation--Spatial variability in emergence was related to bottom type and its concomitant distance from shore, and probably also to clumping of pre-emergent larvae (Figure 7). Analysis in terms of observable physical and biological correlates of emergence explained at best only about one-third of the total sampling variation on any date.

Sampling was adequate to compare emergence over various bottom types only for the last six sampling periods. Most productive types were broken rock and sand; least was
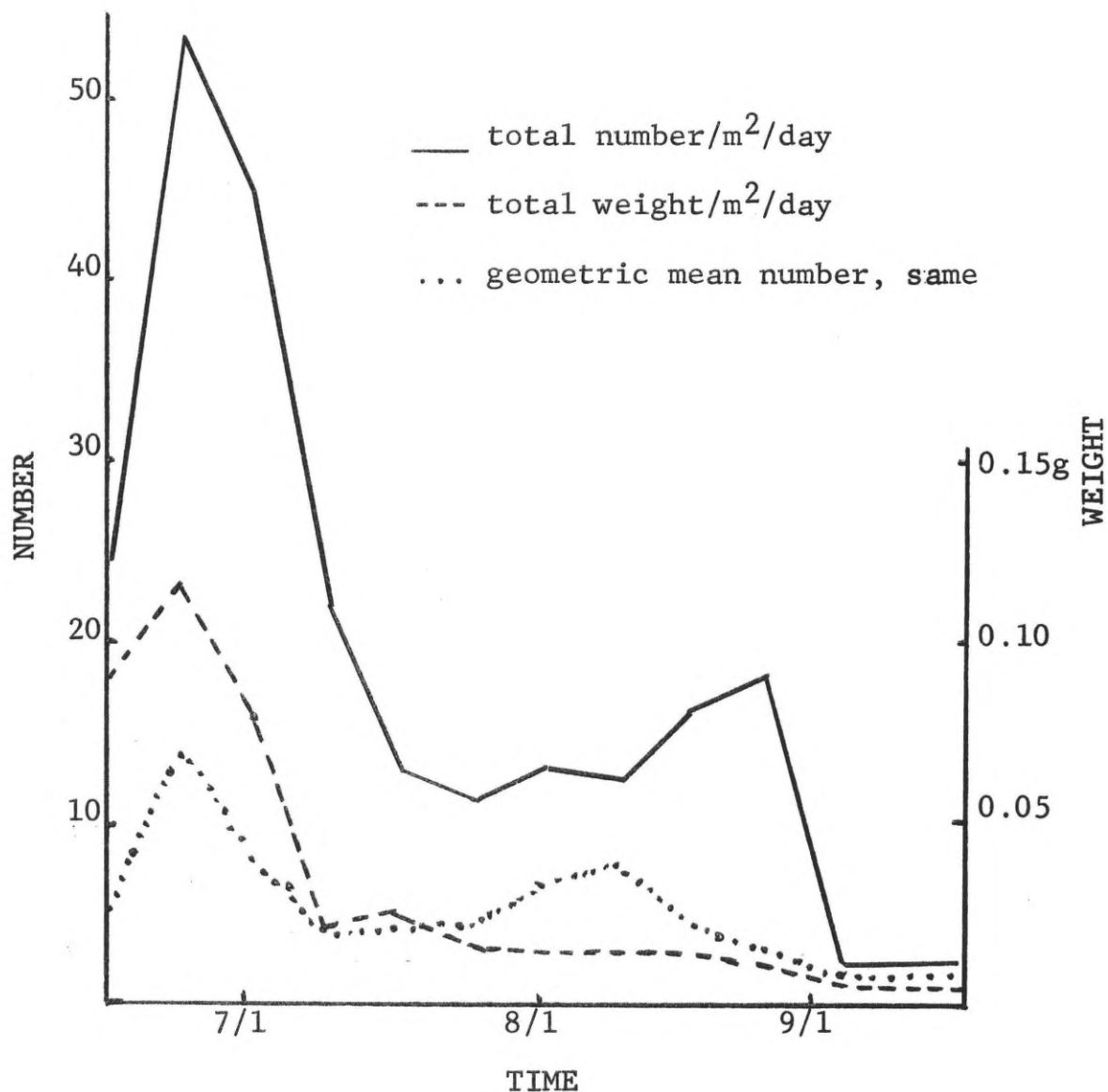
Figure 6. Number and weight of insects emerging per m^2 per day, summer 1966, Emmaline Lake. Geometric mean number estimates are antilogs of mean logarithms (base 10) of total counts (estimates obtained by treating counts as log-normally distributed).

Mud bottom

Broken rock bottom

Large boulders

Solid rock bottom

Sand bottom

50

Number/m^2/day

0
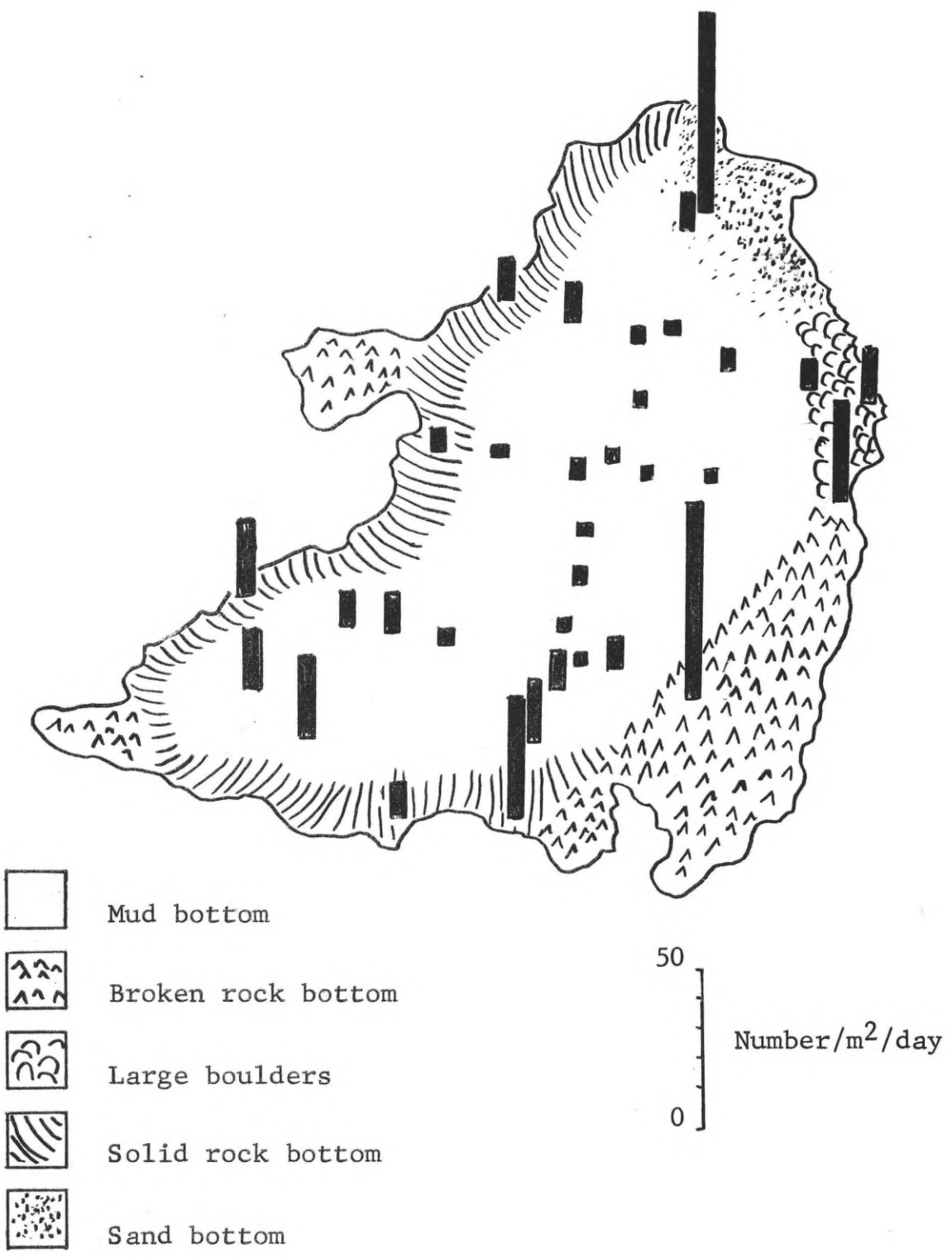
Figure 7. Distribution of mean numerical emergence,
summer 1966, Emmaline Lake.

offshore mud (Figure 5; Table 1). Analyses of variance of mean total counts and weights, blocked to remove time effects, showed significant differences among bottom types for both types of emergence estimates. While numerical emergence was greatest over broken rock areas, inshore mud zones (mud type A) produced greatest weights of emergent insects (Table 2). This discrepancy was due primarily to emergence over inshore mud areas of the large Tendipes sp., while only smaller types were abundant over rock areas. Relatively low numerical emergence indicated for the sand area is a distortion because one over-sand trap was a considerable distance offshore. It represented conditions

Table 2. Comparison of mean number and weight of emergent insects (per m^2 per day) for principal bottom types, late summer 1966, Emmaline Lake. Weight in mg.

