STUDIES ON THE BOTTOM FAUNA OF LOCH LOMOND.

by

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INTRODUCTION.

In 1947 the University of Glasgow established on the shores of Auchentullich Bay, Loch Lomond, a field station for the study of fresh-:water biology. It was decided soon thereafter, that a survey of the fauna of the bay should be made as a necessary preliminary to future limnological work at the station; particularly so as the only available systematic account of the fauna (Murray, 1910) was so meagre as to be of little use.

In the meantime it had been noted as a result of casual collections, that many of the insect larvae found upon McDougall Bank, though also found along the margin of the loch, were absent from the deep, silt-covered loch bottom which surrounded the bank on all sides. This bank lies about 750 m. from dry land; and, being covered generally with about 4 m. of water, is quite invisible even when one is directly over it. It had to be detected by sounding every time it was visited. Most of the larvae mentioned above are temporary residents; they ultimately leave the bank and the loch as flying insects.

I was asked to make a survey of the benthic fauna and to investigate the problem of the re-population of McDougall Bank. In the hope of getting results from the survey that might be of maximum value in answering the question posed by the insect fauna of the bank I rejected a qualitative survey of the entire bay in favour of a quantitative survey/

survey restricted to a line running from the shore to and beyond the bank, but spread in time over an unbroken period of at least one year.

ACKNOWLEDGMENTS.

It is a pleasure to record my gratitude to Professor C.M. Yonge for all the facilities placed at my disposal in his department; to Dr. H.D. Slack, for help with boats and gear, for advice and encouragement, and for permission to quote from his unpublished investigations on the hydrology of Loch Lomond; to Mr. S. McGonigal for the photographic treatment of my drawings; to the many zoologists whose assistance with the determination of the fauna I have acknowledged within the text; and to all those colleagues and friends who made my stay in Scotland a very happy one, and thus assisted my work.

CHAPTER I.

THE HABITAT.

As it is impossible to appreciate the results of a faunistic survey without some knowledge, at least, of the habitat in which the animals live, I shall briefly describe first Loch Lomond and next that part of it which was specially surveyed.

LOCH LOMOND/

LOCH LOMOND.

MORPHOMETRY AND GEOLOGY.

The more important dimensions of Loch Lomond are summarised in Table 1. p. 3a

An examination of Maps* 1 and 2 will show that the loch is divisible into two portions: a long, deep and narrow "highland" portion, with its drainage basin lying upon lime-poor, metamorphosed sediments of Cambrian or Pre-Cmabrian Age (the Dalradian schists, grits and slates); and a wide, shallow "lowland" portion, with its drainage basin lying chiefly upon Old Red Sandstone rocks and also, in the upper reaches of the Endrick Water (not included in these maps), upon lavas and calciferous sandstones of Carboniferous Age.

The "highland" portion occupies a rock-basin that has been produced by the glacial erosion of a pre-glacial river valley (Peach and Horne, 1910; Read, 1948). It is about 25 km. long and trends roughly north and south, from the head of the loch to a line running from Arrochymore Point (Map 2) to the shore just north of Rossdhu Point (Peach and Horne, 1910; Anderson, 1947). Hills flanking it rise steeply from the shore to reach quite considerable heights (Map 1). A ridge, apparently of the relatively hard Dalradian schistose grits that appear at Inverbeg and at/

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* These maps are based on the 1 in. Ordnance Survey maps, on the $\frac{1}{4}$ in. sheet of the Geological Survey and on Anderson (1947).

Table 1. Dimensions and situation of Loch Lomond.

Length*	36.4 km.
Area*	71.1 sq. km.
Area of drainage basin*	699 sq. km.
Maximum depth* (on 30/5/1903)	192 m.
Mean depth*	37 m.
Volume*	2,691 million cu. m. = 2.69 cu. km.
Variation in surface level June, 1948 - June, 1950	1.8 m.
Height of surface above mean* sea level on 30/5/1903	7.3 m.
Latitude	between 56 18½' N and 56 0' N
Longitude	between 4 31' W and 4 43' W

(Asterisks indicate information derived from Murray & Pullar, 1910) at Rowardennan (Map 2), divides this "highland" portion of the loch itself into two basins connected by a bridge of shallow water less than 15 m. deep. Of these, the northern or Tarbet basin is about 18 km. long, but only 1.0 to 1.5 km. wide, and has a maximum depth of 192 m. The southern or Luss basin is about 7 km. long, 1.5 to 3.0 km. wide, and has a maximum depth of only 62 m. These two basins are so different mor-:phometrically that I believe future investigation will show that they are also limnologically different; just as, for example, are the several depressions of Lake Douglas (Welch, 1927; Welch and Eggleton, 1931, 1934), of Lake Akimoto (Yoshimura, 1921; Miyadi, 1932-3, 8), of Lake Biwa (Miyadi, 1932-3, 9), and of Lake Oziri (Miyadi, 1931-2, 2).

The "lowland" portion of the loch, in which are Auchentullich Bay and McDougall Bank, has its greater axis, almost 8 km. long, coincident with the direction of the prevailing south-west winds, (Maps 1 and 2). A chain of islands which crosses it, marking the course of the Highland Boundary Fault, runs in the same direction and therefore offers no significant obstruction to these winds. Nor do the low and gentle hills lying to the wesr and south-west of the loch in this region afford the water in it much protection from the force of these winds. This "lowland" portion of the loch is everywhere less than 30 m. deep, and is separated from the "highland" portion by a second chain of islands rising from a band of shallow water 9 to 10 m. deep, which stretches from Arrochymore Point to the shore of the loch south-west of Inchta-:vannach/

Table 2. Ca, PO_4, and pH values of main tributary streams near their openings into Loch Lomond.

Name of Stream	pH	Calcium mg./l.	Phosphate mg./l. x 10^{-4}
River Falloch	6.5	2.23	<10
Inveruglas Water	7.1	5.83	<10
Douglas Water	7.4	3.53	250*
Luss Water	7.3	7.74	<10
Finals Water	7.0	5.40	<10
Fruin Water	7.4	10.30	<10
Endrick Water	6.9	15.85	<10

* Drainings from a house 50 m. above the point of sampling is considered to the cause of this high phosphate value.

:vannach.

Maps 1 and 2 also show the seven most important streams draining into the loch. As the geological nature of the drainage basin suggests, all these streams have low H ion concentrations, and are poor in calcium (Table 2). The Endrick Water, running over calciferous sandstone in its upper reaches, and over strata of the Old Red Sandstone lower down, is richest in calcium; but even it has only 15 mgm. per litre.

TEMPERATURE.

The earliest measurements of the deep-water temperature of Loch Lomond were made by Jardine in 1812 (see Buchan, 1871). It is clear that if Jardine had taken his readings at rather shorter depth-intervals the thermocline might well have been discovered in 1812. As it was, this discovery had to await the work of Christisson in 1871 - also on Loch Lomond.

Measurements made during this survey and some made in 1903 by Murray and Pullar (1910) show that in winter the temperature differences in the water are very slight. The lowest bottom temperature recorded in the winter 1948-49 was 5°C. In severe winters ice may cover the "lowland" portion of the loch, as it did in 1947-48 and in 1950-51, but not the deep "highland" portion.

In summer a thermocline is established in the "highland" portion of the loch; it may be only 10 m., or as much as 30 m. below the surface.

None has yet been discovered in the "lowland" portion (Figs. 1 and 2). A thermocline here may have been overlooked, for measurements were not frequent. Its absence is likely to be real and due to this basin's having its greater axis, almost 8 km. long, coincident with the direction of the prevailing winds (Map 1); from the force of which there is no range of mountains to protect it. The "highland" portion which does develop a thermocline is narrow, and lies, with its long axis almost at right angles to the prevailing winds, between high and precipitous moun:tain ranges (Map 1). Thermal stratification probably lasts for about three months, roughly from the middle of June to the middle of September. The duration in any year must vary with the weather. Thus June and July of 1950 were cooler and more windy than usual (Fig. 3); and temperatures as late in the summer as the 18th of July show no more than the beginnings of a thermocline.

I wish finally to draw attention to the fact that the summer tempe:ratures of 1949 were higher than those of either 1948 or 1950. For this difference might well be related to the more numerous benthos found in the winter 1949-50 than in the winter 1948-49 (Fig. 3 and Table 9 p. 30).

DISSOLVED OXYGEN.

Measurements at the Tarbet, Luss and Creinch sampling stations (Table 3) p. 67 (Map 1) show that during the period of complete circulation, water at all levels/

Table 3. Dissolved oxygen, Loch Lomond.
Summer values.

17/7/48 - Tarbet				30/7/48 - Luss			
Depth m.	Temp. °C.	O_2 mg. l.	O_2 %	Depth m.	Temp. °C.	O_2 mg. l.	O_2 %
0	19.0?	7.88	85	0	22.5	7.27	97
18	11.4	7.35	68	15	14.4	7.53	73
37.5	7.7	7.88	67	20	15.6	7.36	73
55	6.1	8.40	67	25	15.0	7.36	73
75	5.8	8.23	65	30	9.5	7.80	68
92.5	5.8	8.05	64	35	8.6	7.62	65
110	5.8	8.23	65	40	8.4	7.71	66
				45	8.3	7.53	63
				50	8.2	7.62	64
				57.5	7.8	7.45	63

5/10/48 - Luss				18/7/50 - Luss			
Depth m.	Temp. °C.	O_2 mg. l.	O_2 %	Depth m.	Temp. °C.	O_2 mg. l.	O_2 %
0	12.8	7.57	71	0	14.8	10.56	104
6	12.4	7.48	69	5	15.0	12.48	113
11	12.4	7.83	73	10	14.5	11.20	109
17	12.4	7.57	70	15	12.6	11.50	107
20	12.4	7.74	72	20	10.8	11.20	101
25	12.2	7.68	70	25	9.8	9.60	84
32.5	11.3	7.74	73	30	9.7	12.16	106
37.5	10.4	7.40	66	35	8.2	11.20	94
42.5	9.0	7.57	65	40	8.4	10.48	89
45	8.6	7.57	64	45	8.2	10.96	92
52.5	8.6	7.31	62	50	7.9	10.88	91

Table 3. Dissolved oxygen, Loch Lomond.
Winter and spring values.

Depth m.	Temp. °C.	O_2 mg. l.	O_2 %
15/1/49 - Luss			
0	6.3	12.52	100
11	6.1	12.52	100
20	6.0	12.55	100
30	6.1	12.60	100
40	6.0	12.50	100
50	6.1	15.0?	120
57.5	6.5	12.41	100
31/1/49 - Creinch			
0	5.9	12.70	101
5	5.5	12.61	99
10	5.8	12.84	102
15	5.7	12.31	97
20	6.0	12.75	102
15/3/49 - Tarbet			
0	6.0	12.05	98
32.5	5.6	12.35	98
60	5.6	12.48	99
90	5.7	12.10	97
120	5.7	12.52	100
150	5.8	12.65	103
180	5.7	12.55	100

levels of the loch is generally saturated with oxygen, sometimes even supersaturated with it (Fig. 5). Oxygen concentration does not then fall below 12.00 mgm. per litre.

With the establishment of a thermocline in the summer, the oxygen content of the lower layers begins gradually to fall. It has, however, never been found to go below 60 % saturation, i.e., 7.31 mgm. per litre (Fig. 5). Should the establishment of a thermocline be delayed, as it was in 1950, then high oxygen concentrations may be found even late in summer. Thus on 18th July, 1950 water at all depths of the Luss basin was saturated or almost saturated with oxygen; even at 50 m., just above the bottom, there were 10.88 mgm. of oxygen per litre of water (Fig. 5).

Mortimer (1941, 1942) has shown that when the oxygen concentration of the bottom layer of water in a lake falls below 0.5 mgm. per litre, the adsorbent oxidised layer of the mud-surface is destroyed by reduction. There is always more oxygen in the water of Loch Lomond than this, and it maintains a permanent adsorbent layer which inhibits the transfer of solutes from the deeper layers of the mud to the water. One should expect to find that the loch is oligotypic for phosphates, nitrates and other biologically important ions.

Redox potentials have not been measured in the loch, but the oxygen values found indicate that they probably do not fall to the critical level (Mortimer op. cit.) of E = 0.25 volts, nor even to E = 0.40 volts. This last/

Table 4. Some physical and chemical values of Loch Lomond.

	Value	Date	Method, Conditions etc.
Colour	faint yellow	17/1/49	
Transparency	6 m.	17/7/49	with Secchi Disc on calm sunny
	5 m.	24/2/51	day about 2 p.m.
Dissolved organic matter	2.86 mg./l.	12/2/51	as O_2 absorbed from $KMnO_4$ by surface water, Auchentullich Bay
Inorganic phosphorus	0.008 mg./l.	7/1/49	in surface water, Auchentullich Bay
Nitrate nitrogen	0.31 mg./l.	7/1/49	ditto
Ammonia (free)	0.0045 mg./l.	7/1/49	ditto
Total solids	11.0 mg./l.	7/1/49	ditto

Table 5. pH and calcium values for Loch Lomond.

pH						Calcium	
17/7/48 Tarbet St.		30/7/48 Luss St.		18/7/50 Luss St.		6/10/48 Luss St.	
Depth (metres)	pH	Depth (metres)	pH	Depth (metres)	pH	Depth (metres)	Calcium (mg./l.)
0	6.9	0	7.1	0	7.0	0	2.9
18	6.9	10	6.9	10	6.8	10	2.8
37.5	6.8	20	6.9	20	6.8	20	2.9
55	6.8	30	6.9	30	6.8	30	3.3
75	6.7	40	6.7	40	6.8	40	2.3
92.5	6.7	50	6.7	50	6.8	50	3.1
110	6.7	59	6.7			63.5	3.0

last is of some interest, for Hutchinson et al. (1939) claim to have demonstrated that redox potentials equal to and above 0.40 volts are associated with a chironomid fauna dominated by the genus <u>Tanytarsus</u>. In Loch Lomond the chironomid fauna is in fact thus dominated, as will appear when the results of the benthic survey are considered.

OTHER PHYSICAL AND CHEMICAL FEATURES.

The colour of the water is a faint yellow, and its transparency as indicated by measurements with the secchi disc is low. The disc disappears at 6 m. in summer and 5 m. in winter. Nevertheless the amount of organic matter in solution, indicated by oxygen absorbed from potassium permanganate in 4 hours at 25°C, is small, namely 2.86 mgm. per litre (Table 4). /8a Hydrogen ion concentration seldom varies by more than 0.1 of a unit above the value 6.9, though the surface waters in summer have yielded values of 7.0 and 7.1. Calcium content is low and varies little from the surface of the loch to the bottom, the range being 2.8 to 3.3 mgm. per litre (Table 5). /8a It is interesting to note in this connection that the water of all the 7 main tributary streams flowing into Loch Lomond has a higher calcium content than the loch water itself (cf. Tables 5 and 2). The extent to which this is due to the diluting effect of rain falling on the surface of the loch is probably small; for the area of the loch is only about a tenth of that of its drainage basin. We may have here an indication of biological transference of calcium from water to bottom/

bottom sediments. Phosphorus, nitrogen,[1] free ammonia,[1] and total solids[1] were found, in the winter 1948-49, to the extent of 0.008 mgm., 0.31 mgm., 0.0045 mgm., and 11.0 mgm. per litre surface water (Table).

THE BOTTOM DEPOSIT.

Casperi (1910) gives an analysis of a typical "brown mud", which he says "is the Scottish loch deposit par excellence". It is a typical "gyttja"[2] such as is found on most of the bottom of Loch Lomond below a depth of about 7 m.. His results are therefore relevant, and they show (a) that organic matter forms about a third only of its dry weight; and (b) that the calcium content is very low.

Stangenberg (1949), searching for some simple index of the producti-:vity of a lake, suggests tentatively that lakes in which the organic nitrogen component forms less than 0.8% of the bottom deposit will have a low productivity. Caspari did not analyse the "gyttja" for its organic nitrogen content. But the results Slack (personal communication) has obtained by using the methods adopted by Stangenberg show that the bottom deposits of Auchentullich Bay contain much less nitrogen than this. At my sampling Stations 4 and 8, where the the bottom deposit is a typical "gyttja"/

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1 Estimations by Dr. H.D. Slack, Zoology Department, Glasgow University.

2 A mud in which the biogenic component is mainly autochthonous and derived from the plankton (Naumann, 1922a)

"gyttja", there is only 0.21 and 0.18% respectively of organic nitrogen (Table 6). Productivity here is low, about 400 individuals per sq. m., on the average. This accords well with Stangenberg's suggestion. Yet at Stations 1 and 2, which are highly productive of benthos, the average being more than 6,000 individuals per sq. m. (Table 6) the organic nitrogen content of the bottom deposit is at least as low as at Stations 4 or 8. At Station 1 it is only 0.07%. My comparison of the benthos of McDougall Bank with that of Auchentullich Bay has led me to suggest that the high productivity is due to the extra amounts of allochthonous detritus which accumulate in these inshore regions, and furnish an abundant supply of food. If this is correct it follows that the nitrogen content is not a satisfactory measure of either the quantity of detritus available as food, or its quality. Indeed Stangenberg herself realises that much more work has to be done before the productivity of a lake may be estimated on the basis of the nitrogen content of its bottom deposits. She even suggests that in lakes "standing under strong allochthonous influences" (pp. 434-35 op. cit.) the nitrogen productivity index is inapplicable.

WATER LEVEL.

The water level of the loch varied by 1.7 m. during the period April, 1948 - August, 1950, the highest values being reached in the autumn and winter, the lowest in the summer months. In Fig. 7 I have given/

Table 6. Carbon and nitrogen content and C/N ratios of bottom deposits at Transect Section.

Station No.	Station Depth (m.)	Depth (cms) from mud-surface of core examined	Carbon in mg.p.g. dry wt.	Nitrogen in mg.p.g. dry wt.	% Dry wt.	C/N	Pop. Density (Avg.)
1	1.0 2	0 - 3	12.07	0.735	.07	16.4	6,140
2	2.5	0 - 2	39.42	2.420	.24	16.3	6,124
3	5.5	0 - 2	52.55	2.860	.29	18.4	1,443
4	11.5	0 - 3	37.75	2.058	.21	18.4	434
5	5.5	0 - 2	8.27	0.172	.02	48.1	1,743
6	2.5	0 - 2	3.04	0.176	.02	17.3	2,330
7	5.5	0 - 2	8.08	0.340	.03	23.7	473
8	9.5	0 - 2	38.77	1.848	.18	21.0	430

given the weekly average depths of water at Station 6, on McDougall Bank. (For purposes of comparison curves for the summer months of 1948 and 1950 have also been included).

In the accounts that follow of the transect line and of the benthos, the depth assigned to a Station will be the maximum recorded there. Its actual depth in any week is very simply obtained by adding to the depth of Station 6 in that week (Fig. 7), the factor appropriate to the Station under consideration. These factors are:-

Stations	1	2	3	4	5	6B	7	8
Factors	-1.5	-0.0	-3.0	-9.0	-3.0	-0.0	-3.0	-7.0

I should point out here, that of the two figures indicating the depth of each contour line in Map 3, the larger indicates its maximum and the smaller its minimum depth in the period April, 1948 - August, 1950.

CONCLUSION.