	Broken rock	Solid rock	Sand	Inshore-mud	Offshore-mud
Numbers	41.98	9.16	16.83	6.92	1.83
Weight	12.14	4.17	18.87	22.03	2.82

intermediate between mud and sand, and had consistently low catches. The sand area trap set against the inlet delta had catches comparable to broken rock areas.

Since the lake is comparatively uniform in shape, one might expect distance from shore to explain part of

Table 1. Mean total number and weight (per m^2 per day) of insects emerging from five principal bottom types, August 1 to September 22, 1966, Emmaline Lake. Weight in g.

Date	Solid rock		Broken rock		Sand		Inshore mud		Offshore mud	
	Number	Weight	Number	Weight	Number	Weight	Number	Weight	Number	Weight
8/2	16.69	.00508	33.36	.01400	48.57	.01834	9.943	.03196	1.58	.00143
8/8	8.46	.00338	37.14	.01367	25.00	.02121	12.37	.03065	3.17	.00455
8/15	20.00	.00478	83.81	.01165	7.80	.00608	7.82	.03315	2.13	.00432
8/22	5.26	.00102	92.42	.01575	1.43	.00120	6.75	.02726	0.55	.00197
9/5	0.92	.00231	2.11	.00517	5.57	.02673	2.75	.00666	1.17	.00200
9/22	3.65	.00848	3.04	.01261	12.42	.03969	1.88	.00252	2.38	.00255

observed sampling variability. Catches by weight and by total number were plotted as a function of distance from shore for a typical sampling date (Figures 8 and 9). A weak decreasing trend outward from shore to the edge of the mud area, increase at the mud boundary, and a second decreasing trend outward from the edge of the mud were apparent. These trends, however, were not statistically significant (linear r = 0.2 within rock, and 0.3 within the mud area for weight estimates). Magnitude of emergence over rock areas did not correlate with that over adjacent mud areas, indicating that no large areas (transcending more than one bottom type) were more productive than others.

Spatio-temporal interactions--Emergence from a given trap or lake area as a relative proportion of total emergence was fairly steady. That is, areas producing relatively high emergence did so throughout the summer, regardless of absolute emergence quantity. An exception was the sandy inlet area. Here, relative emergence depended more on the species emerging over a given time period than on the relative basic productivity of the zone.

Statistical description of emergence sampling--Spatial variation in emergence was extreme (Table 3). Three-hundred fold variation in counts between traps was not
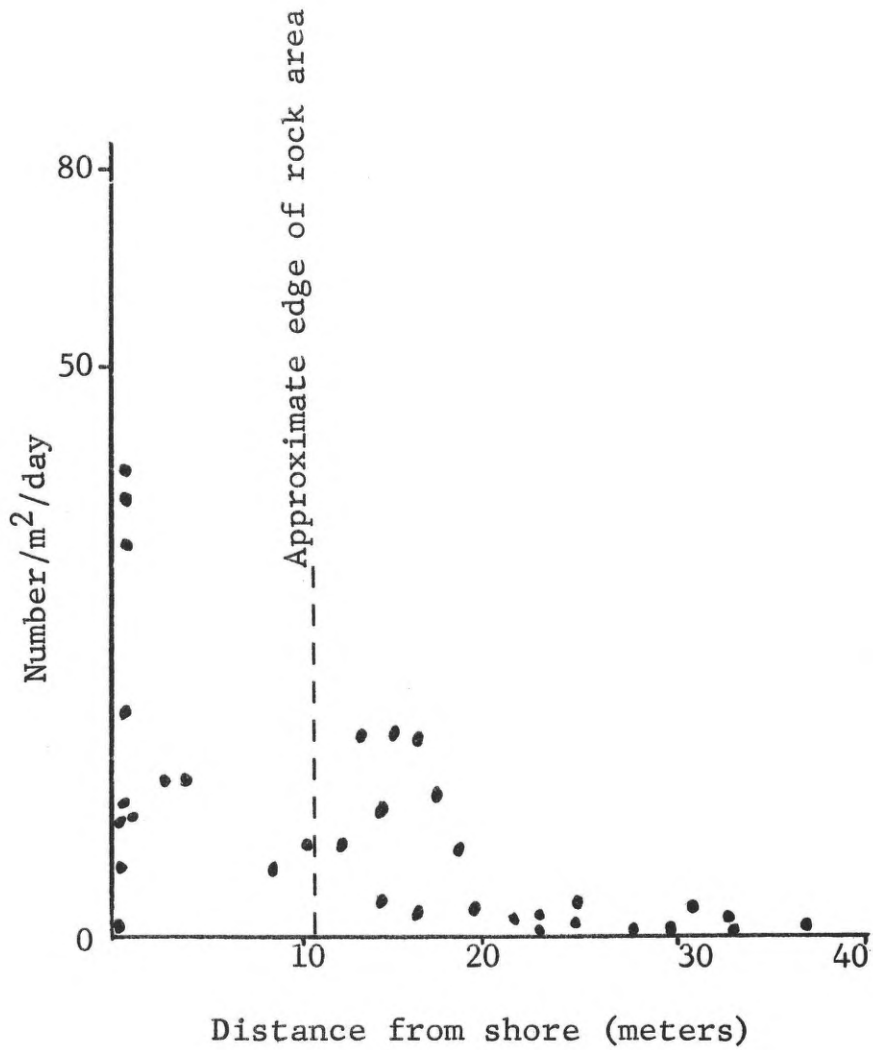
Figure 8. Number of insects emerging on August 1, 1966, as a function of distance from shore. Emmaline Lake.
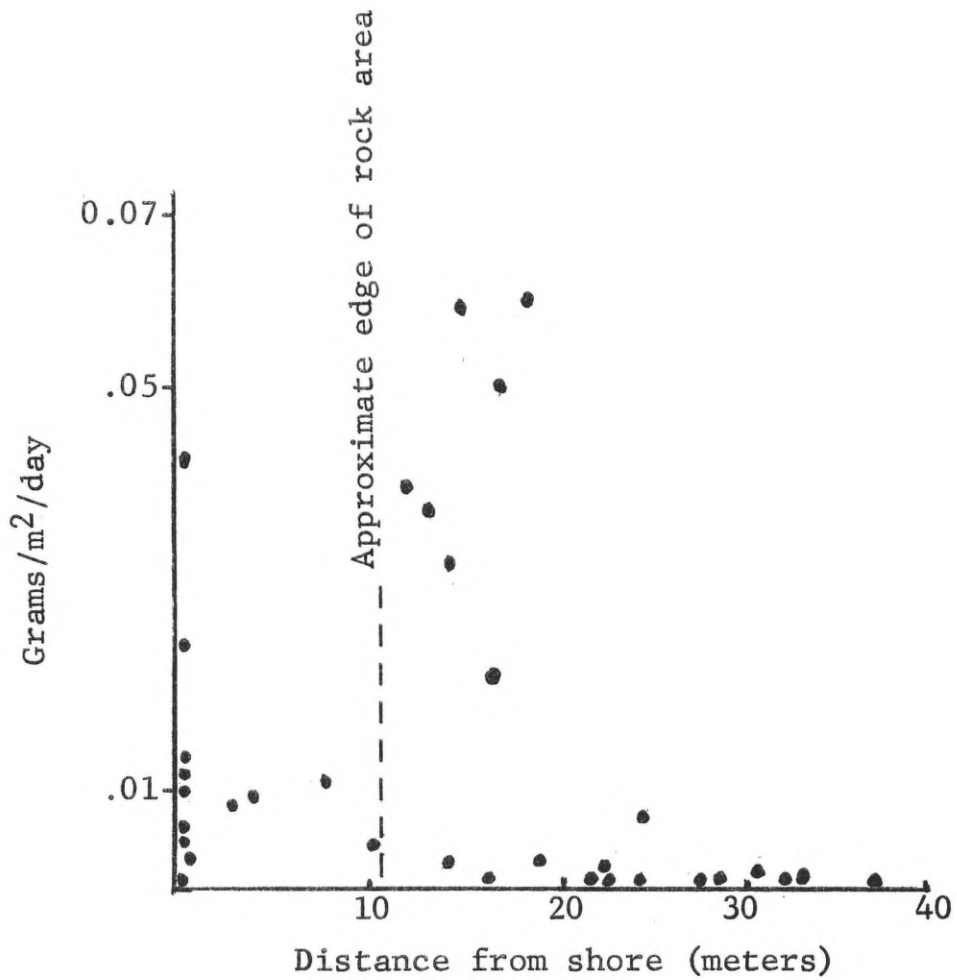
Figure 9. Weight of emerging insects on August 1, 1966, from Emmaline Lake, as a function of distance from shore.

Table 3. Measures of variation of total weight and number of emergence, Emmaline Lake, 1966. Estimates are per m^2 per day.

		Mean			Variance					
Date	N	Number	Log-number[1]	Weight	Number	Log-number	Weight	C.V.N.[2]	C.V.W.[3]	$s^2/\bar{y}$ [4]
6/22	9	24.31	4.20	.08825	1662.868	8.554	.025308	.559	.601	68.403
6/28	12	53.90	14.04	.11769	5229.869	7.070	.032832	.387	.444	97.029
7/2	24	44.33	7.87	.08047	5352.284	7.184	.018147	.344	.349	120.737
7/11	24	22.02	4.00	.02117	2936.032	4.497	.001464	.505	.371	134.561
7/18	24	13.21	4.12	.02161	407.269	3.186	.0009769	.312	.295	30.830
7/25	24	11.39	4.23	.01732	233.769	2.751	.001006	.274	.314	20.524
8/2	34	13.28	6.69	.01485	300.363	1.711	.0004141	.224	.235	22.618
8/9	34	12.29	7.74	.01487	193.456	1.033	.0003331	.194	.211	15.741
8/15	34	16.10	4.43	.01403	2443.195	2.040	.0002723	.526	.202	151.750
8/22	34	19.18	2.88	.01146	5486.166	2.432	.0003040	.662	.261	286.036
9/5	34	2.05	1.69	.00532	3.222	.258	.00007245	.150	.276	1.572
9/22	34	2.44	1.82	.00542	8.209	.408	.00009255	.201	.305	3.364

1--calculations performed on log (base 10) of counts, and final answers converted back to counts

2--coefficient of variation of count data, calculated as standard error of mean divided by mean

3--same as (2), for weight data

4--sample variance divided by simple mean

uncommon; total emergence weight per sample was slightly less variable. Large variance to mean ratios (Table 3) show nonrandomness in the count data (Variance would equal the mean if the data were distributed as a Poisson, or randomly). Treated as Chi-square values (Andrewartha, 1961) with one degree of freedom, these ratios were highly significant for all but two sampling dates.

The negative binomial distribution fit well to emergence counts by sampling period for principal taxonomic types (Table 4), as measured by the approximate Chi-square of Fisher (1950). Total counts, compounded of more simple species-specific distributions, did not follow the negative binomial as closely. "K", the expansion coefficient of the negative binomial, is a measure of nonrandomness, or clumping of individuals being counted (Cassie, 1962). Smaller K values indicate greater clumping; as K becomes very large, distribution approaches random. Most K values in this study were stable between 0.1 and 0.2; Cassie (1959) reported similar values in plankton studies. Standard errors of mean counts, calculated by the formula (Bliss and Fisher, 1953)

$$s_{\bar{y}} = \left[(\bar{y} + \bar{y}^2 / K) / N \right]^{\frac{1}{2}}$$

were approximately equal to those obtained by treating the data as normally distributed.

Table 4. Expansion coefficients (K) of negative binomial distributions fit to emergence counts of principal midge types, summer 1966, Emmaline Lake. Approximate Chi-square values measure goodness of fit to distributions. "Yellows" refers to small types with yellow bodies and dark head capsules.

Date	TOTAL COUNT			TENDIPES			MICROTENDIPES			"GREENS"			"YELLOWS"		
	K	χ^2	D.F.	K	χ^2	D.F.	K	χ^2	D.F.	K	χ^2	D.F.	K	χ^2	D.F.
6/22	.1287	2.619	5		a[1]		.0542	.730	3	.0459	.771	3		a	
6/28	.2441	4.873	9	.5078	3.432	6	.0819	1.447	5	.2736	9.317	9	.2304	2.499	8
7/2	.1864	12.589	13	.1001	9.422	7	.1105	6.303	10	.1859	7.663	10	.1609	10.183	13
7/11	.1680	15.106	13	.1446	8.215	10	.1017	1.834	3	.1508	6.987	9	.1809	6.996	9
7/18	.2509	12.949	11	.1438	2.210	6	.0808	1.424	3	.2590	5.068	7	.1205	13.813	10
7/25	.3172	8.249	14	.1812	2.513	3		a		.3267	4.179	10	.1902	5.359	10
8/2	.6092	16.088	18	.1358	11.002*	4		a		.2319	17.284*	7	.3125	10.554	13
8/9	1.0336	18.390	20	.1690	3.133	5	.0605	1.549	5	.1050	9.708*	4	.4711	9.705	13
8/15	.3364	16.406	16	.2450	6.706	4		a		.0332	2.010	3	.0912	4.382	7
8/22	.1876	20.544*	11	.1550	6.779	4		a			a		.0983	12.838	8
9/5	3.5634	14.316	19	.0590	2.457	4	.1656	6.960*	2		a		.1173	3.848	4
9/22	.7280	11.019	7	.0576	3.053	3		a			a		.2533	5.866	4

1--emergence insufficient for fitting distribution

*--significant at five percent level

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Log-probability plots of total count data, (Figures
10 and 11) indicate a complex frequency distribution for
total emergence counts. Counts seemed to be grouped for
each date into two or three series, each series approxi-
mately log-normally distributed (plot as a straight line
on log-probability paper). Cassie (1962) termed this type
of distribution the "polymodal-log-normal"; it cannot be
easily fitted to empirical data. When used, the only
improvement simple log treatment made in emergence total
count estimates was to prevent confidence intervals from
including zero.

Log-linear groupings of count frequencies corresponded
to different habitats. Groups of low counts occurred over
offshore mud areas; very high count groups occurred over
sand and broken rock areas. Counts over inshore mud and
solid rock areas were not segregated in magnitude.