From the brief account of the loch, I have given, it will be seen that all its characters: the quantities of nutrient salts in its waters, the absence of a period of winter stagnation, the high hypolimnetic oxygen content in the summer, the great depth of the loch, and the geological nature of its drainage basin, all point to its being oligotrophic. In fact Loch Lomond is a ~~loch~~ lake such as Rawson (1939) classes as being truly oligotrophic, in that it satisfies both of Lundbeck's (1934) criteria for oligotrophy/

oligotrophy. For its edaphic factors and its morphology both tend to produce oligotrophy. In Thienemann's system of lake classification (1932) it would fall within the class of harmonic oligotrophic lakes; in Naumann's system (1929) it would fall within the class of oligotrophic lakes sensu stricto, in which all elements of the millieu-spectrum are oligotypic. And yet the lake is possessed of a very rich fauna in its littoral zones - a fauna of the same order of richness as that found in the corresponding zones of typically eutrophic lakes like Esrom for example, (Berg, 1938), or Pereslawskoje (M. Decksbach, 1933), Simcoe (Rawson, 1930), Toro-ko (Miyadi, 1932-3, 7), Nakatuna-ko, Suwa-ko or Ono-ko (Miyadi, 1930-1, 1) (Mendota (Muttkowski, 1918) or Fure-sö (Wesenberg-Lund, 1917). This "anomaly" I shall discuss later (Ch. V, p147)

THE REGION SURVEYED QUANTITATIVELY.

Auchentullich Bay. Both Auchentullich Bay and McDougall Bank form part of the lowland basin of the ~~lake~~ loch, and share in its environmental characteristics. The bay itself is wide, almost 2 km. across its mouth and just over 0.5 km. from mouth to base. It faces east and therefore the inshore waters are sheltered somewhat from the prevailing south-west winds by the gentle hills flanking it. This sheltering effect is greatest where woods extend down to the shore, as they do north of the wall shown in in Map 3.

The countour lines inserted in this map are based upon soundings taken by me in the summer of 1949. They show that for the most part, the floor of the bay is 10 to about 13 m. deep. Along the shore, except to the north-west, it slopes rather steeply down to about 7 m. Thereafter it falls gently to the mouth of the bay where the depth is 15 m.

At the water's edge the bottom is generally composed of cobbles[x] embedded in gravel and coarse sand. This gives place, 0.5 to 1.0 m. be-:low high water level, to sand which extends down to about 3 m. below high water level. Beyond this, silt predominates in the bottom deposit, and, below 7 m., is a typical gyttja, dark brown in colour.

Macrophytic vegetation does not extend much below the 4 m. contour line (Map 3, heavy line) and forms a rather narrow littoral band). At the water's edge Fontinalis antipyretica L. is often found attached to boulders; but wherever there is sufficient sand between the cobbles one finds Litorella uniflora Aschers flourishing. In deeper water where sand completely replaces the shingle the vegetation becomes a carpet of L. uniflora Asch.; that is from 0.5 to 1.0 m. down to about 2.5 to 3.0 m. below high water level Isoetes lacustris L. appears within the outer reaches of this Litorella carpet, and as the sand disappears the Litorella too/

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[x] Named according to the Wentworth classification of coarse sediments (Welch, 1948).

too disappears and is entirely replaced by Isoetes. This plant, however, does not form a carpet but occurs in scattered clumps. Just above and below the 4 m. level the bottom seems silty enough for Nitella opaca Ag. to appear in patches scattered between the Isoetes.

This sequence of the flora is, of course, modified by special con:ditions. Thus the Cross Burn (Map 3) has an unstable delta of small pebbles and gravel. Fontinalis, Litorella and Isoetes are all absent. But at a depth of 2 to 3 m. there is a zone of Potamogeton perfoliatus L. round the outer slopes of the delta. A few scattered plants of Myriophyllum are also found here; and also some Chara, at 1.0 to 2.0 m.. Elsewhere, at 0.0 to 0.5 m., Lobelia portmana L. sometimes replaces Litorella in restricted patches.

McDougall Bank. In the mouth of Auchentullich Bay the bottom of the loch rises very abruptly from the 10 m. contour to a depth of only 4.0 m. below high water level, where it forms a more or less level oval platform. This is the McDougall Bank. It is about 70 m. wide and 250 m. long, and lies with its long axis runningN.N.E. - S.S.W.. It is surrounded by wide stretches of deep water on all sides, except to the north-west, where a ridge jutting out towards it, brings the shallow vegetation zone of the shore within 430 m. of it. The nearest dry land, also to the north-west, is about 530 m. away. An observer in a boat immediately above the bank, can just see it, provided the day is bright and provided the level of the loch/

loch has fallen to such an extent that there are no more than 2.5 to 3.0 m. of water over it.

The northern quarter of the bank is devoid of macrophytic vegetation, the bottom deposit here being mainly a gravel. Elsewhere on the bank the deposit is sandy. Isoetes lacustrus L. appears a little north of Station 6 (Map 3), and becomes more and more abundant the nearer one gets to the southern tip of the bank. Nitella opaca Ag. is also found in patches over the southern half of the bank, especially a little south of Station 6B. As is the case along the shore, the 4 m. contour line is just within the outer limit of the zone of macrophytic vegetation. The Isoetes and Nitella of the bank is less abundant than that of the shore. This may be due to the coarser nature of the bottom deposit or to its poorer nutritional quality or to both these factors.

The Transect Line. The nine sampling Stations which constituted the transect line are shown in Map 3, where they are numbered 1, 2, 3, 4, 5, 6, 6B, 7 and 8.

Station 1 was on the Litorella carpet. The bottom deposit here is sand admixed with large amounts of still recognisable plant remains. Maximum depth (at high water level of the loch) 2.4 m.; minimum depth (at low water level of the loch) 0.7 m.

Station 2. was within the Isoetes zone. The bottom deposit is a dark brownish-gray gritty mud with little in the way of recognisable plant remains. Maximum depth 4.0 m.; minimum depth 2.3 m.

Station 3/

Station 3 had no macrophytic vegetation. The bottom deposit is a reddish brown mud. Maximum depth 7.0 m.; minimum depth 5.3 m..

These three Stations were situated on the shelving margin of the loch. The next two were on the more or less level floor of the bay.

Station 4, a little more than halfway between bank and shore, had no macrophytic vegetation. The bottom deposit was a typical dark brown gyttje with scarcely any recognisable plant remains. It contained, however, large numbers of empty sand-cases of the chironomid Tanytarsus (Stempellina sp. A, (vide p130). Maximum depth a little over 13 m.; minimum depth 11.3 m.

Station 8 lay beyond McDougall Bank. Maximum depth 11.0 m.; minimum depth 9.3 m. In other respects it resembled Station 4.

The remaining 4 Stations were either on the sides of McDougall Bank, (Stations 5 and 7) or on the bank itself (Stations 6 and 6B).

Station 5, on the west side of the bank, supports no macrophytic vegetation; the bottom deposit is a coarse sand mixed with gravel and small pebbles. Maximum depth 7 m.; minimum depth 5.3 m..

Station 7, on the east side of the bank, differs from Station 5 only in bottom deposit, which is a fine sand and silt, red brown in colour. It tends to form a firm plate at a depth of about 4 to 5 cms. beneath its surface.

Station 6 was on the bank and in line with the other Stations. Isoetes lacustris/

lacustris occurs here in scattered clumps. The bottom deposit is sandy and contains little detritus. Maximum depth 4 m.; minimum depth 2.3 m.. *Station 6B*, at the southern end of the bank, resembles Station 6 except for a somewhat greater amount of detritus and the occurrence of *Nitella opaca*.

At various times during the course of the survey the oxygen content, the pH and the temperature of the water just (approximately 0.5 m.) above the loch floor were measured at each of these Stations (Table 7). Such differences as were found between the Stations were small.

The organic carbon and nitrogen in the upper 2 - 3 cms., of the bottom deposits at these Stations were also determined* (Table 6, Fig. 6). Both tend to be higher at the deep Stations than at the shallow ones. They are much lower at the bank-stations than anywhere else. This is a reflection of the smaller amounts of detritus on the bank. The ratio of carbon to nitrogen varied between 16 and 23 (save at Station 5), the lower values being found generally at Stations with a denser benthic population, the higher values at those with a sparser benthic population. This correspondence, however, is not close. Thus Station 3 with a C/N ration of 18.4 has a population over three times as numerous as that at Station 4, which also has a C/N ratio of 18.4. Whilst Station 5 with a/

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* By Dr. H.D. Slack, Zoology Department, Glasgow University.

Table 7. Temperatures, oxygen concentrations and pH along the Transect.

Station	1st March 1949				7th June 1949				12th August 1949				pH
	Depth (m.)	Temp. °C.	Oxygen mg./l.	%	Depth (m.)	Temp. °C.	Oxygen mg./l.	%	Depth (m.)	Temp. °C.	Oxygen mg./l.	%	
1	2.5	5.4	12.77	101	1.5	13.1	11.4	108	1.5	16.2	10.8	109	6.9
2	4.0	5.4	12.83	102	3.0	12.7	11.4	107	3.0	16.0	10.7	109	6.9
3	7.0	5.3	11.72	95	6.0	12.6	8.0	75	6.0	15.7	10.7	108	6.9
4	13.0	5.2	12.95	100	12.0	12.4	11.3	105	12.0	15.4	11.0	109	6.9
5	7.0	5.4	12.79	101	6.0	12.4	11.5	107	6.0	15.8	10.8	108	6.9
6	4.0	5.3	12.59	100	3.0	12.6	11.2	105	3.0	16.0	10.6	107	6.9
6B	4.5	-	-	-	3.5	12.6	11.2	105	3.5	16.2	10.7	107	6.9
7	7.0	5.3	12.74	100	6.0	12.4	11.1	103	6.0	15.5	10.5	105	6.9
8	11.0	5.3	12.62	100	10.0	12.4	11.0	102	10.0	15.6	11.1	110	6.9

a C/N ratio over two and a half times that of Station 4, has a population not sparser than that of the latter Station, but four times as dense (Table 6)., (Table 9) [p. 146 a]

Whilst remaining almost the same, as between the nine Stations, the amount of dissolved oxygen in the bottom layer of water falls from about 12.7 mg. per litre late in the winter (1/3/49) to about 10.6 mg. per litre late in summer (12/8/49). Nevertheless, except at Station 3, the water is always supersaturated with oxygen. Even at Station 3 the concentration was always high - though it did not always reach saturation level.

CHAPTER II.

APPARATUS AND METHODS USED IN THE FAUNISTIC SURVEY.

1. COLLECTION OF QUANTITATIVE SAMPLES.

Each of the 9 Stations on the transect line was marked with a buoy and 3 samples taken from it with a Petersen grab in each of 14 consecutive months, from January, 1949 to February, 1950. From these samples all animals large enough to be retained by a sieve with mesh-opening 0.4 mm. x 0.4 mm. in size were removed by a floatation technique (p. 10). As this technique was in the process of development in January, 1949, that month's collections are not truly comparable with the rest and have been excluded from consideration.

2. THE SAMPLER USED.

The Petersen grab with which the quantitative collections were made, sampled an area of about 370 sq. cms., or roughly one twenty-seventh of a sq. m., down to a depth of about 12 cms.. It worked very well where the bottom deposit was soft, and not covered densely with vegetation. For sampling where there was a dense carpet of vegetation or where the bottom was sandy, the grab was weighted with 4 lead cylinders each weighing 1.5 kgm. dropped over metal rods fixed in its upper surface, (Figs. 8, 9, 10). It was found possible by this means to get very nearly a grabful of sample where, before, a scraping off the loch-bed was all that was obtained.

Berg/

Berg (1938) has shown, by using a "stratification bottom sampler", that though the great majority of benthic animals were found upon and within the uppermost layers of a soft bottom deposit, a few do penetrate to fair depths. Those below 12 cms. would not have been collected by the Petersen grab I used, and there must therefore be a difference between actual faunal densities and the estimated densities (Table 9) [p 146a] based upon my collections. At Stations 1, 5, 6 and 6B the deposit could never be sampled down to the depth of 12 cms., but it is possible that the penetration of animals into these firm sandy deposits is more restricted than in the soft deposits studied by Berg. If so, the difference between real and estimated densities at these Stations will not be much greater than at the other Stations. Upon this assumption I have treated the results at all the 9 Stations as comparable.

Other inaccuracies arising from the use of the Petersen grab have been discussed by Davis (1925) and by Holme (1949).

3. REMOVAL OF FAUNA FROM SAMPLES.

The Floatation Method.

From each sample the fauna was recovered by a series of processes, the sequence of which was rigidly adhered to in order to minimise errors due to the personal factor. It included a modification of the floatation technique first introduced by Ladell in 1936 for the recovery of soil insects. Since examining the animals when they were alive greatly facilitated their preliminary identification, the elaboration of this technique which Salt and/

and Hollick (1944) developed was not adopted. For though it shortens very considerably the time spent on extracting animals from a sample, the use of xylol in the process kills them. Moffett (1943) has used a floatation technique for dealing with sandy lake-deposits. He fixed his sieve residues in 10% formalin and then floated the animals out of them with a solution of calcium chloride. Besides killing the animals this method suffers from a second defect. Calcium chloride is very hygro-:scopic and is therefore inconvenient to use, particularly with samples from muddy or silty substrata,

Stage 1. First Washing.

Each sample was first washed through a wooden sieve (60 x 30 x 10 cms., No. 40 wire mesh) (Fig. 11), floated upon the stream that runs beside the Field Station, and made fast to a foot-bridge. The speed with which the stream flowed was generally great enough to produce an inflow of water through the mesh at the downstream end of the sieve and an outflow at the upstream end. This circulation automatically washed the sample if it was left in the sieve long enough. Unfortunately the longer it remained there, the larger the number of worms entangled in the mesh - by weaving their bodies through it - and lost; for it was impossible to remove them without severe damage.

Instead/

Instead, therefore, of emptying the sample into the sieve, water from the stream was carefully drained through a No. 100 mesh sieve and added to the bucket containing the sample. This was then stirred up, allowed to settle for 15 seconds, and the supernatant muddy water poured away through the sieve floating on the stream. This operation was repeated until most of the mud in the sample had been washed away. The material collected by the sieve from the washings was then added to the residue in the bucket, and the sample was ready for the next stage of the treatment. It now occupied no more than 1/10 - 1/16th of its original volume.

Stage 2. Second Washing.

a) Vegetation. In the laboratory all the macroscopic green plant material in the sample was picked out and attended to first. This green material floats even in water and hence if allowed to remain in the sample would have interfered with the collection of animals floated out with magnesium sulphate solution. The plants were therefore placed, a small quantity at a time, at the bottom of an empty cylindrical jar 24 cms. high and 15 cms. in diameter. A powerful jet of water was then directed at an angle into the jar. This produced a violent swirl in the water as it filled the jar. The swirl detached from the vegetation most of the animals clinging to it, even forms like Limnius tuberculatus which can hold on very firmly with their powerful claws. Tube dwellers were disturbed and left their tubes. When the jet was turned off the green plants soon floated to the surface of the water, whilst the animals, and any dead plant material/

material present sank to the bottom of the jar. The floating plants were picked off and the contents of the jar poured through a No. 40 sieve. This process was repeated, three times for each handful of material, until all vegetation in a sample had been dealt with. The sieve collection, containing all the animals from the vegetation of the sample, was then tipped with a little water into a pie-dish and set aside till the rest of the sample had been washed. The washed plant material is discarded for this treatment has removed all or very nearly all the fauna it contained.*

b) Bottom Deposit

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* Dealing with vegetation in quantities surveys has hitherto been unsatisfactory. The usual method of carefully examining each plant, piece by piece is accurate but is very laborious and time-consuming. Humphries and Frost (1937) allowed weeds to stagnate in a bowl of water and picked off the chironomids when they were forced to the surface as oxygen lack developed in the weed-mass. They saved much labour by this means, but, I suspect, at some expense of accuracy. The method I have described above is not only easy and quick, but also accurate. On one of the occasions when I tested it, two washings yielded 47 animals; the material was then examined piece by piece, and yielded just 2 more animals. On two other occasions the plants were examined piece by piece after they had been subjected to the whole series of three washings. Not one animal was found amongst them.

b) Bottom Deposit. The rest of the sample was now repeatedly washed - also through a No. 40 sieve - till the washings were no longer discoloured with silt. In each washing, water was squirted violently into the bucket containing the sample, so as to churn it up thoroughly. After 15 seconds for settling, the supernatant liquid was poured off through a No. 40 mesh sieve, and the material collected by the latter added to the residue in the bucket, and washed again. The vigorous churning of the sample not only hastened the removal of silt from it, but also disturbed the tube-dwelling animals so much that they left their tubes.* In several samples all the tubes remaining after washing were individually examined. No larvae were found in any of them. This is a very important result of the treatment for as long as the tube-dwellers remain within their tubes they cannot be floated out of the sample by magnesium sulphate solution. It is necessary to point out that even the smallest and most delicate of the fauna were not damaged by this apparently violent treatment.

Stage 3. Examination in Water.

The residues from stages 2a) and b) were thinly spread in 8 to 10 pie-dishes and rapidly examined. Those insect pupae and larvae ready for pupation, from which it was intended to rear adults, were removed now; for/

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* Case-dwelling caddis larvae however remained within their cases.

for contact with magnesium sulphate solution seems to prevent successful metamorphosis. As many of the cased caddis-larvae, and of the snails as possible, were removed. For these, silken-cased larvae and tiny snails excepted, cannot be floated off with magnesium sulphate solution.

Stage 4. First Treatment with Magnesium Sulphate Solution

The entire sample was next placed in a sieve with a No. 100 mesh and drained of most of its water. One or two c.c.s were placed in a glass dish and magnesium sulphate solution of s.g. 1.15* added to it.

Most of the animals and some of the vegetable detritus floated to the surface of the solution. The detritus soon absorbed magnesium sulphate and sank, leaving the surface clear except for the animals floating on it. These were picked off with a bent needle. Solution which has been coloured a dark brown by previous use throws small whitish or almost colourless animals into sharper relief than does clean freshly prepared solution, and was therefore always used.

Not all the animals floated up at once. Some remained at the bottom of the dish, clinging to or accidentally imprisoned within the detritus and mineral sediment. These floated up with sufficient stirring of the sediment. In practice, no sample was considered to be 'completely extracted'/

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* This slightly denser solution has been found in practice to be more suitable for freshwater animals than the solutions used by Ladell or Salt & Hollick (op. cit.)

extracted' by this floatation process until three consecutive stirrings brought no single extra animal to the surface.

When this test was passed the contents of the dish were poured into a No. 100 mesh sieve. The solution which passed through it was brought up to correct strength by adding concentrated magnesium sulphate solution to it and checking its s.g. with a hydrometer. The residue in the sieve was washed in running water and then placed in a dish in contact with a large volume of water in order to remove the magnesium sulphate from it.

In this manner the entire sample was treated with magnesium sulphate solution. As the animals were picked out they were immediately separated into groups, by their appearance and movement. Often it was possible to recognise species by this means, and save much time later on when the preserved specimens had to be identified. All specimens except the Mollusca were preserved in 4% formalin solution. The Mollusca were preserved in 70% alcohol.

Stage 5. Second Treatment with Magnesium Sulphate Solution.