Stratification of samples by bottom type gave little
improvement in precision of mean total number or weight
estimates. Further division, to making separate estimates
by taxonomic type stratified on bottom type, also gave no
better precision. Standard errors of mean estimates were
usually about one-third or more the size of the means.
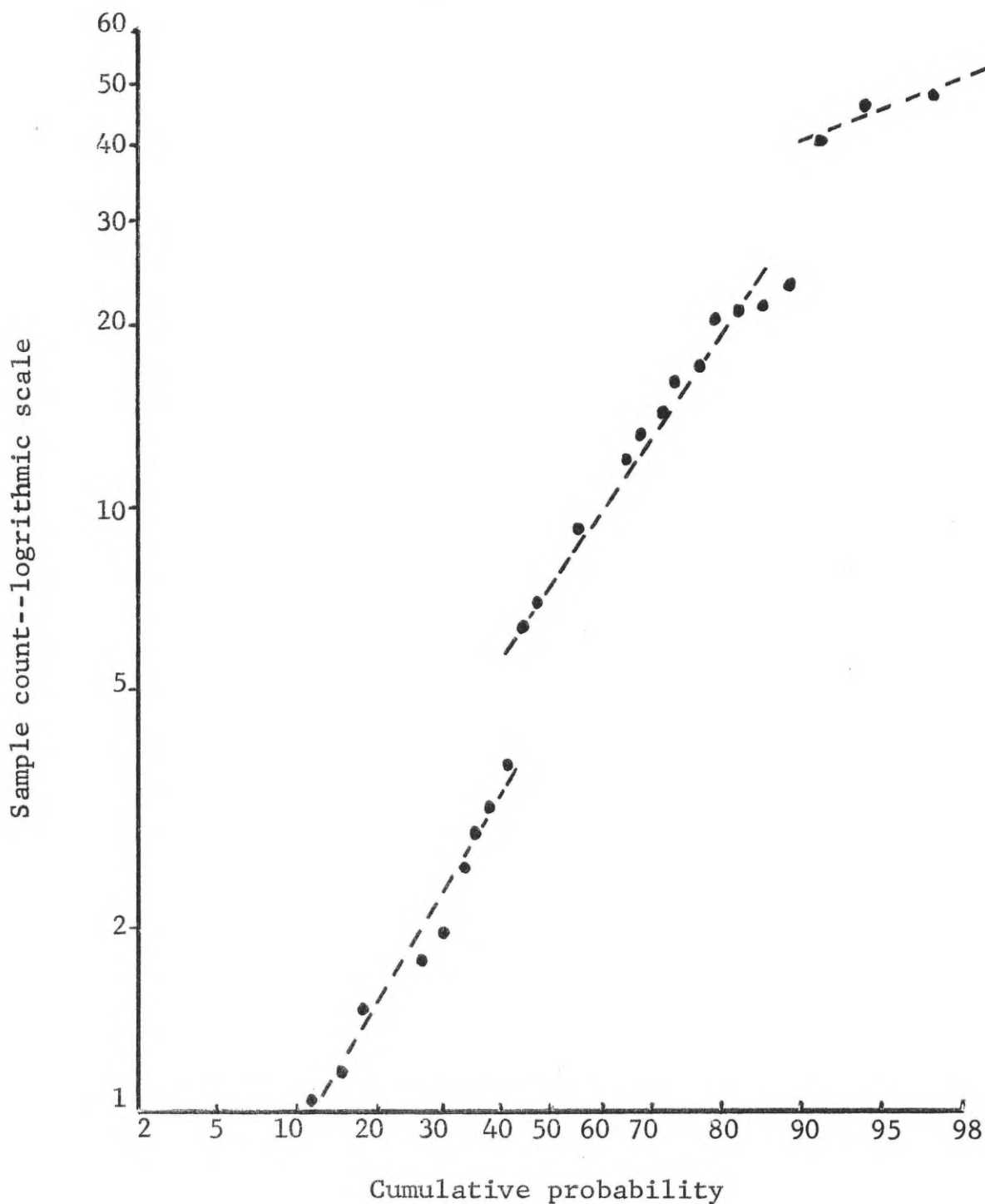
Figure 10. Log-probability plot of total emergence counts
(per m² per day), August 1, 1966, Emmaline Lake.
Each point represents cumulative probability of
a smaller count. Lines fitted by eye.
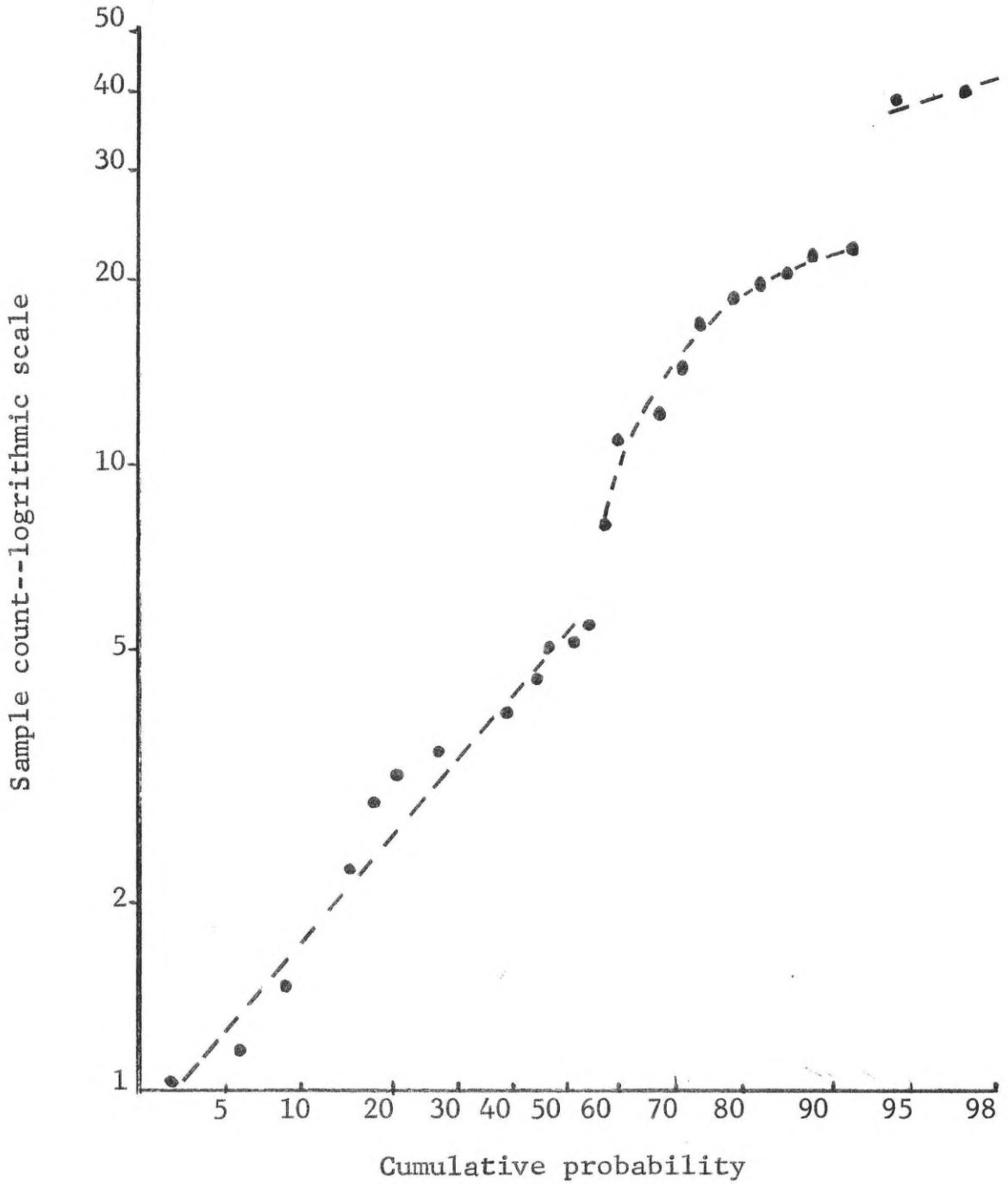
Figure 11. Log-probability plot of total emergence counts
(per m^2 per day) August 8, 1966, Emmaline Lake.
Each point represents sample cumulative
probability of a smaller count. Dashed lines
fitted by eye.

Even this estimate of variation may be too low; Cochran (1963) indicated that stratification after sampling gives deflated estimates of error.

LARVAL POPULATIONS

Quantitive bottom sampling was possible only in mud bottom areas. Rock dwelling larvae were not sampled. Mud areas were dominated by a <u>Tendipes</u> <u>sp</u>.; other larval types were occasionally observed. Larvae of the dominant <u>Tendipes</u> with both one and two year life cycles were present.

<u>General abundance</u>--Four phases of population change were apparent (Figure 12):

(1) A weight growth period, from ice melt to about July 20. Numbers remained stable, while biomass increased.

(2) An emergence, or mortality period, during the third week in July, when numbers declined drastically.

(3) A late summer hatching period, when small larvae appeared, and larval growth was rapid.

(4) A fall period of numerical decline with no individual larval growth.