The foregoing treatment left behind in the sample all the Sphaeridae; and those snails and sand-cased Trichoptera that had escaped attention during the examination in stage 3. Of these the cased Trichoptera are as little buoyant as the mineral matter in the sample; whilst the sphaerids and snails though more buoyant than the mineral matter are less buoyant than the detritus. The subsequent treatment makes use of these differences/

differences in order to remove by floatation in magnesium sulphate, first the detritus, then the sphaerids and snails; and thus leave behind in the sandy residue the sand-cased caddis larvae.

The residue from stage 4 was well washed so as to remove all the magnesium sulphate that had been absorbed by the detritus. It was then drained of its water (through a No. 100 mesh sieve) and magnesium sulphate solution, s.g. 1.15 added to it. The detritus floated to the surface and was gently decanted away. To the residue at the bottom of the dish was then added a saturated solution of magnesium sulphate at 47-50° C.. At this concentration the solution is dense enough to float all the sphaerids and all except the largest snails. It was decanted away through a No. 40 sieve which therefore retained the molluscs. The sand-cased caddis larvae and also the few specially large snails which were too heavy to be floated even by the hot saturated solution of magnesium sulphate, were then picked out with ease from the small quantity of sand that remained in the dish. It is essential, however, that immediately after decantation the residue in the dish as well as the collection in the sieve be placed in water. Otherwise the magnesium sulphate crystallises to form a solid mass from which it is difficult to recover the animals.

OTHER COLLECTIONS.

The regular quantitative collections were supplemented with others, mainly/

mainly qualitative and taken by hand, or with hand net or dredge. Some of these sampled the area from the water's edge down to about the level of Transect Station 1; others sampled areas near Stations 1, 2, 6 and 6B; a few sampled the mud at 180 m. near the Tarbet sampling Station (A in Map 1). Some quantitative samples were also collected from the Creinch (20 m.), and the Luss (60 m.) sampling Stations (C and B in Map 1).

CHAPTER III.

THE ANIMALS FOUND.

COELENTERATA.

(Table 8).

The only representative of this group is <u>Hydra vulgaris</u> (Pallas) which occurs wherever there is macrophytic vegetation, except perhaps where the water is much disturbed by wave action. It was found mainly in April and August, when there were almost 260 of them per sq. m. of the <u>Litorella</u> carpet along the loch margin, and 180 per sq. m. amongst the <u>Isoetes</u> and <u>Nitella</u> of McDougall Bank. In most other months of the year none was taken by the bottom sampler. This points, I believe, to an extreme scarcity of polyps during this period, rather than to their com:plete absence.

In April and August nearly 50% of the chironomid larvae, <u>Limnochiro:nomus</u> sp., in the vegetation zones are covered with large numbers of nematocysts. These larvae could have been stung whilst merely moving about a microhabitat crowded with <u>Hydra</u> polyps. If so it is a little surprising that no other chironomid species was similarly stung. The coating of nematocysts on this single species of chironomid seems to me to indicate a closer relationship between polyp and larva than that of being close/

Table 8. Proportional representation of various groups in collections from each Station and in entire collections.

Group	1	2	3	4	5	6	6B	7	8	All Stations
Coelenterata (Hydra)	0.3	0.3	0	0	1.0	0.5	0.9	0	0	0.3
Turbellaria	0.7	0.3	0.9	0.1	0.7	1.7	1.7	1.9	0	0.8
Nematoda	4.6	4.9	5.0	3.6	17.6	5.1	8.8	30.8	4.2	6.6
Lamellibranchiata (Sphaeridae)	6.6	1.8	3.2	3.0	15.3	7.6	3.2	14.1	2.1	5.0
Gastropoda	0.8	0.6	0.4	0.4	4.7	4.7	5.1	4.8	0.3	2.0
Hirudinea	0.1	0.1	0.1	0	0	0	0	0	0	0.1
Oligochaeta	19.9	14.7	21.0	55.3	23.6	12.6	9.3	17.1	57.9	17.8
Hydracarina	2.8	2.8	4.8	1.8	5.1	1.4	0.7	3.9	1.7	1.8
Copepoda	1.0	0.6	1.0	4.2	1.1	1.7	3.1	1.9	1.5	1.3
Ostracoda	0.5	0.4	0.4	0.1	0.1	1.7	0.7	0.1	0	0.5
Cladocera	3.2	1.0	2.4	0.9	4.5	9.6	4.8	1.4	0	3.3
Amphipoda (Gammarus)	0.1	0	0	0	0	0	0	0	0	0.1
Isopoda (Asellus aquaticus)	15.9	0.5	0	0.1	0.7	8.1	6.4	0	0.3	6.4
Hemiptera	0.1	0	0	0	0	0	0	0	0	0.1
Plecoptera	0.5	0.1	0	0.1	0	0	0.1	0	0.2	0.2
Odonata	0	0.1	0	0	0	0.1	0.1	0	0	0.1
Ephemeroptera	4.5	9.8	5.8	0.1	0.7	1.4	1.6	0.3	0.2	5.0
Trichoptera	4.1	2.7	0.6	0	1.3	3.1	3.4	1.4	0	2.9
Coleoptera	6.9	0.3	0.1	0	0.1	4.2	1.5	0.5	0.3	2.7
Coleoptera (Limnius only)	6.3	0.2	0.1	0	0.1	4.2	1.5	0.5	0.3	2.5
Diptera - Chironomidae	22.5	53.7	48.3	28.5	21.3	34.6	46.4	21.7	29.6	38.1
Diptera - Ceratopogonidae	3.2	3.9	5.6	1.2	1.3	1.5	1.1	1.1	1.1	2.9
Diptera - Empididae	2.0	1.4	0.3	0	0.1	0.1	0	0	0	1.0
Diptera - other families	0.1	0.1	0.1	0.1	0	0	0	0	0	0.1

close neighbours. I suspect the larva feeds on the polyp.

PORIFERA.

A species of Spongilla (= lacustris ?) grew upon the buoys marking the sampling Stations but no specimens were ever taken in the samples.

PLATYHELMINTHES.

TURBELLARIA.

(Table 8 and Figs. 13 and 38).

Turbellarians are, numerically, an unimportant group of benthos, and never form more than 2% of it (Table 9, 30a, Fig. 38). The triclads, Dendrocoelum lacteum (Mull.), Bdellocephalla punctata (Pallas), and Polycelis nigra Ehrnbg. are commonest on boulders and cobbles at the water's edge, but are also found in the vegetation zones of the bay and of McDougall Bank. Of the three, P. nigra Ehrnbg., with an average density of about 25 per sq. m., is the most numerous in these vegetation zones. Sexual reproduction apparently occurs from May to August, for cocoons were frequently found then - and successfully hatched - and there was a pronounced increase in individuals captured during August and September (Fig. 13). D. lacteum (Mull.), and B. punctata (Pallas) are generally less than a third as frequent as P. nigra Ehrnbg.. In them also, reproduction seems to take place in the period May - August, cocoons being often found then.

The/

Table 9. Seasonal variation in population density of benthos (estimated no. per sq. m.).

Station	1	2	3	4	5	6	6B	7	8
February	3634	2610	621	531	936	1,188	1680	513	351
March	4293	3816	1314	405	495	1404	2448	999	72
April	5535	2781	1818	297	1170	1107	1521	216	324
May	4752	3065	639	135	738	1773	1269	351	288
June	4715	7515	1350	117	522	2115	2214	423	135
July	10863	8055	4437	1080	2232	2511	3402	576	477
August	9180	7002	1710	747	1863	4032	2790	324	549
September	7677	5976	999	324	1899	4041	2853	567	99
October	7164	8721	567	126	963	1521	3771	126	251
November	6174	6003	963	135	270	1440	2781	117	171
December	5535	9108	927	486	783	4941	4581	846	999
January	5382	7470	1350	774	1008	3267	3690	315	414
February	4923	7497	2070	494	783	855	3429	783	567
Average	6140	6124	1443	434	1743	2330	2802	473	430

The rhabdocoeles, including a species of *Mesostomum* are rarer than the triclads, but extend beyond the vegetation zones even to depths of 13 m.. There are more of them in the summer than at other times.

NEMATHELMINTHES.

NEMATODA.

(Table 8 and Fig. 39).

Nematodes form one of the six most important groups of animals in the loch (Table 8). In shallow waters there are generally almost 300 of them in a sq. m.. This number decreases rapidly below 4 m. though even at 13 m. it is still about 15 per sq. m.. No nematodes were found at 20, 60 or 190 m. on the few occasions when mud from these depths was examined, and it seems unlikely, therefore, that they extend much below 13 m. (Fig. 39). Nematodes of Innaren, also an 'oligotrophic' lake, have a similar distribution (Brundin, 1949) though they are almost six times as numerous there as in Loch Lomond.

I did not separate my catch of nematodes into species, and have not been able, therefore, to discover the existence of seasonal variations in density. Numbers of all species together, vary erratically in each month's collections at each Station. Along the whole transect line nematodes were more than twice as numerous after the 1949 summer as before it.

A/

A similar increase has been found in other animals too - e.g. Eurycercus lamellatus, Asellus aquaticus, the oligochaetes, the ceratopogonids and the chironomids (q.v.) - and is reflected in the richer benthos, both stenotopic and heterotopic, found in the winter 1949-50, than in the winter 1948-49 (Table 9, Fig. 34). It probably indicates that a warm and fine summer, such as was experienced in 1949 (Fig. 3) favours repro-:duction in these groups and leads to an increase in their populations in the loch. What factors in the environment, and what stages of the life cycle are involved have yet to be worked out. As regards many insects, I have gathered some evidence (see Ch. III, p. 81 et seq.) that wind strength is one of these factors and that it effects mating and oviposition.

Larvae of the ceratopogonids Probezzia venusta (Meigen), Palpomyia quadrispinosa (Goetghebuer) and Bezzia sp., and of the chironomids, Pentaneura sp., and Spaniotoma sp. often harboured nematodes. Each nematode when full-grown, is three or four times as long as its host, within whose haemocoele it lies folded on itself. Here it occupies a region extending from the second or third thoracic to the penultimate or last abdominal segment. No host was ever found with more than one nematode in it. I have on occasion watched a parasite escape from its host. Escape was preceded by a period of half to one hour during which the cephalic end of the previously quiescent parasite probed about within the thorax and head capsule of its host. The latter generally stopped wriggling/

wriggling or swimming soon after these probing movements began; and was quite dead by the time the parasite had left it. As a result of its probings the parasite ultimately forced an opening through the cuticle of its host. In three instances this opening was in the membrane joining head and thorax; in the fourth it was in the floor of the buccan cavity near the mouth. The parasite then slid out through the opening, its body being thrown into a series of waves which must in some way have assisted its movement. When it was outside the host, these waves disappeared, and the parasite assumed a flat spiral shape rather like a watch spring. Many of the nematodes found free in the samples, were coiled in this manner, and it therefore seems likely that an important proportion of the nematode fauna of the loch consists of free-living stages of parasitic species. Dr. W.A. Baylis of the British Museum (Natural History) has kindly examined some nematodes I found in larvae of Spaniotoma sp., and informs me that they are larval Mermethidae.

EUBOSTRICHUS.

In his account of the fauna of the Scottish freshwater lochs Murray (1910) has included the following note in his list of the nematodes (p. 318, op. cit.):-

"Eubostrichus ? sp. - Loch Lomond".

The/

The genus Eubostrichus was erected by Greef (1869) for an animal type, two species of which he then described and figured. Both were marine and Murray's discovery of a species of the genus in freshwater is, at least, unusual. I kept careful watch during the survey for any animal that belonged to this genus or might reasonably be mistaken for it. None was ever found. Greef gives no measurements in his text, but from his figures it appears that Eubostrichus spp. are small animals about 8 mm. long and about 60 μ wide. It is possible that an animal as slender and as long as this might have been destroyed or lost by the washing and sieving methods I adopted (see Ch. II). I have, however, recovered typical nematodes not much thicker than this by the same methods, and feel justified in concluding that Eubostrichus sp. was never captured during my survey. Since Murray himself had some doubt as to the correctness of his determination of the genus I should be surprised if the genus does occur in the loch.

POLYZOA.

No polyzoan colonies were found during the survey but statoblasts of Cristatella mucedo were common in silt, particularly at Stations 4 and 8 (i.e. at 11 and 13 m.). Here between May and December, 5-10 statoblasts were generally found in each sample, but on one occasion there were 80 and on another 121. One or two were taken in each grabful of silt from 60 m. at the Luss Station, but none was ever found in the phytal zones of/

of the loch margin or of McDougall Bank.

The fate of these statoblasts is as puzzling as their source - for the colonies usually live in shallow waters.

It is also worth noting that the statoblasts had not lost their usual buoyancy, for when removed from the samples and placed in water they floated.

MOLLUSCA.

LAMELLIBRANCHIATA - SPHAERIDAE.

(Table 8, Fig. 40).

Time did not allow the complete identification of the one and a half thousand sphaerids collected, but amongst them I found the following*:-

Sphaerium corneum L., *Sphaerium lacustre* Mueller, *Pisidium cinereum* Alder, *P. conventus* Clessin, *P. nitidum* Jenyns, and *P. subtruncatum* Malm.. The genus *Pisidium* makes up the bulk of the collection.

This family is almost as numerous in Loch Lomond as the nematodes (Table 8) and has a rather similar distribution. It extends, however, to much greater depths, 14 *Pisidium* per sq. m. being found in mud at 60 m., (Luss Station) in March and in September, and some even at 180 m. (Tarbet Station/

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* Names after Ellis (1940).

Station). Nevertheless it is relatively more numerous in shallow zones, particularly if the bottom is sandy. Thus at Station 1 there are on an average about 400 of them per sq. m. (Fig. 40). On McDougall Bank, however, the density is about a third of this - possibly because of the relatively smaller amount of detritus available there.

No seasonal variation in density was detected for the family as a whole.

GASTROPODA.

(Table 8, Figs. 41, 13).

The following species* occur in Loch Lomond:-

Ancylastrum fluviatilis Muell.	Pulmonata.
Limnaea (Radix) pereger Muell.	do.
Planorbis (Gyraulus) albus Muell.	do.
Planorbis (Gyraulus) laevis Alder	do.
Physa fontanilis L.	do.
Valvata piscinalis Muell.	~~Opisth~~ Prosobranchiata.

All these are species which Boycott (1936) has found generally to inhabit soft-water lakes.

Ancylastrum fluviatilis, a freshwater limpet, is confined to the cobble and boulder strewn margins of the loch, and may be locally quite abundant/

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* Names after Kennard and Woodward (1926).

abundant. Limnaea pereger is commoner than Ancylastrum fluviatilis in this region but is not confined to it. For this snail is also found in small numbers (less than 10 per sq. m.) at Stations 1, 6 and 6B, where the bottom is a firmly packed sand with Litorella or Isoetes growing on it. It does not occur on silt or mud. Moon (1934) and Humphries (1936) indicate that it has similar habitat preferences in Lake Windermere. Planorbis albus and P. laevis, on the other hand, are commonest in such sandy, weed-covered regions, where their population density is about 20 per sq. m., on an average. They may reach much greater values when Nitella is present among the weeds. Thus at Station 6B on McDougall Bank densities of about 100 per sq. m. have been found. These two species do not inhabit silt or mud; the very rare specimens taken there have, I believe, been carried thither accidentally. Physa fontinalis resembles the two species of Planorbis in being restricted to zones containing plants like Litorella, Isoetes and Nitella, but differs from them in that it does not seem to find a sandy bottom deposit essential. Thus at Station 2 where Isoetes and Nitella occur in scattered clumps separated by mud, there were on an average 20 Physa fontinalis but not even one Planorbis per sq. m..

There is a marked seasonal variation in population density of this snail, with a maximum in August and a minimum in July. Furthermore, its population in the winter 1949-50, was two to three times as high as in the winter 1948-49 (Fig. 13). For this I believe the specially warm and fine summer/

summer ~~1950~~ 1949 was responsible (cf. Nematoda, p. 32).

Valvata piscinalis, the only prosobranch, is also the only snail which extends beyond the vegetation-covered zone. But it, too, favours the latter habitat, which generally contains more than 20 of them per sq. m.; whilst on silt the average is about 5 per sq. m. at 7 m., an occasional specimen at 13 m., and none at depths of 20 m. or more. Densities on McDougall Bank are exceptionally high, the average in the weedy area being about 90 per sq. m., and the maximum about 200 per sq. m.. Less disturbance in the water over the bank might be the reason for this; so also might the absence of possible predators like the leech, Helobdella stagnalis, which is found inshore. A seasonal variation in the density of this snail was not discovered.

As a group the gastropods are inhabitants of shallow waters (Fig. 41) and are numerically unimportant. Except on McDougall Bank they constitute less than 1% of the benthos (Table 8). Members of all species have poorly calcified shells and are relatively smaller than those living in harder waters. Very few empty shells were found in the survey and all of them, soft and translucent, showed unmistakable signs that the calcium in them was rapidly dissolving away. There is in Loch Lomond no trace of the "shell zone" which is so characteristic of "eutrophic" lakes, like Esrom (Berg, 1938), Mendota (Juday, 1922, Muttkavski, 1918) and the many north German lakes studies by Lundbeck (1926).

ANNELIDA/

ANNELIDA.

HIRUDINEA.

(Table 8, Fig. 42).

Leeches are rather uncommon in Loch Lomond. Glossisiphonia complanata L. occurs on stones in the shallow waters along the margin of the loch, but was not taken on the transect. Helobdella stagnalis L. (Fig. 42) finds its optimum habitat amongst Isoetes and Nitella in the neighbourhood of the 4 m. contour line, and here occurs in small but fairly constant numbers throughout the year (average density 10 per sq. m.). It does not occur at depths greater than about 7 m., nor on McDougall Bank.

OLIGOCHAETA.

(Table 8, Figs. 43-51, 14-17, 6)

Oligochaetes outnumber all other groups of the benthos, except the Chironomidae (Table 8). They attain their greatest densities in the shallow regions of the loch, where, at depths between 0.7 and 4.0 m. the average annual population is about 1,200 per sq. m. (Fig. 43), and the summer maximum twice as great, (at Station 1, in July). Numbers decrease below 4 m., at first very rapidly, for at 7 m. the population is only 300 per sq. m., and later gradually, for at 12 m. there are still 250 worms per sq. m.. A few collections made in the Luss basin (September, 1949 and March, 1950), and in the Tarbet basin (May, 1951)* indicate that at 60 m./

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* Collections by Dr. H.D. Slack.

60 m. there are perhaps 60 worms per sq. m., and at 180 m., perhaps 15 per sq. m.. The decrease apparently continues to be gradual.

Nevertheless increase in depth finds the worms becoming a steadily more important fraction of the benthos (Table 8), since other animal groups are even more restricted to the shallow zones of the loch than are the worms.

A very pronounced seasonal increase in density occurs beginning about May and reaching its peak in July (Fig. 14). At Station 1, a second peak, due mainly to Peloscolex ferox Eisen, occurs in October. Unlike the first peak this second one seems to involve the worm population of McDougall Bank hardly at all. The occurrence of two peaks might be due to certain species multiplying early and certain other species multiplying late in the summer. But then both peaks should be shown by the worm population of McDougall Bank - for on it are found all those species of worms that occur at Station 1. Besides the same two peaks are still evident when one considers the seasonal variation at Station 1, of Peloscolex ferox E. alone, the species which is mainly responsible for the second peak (Fig. 17). It seems more likely, therefore, that the October peak is the result of a second period of reproduction in the species that have already reproduced in the summer.

The reason for the very poor development of this second reproductive phase on McDougall Bank must, I feel, be sought in the special conditions regarding/

regarding warmth that occur at the margin of a loch. Here the loch floor is in direct contact with the relatively shallower layer (about 1 m. thick) of warm water produced by daily insolation of the loch surface; or as at Station 1 is never far removed from its influence. The animals living in the margin of the loch will therefore be subject to special conditions of warmth, which might well be sufficient to induce a second reproductive phase in at least some of the worms. In addition the extra warmth might so hasten the growth and maturity of the first summer generation that it is able to reproduce itself before the winter sets in (Wesenberg-Lund, 1912). McDougall Bank on the other hand is always at least 2 m. below the surface of the loch; and must be much less influenced by the layer of warm water at the surface. The second reproductive phase would therefore be absent or very poorly developed.

I was unable to identify 311 of the 5,412 oligochaetes collected; the others were separated into the following 14 species:-

Family Naididae:

Vejdovskyella comata Vedj.*
Slavina appendiculata Udek.
Pristina longiseta Ehrenbg.
Paranais sp. (= uncinata ?)
Chaetogaster diaphanus Gruith*
Stylaria lacustris L.
Arcteonais lomondi/

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* Determined by Miss S.M. Davies, British Museum (Natural History), London.

	Arcteonais lomondi Martin
Family Tubificidae:	Tubifex tubifex Müll.
	Peloscolex ferox Eisen
	Limnodrilus sp.
Family Enchytraeidae:	Marionina sp.*
Family Lumbriculidae:	Lumbriculus variegatus Müll.
	Stylodrilus heringianus Clap.
Family Lumbricidae:	Eiseniella tetraedra Sav.

Of these, *E. tetraedra*, *Marionina* sp. and all except two of the Naididae are generally limited to the vegetation covered deposits in shallow water. The other species, including the naids *A. lomondi* and *Paranais* sp., extend beyond this zone to various depths. *P. ferox* has been found even at 180 m.; *T. tubifex* at 60 m.; and *S. heringianus* at 20 m..

All 14 species are found on McDougall Bank. But as will be evident from the accounts of each species that will follow, they are much scarcer there than at the comparable Stations, 1 and 2, along the shore. Since these worms, except *C. diaphanus*, seem to be detritus feeders their scarcity/

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* Determined by Miss S.M. Davies, British Museum (Natural History), London.

scarcity on the bank suggests that there is less detritus of nutritive value there than at Stations 1 and 2 (see p.10).

It is unfortunate that there is as yet no means of measuring differences in nutritive value of detritus. Neither organic nitrogen nor organic carbon content of the deposit, as estimated by the methods referred to earlier is a measure of this, as a comparison of the "organic carbon"* and the oligochaete density curves in Figure 6 will show. For example, Station 4 was found to have almost three times as much organic carbon as Station 1, and yet has only a fifth as many worms; whilst Station 2 which also has about three times as much organic carbon as Station 1 has almost the same number of worms.

Vejdovskyella comata is a very small worm, 1.5-2.0 mm. long, which occurs associated with Nitella, Isoetes and Litorella, upon McDougall Bank and down to 4 m. in the bay. There are generally about 10 of them per sq. m.. Reproduction is by budding and was noticed in February and September. Slavina appendicullata is found in the same regions as V. comata but is rather less frequent. Whilst two specimens only of Pristina longiseta were taken during the survey. Both were from McDougall Bank though there seems no reason to suppose that this species does not occur/

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* Organic nitrogen content of the bottom deposits is given in Table 6. They closely follow the carbon values and have not been graphed.

occur inshore as well.

In July, 1949, 50 individuals of Chaetogaster diaphanus, a small predatory worm, were found in three samples collected from Station 1. A month later only two specimens were obtained here from a similar number of samples. None was taken at this Station before or after these dates. This restricted distribution in time is peculiar, for Borner (1922) re:ports that in Lake St. Moritz C. diaphanus is abundant in all months of the year (except November) amongst rooted vegetation at depths of 0.0 to 5.0 m.. Lehmann (1932) in his studies on the food of this species, remarks that though it will eat a variety of cladocerans, and sometimes even chironomid larvae and turbificid worms, it feeds mainly upon species of Chydoridae. Of the four chydorids I have found in Loch Lomond, one, Eurycercus lamellatus is rather too large to serve as food; two others, Camptocercus rectirostris and Alonopsis elongata are extremely rare at all times of the year. The fourth species, Alona affinis is not too large to be eaten; and has a seasonal distribution remarkably similar to that of the worm (Fig. 16). Furthermore, it resembles C. diaphanus in being much scarcer on McDougall Bank than along the shore. This points to a close relationship between these two species, probably a predator-prey relationship, which controls the seasonal distribution of the worm.

A similar seasonal distribution of A. affinis in Lake St. Moritz need/

need not impose a restriction upon the C. diaphanus population there, if the seven other chyorids (including two other species of Alona) which Borner (op. cit.) found in that lake are so distributed as to afford the worm an abundant supply of food throughout the year.

Stylaria lacustris. This worm, like Chaetogaster, shows a pronounced maximum in summer (Fig. 15). It seems to prefer an environment of sand covered with vegetation and vegetable debris and is seldom found on deposits of silt even in the presence of vegetation. It was never taken at depths greater than 7 m.. Reproduction is generally asexual, but sexually mature individuals were found in July.

Arcteonais lomondi. This species was described by Martin (1907) from specimens taken in mud at depths of 4-7 m., off Tarbet, Loch Lomond. The present survey shows that it has a wider range - namely, from the vegetation covered sandy deposits at 0.7 m. of water down to the fine silt at 13 m. (Fig. 45). It is, in fact, the only naid, besides Paranais sp., which is not confined to the vegetation covered zones of the loch floor.

Population densities on mud decrease from an average of 27 per sq. m. at 4 m. to about 10 per sq. m. at 13 m.. No specimens were found at 20 m. (Creinch Station - Map 1), and it may be presumed that the outer limit of the range of A. lomondi lies at some depth between 13 and 20 m.. On sandy deposits, however, the worm is distinctly scarcer than on mud. Thus at Station 1, in 0.7 to 2.4 m., there were 7 per sq. m., and on McDougall Bank only 4 per sq. m.. It is worth noting that Stylaria lacustris/

lacustris, a worm very similar to A. lomondi in shape and movement, has just the opposite habitat preferences; so that its maximum densities are on sandy and its minimum on muddy deposits. The two worms may occupy similar ecological niches in the two habitats.

Very high concentrations of A. lomondi were found in the sand and gravel of Station 5 when they became sexually mature in July-September; forming an exception to the normal habitat preferences of this worm, but possibly connected with sexual reproduction.

Apart from the concentrations referred to above there was no evidence of a seasonal variation in density of population. Reproduction by budding seems to occur at most times of the year.

An interesting feature of A. lomondi populations is the presence in them of many individuals lacking the proboscis so characteristic of the species. In all other respects these individuals resemble typical A. lomondi. I believe that this is because a bud separates from its parent before it has developed a proboscis. None of the many buds exa-:mined by me whilst they were still attached to their parents showed any trace of one.

Paranais sp.. This small whitish worm occurs, like A. lomondi, at all depths along the transect line from 0.7 to 13.0 m.. Densities, however, were greatest within the vegetation-covered zones (about 210 per sq. m. on an average), and fall gradually to about 120 per sq. m. at 13 m.. The outer limit of the range of this worm lies somewhere above 20 m./

20 m. (Fig. 44). On McDougall Bank densities were never more than a third of those in similar habitats along the loch margin.

Reproduction is by budding.

Eiseniella tetraedra, is confined to sandy deposits with a cover of vegetation, and has been found from the edge of the loch down to a depth of 2.4 m.. Here it has an average density of 20 per sq. m., but on McDou:gall Bank there is seldom more than one per sq. m.. Sexually mature individuals with well developed clitella were found from February to the beginning of June.

Marionina sp. (Fig. 49) inhabits the same region as E. tetraedra but extends somewhat on to mud. Thus at Station 1 (0.7 to 2.4 m.) there are on an average 140 of them in a square metre, whilst at Station 2 (4 m.) and Station 3 (7 m.) the population is only 4 and 2 per sq. m. respectively. It must be noted, moreover, that on McDougall Bank there are seldom more than a fifth as many of these worms as at Station 1, an apparently similar habitat.

Sexually mature individuals seem uncommon; 6 specimens were taken in February at Station 1.

Lumbriculus variegatus (Fig. 50). Populations of this worm are densest in the shallow weedy zone of the bay (about 90 per sq. m.) and fall gradually with increase in depth till there are just one or two per sq. m. on silt at 13 m.. Next to E. tetraedra this is the largest animal in the benthos.

Stylodrilus heringianus/

Stylodrilus heringianus, the other lumbriculid, has a very extensive range, from the margin of the loch down to a depth of at least 60 m. (Fig. 51). It is not, however, particularly abundant and, except at 4 m., is generally present in populations of about 15 to 20 per sq. m.. No marked seasonal variation in population density occurs. Large sexually mature worms were met with in April and in August. This is the only worm which is not markedly scarcer on McDougall Bank than inshore.

Peloscolex ferox is the most abundant oligochaete in the area sur:veyed and formed fully a quarter of all the worms collected. Along the margin of the lake down to depths of about 2.4 m., there are almost 540 of them per sq. m. (Fig. 47). Population density then falls rapidly with increase in depth to about 30 per sq. m. at 7 m.. Thereafter it decreases very gradually indeed; for at 60 m. there are still about 30 per sq. m. and at 180 m. the figure is probably about 15 per sq. m..[1]

On McDougall Bank the population is generally about a thirteenth of that at Station 1 where the habitat seems to be very much the same.

Clitellate individuals were found first in February, 1949[2] and then from/

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(1) Based on two quantitative samples collected by Dr. H.D. Slack in May, 1951.

(2) Though the January collections have not been included for the reasons given on p. 19 , nevertheless all animals as large as the clitellate P. ferox would have been extracted. None of these clitellate forms was present.

from April to September, 1949. Sexual reproduction must therefore occur over this long period. Water temperatures (at the edge of the loch), which had been steadily falling through the winter, began to rise shortly before February (Fig. 3); and in October, when sexual reproduction had ceased, they were much higher than in February. This suggests that a rise in temperature may by itself induce the onset of sexual reproduction at a time when the environment is much colder than it will be when sexual reproduction ceases at the end of summer. Hence the presence of the spring increase in Peloscolex populations at Station 1 near the edge of the loch, and its absence on McDougall Bank (Fig. 17) which is covered by 3-4 m. of water during this period and thus well screened from the direct effect of insolation (p. 40). On the other hand the high tempe-:ratures of summer (see p. 40) must themselves favour growth and repro-:duction. Otherwise it would be difficult to understand the presence of the second increase in population density that one finds at Station 1 (Fig. 17). If high water temperatures accelerate growth the first summer generation of Peloscolex might in a specially warm summer be able to attain maturity and reproduce itself before the low tamperatures of autumn inhibited sexual reproduction. Should this reproduction occur between September and October it would easily account for the October peak in population (Fig. 17). And it would also account for the fact that population densities of Peloscolex after the exceptionally warm summer/

summer of 1949 were two to three times as high as they were in the preceding winter.

Tubifex tubifex. Of the worms found in Loch Lomond this is the most nearly bathyphilous. It is poorly represented on sandy deposits in shallow waters, but quite numerous in silt from 4 m. downwards (Fig. 46). Average density at 4 m. and at 11 m. is about 70 per sq. m.; whilst at 20 and 60 m. there are probably 50 and 25 of them per sq. m.. Densities on McDougall Bank (about 7 per sq. m.) are as usual lower than at Station 1.

There is little evidence of a seasonal variation in population density. Sexually mature individuals were found from February to October; very small individuals from March to November.

Limnodrilus sp., resembles T. tubifex in being scarce on sandy de:posits at depths of 0.7 to 2.4 m. (average density 12 per sq. m.), and in reaching a maximum density at 4 m. (140 per sq. m.). It does not, however, reach to as great depths, for at 11 and 13 m., an occasional specimen only was found and none was ever taken at 20 or 60 m. (Fig. 48).

There is no marked seasonal variation in population density.

ARTHROPODA.

HYDRACARINA.

(Table 8, Fig. 52).

Water/

Water mites are infrequent in Auchentullich Bay, except amongst the vegetation in shallow waters, that is from 0.7 to 4.0 m. in depth. Here there are on an average 175 of them per sq. m.. Outside this zone they become rapidly scarcer with increasing depth so that at 11 and 13 m. there are about 7 per sq. m., and it is unlikely that they range much below these depths (Fig. 52). Like most other animals of Loch Lomond they are much scarcer (density about 30 per sq. m.) on McDougall Bank than they are amongst the vegetation inshore.

Reproduction seems to occur mainly in summer and populations in July and August are almost twice as great as in other months of the year.

Of 797 mites collected during the survey almost a third belonged to the species Mideopsis orbicularis Mull., a small brownish mite easily distinguished from the others by its flattened upper surface. The remaining mites belonged to thirteen different species. All are hygrobatids and are listed below.

Sub-family Aturinae:	Mideopsis orbicularis Müll.
Arrhenurinae:	Arrhenurus sp.
Sperchoninae:	Sperchon sp.
Lebertiinae:	Lebertia porosa Thor.
	Lebertia sp.
Limnesiinae:	Limnesia koenikei Piersing
	Limnesia sp.

Hygrobatinae/

Hygrobatinae:	Hygrobates nigromaculatus Lebert
	H. titubans Koenike
	H. longipalpis Hermann
Unionicolinae:	Unionicola crassipes Müll.
Pioninae:	Piona carnea Koch
	P. longicornis Müll.
	P. longipalpis Kendrovsky
	Hydrochoreutes ungulatus Koch

CRUSTACEA - COPEPODA.

(Table 8, Fig. 53).

At all times of the year, and at all depths these small animals form an insignificant proportion of the benthos. Most frequent among vegetation (about 50 per sq. m.) they occur in gradually diminishing numbers down to depths of 13 m. at least (Fig. 53). None was found at 20, 60 and 180 m.. They are as frequent on the vegetation covered surface of McDougall Bank as they are inshore. A seasonal increase in population occurs in July-September.

Of the 425 copepods captured, 11 were Diaptomus gracilis Sars, a planktonic species whose presence in the bottom samples must be considered accidental. Cyclops viridis Jurine accounted for the great majority of the/

the others, all truly benthic. *C. albidus* Jurine, *C. strenuus abyssorum* Sars and *C. macruroides* Lilljeborg were also present.

CRUSTACEA - OSTRACODA.

(Table 8, Fig. 54).

These crustaceans inhabit the vegetation covered deposits of bay shore and bank and are very seldom met with elsewhere. Only two species were found, *Candona candida* Müller - Varva and *Cypridopsis vidua* Müller. Both of them are rare, seldom more numerous than 20 per sq. m., the former preferring deposits where mud predominates, the latter those where sand predominates. As with the copepods, populations on McDougall Bank are the same as those at Station 1 inshore.

Seasonal variation in density, with a peak in summer, is most pronounced in *C. vidua* populations.

CRUSTACEA - CLADOCERA.

(Table 8, Figs. 55, 16, 18).

Twelve species of cladocerans were found. Four of these, namely *Daphnia hyalina* Leydig, *Bosmina obtusirostris* Sars, *Polyphemus pediculus* L., and *Bythotrepes longimanus* Leydig are planktonic organisms whose presence in the bottom samples must be considered accidental. Besides, they/

they accounted for 5 only of the 1,020 cladocerans captured.

The eight benthic species were:-

Family Sididae:	Sida crystallina Müll.
	Latona setifera Müll.
Daphnidae:	Simocephalus vetulus Müll.
Macrothricidae:	Ilyocryptus acutifrons Sars
Chydoridae:	Eurycercus lamellatus Müll.
	Camptocercus rectirostris Schödler
	Alonopsis elongata Sars
	Alona affinis Leydig

L. setifera, C. rectirostris, A. elongata and S. vetulus are extremely rare along the transect line, but somewhat more numerous in collections from stones and vegetation in very shallow water.

The other four species, namely S. crystallina, E. lamellatus, A. affinis and I. acutifrons constituted almost 97% of all the cladocerans in the samples. The first three of them inhabit areas covered with macrophytic vegetation and are very seldom found outside such areas. The fourth seems to prefer a bare, muddy bottom deposit. This species is chiefly responsible for the extension below the 4 m. level, seen in Fig. 55.

Seasonal variation of population density is so very marked that these/

these four species would appear to occur in summer months only. They are in fact, however, not completely absent in other seasons; for, if large enough samples are collected a few specimens can generally be found. Moreover, one specimen of A. affinis and two of I. acutifrons were taken in mid-winter even with the Petersen grab.

Nevertheless "overwintering" in all these cladocerans is generally by "winter-eggs" contained within ephippia. In each species these begin to appear in samples about the time when its population is at its peak, and continue to be found until shortly before the next summer's "flowering". Ephippia of A. affinis for example are found between July and the succeeding March; whilst its population is densest in July.

Sida crystallina spends much time attached to plant leaves and stalks by a gland on the back of its head. It is not surprising, therefore, that it is confined to weedy zones. It is found mainly from June to August, being most frequent in July, when there are almost 500 of them in a sq. m. of the Litorella carpet at Station 1, and almsot 330 in a sq. m. of the Nitella-Isoetes community on McDougall Bank.

Eurycercus lamellatus is the commonest of the species found. Maximum densities occur in August (Fig. 18), when there were over 1,100 of them per sq. m. at Station 6 and 600 per sq. m. at Station 6B on McDougall Bank. At Station 1 the population even in August is only 325 per sq. m.. Wave distrubance at Station 1 might account for this, but it is also possible that/

that the optimum habitat inshore was not found.

Ephippia, each with 3 to 6 winter eggs, are first produced in August, when the population is at or near its peak; they continued to be taken in samples till the succeeding February.

Alona affinis occurs in very small numbers except in July when there are suddenly over 1,300 of them per sq. m. at Station 1. This "flowering" comes to an end almost as rapidly, for by the next month there are not even 75 per sq. m. (Fig. 16). Ephippia, each usually containing one egg, are produced in July and are found in enormous numbers towards the end of that month (at Station 6 where Alona is ten times scarcer than at Station 1, there were about 300 ephippia per sq. m.). Thereafter they were taken in ones and twos till the succeeding February.

Ilyocryptus acutifrons. I have already mentioned that this is the only cladoceran that favours a muddy bottom deposit devoid of weeds. In August, when populations are largest, there were about 230 of them per sq. m. on the mud at Station 3 (7 m.), and less than 10 per sq. m. at Station 1. On McDougall Bank they are even rarer.

CRUSTACEA - AMPHIPODA.

(Table 8)

Gammarus pulex L. was found on and under stones in shallow water along the shores of Auchentullich Bay. Only 3 specimens were ever taken outside this/

this habitat.