Maximum density observed was 215 larvae per 1/4 ft^2, in a late September sample; maximum weight observed, also in late September, was 1.80 g per 1/4 ft^2. Samples with no larvae were rare (3 percent).
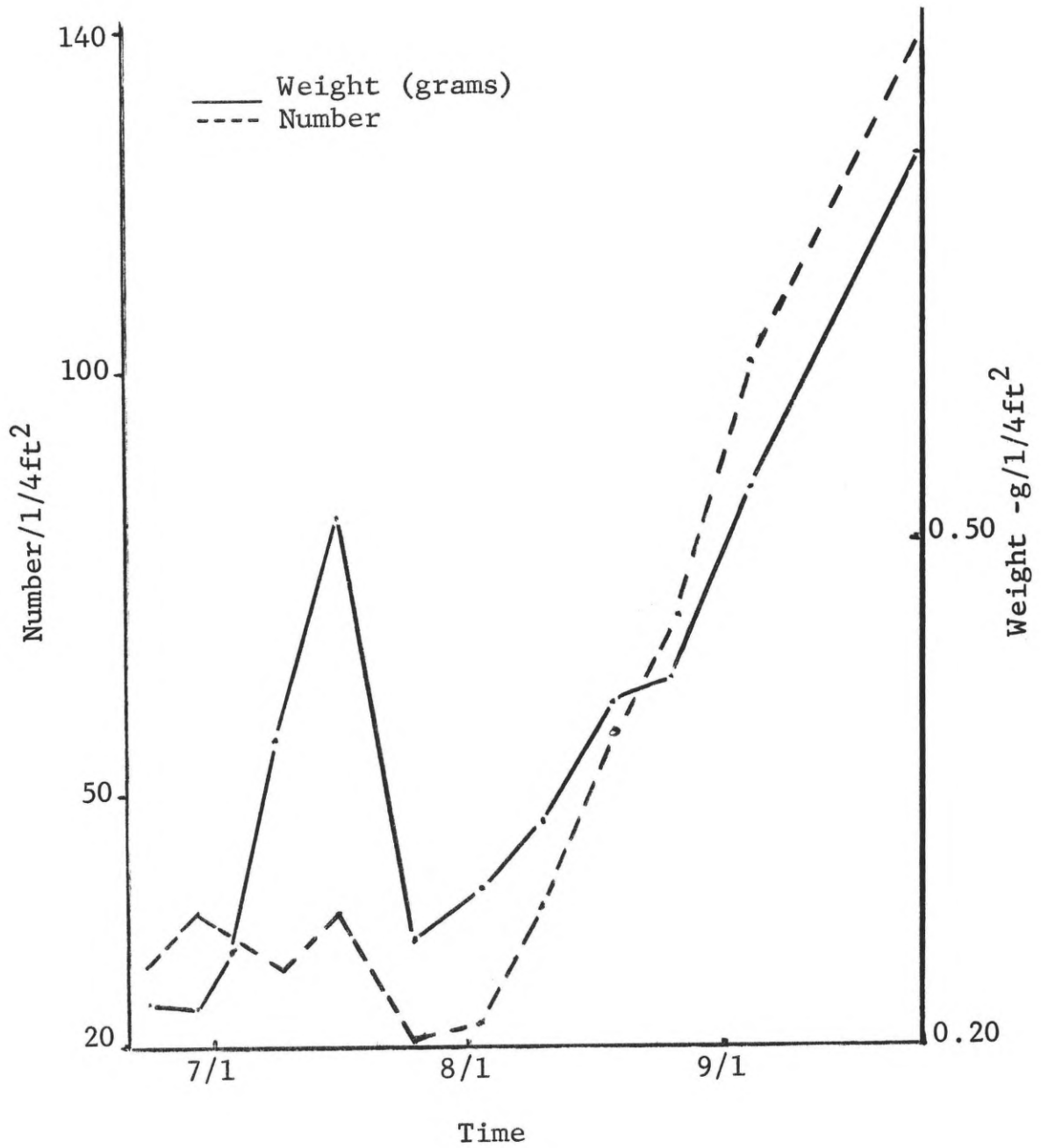
Figure 12. Total number and weight of mud dwelling insect
larvae, summer 1966, Emmaline Lake.

Sampling variability--Statistical variability in bottom sampling was high (Table 5). Standard errors of mean estimates were usually around 20 to 30 percent as large as their means, both for number and weight estimates.

Again, high variance to mean ratios indicate nonrandomness in spatial distribution of larvae. Correlation between 54 sample pairs collected less than 10 m apart was low, but statistically significant (r = 0.49 for weight, and 0.43 for numbers). Correlation indicates clumping of larvae, or presence of differentially productive bottom zones (to be discussed later).

Sampling variability was probably inflated by the semi-systematic distribution of samples. Analysis of variance (total sample weight) of four sample series taken on August 8 and 9 (Table 6) indicates this by the low among series mean square (series means varied less than would be expected from within-series variance estimates).

Table 6. Analysis of variance of total sample weights of four bottom sample series taken August 8 and 9, 1966, Emmaline Lake.

Source	D.F.	Mean square	F
Among series	3	0.01502	0.236
Within series	32	0.06370	
Total	35	0.05952	

Table 5. Measures of variability in bottom sampling, summer 1966, Emmaline Lake. Number of observations per series was 9; series 3-4, 8-9, and 10-13 are within date replications. Number and weights (g) are per $1/4 ft^2$. Coefficient of variation (C.V.) was calculated as standard error of mean divided by mean.

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Series	Date	MEAN		VARIANCE		C.V.		VAR./MEAN	
		Number	Weight	Number	Weight	Number	Weight	Number	Weight
1	6/22	30.22	.2284	1390.98	.11404	.390	.467	46.03	0.49
2	6/29	36.44	.2238	1526.95	.04580	.339	.302	41.80	0.20
3-	7/3	37.89	.2878	1532.89	.07763	.326	.306	40.40	0.27
4	7/3	28.89	.2314	666.32	.03653	.281	.261	23.06	0.16
5	7/12	29.89	.3842	535.09	.20175	.244	.369	17.92	0.52
6	7/19	36.67	.5166	274.16	.07048	.142	.162	7.48	0.15
7	7/26	20.33	.2625	346.57	.10670	.289	.393	17.05	0.41
8	8/2	21.89	.3228	243.64	.07118	.225	.261	11.13	0.22
9	8/2	23.67	.2686	644.17	.06454	.339	.299	27.21	0.24
10	8/8	34.11	.2822	540.08	.08259	.215	.322	15.86	0.29
11	8/8	34.11	.3397	967.27	.06793	.288	.242	28.33	0.20
12	8/9	37.67	.3328	649.31	.05619	.213	.225	17.21	0.17
13	8/9	45.00	.3811	1352.34	.11000	.258	.275	30.00	0.29
14	8/16	57.89	.4065	5294.69	.10390	.397	.250	91.50	0.26
15	8/22	71.89	.4204	4767.24	.11556	.303	.255	66.30	0.27
16	9/6	101.44	.5336	5049.46	.34790	.221	.349	49.70	0.65
17	9/22	140.78	.7350	5893.73	.16494	.172	.174	41.80	0.22

There seemed, as in emergence sampling, to be at least two distinct groups, or sampling populations. Simple and log probability plots (Figures 13 and 14) of total numbers on August 8 and 9 show these groups, and also show extreme variability of the data. Not enough observations were taken on any date to statistically test for group separation, or to test for fit to separate log-normal or negative binomial distributions.

Statistical groupings in the data have biological basis. Samples in high count groups were all taken near shore, within 18 m of mud-rock boundaries, while low counts occurred only in the lake center.

Distribution patterns--Larvae were numerically concentrated in inshore mud areas throughout summer, 1966. Young (second instar) individuals appearing in August were found only close to shore, but spread into offshore areas as larval growth progressed and inshore density increased (Table 7).