This restricted bathymetric distribution cannot be related to the high oxygen stenoxybiosis which Wundsch (1922) has shown to be characteristic of the species. For water at all depths of Loch Lomond is well oxygenated even in summer beneath the thermocline. Species of Gammarus have been found to inhabit very deep areas of certain lakes. There are, for example, 260 of them per sq. m. at a depth of 37 m., and 104 per sq. m. at 42 m. in Toya-ko; and 52 per sq. m. at a depth of 155 m. in Sikotu-ko (Miyadi, 1932-3, 7). Both are deep, well-oxygenated, oligotypic lakes; but they are clearer lakes with little silt deposited at the bottom. In Toya-ko, Miyadi (op. cit.) states that "samples contained pebbles even from the deepest bottom" and that where Gammarus was found "the bottom is very often rocky". In Sikotu-ko, similarly, "pebbles may occur even at depths of 192 and 216 metres". It seems likely, therefore, that nature of bottom deposit is a factor controlling distribution. The animal seems to require a solid substratum to move and to rest. Where stones and pebbles that provide such a substratum are absent, as at all my sampling Stations, the animal is not found (except accidentally).

But in Loch Lomond even in such habitats G. pulex is never abundant. This is not to be wondered at since Wundsch (1922) has shown that in Germany, it does not occur in those streams in which there is less than about 10 mgm. calcium per litre of the water. In Loch Lomond the calcium content is only about 3 mgm. per litre.

CRUSTACEA - ISOPODA/

CRUSTACEA - ISOPODA.

(Table 8, Figs. 19, 56).

In Auchentullich Bay Asellus aquaticus L.[x] occurs from depths of a few cms. down to 4 m.. Populations are largest at Station 1 (0.7 to 2.4 m.) where they average over 950 per sq. m. and reached 1,900 per sq. m. in November (Fig. 19). Below 2.4 m. the density falls very rapidly so that at 4.0 m. there were only 30 per sq. m. and only one or two were ever found at 7, 11 and 13 m.. It also occurs in fair numbers on McDougall Bank, though it is much scarcer here than on similarly sandy bottoms in-:shore, i.e. at Station 1.

Two important questions arise out of this bathymetric distribution. First, why does the population thin out so rapidly between Stations 1 and 2 especially since A. aquaticus is found in fair numbers on McDougall Bank, which is at the same depth below the surface as Station 2? Conditions at Station 2 as regards depth, light intensity, O_2 content, pH and C/N ratio are much the same as on McDougall Bank. The Isoetes on the bank is no more profuse than at Station 2. The available food at Station 2, if/

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[x] I have not found A. meridionalis Racovitza in Loch Lomond though Collinge (1946, 21) states that this species has also been reported to occur in Scotland.

if numbers of worms and chironomids etc., may be taken as an indication, is greater than on the bank. Yet there are on an average about 190 Asellus aquaticus per sq. m. on the bank and only 30 per sq. m. at Station 2.

I suggest that the nature of the bottom deposit is the controlling factor, that A. aquaticus avoids silty bottoms and prefers sandy ones. For it is sandy at Station 1 and McDougall Bank but silty at Station 2.

Berg (1938, pp. 69-70) has found large populations of A. aquaticus down to depths of 14 m. in Esrom Lake. At 14 m. the average for the year was about 200 per sq. m.. It is important, therefore, to find (Berg, 1938, pp. 14 and 35) that though macrophytic vegetation does not extend much beyond 6.5 m. in that lake, the bottom even at 14 m. contains much sand. Beyond 14 m. silt predominates; and A. aquaticus disappears. This disappearance is not likely to be due to the low oxygen content of water in the hypolimnion of Esrom in summer. For Berg (1948, p. 76) reports that A. aquaticus occurs in fair numbers at Möellebro on the River Susaa where, due to pollution, the bottom of the river is a black mass smelling of H_2S.. At any rate it is certain that in Loch Lomond, dissolved oxygen is not the controlling factor for there is as much of it at Station 2 as on the bank or at Station 1 (Table 2).

The second striking feature is this: though Loch Lomond is oligotypic the numbers of A. aquaticus found in the shallow waters along its margin are almost as great as those in similar regions of Esrom, a typically eutrophic/

eutrophic lake. Thus the maximum at my sampling Station 1, namely 1,900 per sq. m., is not much lower than that which Berg (1938, pp. 68-70) found at a depth of 2 m. in Esrom - 2,100 per sq. m.. It is interesting to note that Brundin (1949) found even higher densities in another oligotypic lake, Lake Innaren. Here the average density at 1.5 m., about 3,800 per sq. m., is almost four times as large as the average, 1,000 per sq. m., at a corresponding depth in Lake Esrom.

Yet in deeper regions, below 4 m., both oligotypic lakes everywhere contain very much fewer A. aquaticus than the eutrophic lake. For example, there 760, 170 and 30 individuals per sq. m. at 7 m. and 200, 0, 0, per sq. m., at 14 m. in Esrom, Innaren and Lomond respectively.

Asellus aquaticus feeds on decaying vegetation (Cooper, 1925, Collinge, 1946, 20). In deep areas of these large lakes, the major part of the vegetable detritus will derive from the rain of dead phytoplankton from the waters above. The two oligotypic lakes will have much smaller amounts of plankton than the eutrophic Esrom, and therefore much smaller amounts of decaying vegetable matter. This I suggest accounts, in the main, for the differences in size of A. aquaticus populations in deep zones of the three lakes.

In the shallow areas, which are close to the margin of the lake, leaves and other plant material falling upon or carried by streams into the lake, form an important addition to the autochthonous detritus derived from plankton/

plankton and benthic vegetation, and I suspect that this allochthonous component is large enough in the two oligotypic lakes under consideration completely to mask the poorer autochthonous component. Lomond and Innaren have much forest along their shores, Esrom very little.

It has already been pointed out that a silty bottom provides an unfavourable habitat for A. aquaticus, and that bottom deposits of Lake Esrom, down to 14 m., are somewhat sandy. It may be urged that the low populations in deep areas of Lomond are due to the fine silt in these areas. There can be little doubt that this must be a contributory cause. But it cannot be the sole cause. For the surface of McDougall Bank, only 4 m. deep, is sandy and on it grow Isoetes and Nitella. It is in fact a habitat very like Station 1. Yet Asellus aquaticus is on an average not even a sixth as numerous here as it is at Station 1. If the physical nature of the bottom deposit were entirely responsible for the low popula:tions in the deep zones of Lomond, then McDougall Bank should have a population as great as that at Station 1. On the other hand if the amount of decaying vegetation is also of importance then the population of McDougall Bank is what might be expected. For it is 700 m. away from the woods along the shore and must receive very little if any allochthonous material.

Seasonal Distribution and Reproduction. Gravid females were found both on McDougall Bank and inshore in April, May, July, August and September; whilst animals have been found in copulo in April and September. But breeding/

breeding does not occur with equal intensity throughout this long period; for the population shows two peaks in density, one in September and the other in November-December (Fig. 19). These must indicate that breeding activity is especially pronounced during two periods in the long breeding season.

Examination of the brood pouches of 16 gravid females showed that the brood size (22 per female on an average) resembles that of A. aquaticus in Esrom Lake (Berg, 1938, p. 70) but is less than that reported by Janke (1924, p. 276 - 80-150 per female), by von Kaulberg (1913, p. 304 - 50-60 per female) and by Collinge (1946, 20, p. 153 - 40-50 per female).

Females found in March had no eggs in their brood pouches, whilst those found in April had well-developed embryos very near the hatching stage. It is probable therefore that the length of embryonic life differs little from the 3 to 6 weeks ascribed to it by Wesenberg-Lund (1939, p. 528). When about to hatch, embryos are much the same length as the smallest specimens found free in samples, i.e. 1mm.

Adult A. aquaticus do not attain any great size in Loch Lomond. As a rule they do not exceed 8 mm. in length, only one specimen out of a total of nearly two thousand, attaining 11 m.. Gravid females ranged from 5 to 8 mm. in length. In its small size A. aquaticus of Loch Lomond resembles that of Esrom Lake (Berg, 1938) and differs from those of Central European streams. In these males are 20 and females 13 to 15 mm. long (van Emden, 1922, p. 97). The tendency for individuals from lakes to be smaller/

smaller than those from streams has already been noted by Ekman (1915, p. 333).

INSECTA - HEMIPTERA-HETEROPTERA.

(Table 8).

The corixid bugs, Micronecta poweri Douglas and Scott and Corixa distincta Fieber,* occur in Loch Lomond. They are powerful swimmers and it is perhaps questionable whether they are to be considered as truly members of the benthos. Certainly they can easily escape capture by the bottom sampler, and this may account for the very small numbers found in the quantitative collections.

At certain times of the year particularly in July and August both species are frequently to be seen swimming in shallow water (0.0-0.5 m. deep) near the edge of the loch. Four specimens of M. poweri were taken at Station 1 and I suspect it extends as far down as the outer limit of macrophytic vegetation, i.e. about 4 m.. Both species were taken in net samples from vegetation on the surface of McDougall Bank.

INSECTA - ODONATA/

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* Nomenclature after Kloet and Hinks (1945), and China (1943). Determination by Dr. H.D. Slack, Zoology Department, Glasgow University.

INSECTA - ODONATA.

(Table 8).

Two larvae of the damsel-fly Enallagma cyathigerum Charpentier[1] were taken with the Petersen sampler from Station 2 and one from McDougall Bank. Larvae have also been collected with a net in depths of about 1 m. along the shore - amongst Litorella. It is always infrequent.

The female E. cyathigerum crawls down emergent vegetation into the water to lay her eggs (Perry, 1949). There was no emergent vegetation on McDougall Bank at any time during 1948 and 1949, but in 1949 there were two buoys anchored at Stations 6 and 6B. She could have crawled down an anchoring wire in the 1949 summer to lay eggs from one of which hatched the larvae which were captured in October 1949. Otherwise the larvae must have been transported across from inshore waters.

INSECTA - PLECOPTERA.

(Table 8, Fig. 57).

The following species[2] occurred in my collections:-

Nemoura avicularis Morton

Leuctra nigra

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(1) Determination by Dr. F.C. Fraser, Bournemouth.

(2) Determination by Miss R.M. Badcock, Zoology Department, Glasgow University.

Leuctra nigra Olivier

Leuctra fusciventris Stephens

Leuctra hippopus Kempny

Leuctra sp. (? - *L. moseleyi* Morton).

Nemurella inconspicua Pictet

Amphinemura cinerea Olivier

Chloroperla torrentium Pictet.

Of these there were twice as many *Nemoura avicularis* as all the other seven species together. It occurs from the water's edge down to 2.4 m. (Station 1) where the population is about 10 per sq. m. except during the pronounced seasonal maximum at the end of summer; in August there were more than 130 of them per sq. m.. It is very likely that Station 1 is near the outer limit of its range, and that the stony region inshore is more densely populated with this species.

Leuctra nigra has a similar range but is more infrequent. The remaining six species account for only 15% of the stoneflies collected. They appear to be even more strictly confined to the stony region near the water's edge than the two species already referred to.

In numbers the plecopterans are a very insignificant group and formed less than 0.5% of the animals collected (Table 8). The interest in the group, however, lies in the fact that living specimens have been found on silty deposits, 400-600 m. away from the stony margin of the loch which/

which is their habitat.

Thus in June, 1949 one very young specimen of Leuctra sp. (? - L. moseleyi) was found in a sample of mud taken from Station 4 whose depth at the time was 11.6 m.. And in December, 1949 a young specimen of L. hippopus was similarly found at Station 8, then about 10.5 m. deep. Both specimens were alive and active. They could not have entered the samples as contaminants from the stream as great care was taken to prevent any such accident (see Ch. II).

Stoneflies oviposit under and amongst stones at the very edge of the water, generally crawling under them to do so (Brink, 1949). I have not actually seen the way females of Leuctra moseleyi and L. hippopus lay their eggs but there seems little reason to suppose that they differ in this respect from the generality of stoneflies. In that case the two larvae referred to must have been washed away from the shore by currents and carried down to the deep silt covered regions in which they were found. A third young larva (L. hippopus) was found in November, 1949, at Station 6B on McDougall Bank. Its occurrence there must have a similar explanation and suggests a way by which the bank may periodically receive its heterotopic benthos (see Ch. VI).

INSECTA - EPHEMEROPTERA.

(Table 8, Figs. 58, 59 and 20).

The/

The following mayfly larvae[x] occur in Loch Lomond:-

Ephemera danica Müll.

Leptophlebia sp. (? - L. marginata L.)

Ephemerella ignita Poda

Caenis horaria L.

Centroptilum luteolum Müll.

Cloeon simile Eaton

Ecdyonorus dispar Curtis

Ephemerella ignita is the mayfly larva most frequently found on stones and boulders along the margin of the loch. In such situations there are about 20 of them per sq. m.. The larva also occurs, but in much smaller numbers upon the Litorella sward in shallow waters. Only 2 specimens were taken from Station 1, and that at a time when the water at this Station was only 1.3 to 1.5 m. deep.. It does not occur, even at the margin of the loch, upon pebbles or gravel. Nor does it occur upon stones and boulders if these are particularly exposed to wave action - as they are, for example just south of the wall shown in Map 1. In such situations E. ignita/

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[x] Identification of all larvae except E. dispar Curtis has been confirmed by the examination of imagines reared from larvae, or from subimagines captured whilst emerging from the loch.

E. ignita is replaced by *Ecdyonurus dispar*, whose body is much more flattened dorso-ventrally than that of *E. ignita*, and therefore probably better adapted to withstand the more disturbed conditions here. I have also found *E. dispar* larvae on the western, exposed shore of Inchmurrin, the island opposite Auchentullich Bay. *E. dispar* populations are about 20 per sq. m. in density.

Cloeon simile occurs in small numbers on the *Litorella* sward in very shallow waters. It was never taken along the sampling line.

Caenis horaria is easily the most abundant ephemerid in Loch Lomond. It occurs at depths of about 0.5 to 7 m., with maximum populations of about 515 per sq. m. on an average, at Station 2 (4 m.) where the bottom is silty and covered with scattered plants of *Isoetes lacustris*. Population densities fall as silt gives way to sand in shallower waters. But they also fall with increase in depth even though the bottom deposit becomes more silty (Fig. 59). Only one specimen was taken at each of the Stations 8 and 4 whose depth was 11 and 13 m. respectively.

Larvae of this species are especially suited for life upon fine sediments. Their gills are protected from clogging by a pair of gill-covers, especially modified for the purpose from a pair of gill lamellae. They feed upon the sediment itself utilizing the organic detritus in it (Moon, 1939, Lithgow, 1949, Weir, 1951). Weir (1951) has found that their guts contain the same components as he found in the surface layer of the /

the sediments from Stations 2-4. The oxygen content, pH, and temperatures of the water at Stations 4 and 8 are the same as those at Station 2 (Table 2). One should therefore expect the populations of C. horaria at all these three Stations to be the same. But this is not so; there is instead a sharp drop in population at depths below that of Station 2, and no C. horaria populations at all at 11 and 13 m..

In dealing with the distribution of detritus feeders like Asellus aquaticus and the worms (q.v.) I have suggested that in Auchentullich Bay the nutritive value of the detritus falls rapidly with increasing distance from the water's edge. Since C. horaria is a detritus feeder its distri:bution must depend upon the amount of food available in the bottom sediments, and will decrease in number with increase in distance from the shore. Indeed some of Weir's results (op. cit.) support this explanation. In the guts of C. horaria larvae he found the following classes of material: "algal fragments", "higher plant fragments", "brown material", "unidenti:fiable detritus", and "quartz grains". He has also examined the surface layer of sediments from my Stations 2-4, and found that the first four components decrease significantly in quantity from Station 2 to Station 4.

Though this does not prove that the quality of the food decreases, it does show at least that the quantity of the sort of food that C. horaria consumes does decrease in the sediments with increase in depth and distance from the shore.

Caenis horaria/

Caenis horaria is the only mayfly larva which is a regular inhabitant of McDougall Bank, on which there are about 40 of them per sq. m. (Fig. 20). This population is nearly one half as large as that on a similar bottom inshore, namely 100 per sq. m. at Station 1, and does not show any trace of the enormous seasonal increase produced at Stations 1 and 2 in August and September by the newly hatched larvae (the significance of this is discussed in Ch. ~~VII~~ VI). Emergence occurs during June; in this month and in July populations are minimum. In August and September the new generation of larvae appears and populations become extremely large - almost 1,600 per sq. m. at Station 1 on13/8/48, and 2,300 at Station 2 on 30/8/48. A month later populations are back to normal (Fig. 20). This suggests (i) that the laying period like the emergence period is of short duration and (ii) that eggs are laid near the margin of the loch, and the newly hatched larvae soon dispersed thence over their future habitat.

Ephemera danica is found at depths of 0.7 to about 7 m.. Along the transect line it is most abundant at Station 1 (0.7 to 2.4 m.) where the density is 33 per sq. m. on an average. This decreases to zero at a depth a little greater than 7 m..

Weir (1951) using cores about 25 cms. long obtained with a corer from the bottom of this loch, has shown that full-grown larvae from Station 2 are capable of burrowing to a depth of 25 cms., as easily in undisturbed cores from Station 4 as in those from Stations 1 or 2. Nor did/

did he find any evidence whatsoever that the finer texture of the deposit from Station 4 impeded the functioning of the larval gills. Obviously, therefore, the fine texture of the deposit does not account for the absence of E. danica larvae from Station 4, nor for their rarity at Station 3. Though Weir himself believes that it does affect the young larvae, I am not satisfied that his experiments can be taken to disprove the influence of the food factor. E. danica is a detritus feeder and I suspect that it is the food value of the detritus that is responsible for the disappearance of this species below 4 m., in much the same way as it is for that of C. horaria (q.v.).

E. danica is absent from McDougall Bank though the bottom deposit there closely resembles that at Station 1, and leads one to expect the larva. The burrowing habit of this species is probably responsible for this as it will keep the larvae from being swept away by off-shore currents and carried to the bank (see Ch. ~~VII~~ VI).

Larvae ranging in size from about 3 mm. to about 22 mm., and falling roughly into three size groups, occur at all times of the year and suggest that the larval life is at least two years long. Nevertheless there is some indication of a seasonal variation in population with a minimum in June-July and a maximum in August.

Leptophlebia sp.. This species like E. danica inhabits the margin of the loch, but it has a wider range (0.5 to 4 m.). It does not occur outside/

outside the zone of macrophytic vegetation and is most frequent at Station 1, where the carpet of Litorella is thickest.

The animal feeds on algal fragments in the detritus (Moon, 1939, Lithgow, 1949), and probably browses off small epiphytic algae too. And its distribution is no doubt related at least as much to these food requirements as to its habit of clambering about vegetation.

In very shallow ($<$0.5 m.) waters the larva becomes infrequent in spite of the presence of suitable vegetation, presumably becuase of the increased disturbance due to wave action.

Though conditions on the top of McDougall Bank must be suitable, it is not found there as a regular inhabitant. In the thirteen months of collecting just three larvae were taken at the two Stations on the bank, 6 and 6B.

Centroptilum luteolum has the same habitat as Leptophlebia sp. and its range is rather similar. It does not occur regularly on McDougall Bank, whilst in the bay it is confined to the zone of macrophytic vegeta-:tion. There are about 30 of them per sq. m. at Station 1, but the optimum habitat is probably in somewhat shallower waters. Lithgow (1949) and Weir (1951) have shown experimentally that the larva is mainly depen-:dent upon filamentous algae for its food. This must be an important factor contributing to the abundance of the larva in the 0.5 to 2.4 m. zone where cobbles and Litorella, upon which such algae grow, are found; and/

and for its rarity or absence at greater depths.

As a group mayfly, larvae are confined to a narrow zone along the shores of Auchentullich Bay (Fig. 58) - with the one exception of C. horaria which extends into somewhat deeper waters and is also found on McDougall Bank. But in spite of this restricted distribution they form an impor:tant part of the benthos; nearly 5% of all the animals collected were mayflies (Table 8). This is due mainly to the great abundance of Caenis horaria.

A NOTE ON EMERGENCE, SWARMING AND OVIPOSITION.

Emergence. For most of the mayfly fauna of Auchentullich Bay, emergence of the sub-imagines occurred at all times of the day from June to August, 1949. In E. ignita the period was somewhat more restricted: 7 to 8.30 p.m. in June and July; in C. horaria it was even more so: mid-June to the first week of July, and especially during the hour before sunrise and a couple of hours after sunset; for example from 3 to 4 a.m. on 25/6/49 and 8.30 to 10.30 p.m. on 22/6/49. Emergence was not observed in E. dispar.

Swarming. I have not met with male swarms of E. danica,* C. horaria and Leptophlebia sp.. In the other species they appear from June to August as soon as the sun has sunk sufficiently for the beach to be screened from its direct rays - generally about 7 p.m. - and remain until/

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* Described by Percival and Whitehead (1926).

until the evening begins to darken at about 8.30 to 9.30 p.m.. On dull, overcast days, of course, swarms may appear as early as 6 a.m.. Rain does not prevent swarming but all winds, except light ones, do. (As was found to be the case in E. danica by Percival and Whitehead, 1926, also).

Oviposition. This has been observed only in E. ignita. It begins as soon as the beach is screened from the direct rays of the sun - about 7 p.m. - and continues till about 10 p.m.. The females, each with a little spherical mass of eggs at the tip of her abdomen, fly to and fro over the water at a height of 10 to 30 cms., usually only from the margin of the loch to where the water is 0.5 m. deep. I have not actually seen the way the egg-mass is dropped into the water, but I have picked up so many spent females off the surface of the loch that I suspect that she alights on the water to liberate her egg-mass.

INSECTA - TRICHOPTERA.

(Table 8, Figs. 21, 60).

During the period June, 1948 to August, 1950, and especially in the summer 1949, adult caddis flies were captured, some of them flying over the loch, some flying over its shores and some by means of funnel-traps* as they emerged from the loch. The species which I found in this collection/

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* For a description of these traps see Brundin (1949).

collection of almost 1,400 caddis flies are:-

Phryganeidae:	*Phryganea* sp.
Limnophilidae:	*Limnophilus marmoratus* Curt.
	Halesus digitatus Schrank
	Chaetopteryx villosa Fabricius
Sericostomatidae:	*Sericostoma personata* Spence
	Goëra pilosa Fabricius
	Lepidostoma hirta Fabricius
Leptoceridae:	*Leptocerus* spp.
	Mystacides azurea L.
	M. longicornis L.
	Oecetis ochracea Curt.
	O. lacustris Pictet
Polycentropidae:	*Cyrnus trimaculatus* Curt.
	C. flavidus McLach.
Psychomyidae:	* *Tinodes* sp. ? = T. waeneri L.
	* *Lype* sp. ? = *L. phaeopa* Stephens
Hydroptilidae:	*Hydroptila* sp. ? = *H. femoralis* Eaton
	Oxyethira simplex Ris

It is probable that not more than twenty species are represented in the part of Loch Lomond that was studied. The seven that are referred to/

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* Determined by Miss R.M. Badcock, Zoology Department, Glasgow University.

to below are infrequent.

Phryganea sp. occurs upon the Litorella carpet in shallow waters down to about 1 m., but is probably never more numerous than 1 per sq. m.. On McDougall Bank it is even more infrequent for only one specimen was ever taken and that too after prolonged dredging with a miniature beam trawl. It is probably not a regualr inhabitant.

The gravid female climbs down emergent vegetation and attaches a ring-like mass of eggs to it, close to the floor of the loch. Some of these egg masses were collected in July, 1949 and hatched in the laboratory. Each of the first instar larvae had a tiny case composed of detritus, some of it probably torn off the jelly in which the eggs had been embedded. It maintained itself suspended almost vertically in the water by vigorous swimming movements of its legs. In short, first instar larvae of this typically benthic species are planktonic, a fact the significance of which I shall discuss later when dealing with the problem of how insect larvae reach McDougall Bank (see Ch. VI).

Halesus digitatus, Chaetopterix villosa and Goëra pilosa are typically fluviatile larvae and occur in the shallow margins (0.0 to 1 m. deep) of Loch Lomond, where the substratum is sandy or stony and is disturbed by wave action. Two specimens of G. pilosa were also taken on the Litorella carpet at Station 1. All are rare and it is not likely that densities greater than 1 per sq. m. are attained. Two other typically fluviatile forms/

forms, the tube dwelling Lype sp. and Tinodes sp. have also been found, just one specimen of each, on the boulders at the water's edge. And four specimens of the tiny cased larva Hydroptila sp. were taken at Station 1. It is probably a little more frequent between this Station and the water's edge.

The remaining larvae are as a rule somewhat more numerous, but the Trichoptera as a group are not a numerically important part of the benthos - they formed under 3% of the entire collections (Table 8). All the species are limited in their range by the outer limit of the vegetation zone, few specimens being found beyond that (Fig. 60). Oxyethira simplex, the leptocerids, particularly M. longicornis, and the polycentropids are also regular inhabitants of McDougall Bank.

Limnophilus marmoratus builds its case with sections cut from the leaves of Litorella and Isoetes plants, and occurs where these plants are found, that is down to a depth of 4 m. along the loch margin. There are generally about ten of them per sq. m. here. Though the vegetation and substratum on McDougall Bank are suitable it is not found there. This absence is significant in view of Siltala's report (1907) that the first instar larvae of the Linnophilidae do not swim, unlike those of most other trichopteran families, and it will be discussed later in Chapter 6.

Oxyethira simplex on the other hand builds an entirely silken case but is also confined to areas with macrophytic vegetation. This seems to be/

be due to its habit of crawling over plants rather than on the substratum itself, a habit which also accounts for the larger numbers of this larva found in collections made with a trawl dragged over the bottom, than of most other caddis larvae. For it is in fact one of the less numerous species and seldom occurs in densities greater than about 5 per sq. m.. It is not less common on the bank than inshore.

The two sericostomatids, Sericostoma personata and Lepidostoma hirta have very similar distributions. There are generally about 40 of each* per sq. m. at Station 1, about 15 per sq. m. at Station 2, and none at Station 3. This fall in density seems to be correlated with the fact that both of them utilise sand grains for building their cases (Lepidostoma uses plant material in addition). A soft silty substratum such as begins to appear near Station 2, can provide little of this material, and must also suffer from the disadvantage of being difficult to crawl over for a larva encased in a heavy case of sand grains.

Both species are very rare on McDougall Bank though it affords a habitat as suitable as that at Station 1. 11 specimens of L. hirta and 1 of S. personata were all that were taken there. The reason for this is probably the same as that which accounts for a similar distribution of the mayflies Leptophlebia sp. and Centroptilum luteolum (q.v.) and will be discussed in Chapter 6.

Both/

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* L. hirta is perhaps a little more numerous than S. personata.

Both show quite clearly a seasonal minimum of population in early summer and a seasonal maximum in late summer-early autumn.

I have captured imagines of Cyrnus flavidus and Cyrnus trimaculatus over Auchentullich Bay. Of the larvae some agreed with the descriptions given by Lestage (in Rousseau, 1923) and by McDonald (1950) of C. flavidus. Others did not, but showed in varying degree some of the features which Lestage (op. cit.) states are characteristic of C. trimaculatus, and serve to distinguish it from C. flavidus. It is probable therefore that larvae of both species are present in Auchentullich Bay, though this will not be known for certain until both imagines have been obtained from larvae in the loch, or until a detailed description of the C. trimaculatus larva is available.

Larvae of Cyrnus spp. inhabit silken nests which they build generally on plants. It is therefore not surprising to find that they do not occur much beyond the outer limit of the vegetation zone. Within this zone there are on an average 40 per sq. m. at Station 1 (0.7 to 2.4 m.), 80 per sq. m. at Station 2 (4 m.), and 35 per sq. m. on McDougall Bank.

Cyrnus larvae of all instars are capable of swimming rapidly for short periods of time. They do so by vigorous undulating movements of the abdomen which carry them backwards. This ability to sqim is probably not unconnected with their fairly high populations on McDougall Bank (see Ch. VI). The fact that they live in silken cases would not remove them/

them from the danger of being carried away by off-shore currents, for they seem often to leave these silken nests in search of prey.

Large and small sized larvae were found at all times of the year, and though there is some indication of a seasonal maximum in Cyrnus populations in summer, it would appear that the larval life is two years.

Leptoceridae. None of the three genera of the leptocerids present in Auchentullich Bay is outstandingly numerous; and in view of the impos-:sibility of satisfactorily distinguishing between the species of each genus with the descriptions and keys available at present (Ulmer, 1909, Lestage (in Rousseau), 1921, Hickin, 1943, MacDonald, 1950), I shall deal with this family as a unit.

The Leptoceridae occur down to depths of about 4 m., but may extend somewhat farther if the bottom remains sandy, as at Station 5 on McDougall Bank. There are on an average 60 per sq. m. at 0.7 to 2.4 m., and 45 per sq. m. at 4 m. inshore. At 7 m. an occasional specimen is all that is found. On McDougall Bank the population is about 40 per sq. m..

With the advance of summer, populations at the inshore Stations decrease to a minimum in July and August, then increase suddenly to a very pronounced maximum in September and October, before returning to the average characteristic of winter and spring (Fig. 21 - curve for Station 1). There is no reason to suppose that the fall in number is not due to the emergence from the loch as winged adults of the previous winter's generation of/

of larvae; or that the sudden large rise is not due to the hatching from eggs laid by these imagines of the succeeding generation of larvae. It is therefore remarkable that whilst the population of McDougall Bank clearly shows the summer fall, it does not show the sharp increase that follows this fall at Station 1. Instead, the population on the bank merely rises gradual-:ly to the size characteristic of winter (Fig. 21 - curve for McDougall Bank). This must indicate that whilst the larvae of the bank emerge as and when they do inshore, they do not return in the same manner. That is to say, they are not hatched on the bank from eggs. I have been led by other studies, described in Chapter VI, to suggest that the larvae are transported to the bank by water currents. If this suggestion is correct, then the variation in population density on the bank, is just what one might expect - a gradual fall in summer as the larvae metamorphose and emerge from the loch, followed by a gradual rise as some of the new genera-:tion of larvae produced inshore are transported to the bank.

NOTES ON THE SWARMING AND OVIPOSITION OF CADDIS FLIES AT AUCHENTULLICH BAY.

Observations were made on the behaviour of these insects in ths summers of 1949 and 1950. In 1949 I lived at the Field Station on the shores of Auchentullich Bay from mid-June to mid-September and the observations were therefore much more detailed than those made in 1950, when I spent only 39 days/

days there during the three months June-August. Though the conclusions I have drawn are still tentative it will be seen that they have been based upon a fair amount of field work.

Identification of swarms was verified by actual capture and examination of members of the swarm.* Upon capture each insect was transferred from the net to a 3" x 1" tube of glass. On the cork stopper of each tube was marked the serial number given to the note in the Field Notebook regarding the capture. In the case of female insects a 3" x 1" strip of blotting paper was inserted into and pressed against the side of the tube. Just enough water to keep the paper sodden was then added. Experience had shown that in such conditions a female ready to oviposit when captured, would lay her egg mass upon the moist blotting paper. She did this as a rule within 6 hours after insertion into such a 'culture' tube. Nevertheless no females were killed and preserved until at least a further 24 hours had elapsed. All those which had not laid their eggs by the end of this time were classed as not ready to oviposit, and therefore not likely to be on their ovipository flight when captured. I am aware this method of dividing the females into those about to lay, and those not so prepared, is open to objection on many counts. It was however the only one that the/

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* Over 400 caddis flies were thus captured and identified.

the circumstances in which these observations were made, gave me time to adopt.

Light and temperature measurements - light in arbitrary units - were made at regular intervals. Extent of cloud cover, conditions of wind and rain were also noted.

It must be pointed out that Auchentullich Bay faces east. It there:fore receives the rays of the morning sun but is screened by the woods and the hills behind them, from the rays of the setting sun.

Flight in swarms generally occurs when the air temperature is above 13°C., though single specimens were found flying when the air temperature was as low as 8.4°C.. A glance at the graph of daily variation in air tem:perature (Fig. 4) shows that swarming should therefore be possible at any time of the day except for a short period between about 1 a.m. and 7 a.m..[*] No upper limit of air temperature has been found for swarming. <u>Mystacides azurea</u> swarms have been found at noon when the temperature was 21.8°C.. <u>Leptocerus bilineatus</u> swarms were found at 22°C.: a temperature which is just 3 below the maximum recorded in the hot summer of 1949. Nevertheless swarming generally occurs even for diurnal species after 7 p.m. in the evening. Thus <u>M. azurea</u> generally swarms between 8.30 and 10.15 p.m. in July and between 1.30 and 9.15 p.m. towards the end of August.

There are two reasons for this: 1) for diurnal species like <u>M. azurea</u> or/

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[*] These and all subsequent indications of time refer to Greenwich Mean Time.

or Leptocerus bilineatus etc., observation shows that it is essential that the direct rays of the sun do not fall upon the insect. From this it follows that on cloudless days or days with very little cloud, swarming cannot occur till the bay is screened from the diráct rays by the woods and hills behind it. This happens after 7 p.m. in June and July, and the swarms then form over the shadowed waters near the shore. On days when there is an extensive or complete cloud cover, the swarms begin to form early in the morning, as soon as the air temperature reaches the value of 13.0°C.. On 20th July, 1949, for example, this happened at 7.15 a.m. and within 15 minutes, swarms of M. azurea were found dancing over the water. They continued throughout the day, disappearing only at about 9 p.m. when light became too poor. On many occasions it was observed that such swarms disappeared as soon as the cloud cover moved away from the face of the sun, or even thinned sufficiently for the sun to be seen clearly through it. This behaviour of M. azurea and other diurnal-swarming caddis flies in the field is very like that which Gibson (1942) found to characterise the chironomid Spaniotoma minima in the laboratory.

2) The other reason why swarming is restricted to the late evening operates in the case of the crepuscular species like Mystacides longicornis. These, in addition to having a minimum air temperature below which swarming does not take place, have also a limit of light intensity above which swarming does not take place either. Thus M. longicornis requires very/

very weak light intensities; in arbitrary units these intensities fall between the limits 0 to 45, where 500 represents the brightness of a clear July day at about 6 p.m.. At these intensities the reading of an ordinary printed page was difficult. In July such intensities generally occurred between 9.30 and 10.30 p.m., i.e. about $1\frac{1}{2}$ hours after sunset; and between 2.30 and 3.30 a.m., i.e. about 1 to $1\frac{1}{2}$ hours before sunrise. Swarming occurred in the evening period since temperature then was also suitable, but not within the morning period since the temperatures were then too low - this being almost the coldest time of the 24 hours in summer (Fig. 4).

One other factor was found to influence swarming importantly and indeed flight of any kind. This was wind strength. Complete calm, or very gentle breezes, alone permit swarming or oviposition. I have unfortunately not been able to measure exact wind strengths, but it is a near enough estimate to say that wind strength above 1 on the Beaufort Scale prevents swarming and oviposition. North-easterly winds blowing into Auchentullich Bay often leave little pockets of calm over the water along the edge of the woods. These pockets of calm are clearly marked by an absence of ripples, and over them caddis flies swarm whilst just outside the pockets where conditions are otherwise exactly the same, no swarming occurs. The pockets themselves seem to be the result of the air current rising upwards to clear the barrier of trees, and one often sees a rather stronger gust sweeping the fluttering insects before it into the woods. As soon as the gust/

gust is spent the swarm returns to dance over the pocket of calm.

The water surface over which swarming or oviposition occurs may be either calm and flat or covered with ripples or even waves. These do not prevent swarming if they are not accompanied by unfavourable winds.

Drizzle and rain of the type generally met with in Scotland does not prevent swarming or oviposition. Heavy rain did fall on a number of occa:sions but was generally accompanied by strong winds so that it is impossible to say what the effect of heavy rain alone might be.

Oviposition in the case of both diurnal and crepuscular species is at dusk and later. The conditions of wind, rain, and waves which are necessary for swarming, are necessary here also. Air temperatures when oviposition occurred varied between 15.1 and 20.8°C..

Though gravid females have been observed and captured at great distances from the shore, they are rare here and are most numerous over the shallow inshore waters. Oviposition seems to be more or less confined to this region. Evidences for this view I ~~have already~~ shall discuss~~ed~~ in another section of this thesis (Ch. VI), and shall not recount here. The factors respon:sible for this restriction of the laying zone were not discovered; but it seems quite likely than an important one is time. As the gravid females move out of the woods towards and over the loch, most of them will lay within a short time of their reaching water. Fewer and fewer will have the time to move farther out over the loch before they have to lay. The assumption/

assumption here is that a gravid female is unable except perhaps within relatively narrow limits, to control the time of her laying. I believe this is not an unwarrantable assumption since a number of captured females have laid within a few minutes of being introduced into glass tubes - though in each case the tube was so dry that she was unable to free herself from the extruded egg mass, which stuck to her and to the wall of the tube, binding her helplessly to it. But whatever may be the real reasons for this restriction of the laying zone, its existence is a further reason for the well-known fact that of two similar lochs that which has the longer shore line is the more productive.

Mystacides azurea. This species first appears at the end of June or the beginning of July (3rd July in 1949 and 25th June in 1950). It is most abundant in July and early August, after which it seems to become scarcer so that by mid-September very few are present.

As has already been mentioned the male swarms appear when conditions are suitable, about 8.30 p.m. in July. As the season advances this time gets earlier, till late in August swarming begins at about 7.30 p.m..

The swarm consists of immense numbers of males, each performing a little skipping dance at a height of 6 in. to 1 ft. above the surface of the water. The swarm extends from the water's edge outwards over the loch for a distance of about 15 m.; so that at the outer limit of the swarm the insects are dancing over water 4 to 5 m. deep. As the evening gets later/

later, the swarm becomes less dense, by members leaving it. In addition, its outer edge seems to draw steadily inwards closer to the shore, until ultimately at about 10.15 p.m. in July, (9.15 p.m. in late August) the swarm has completely disappeared. This behaviour I believe follows from the habit M. azurea has of using solid objects above the water surface - trees, emergent aquatic vegetation, the beach, etc. - as landmarks in order to maintain a relatively constant position whilst performing its skip-dance. It does change this position from time to time, but only in order to reach and maintain some new position. I believe that these landmarks are detected by means of sight. For when a boat is rowed through a swarm of M. azurea it "collects" a retinue of insects from the swarm. These alter their landmark to the boat passing near them, and whilst maintaining a constant position relative to it, are taken out of the swarm when the boat passes beyond it. Another fact pointing to the use of landmarks is the difficulty one meets with in attempting to capture insects from a swarm; especially if one approaches the swarm slowly. After one is within about 2 m. of the swarm, each additional step forward makes the whole swarm in one's vicinity retreat an equal distance backwards. The observer has himself become a landmark. The only way then of effecting a capture is to make a sudden lunge at the swarm with a long-handled net.