Analysis of differences between inshore, intermediate, and offshore mean numbers of different sized larvae, blocked over time, showed significant differences among areas and a significant area-size interaction (Table 8). The significant area-size interaction indicates that the relative proportion of larvae of a given size in an area
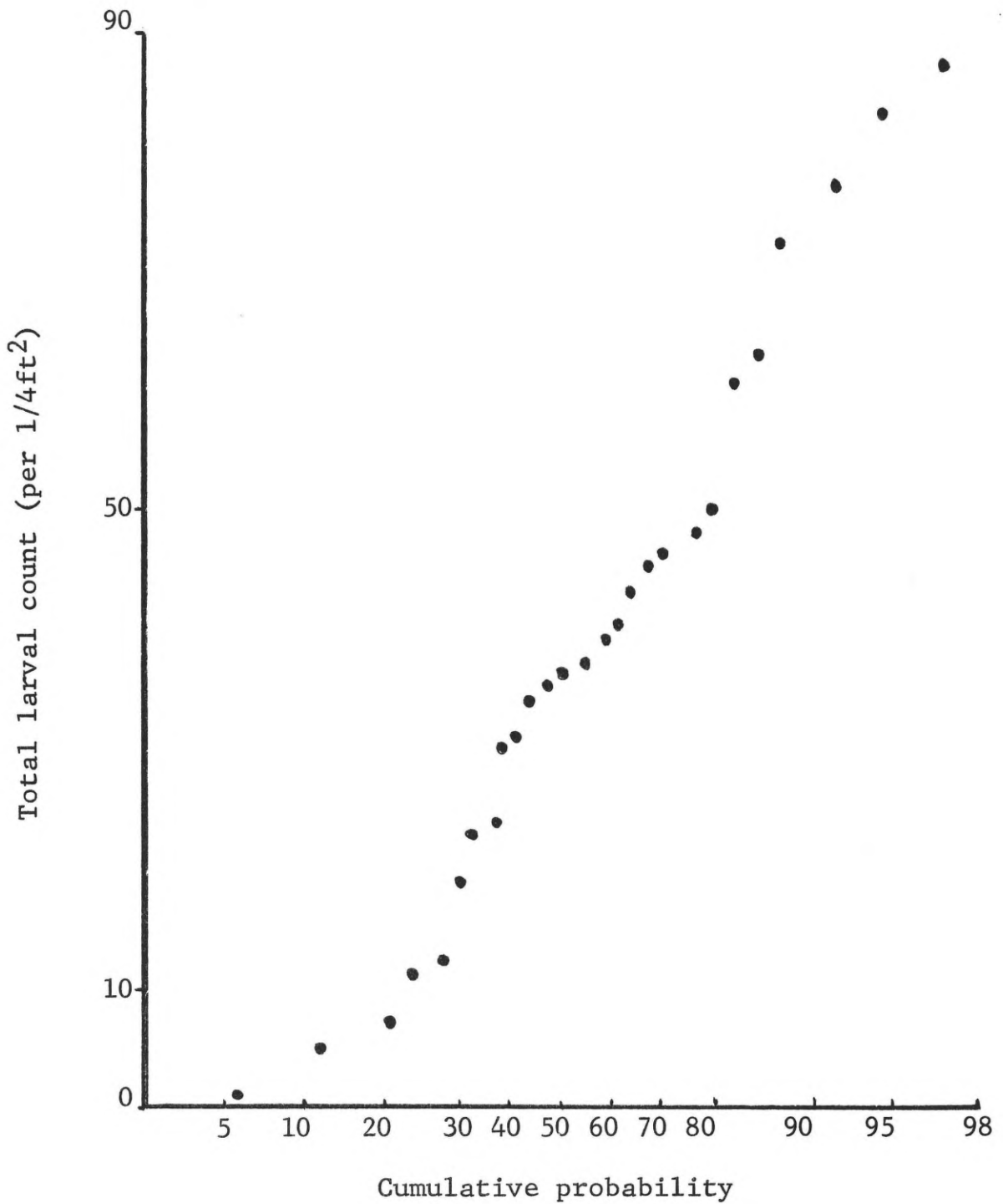
Figure 13. Probability plot of total larval counts, August 8 and 9, 1966, Emmaline Lake, as a function of cumulative sample probability of a smaller count.
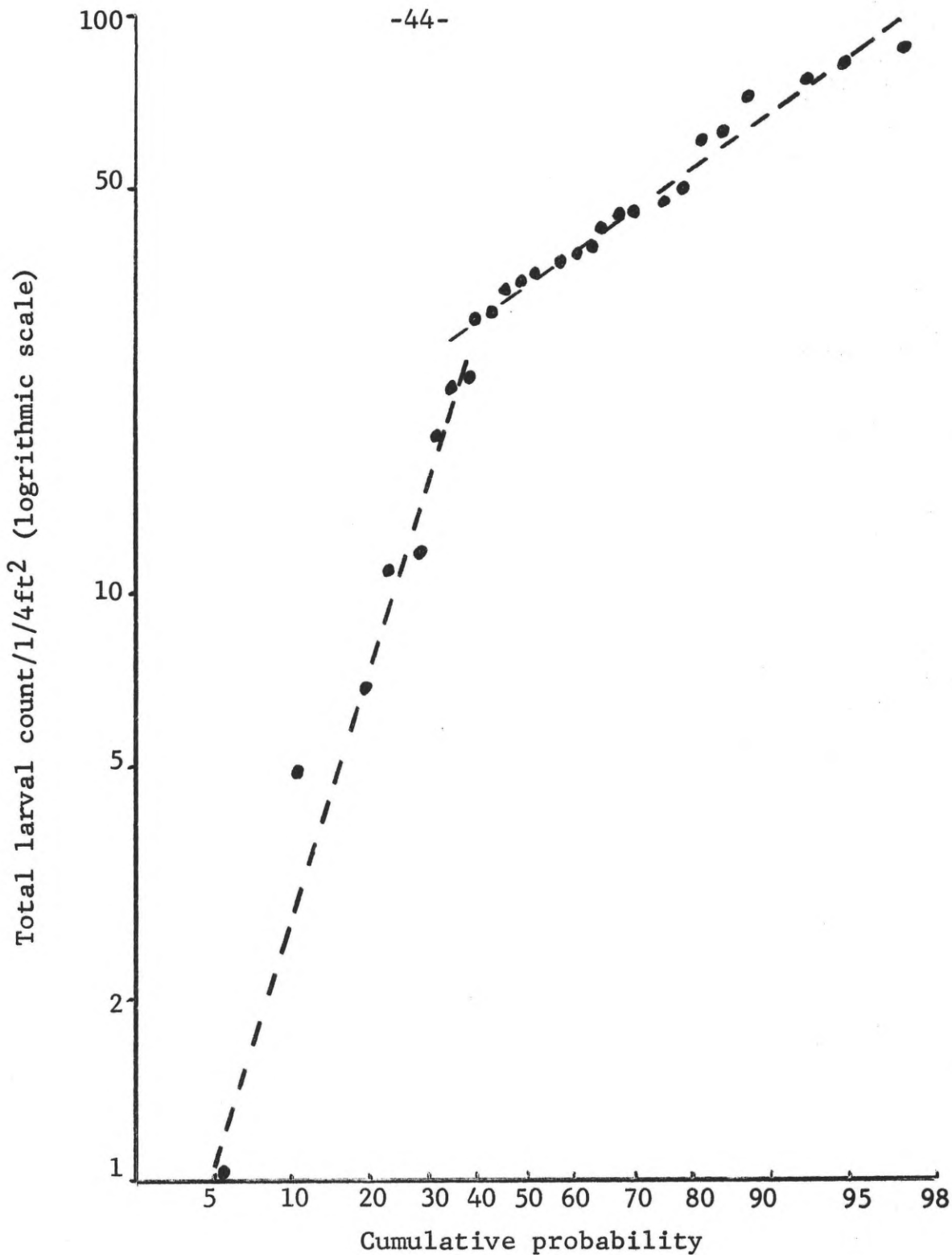
Figure 14. Log-probability plot of total larval counts, August 8 and 9, 1966, Emmaline Lake, as a function of cumulative sample probability of smaller count. Lines fitted by eye.

Table 7. Mean number of three larval size classes for inshore, intermediate, and offshore mud areas, summer 1966, Emmaline Lake. Inshore areas were defined as less than 10 m from rock-mud interfaces, and offshore areas as greater than 20 m from these interfaces. Counts per $1/4\text{ft}^2$.

Date	NO. OF SAMPLES IS	IM	OS	INSHORE <10mm	10-16mm	>16mm	INTERMEDIATE <10mm	10-16mm	>16mm	OFFSHORE <10mm	10-16mm	>16mm
6/22	7	2	1	0.5	12.1	3.7	1.0	3.5	2.0	1.0	0.0	3.0
6/29	4	3	2	11.6	13.9	6.5	2.0	11.6	3.7	1.5	4.5	0.0
7/3	9	6	3	11.4	15.0	8.2	1.3	8.6	2.5	0.3	4.6	0.3
7/12	4	4	1	5.7	26.0	11.7	0.3	7.0	2.5	1.0	5.0	0.0
7/19	4	4	1	0.3	30.5	8.0	0.0	29.8	8.0	0.0	13.0	3.0
7/26	4	3	2	4.0	18.2	5.7	1.3	10.6	5.6	0.0	3.0	1.0
8/2	11	6	1	13.0	20.0	7.9	0.2	5.0	1.8	0.0	15.0	4.0
8/8	20	5	11	19.9	21.8	8.8	24.0	11.8	6.8	2.4	6.5	2.1
8/16	5	2	2	60.0	16.4	11.4	3.0	9.5	5.5	4.5	4.0	9.0
8/22	5	2	2	57.8	23.4	8.2	47.5	25.0	12.0	0.0	1.5	4.5
9/6	5	3	1	74.6	43.6	5.2	11.1	67.6	0.0	2.0	16.0	13.0
9/22	4	3	2	121.7	80.5	7.0	24.6	85.0	7.7	7.0	39.0	0.5

Table 8. Analysis of variance of mean counts of three
larval size classes found in inshore,
intermediate, and offshore mud zones, during
summer 1966, Emmaline Lake. Table 7 gives means
used in the analysis.

Source	D.F.	Mean Square	F[1]
Length groupings	2	2635.063	4.361*
Spatial zone	2	1545.451	2.267
Weeks	11	1078.775	4.219**
Zone-Length	4	609.265	3.235*
Zone-Weeks	22	183.210	0.973
Length-Weeks	22	260.718	1.384
Error (Length-Zone-Week interaction)	44	188.279	
Total	107		

* significant at five percent level

**significant at one percent level

1--testing, or error mean squares for primary treatments
found by considering main treatment effects random
(completely randomized three way factorial design of
Snedecor, 1956).

depended on the area under consideration. Young larvae
made up a disproportionately large fraction of inshore
abundance but were relatively less numerous in offshore and
intermediate areas. This analysis of variance must be
interpreted with caution. Mean counts were used because of
unequal cell sizes. Counts were not normally distributed.
Also, length categories from a sample are not strictly
treatments in the sense of analysis of variance.