As the light becomes poorer with the advance of the evening, the insects have to move nearer and nearer to the shore to keep these trees in sight. Hence the inward movement of the swarm each evening.

A/

A train of waves moving inshore gradually displaces the swarming in-:sects backwards towards the shore. After the insects have been carried back some distance they fly forward to regain their lost positions. This happens as long as waves are moving inshore. It seems to indicate that though the insects maintain a constant position relative to some object on the shore, the water surface is also observed, and a train of waves in it tends to disturb that position, gradually displacing the insect till it is out of alignment with its landmarks. The forward flight then occurs to bring the landmarks into position once more.

I have not been able to gather any evidence that the bottom of the loch is kept under observation through the water. What evidence there is points to the opposite conclusion. Thus the attendant insects collected by a boat rowed through a swarm of M. azurea, have been taken out to positions where the loch bottom was 13 m. below the water surface (at Station 4). Here they have continued to perform their swarming dance although the bottom could not have been observed by them.

They have also followed a boat out to McDougall Bank, a fact which proves that the bank is not beyond the flying range of these insects. Yet natural swarms of M. azurea were never observed over McDougall Bank, although the bottom here is covered by 2 to 4 m. of water, whilst off-shore, insects swarmed over waters 4 to 5 m. deep. From this it is evident that depth of water does not limit the outward range of the swarm. Nor does light/

light itself. For as the evening gets later, suitable light conditions - intensity and absence of direct rays of sun - are found farther and farther out towards the centre of the bay. And I have already mentioned that swarms "attendant" upon a boat can be taken far beyond the normal limits of the swarm and will continue to swarm in these new positions.

All this points to the conclusion that the outermost limit of the swarm is the maximum distance from which the swarming insects can keep landmarks on the shore in view.

It also explains why swarms of M. azurea have never been found dancing over McDougall Bank even when all the conditions favouring swarming have been present there; for insects moving out of their resting places within the woods are "trapped" within a relatively narrow band along the shore by their sighting habit. They are never found beyond this zone except when they have been detached from the swarm and blown out over the loch by gusts of wind. Such specimens, flying vainly shorewards and carried in the opposite direction by the wind have been observed on several occasions over McDougall Bank.

The female M. azurea enters the swarms from time to time; and as far as I have been able to make out seems to join in the dance - performing the same sort of movement as does the male - until a male successfully unites with her. The mated pair, both members pointing in the same direction and both flying, leave the swarm, moving upwards and shorewards. Within a few seconds they are generally lost to view as they gain height. From/

From the circumstance that I have once found a pair completing the copulatory act whilst resting upon a door of the Field Station hut, I presume that these mated pairs which leave the swarm make for a resting place in the trees and there complete the copulation.

Relatively few of the females captured showed, by laying in the 'culture' tubes, that they were about to oviposit. These were found in very poor light (arbitrary units: 0 to 90) after the male swarms had disap-:peared, that is between 9.30 and 10.30 p.m.. It seems very probable that in this otherwise diurnal species oviposition occurs at dusk or, even later, at night. Support is lent to this view by the fact that of four females (in a light trap) captured during the night of 22nd August, 1941,[x] three were spent, having laid their eggs beofre capture, whilst the other laid her eggs immediately after capture.

In ovipositing the female dives from a height of about a metre on to the surface of the water. Here she rests for about a second before flying off. She does this a number of times before a spherical egg mass is extruded at the tip of the abdomen and is washed into the water. The pre-:liminary contact with the water provided by this succession of dives seems in some way necessary for the extrusion of the egg mass, though I am unable to/

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[x] This trap was set up by Mr. W.W. MacDonald, and I must thank him for letting me examine the caddis flies captured.

to suggest what function it serves.

Nor am I able to say how long a period has to pass after copulation before the female is ready to lay. The single female I captured immediately after she had finished copulation, did not lay in the culture tube though she was kept in it for three days before she was killed. When eggs are laid it is generally done within 6 hours of the female's being introduced in:to the tube. But though the behaviour of this female might indicate a fairly long period between copulation and oviposition, I hesitate to draw such a conclusion from a single instance.

I wish finally to draw attention to a case of aberrant laying in this species. The 30th July, 1949 had been heavily overcast with cloud and there had been a steady drizzle all day. At about 8.30 p.m. I went to the datum pole to take a reading of the loch level. This is a wooden pole painted white, and on the evening in question was wet and completely sur:rounded by the waters of the loch. The entire pole was dotted over with caddis egg masses - there were at least half a dozen of these to every foot of pole-length. Also on the pole were several female M. azurea, and a much smaller number of Sericostoma personata and Oecetis lacustris. The egg masses, of which the majority resembled those of M. azurea, were firmly stuck to the pole. Why these females had laid upon this pole when all around it was water suitable for laying in, and when other conditions were also suitable for oviposition, is difficult to understand. In the dull/

dull wet condition of that evening, the pole was brighter than either the sky above or the water around it. Whether this was in any way connected with the aberrant laying or not is uncertain.

Leptocerus cinereus, L. dissimilis and L. bilineatus though not observed in as great detail, seem to behave, in essentials, like M. azurea. Unlike the mated pair of M. azurea, the male alone of L. cinereus flies, dragging the female behind him, and she points in the opposite direction.

Mystacides longicornis was found from the beginning of July to the beginning of September in 1949. It is most abundant in July.

Whether singly or in swarms, the males appear in very poor light (arbitrary units: 0 to 40) about half an hour after the disappearance of the swarms of M. azurea, i.e. between 10.30 and 11.15 p.m. in July. Air temperature is always over 13.0°C., generally between 13.6 and 16.7°C. at times of swarming. Swarms are not very extensive, and in them the insects seem to dance up and down almost vertically, over a distance of a few inches. It is noteworthy that such swarms have been met not only inshore, but also over McDougall Bank and at Station 4 over water almost 13 m. deep. It seems as though this species, swarming as it does in very poor light, is not restricted to a narrow band of water near the shore, but can and does range widely over the loch. The swarms I observed gathered near the boat and may have been using it as some sort of landmark for purposes of orientation. But I am not in a position to suggest how the boat was kept under/

under observation.

Very few females of this species were captured, but all of them were found at about 10.30 p.m., i.e. in very poor light (arbitrary units 0 to 4). Some of these laid egg masses in the culture tubes and since no females were ever seen to oviposit in good light, I feel it is safe to conclude that M. longicornis oviposits at dusk or after.

Lepidostoma hirta. No males of this species were ever observed to swarm over the loch, or near it. In fact only one male was captured, and this was very probably a newly emerged specimen. I captured it over McDougall Bank at 4.40 a.m. G.M.T. on 7th July, 1949, i.e. about half an hour after sunrise, and in very bright light.

Females of this species were found from mid-June to mid-July, in very poor light (arbitrary units 0 to 10) between 10.30 and 11.30 p.m.. Most of them were about to lay (and did lay readily in the culture tubes) and were captured over the water's edge. A very few were found farther out, even as far as Stations 4 and 6, but I am not certain whether these had been blown out accidentally or had been ranging as far out of their own accord. As with M. azurea, the female dives a number of times on to the water before the egg mass is extruded from the abdomen.

Sericostoma personata behaves like L. hirta except that the females appear to lay a few minutes earlier in the evening.

Oecetis lacustris. 75 of the 116 caddis flies captured by a light-trap/

trap* on 22nd August, 1947 were of this species, 32 females and 43 males. The species is found mainly in August. Males are definitely nocturnal, appearing after complete darkness has set in, i.e. after 10 p.m.. They were attracted to light in ones and twos and though I am unable therefore to say that swarms do not occur, it does not seem likely that they do.

Females are similarly nocutrnal. And since 23 out of the 32 females captured by the light-trap on 22nd August, 1947 were spent, it seems probable that oviposition occurs during the hours of darkness. Neverthe-:less, I have also observed females flying along the edge of the loch between 7 and 8 p.m. G.M.T., when there was still much light (arbitrary units 180 to 300). Five of these were captured and three of them laid eggs in the culture tubes. This seems to show that oviposition may occur in the evening as well.

By way of conclusion I wish to draw two generalised inferences from these observations. The first is that bright sunny summer and a windy one will both of them have an unfavourable influence upon the productivity of a loch: the one by reducing the amount of time spent on swarming, and thereby the number of successful copulations, the other by reducing the number of ovipositing flights. Both will tend to reduce the total number of eggs laid. Other things being equal, this will mean a smaller number of/

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* See footnote on p. 91.

of caddis larvae in the benthos during the succeeding autumn-spring than after largely overcast but calm summer. There will in short be a reduction in the productivity of the loch. Whilst my observations on other insects, e.g. mayflies (see Ch. 3) and chironomids, are scanty. I am inclined to believe that these will in general be affected in much the same way as are the caddis flies.

The other inference follows from the fact that trees along the edge of Auchentullich Bay provided areas of calm shadowed water by their screen-:ing effect upon the sun's rays and upon the wind. In these areas swarming and oviposition occurred even when conditions elsewhere were too bright or too windy. The growing of woods along the margins of a lake is therefore a means by which we may modify and counteract the unfavourable weather conditions referred to earlier, and thus increase the productivity of a lake.

INSECTA - COLEOPTERA.

(Table 8, Figs. 22, 61).

In the following list* of the beetles of Auchentullich Bay the letter "A" indicates that imagines have been found and the letter "L", larvae/

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* All identifications are due to Mr. R.A. Crowson, Zoology Department, Glasgow University.

larvae:-

Haliplidae	Haliplus ruficollis Degeer	A.
	* H. variegatus Sturm	A.
	* Haliplus sp. (? H. lineolatus Mannerheim)	A.
Gyrinidae	Orectochilus villosus Müll.	A.
Dytiscidae	Platambus maculatus L.	A, L.
	Deronectes duodecempustulatus Fabric.	A, L.
	* Hygrotus novemlineatus Stephens	A.
Elmidae	Riolus cupreus Müll.	A, L.
	Esolus parallelopipedus Müll.	A, L.
	Latelmis volkmari Panzer	A, L.
	Limnius tuberculatus Müll.	A, L.
	Elmis sp.	L.

All these were infrequent except Limnius tuberculatus which formed about 94% of the 838 beetles collected along the transect. Only a few specimens of each species of Haliplus, Riolus, Esolus, Elmis and Hygrotus were taken. The haliplids and Hygrotus occur in very shallow water, 0.0 to about 0.3 m. deep, upon substrata of cobbles and Litorella. Riolus and Esolus extend somewhat further out, at depths of about 0.7 to 4 m., where/

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* These specimens were collected by Mr. F. Sinclair, Glasgow.

where *Litorella* and *Isoetes* grow. The single *Elmis* sp. larva curiously enough, was found at Station 2 (4 m.) though it is a fluviatile genus.

Orectochilus villosus. This species is confined to the very edge of the loch. The adult spends the day beneath cobbles and boulders, and comes out after dusk in search of prey. It is gregarious and may be quite numerous where the substratum is suitable. Larvae were not found, pro-:bably because they also are rather localised in their distribution. Berg (1938) reports finding them in Esrom Lake at depths of 0.1 to 0.4 m. where the substratum was pebbly.

Platambus maculatus occurs in shallow waters, 0.0 to 0.5 m. deep, on a substratum of stones, sand and *Litorella*. There are probably about 1 or 2 of them per sq. m.. Larvae extend to somewhat greater depths than the adults, a few specimens having been taken at depths of 2 to 4 m..

Deronectes duodecempustulatus seems to occupy much the same habitat as *P. maculatus* but is somewhat more abundant - about 10 larvae per sq. m.. The adults are very rapid swimmers and were seldom captured with the Petersen sampler. Egg-laying must begin very early in the year for an egg was collected from the mud of Station 2 on 22/4/49. Embryogeny was well advanced and the larva emerged in a fortnight. Nevertheless larvae were most frequent in July and August.

Latelmis volkmari. About 20 of these larvae occur per sq. m. of the *Litorella* sward at depths of about 0.5 to 2.4 m.. None was found at Station 2 nor on McDougall Bank. The adults are infrequent and though also/

also occurring on the *Litorella* sward are confined to that part of it which lies in shallower waters, i.e. above 0.3 m..

Larval life probably lasts for more than a year for both large and small larvae were found at all times.

These larvae have their legs adapted for crawling over and clinging firmly to the stems and leaves of aquatic plants and are unable to make any progress upon silt. It is therefore worth noting that a single speci:men was collected from the silt at Station 3 in August, 1949; for this seems to indicate that these larvae are sometimes carried out of their habitat by off-shore currents.

Limnius tuberculatus. Like *L. volkmari*, larvae and adulst of this species seem to be adapted for crawling about and clinging to plants like *Isoetes* and *Litorella*; and are found in Auchentullich Bay wherever these plants grow. Between 0.7 and 2.4 m., where *Litorella* forms a closely packed carpet or sward, there are about 370 larvae and 12 adults per sq. m.. As with increase in depth, the *Litorella* carpet gives way to scattered groups of *Isoetes*, the species becomes less frequent and at 4 m. (Station 2) there are only 15 larvae and perhaps one adult per sq. m.. On bottom deposits without macrophytic vegetation the species does not occur as a member of the benthos (Fig. 61).

Nevertheless in the thirteen months of collecting a very few larvae were obtained from such places: one from the mud at Station 3 (7 m.), one/

1 in each of four months from the mud at Station 7 (7 m.) and 1 in each of two months from the silt at Station 8 (11 m.).

Limnius tuberculatus is a regular inhabitant of McDougall Bank, on the vegetation of which there are on an average about 70 larvae and 3 adults per sq. m.. Since the adults are there, the occurrence of the larvae of this insect on the bank does not present one with a problem re:quiring special explanation. But the fate of the larvae themselves is somewhat puzzling. For pupation in this species usually occurs in a little chamber built by the larvae on the beach, above water level; and unless the larvae of McDougall Bank can get to the beach when they are ready for pupation they must all perish. Since the larvae cannot crawl across, it is suggested that they are able to float up to the surface of the loch when ready to pupate and are transported to the beach by surface water currents. This difficulty of reaching the edge of the loch must also confront many of the inshore larvae, those living at depths of about 4 m. where a clump of Isoetes is often surrounded by a patch of bare mud; and the method by which the McDougall Bank larvae reach the beach is pro:bably common to all Limnius tuberculatus larvae.

SEASONAL VARIATION.

Numbers of larvae decrease from January to a minimum in May, and then increase to a maximum in December and January (Fig. 22) - curve for Station 1) consistent with larvae leaving the loch to pupate. and the appearance of a new generation

It is worth noting that in this respect the population on McDougall Bank/

Bank behaves in the same way as that inshore; a resemblance which is in marked contrast to the divergence in behaviour of bank and inshore popula-:tions of insects like Caenis horaria and the leptocerids (q.v.) during those months when the new generation begins to appear.

INSECTA - DIPTERA - EMPIDIDAE.

(Table 8, Figs. 23-25, 62).

Larvae of the empid Hemerodromia sp.* are quite common in the margin of Auchentullich Bay. They have a set of powerful claws upon each of their prolegs and in the laboratory crawl over plants but seem to be quite help-:less upon silt. It is not surprising therefore that their populations are largest where macrophytic plants are numerous - for example, about 120 per sq. m. on the carpet of Litorella at depths of about 0.7 to 2.4 m.; and about 90 per sq. m. at Station 2 (4 m.) where Isoetes and Nitella occur only in scattered clumps. Outside the zone of vegetation, numbers must fall very rapidly for at a depth of 7 m. at Station 3 the samples seldom yielded more/

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* Imagines I reared from these larvae resembled H. oratoria Fallen (see Lundbeck, 1910), but in the absence of a complete key for the British species of this genus, I cannot ascribe them to this species.

more than 1 specimen per month, often none at all (Fig. 62). If the presence of these is not accidental and due to their being washed away from the vegetation zone by currents, then some movement upon an undisturbed mud surface at depths of 4 to 7 m. in the loch must be possible despite their behaviour in the laboratory.

Though the conditions on top of McDougall Bank are suitable Hemerodromia is not a member of the benthos there.* This absence indicates a) that the gravid females of this species do not detect McDougall Bank nor lay their eggs thereon; and b) that though the larvae, well adapted as they are for clinging to vegetation, may sometimes be carried away from the in:shore vegetation by currents, their complete inability to swim mitigates against their being transported over long distances; and therefore pre:vents them from populating McDougall Bank to any significant extent.*

The seasonal variation in population density of Hemerodromia sp. is remarkable in that the summer maximum does not succeed but is followed by a minimum (Fig. 23). An enumeration in the monthly collections from Stations 1 and 2, of small larvae on the one hand, and of pupae and mature larvae on the other, showed that the proportion of the latter in the collection increases during summer to a maximum of 100% in July, and then falls, as emergence of the adults occurs, to zero in October-December. Whilst/

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* In 156 samples collected during thirteen months from the bank Stations 5, 6, 6B and 7, just 3 specimens were found.

Whilst the proportion of small, i.e. recently hatched larvae increases from the end of summer to a maximum of 88% in October, and then gradually falls to minimum values of zero in the succeeding spring and early summer (Fig. 25). This sequence is what usually occurs in the larval populations of the loch. An unusual feature here, is that in addition to the increase in proportion of pupae and mature larvae, there is a very large simultaneous increase in the total population itself. This increase is not due to the new but to the old generation of larvae (Fig. 23, 24). It is not clear why this should happen though there is some evidence which suggests that mature larvae when nearing pupation migrate shorewards in summer. As this migration goes on they will accumulate in the shallower regions of their habitat, and thus produce the increase in density noted above. The evidence referred to resides in the fact that the summer maximum is reached at Station 2 in 4 m. of water at least one month before it is reached at Station 1 in about 2 m. of water. And that when the population at Station 1 is at its maximum in July, that of Station 2 has fallen very near to its minimum (Fig. 24 - curves for mature larvae and pupae).

In the case of the small larvae on the other hand the situation is just the reverse. Their maximum density is reached at Station 1 about two months before it is reached at Station 2 (Fig. 24 - curves for small larvae). This suggests that in addition to the shoreward migration of the mature larvae, there is an outward migration of the newly hatched larvae.

Migration/

Migration of this sort is not unknown in benthic animals; Wesenberg-Lund (1912), Lundbeck (1926), Lang (1931), Miyadi (1931-2, 2) and Berg (1938) for example, have detected several instances of it, and have speculated about the probable stimuli involved, particularly in the initiation and directional control of the shoreward movement. But in none of these instances do we have a clear understanding of the process; indeed we often do not even know how the movement itself occurs. Thus Berg (1938) assumed that the shoreward migration of ceratopogonid larvae occurred on the lake bottom, but my observations (Weerekoon, in press) suggest that it takes place at or near the surface of the lake.