Larval growth and production--Growth rates of larvae
were calculated by following weight and length per indivi-
dual changes through the summer (Figure 15). Based on the
one and the two year life cycle phases of the dominant
Tendipes sp., two types of larval growth pattern were
observed. For discussion, larvae with one year life cycle
will be called "Alpha", and those with two year life cycle,
"Beta." However, rehabilitation of the lake in 1964
removed the group of Beta larvae that would have emerged
in 1966, so no exact determination of final larval size
for this phase was possible.

No exact estimate of variation in weight per indivi-
dual was possible, because mean weight per individual used
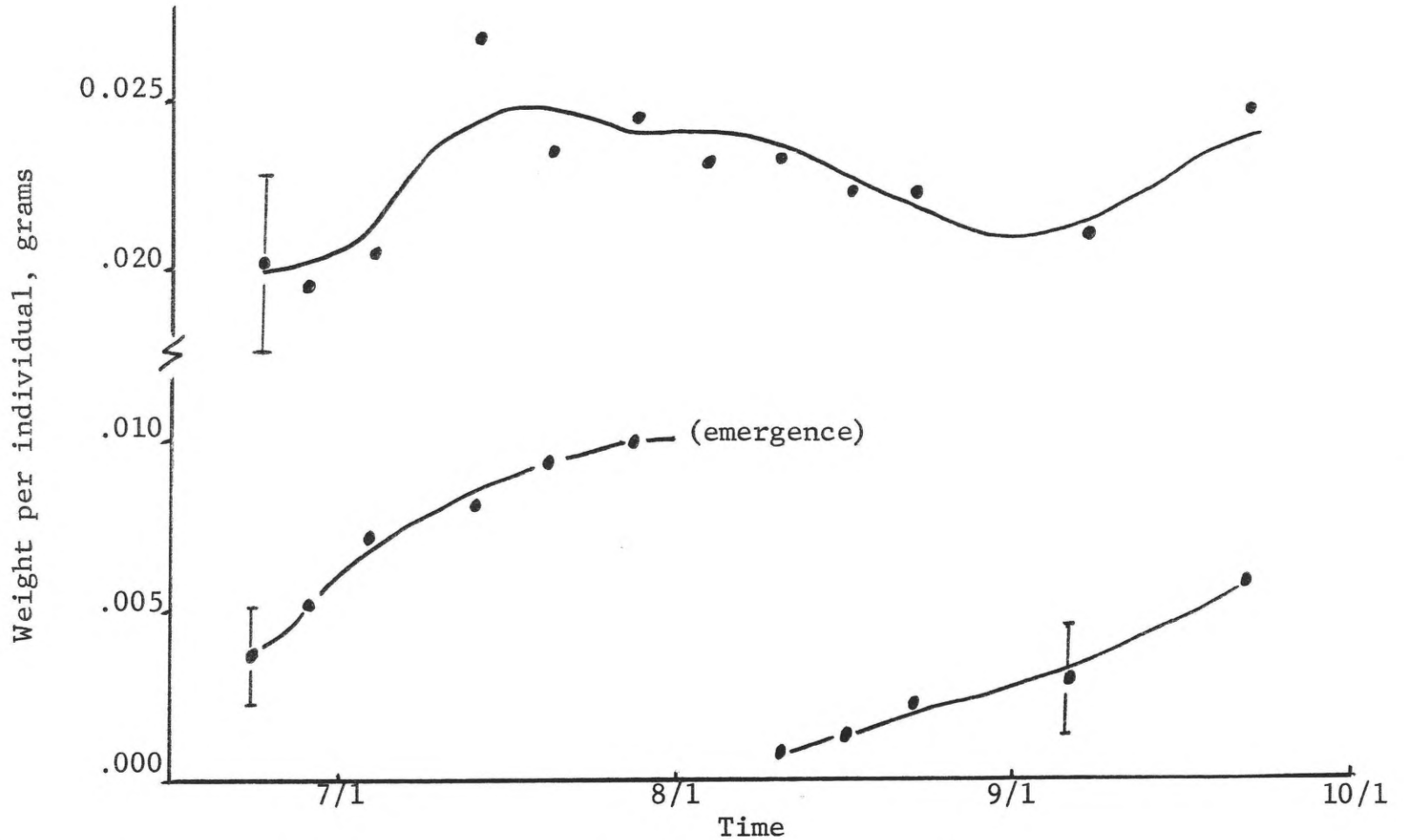
Figure 15. Apparent growth rate of two larval types, summer 1966, Emmaline Lake. Lower two curves are "Alpha" phase, and upper is "Beta" phase of the dominant <u>Tendipes</u> <u>sp</u>. Curves drawn by hand; vertical bars show approximate 95 percent limits on weight per individual.

in growth calculation was obtained as slope of the re-
gression of total sample number on total sample weight for
each size grouping. Regression estimates of variation
(Cochran, 1963) provided approximate confidence belts
(Figure 15); these error estimates were stable over time
for each type of growth pattern.

Net larval biomass production over a time period can
be calculated as the area under the curve relating larval
number to individual weight. Production of biomass to
emergence can be calculated as population weight loss at
the time of emergence (Neese and Dugdale, 1959). Calcula-
ted in this manner, production during summer 1966 of Beta
larvae was zero (0 net weight gain times constant numerical
abundance). Production of Alpha larvae emerging during
the summer (hatched one year previous), from the start of
summer to the time of emergence, was 0.805 g/m^2/ week (or
.0075 g net weight gain times constant abundance of 752
individuals/m^2 divided by 6 weeks); and production of
Alpha larvae hatched during the summer, from the time of
first appearance to September 22, was 0.197 g/m^2/week.
Calculations for the second group of Alpha larvae are
confounded, however, because individuals were being added
throughout the period of calculation. A better estimate

of the net production of this generation is the total gain
in larval biomass attributable to their appearance, equal
to 22.65 g/m^2 between time of first appearance and September
22.

Except for larvae hatching during summer 1966, non-
emergence mortality rate appeared to be zero. Abundance of
1966-hatched larvae increased to a mean of 5160 individuals
per m^2 in late September, then decreased to approximately
1720 per m^2 in samples taken on November 24, 1966. Peak
abundance was not sampled, so no reliable mortality rate
can be calculated for the period.

DISCUSSION

Midges of Emmaline Lake form a complex biological entity that is diverse in habitat requirement, and potentially very productive as a source of fish food. The alpine lake presents a mosaic of habitats with widely varying productivity.

Three basic weaknesses that confound results of this study must be mentioned. First, species identification of midges was impossible. (No complete life history studies were carried out because larvae could not be linked to adult forms.) Second, rock dwelling larval populations were not sampled; their magnitude and potential as fish food can only be approximated. Third, no measure was available of absolute quantitative efficiency of the emergence traps; other studies have given contradictory results (Wiltzius, 1965; Morgan and Waddell, 1963; Guyer and Hutson, 1955), but all indicate that it is high.

Two conclusions can be drawn about productivity of rock areas from emergence over these areas, assuming that emergence over them is primarily of taxa with rock dwelling larvae, and not of individuals moving inshore from mud areas to emerge.

First, more emergence over broken rock and sand areas than over solid rock areas indicates that larval density on rocky slopes may be a simple function of available surface area, as it affects periphyton production. That abundance of rock dwelling larvae may be directly dependent on amount of periphyton was shown by Dusoge (1966). If the assumption that abundance of rock dwelling larvae depends on periphyton were correct, a peculiar problem may arise in alpine lakes when fishes are present. Periphyton increased drastically after fish were removed from Emmaline Lake (personal observation); fishes apparently tie up nutrients otherwise cycled through periphyton. Thus, besides directly affecting rock dwelling midges through predation, fishes may indirectly affect them by slowing cycling of nutrients essential to the periphyton. A reduction in nutrient cycling rate may favor survival of larger, less metabolically active midge species, with consequences for fingerling fish that are dependent on smaller midge species for food.

Second, because emergence over rocky areas was mostly of small but very numerous individuals, such areas must be of great importance for young fish. Rocky areas can provide food supply of proper size, as well as protection, for fingerlings.

Three characteristics place the midge community of
rocky areas in Emmaline Lake as a remarkable alpine lake
counterpart to midge associations found on rooted aquatic
plants in littoral zones of low elevation lakes (described
by Buscemi, 1961; Frank, 1965; Macan, 1965; Anderson and
Hooper, 1956; and others). These are predominance of small
individuals, probable taxonomic diversity, and great
numerical abundance.

Emergence over mud zones bore no clear relationship to
larval populations in these zones. Emergence throughout
the summer of a large _Tendipes_ _sp._ was not accompanied by
significant decreases in any size group of mud dwelling
larvae; no small larvae were found in mud areas to account
for emergence of small types observed there occasionally.
Apparently, emergence of small species over offshore areas
was due to "pupal drift" from rocky zones. Sudden decline
in number of larvae in late July presumably was due to
emergence of the first observed group of Alpha individuals.
The decline was accompanied by increased emergence over
inshore mud areas, but no observable change in species
composition of emergence. Apparently, imagoes from this
larval group are morphologically indistinguishable from

species whose larvae normally inhabit rocky areas and emerge near shore (not uncommon with Tendipedids, Fittkau, 1961).

A quantitative description of some life history aspects of the dominant Tendipes was possible, and may give insight into population dynamics of species that are less easily sampled.

Alpha larvae were concentrated near mud-rock interfaces and were strongly clumped in some areas, while Beta larvae were more randomly distributed over mud bottoms. No emergents of the Beta group were observed; larvae that would have been two years old in 1966 were apparently killed by rotenone.

Distribution of Alpha type larvae, with younger individuals concentrated near shore, has been reported by Wülker (1961), Jonasson (1965), and others. Three factors seem to be important in development of this distributional pattern. First, adults are weak flyers and are forced by wind to breed in protected shoreline areas. Second, wind generated currents along shore may affect distribution of egg masses and movement of planktonic first instar larvae. Patterns such currents take in arctic lakes have been described by Rex (1960). Based on his findings, a probable

late summer current pattern for Emmaline Lake, and the
relationship to larval concentrations, are shown in Figure
16. Credibility is imported to the postulated current
pattern by observations of plankton concentrations along
windward shores in high lakes (Reimers, 1958), and by
presence in Emmaline Lake of benthic detritus concentra-
tions in eddy areas indicated. Third, larval food supply
may be concentrated in shoreline areas. Inshore muds
probably receive a concentrated rain of detritus deposited
by eddy currents and of periphyton washed free by wave
action. In general, the same environmental factors that
may concentrate food supply in certain mud bottom areas may
also concentrate eggs and larvae of mud dwellers in those
areas.

Alpha phase larvae were present at the start of summer
1966 at mean density $752/m^2$. No measurable mortality
(decrease in mean density) occurred prior to emergence in
late July. From total emergence estimates in late July,
mean survival of adults to breeding time could have been no
more than 20 to 30 individuals per m^2 . However, if pupae
moved up almost exclusively among and directly upon rocks,
catches for shoreline emergence traps would be too low;
only small portions of their circular bases were in direct

Dominant wind direction
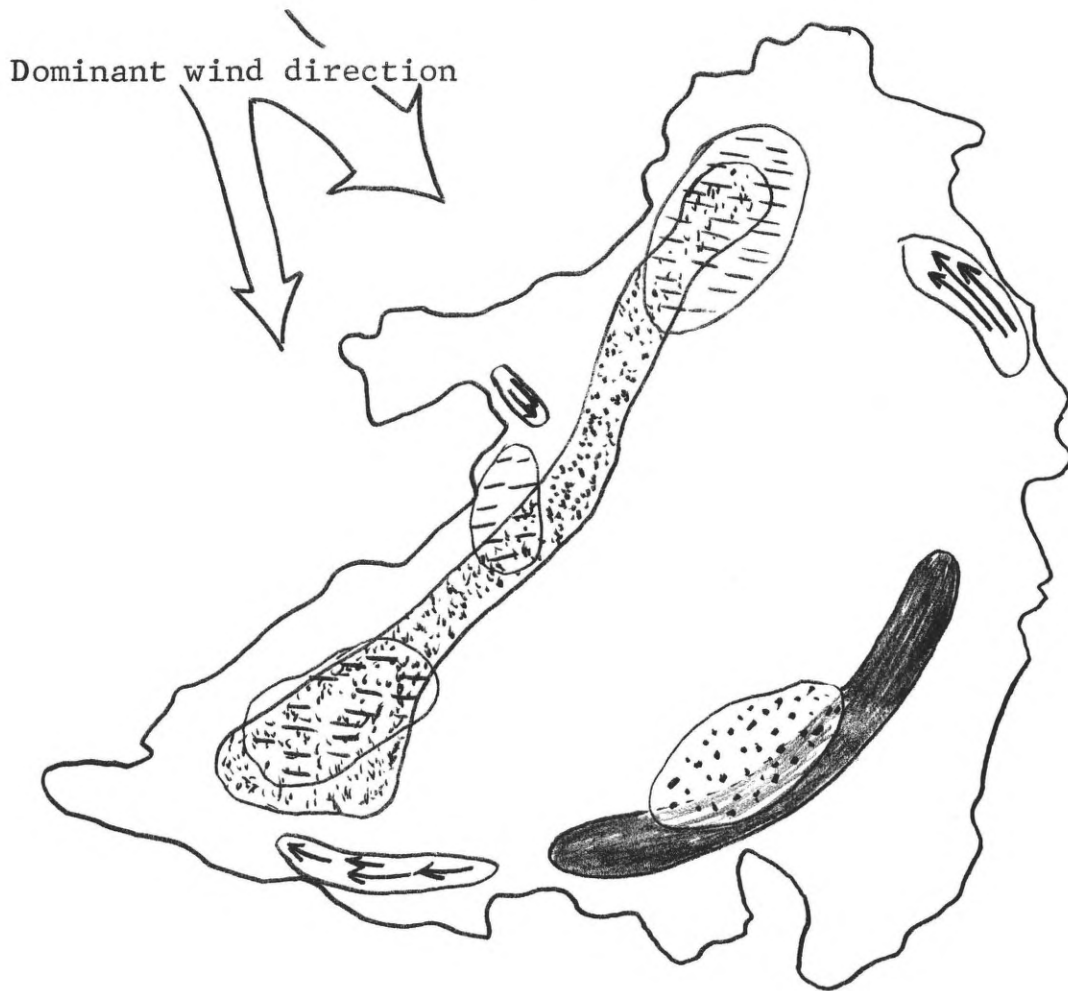
▮ Zones of zero lateral movement along shore

▦ Eddy currents

▧ Zones of maximum lateral current along shore

▨ Larval concentrations

Figure 16. Probable current patterns and observed concen-
trations of young larvae, late summer 1966,
Emmaline Lake.

contact with rock surfaces. Pupal survival was accordingly very low, even in the absence of fish predation. Further study will be needed to determine whether pupal mortality occurs: (1) in the mud during transformation from larvae, (2) during movement through the water column, or (3) at the water surface during transformation into adults.

The few surviving Alpha adults produced enough eggs to yield a mean larval population density of at least 5000 per m^2 by late September. By late November this second Alpha group had declined in abundance to approximately 1700 per m^2 --not greatly different considering further potential mortality through the winter from abundance of pre-emergent larvae of the previous generation. Also, weight of individual Alpha larvae declined in the fall to a level comparable to that of individuals of the previous generation at the start of summer. Lack of autumnal growth contrasts sharply with findings of Jonasson (1961) that growth of Chironomus anthracinus is greatest during the fall.

Thus, fish predation on young larvae, on pre-emergent larvae, and on pupae could be great without damaging population reproductive potential, assuming that predation would act as replacement rather than additive mortality.

Was the sampling program sufficient to justify quantitative comparisons and to detect statistically the effects of "normal" levels of fish predation? From confidence limits, most mean estimates in emergence and bottom sampling may have been in error by at least 50 percent. Gross late summer and fall mortality in Alpha larvae, and low emergence success by the Alpha group were thus reasonable conclusions. But, effects of fish predation may be much more subtle (Lellak, 1965). To detect fish-induced changes in midge populations will require comparison not of gross sampling means, but of changes occurring at individual spatial sites. Environmental factors can be expected to remain relatively stable over small areas. Otherwise, to detect even 20 percent changes in midge abundance would require approximately 300 samples per sampling date.

Perhaps the most important result of this study is that ordinary limnological sampling techniques, suitable only for studying larval abundance in mud habitats, give no real estimate of midge productivity in high mountain lakes like Emmaline Lake. Rocky shoreline areas may be very important in fish food production.

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