Unless one makes the unreasonable assumption that gravid females of Hemerodromia lay closer to the shore at the beginning of the laying season, and farther away later in the season, then the fact that newly hatched larvae reach their maximum earlier in shallower waters and later in deeper waters, must indicate not only that there is an outward migration of these larvae, but also that eggs are not laid all over the region that will later be inhabited by the larvae hatching from these eggs. Thus the presence of larvae in any suitable habitat is no indication that ovipositing females have detected that area or laid eggs over it. This conclusion affords strong support to my view that in general the heterotopic species of the McDougall Bank benthos do not reach it in the egg-stage (see Ch. VI).

Emergence of the adult has not been observed. The pupa is motionless save/

save for an occasional and slight bending of its body. It is also provided with 8 pairs of very long slender tracheal filaments which project from its sides. Even if the pupae could wriggle these appendages would greatly hinder progress. Yet healthy pupae from which imagines have subsequently emerged have been collected from depths of 0.7 to 4 m.. Though I have reared a number of adults from pupae I have not been fortunate enough to observe the act of emergence.

It is tempting to suppose that as in the Ceratopogonidae (Weerekoon, in press) Hemerodromia larvae pupate outside the loch - upon damp stones and debris; and to explain the presence of pupae in samples from Stations 1 and 2 as due to pupation of larvae subsequent to the collection of samples - in the period when the sample, washed and incompletely covered with a thin layer of water, awaited attention in the laboratory. But this could not have happened in June, July and August, when each sample was examined im:mediately it was collected. Pupation must therefore occur within the loch, and often beneath considerable depths of water; and the problem of how the adults reach the surface of the loch remains.

INSECTA - DIPTERA - CERATOPOGONIDAE (HELEIDAE).

(Table 8, Figs. 63, 64, 65).

Satisfactory keys for the identification of most ceratopogonid larvae are/

are not available, but it has been possible by the examination of imagines reared from larvae and pupae from the loch to find the following general and species[*] and to distribute most of the collection of 895 larvae amongst them:-

Dasyhelea sp. (? = *D. holosericea* Meigen)
Culicoides cubitalis Edwards[**]
Stilobezzia sp. (? = *S. ochracea* Winnertz)
Palpomyia quadrispinosa Goetghebuer
Bezzia sp. (? = *B. ornata* Meigen)
Johannsenomyia sp. (? = *J. nitida* Macquart)
Probezzia venusta Meigen

Dasyhelea sp.. This rather sluggish larva is a regular though rare member of the benthos of Stations 1 and 2. There are here about 5 to 8 of them per sq. m., but it is possible that in shallower waters, i.e. less than 0.7 m., populations may be a little greater. None has ever been found at depths greater than 4 m., a fact which may be due to the food preferences of the larva. For members of the genus seem to feed upon filamentous and unicellular/

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[*] Nomenclature after Kloet and Hincks (1945).

[**] Mr. D.S. Kettle and Dr. J.W.H. Lawson of the Zoology Department, Glasgow University, identified the imago and the larva respectively of this species.

unicellular algae (Mayer, 1934b, Lawson, 1951, and Thomsen, 1937) and should therefore be confined to the relatively shallow region of the loch (0 to about 5 or 6 m.) into which sufficient light penetrates for these to grow.

Dasyhelea does not occur on McDougall Bank, an absence very probably due to the fact that the animal is a burrower in mud and hence little liable to be washed away from the shore by currents (cf. E. danica).

Stilobezzia sp.. This species is almost uncommon in the loch. A single pupa was found in a sample taken in July, 1949 from Station 1 which was at that time 0.8 m. below the surface. This particular sample had had to wait for some hours before I found the time to examine it and there is little doubt that pupation occurred during this period. It was upon the imago reared from this pupa that the determination of the genus and species was made. Since, however, I had not seen the larva from which the pupa emerged, I have been unable to distinguish any more of this species in my collection; and it is very likely that some of the larvae placed under the group "others" belong to it.

Culicoides cubitalis Edw. is found at depths of 0.7 to 7 m., but more frequently in the shallower than in the deeper portions of its range. The population decreases from an average of nearly 35 per sq. m. at Station 1 to only 4 per sq. m. at 7 m. (Station 3). No larvae were ever found at greater depths (Fig. 64).

Members of this genus feed upon detritus* (Lang, 1931, Mayer, 1934a and

b/

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* Thomsen (1937), however, states that it is carnivorous.

b) and it is interesting to note the resemblance between the distribution of *C. cubitalis* and that of the mayfly larva, *E. danica* (q.v.), another burrowing, detritus feeding species. For it suggests that in *C. cubitalis* also the main factor controlling its bathymetric distribution is the rapid decrease in the nutritive value of the detritus in the bottom deposits, with increase in depth.

Only 3 specimens were taken on McDougall Bank in all the thirteen months of sampling, a fact which fits in well with my suggestion (see Ch.VI.) that insects do not generally lay their eggs over the bank and that of the larvae which are restricted to shallow regions of the bay, only those which are specially liable to be carried by currents from their habitats inshore will be found in significant numbers on the bank.

C. cubitalis like most ceratopogonids can swim rapidly but does not do so if there is mud for it to burrow into (cf. Lawson, 1951 on *C. nubeculosus*). It will therefore be exposed only very rarely to the action of these currents.

Larvae of *C. cubitalis* have hitherto been reported from marshy habitats (Kettle and Lawson, ~~in press~~ 1952), and this is the first report of them from a loch. For though there are many references in limnological literature to the existence of *Culicoides* in lakes (e.g. Brundin, 1949, Valle, 1927, Järnefeldt, 1925, Lenz, 1923, Thienemann, 1920, and Reith, 1915) none of them states what the species concerned is. Thus Brundin (1949) merely refers to them as larvae of the "*Culidoides-nubeculosus* group", and Lang (1931)/

(1931) refers to "Culicoides sp.". It may be noted in passing that all these investigators found the larvae to inhabit in the main the shallow vegetation covered margins of the lake, and to be less frequent in the up:per part of the aphytal zone. The distribution of C. cubitalis in Auchentullich Bay, Loch Lomond, is the same.

Bezzia sp.. Like C. cubitalis this larva can both swim in water and burrow rapidly through mud; and generally does the latter. One might therefore expect a similar distribution, namely a large population within the shallow, phytal zone; a rapid fall in population density to zero outside this zone; and an almost complete absence from McDougall Bank. In fact the distribution of Bezzia larvae is quite different. Though most numerous in shallow waters - about 25 per sq. m. at 0.7 to 2.4 m. - they occur at all depths along the transect line, right down to 13 m. and pos:sibly beyond. And they are almost half as numerous on McDougall Bank as at Stations 1 and inshore (Fig. 64).

I have already indicated that in all probability C. cubitalis is not found at depths greater than 7 m. because it is a detritus feeder and be:cause the nutritive value of the detritus in Loch Lomond falls rapidly beyond the relatively narrow phytal zone inshore. It is significant therefore that my observations on Bezzia sp. have shown that it is carnivo:rous (Weerekoon, in press). Unless its prey is restricted to one species which is itself confined to the margin of the loch, there is no reason why Bezzia/

Bezzia larvae should not range widely over the loch floor.

There is no evidence that the diet is thus restricted. Though little is yet known about the food of carnivorous ceratopogonids, such reports as there are show that a variety of animals is eaten. As for the Bezzia sp. larvae of Loch Lomond, I have found that they feed upon Palpomyia quadrispinosa larvae; and also that they probably feed on worms and on chironomid larvae for their guts often contain a red emulsion-like liquid which can only have come out of some haemoglobin containing animal of which there are quite a number amongst these two groups in the loch; for example, the chironomid larvae Chironomus (Microtendipes) spp., C. (Cryptochironomus) spp., C. (Pentapedilum) spp. and C. (Polypedilum) spp.; and the tubificid worms Tubifex tubifex, Peloscolex ferox, Limnodrilus sp., or the lumbricu-:lids, Lumbriculus variegatus and Stylodrilus heringianus. Of these, tubificids and C. (Cryptochironomus) spp.(q.v.) extend to very great depths.

This carnivorous habit is therefore very probably the reason why the Bezzia sp. larvae have been found even at Station 4 which is 13 m. deep, and at least 600 m. away from the detritus-rich margin of the loch. Ranging thus widely over the loch floor, the larvae can easily reach McDougall Bank where the rich benthos will support a correspondingly greater number of them.

Palpomyia quadrispinosa. Like Bezzia sp. P. quadrispinosa is found mainly in the shallow phytal margin of the loch (50 per sq. m.) but also extends/

extends in small numbers to very great depths (~~Table 33 (7)~~, Fig. 65). Thus a specimen was found in two samples collected with the Petersen grab from 60 m. (Luss Station).

This distribution suggests that Palpomyia like Bezzia, is a carnivore. Some of the Palpomyia larvae found contained the same sort of red emulsion as did the Bezzia larvae; and Thomsen (1937) states that members of the genus are carnivorous, though Mayer (1934b) believes they are detritus feeders.

The species occurs on McDougall Bank but in small numbers.

Probezzia venusta and Johannsenomyia nitida. Larvae of these two species look so much alike that their separation required detailed examina-:tion and was not possible within the time at my disposal. I shall there-:fore deal with them together. This is not as unfortunate as it might have been for both species seem to be carnivorous, and from what has been found in the case of Bezzia sp., Culicoides cubitalis and Palpomyia quadri-:spinosa, should resemble each other in their bathymetric distributions. Besides it is probable that J. nitida accounts for a very small fraction of the total of 456 individuals. For amongst the imagines reared from larvae that had made their way out of the loch in order to pupate upon the damp stones and debris near the water's edge there were at least 20 of P. venusta to every one of J. nitida.

Larvae of these two species together formed over half of all the ceratopogonids collected during the survey, and P. venusta must therefore easily/

easily outnumber all the other ceratopogonids in the loch. There are between 75 and 140 of them per sq. m. within the phytal zone of the bay. Outside this zone the population decreases in size but even at 13 m. there are still 4 per sq. m., whilst specimens have been taken even at 20 m. (Creinch Station). On McDougall Bank the population has a density of about 17 per sq. m..

Though densities are as a rule higher, this distribution resembles that of Bezzia sp., which is also carnivorous, and differs from that of the detritus feeder C. cubitalis. The suggestions I have made to explain the distribution of Bezzia sp. (q.v.) are equally applicable in the case of these species.

Of the ceratopogonid fauna of Loch Lomond it can be said that all species are most numerous within the phytal zone where they contribute 3 to 4% of the benthos (Table 8). Beyond this shallow phytal zone their numbers begin to fall (Fig. 19); rapidly in the case of detritus feeders like C. cubitalis and Dasyhelea, which disappear at depths of about 7 m. or even before; gradually in the case of carnivores like Bezzia sp., P. venusta and Johannsenomyia sp., which may even be found at depths of 20 m.. The former group is virtually absent from McDougall Bank while the latter constitutes a prominent part of its benthos.

INSECTA - DIPTERA - CHIRONOMIDAE.

The/

The chironomids are the most important members of the benthos in Loch Lomond. They formed almost 40% of the collections (Table 8) and are the dominant family at all depths down to at least 13 m.. At 20 m. the Tubificidae (Oligochaeta) take first place, the Chironomidae second. There are, however, over 40 species of them and no single one is as numerous as the isopod Asellus aquaticus, the tubificid Peloscolex ferox or the ephemerid Caenis horaria.

Densities are highest within the phytal margin of the loch, especially where the substrate is silty, e.g. about 3,300 per sq. m. at Station 2 in 4 m. of water (Fig. 66). Outside this zone populations decrease, at first very rapidly (in 7 m. of water there are only about 700 per sq. m.) and then gradually. There are about 150 per sq. m. at 13 m., mainly Procladius spp., C. (Cryptochironomus) spp. and C. (Pentapedilum) rubens; whilst populations at 20 m. are probably little smaller. By 60 m., however, density is nearer 20 per sq. m., mainly Procladius and C. (Cryptochironomus).

SUB-FAMILY TANYPODINAE. (Figs. 26, 79, 80).

Though members of this sub-family formed less than a quarter of the chironomids collected, they are probably of considerable importance in the economy of the loch. Being carnivores they must be responsible for the annual destruction of other species many times their number.

At least 8 species occur in Loch Lomond, and have been identified but I have been able to sort the larvae collected into just 4 groups:-

Anatopynia/

Anatopynia (Macropelopia) goetghebueri Kieffer

A. (Psectrotanypus) trifascipennis Zett.

Pentaneura spp.

Procladius spp.

A. (M.) goetghebueri and *A. (P.) trifascipennis* are two relatively uncommon species. The former, a large, brownish red larva, occurs amongst *Litorella* and *Isoetes* to an extent of about 8 per sq. m., is not found on bare mud or silt, and is very rare on McDougall Bank. The latter, easily distinguishable from the other tanypodines in the loch by its dark brown head, attains its maximum along the outer border of the vegetation zone - 55 per sq. m. at 4 m. - disappears rapidly as sand replaces silt at shallower depths, but only gradually with increasing depth.

Pentaneura spp.. This genus of which 4 species have been found is best represented in the margin of the loch, particularly on the *Litorella* carpet at 0.7 to 2.4 m., where densities of about 260 per sq. m. (average) and 980 per sq. m. (maximum) were attained. Beyond this the population steadily decreases in size down to a depth of about 8 m., after which it remains fairly constant at about 3 per sq. m. (Fig. 79). *Pentaneura* was found even at 20 m. (Creinch Station). On McDougall Bank there are about 170 *Pentaneura* per sq. m. - a fairly large population. Actual densities apart, this distribution is rather like that of the carnivorous ceratopogo-:nids. *Pentaneura* spp. are also carnivorous.

At Station 1 there is a very marked seasonal variation in the size of the/

the *Pentaneura* population. Densities of about 330 per sq. m. in the months February to May, 1949, suddenly increased in June to a value three times as large, namely 980 per sq. m., due to the appearance of a new generation of larvae. As these dispersed over the loch floor, the density fell sharply during July to about 100 per sq. m., a value which was maintained more or less steadily thereafter (Fig. 26). A similar variation occurred at Stations 2 and 3.

At Station 3 which was very much farther away from the shore than the other two, the peak occurred in July, a month late (Fig. 26). This delay suggests that egg-laying and hatching takes place at or near the water's edge and that the young larvae gradually spread outwards over the loch floor, a view which is afforded support by what happens on McDougall Bank. Here the summer peak is completely absent; populations remain very much the same throughout the year (Fig. 26). Since the peak is due to the hatching of eggs it follows that eggs of *Pentaneura* are not present on the bank; that they are neither laid there nor carried there by currents; and the bank must receive its population of larvae gradually throughout the year. The movement itself may be a combination of crawling and swimming - these species being capable of both, and the deep silted loch floor which surrounds the bank is not an obstacle to these larvae for they live in it.

Procladius spp.. By far the commonest species of the genus *Procladius* in Loch Lomond is *P. (Procladius) crassinervis*. At least one other/

other species P. (Psilotanypus) rufovittatus is also present.

The larvae are found at all depths from the water's edge down to 180 m.. ✱ Population densities are highest within the phytal zone - 410 per sq. m. at 4 m. - and decrease to about 100 per sq. m. at 7 m.; thereafter there is very little decrease and at 13 m., and probably 20 m., there are still nearly 80 of these larvae per sq. m. (Fig. 80)

In the sandy areas of the phytal zone inshore and on McDougall Bank where the bottom deposit is likewise sandy, the larvae though still very common, are relatively less numerous - 90 and 45 per sq. m. respectively.

These larvae are carnivorous, (cf. Morgan, 1949, Johannsen, 1937a) and this wide distribution from the shallows to the deepest waters seems to be characteristic of many carnivorous insect larvae in Loch Lomond, e.g. Pentaneura spp., Bezzia sp., Palpomyia quadrispinosa, Probezzia venusta and Johannsenomyia sp. (q.v.).

There were distinctly fewer of these larvae in the winter of 1949-50, than in the previous one. This, it has already been seen, also characterised the populations of Pentaneura spp. at Station 1 (Fig. 26) and in neither case can I offer an explanation, for behaviour in such marked contrast to that/

✱ No specimens have yet been found at 192 m., the greatest depth in the loch, but this is probably because very few samples have been collected from there.

that of the benthos as a whole, (Figs. 34, 35), and of so many of the species in it, all of which were more numerous in the 1949-50 winter than in the previous one.

SUB-FAMILY DIAMESINAE.

This sub-family, of which the two species Diamesa (Psilodiamesa) lacteipennis Zett. and Prodiamesa olivacea Meigen have been found, is very poorly represented in the loch. The larvae inhabit the phytal zone but even at Station 1 (0.7 to 2.4 m.) where most of them are found, populations are seldom larger than 10 per sq. m.. Though areas shallower than this were sampled only qualitatively the impression was received that populations are not any larger there. Upon McDougall Bank just one diamesine larva, a P. olivacea, was taken during the survey.

In the oligotypic Lake Innaren (Brundin, 1949) and the meso- to oligotypic Lake Windermere (Humphries, 1936) diamesines are similarly rare but include the bathyphilous species, Monodiasmesa bathyphila Kieff., which I have not yet found in Loch Lomond.

SUB-FAMILY ORTHOCLADIINAE.

This sub-family is somewhat better represented in the loch than the diamesines. In the phytal zone both on McDougall Bank and inshore, there are generally about 90 orthocladiines per sq. m., except in July when the population inshore, but not on the bank,* increases almost tenfold. Outside the/

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* Cf. Pentaneura spp., Caenis horaria, etc..

the phytal zone numbers fall rapidly to about 18 per sq. m. at 7 m.; there-:after the fall is slow for there are about 10 per sq. m. at 13 m. and a few even at 60 m..

The sub-family seems to have a similar distribution in Lakes Winder-:mere (Humphries, 1936), Esrom (Berg, 1938) and Innaren (Brundin, 1949), but is about twice as abundant in the last named lake as in Lomond.

There are at least 12 species in Loch Lomond though I shall be able to deal separately with only 5 of them, for my collection of 890 orthocladiines has not been completely classified.*

The two species lacustris and scutellata of Corynoneura are extremely rare, a few specimens only having been taken during the whole survey, but are found in the phytal zone both on McDougall Bank and inshore. Hydrobaenus (B.) curtistylatus is somewhat more frequent (average density 10 per sq. m.) and seems to be confined to the upper part of the phytal zone, 0.0 to 0.7 m. in depth. It has a similarly restricted range but seems to be much more frequent, about 180 per sq. m., in Lake Innaren (Brundin, 1949). Hydrobaenus (B.) apicalis is also comparatively uncommon (about 5 per sq. m.) in Loch Lomond; where moreover they seem to be confined to the phytal zone though in Lake Innaren, Brundin (1949) found that they extended/

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* This was due mainly to lack of time, for given the existing keys for larvae, the breeding and identification of imagines is often necessary for the separation of larvae into species.

extended to great depths. Metriocnemus (H.) marcidus is another infrequent species for there are seldom more than 12 per sq. m. in the upper part of the phytal zone, 0.7 to 2.4 m.. They differ from the 4 species already mentioned in extending into waters as deep as 13 m., where there are about 3 per sq. m.. Also more or less restricted to the upper phytal zone, are the two species, lacuum and sylvestris of Cricotopus, which are particularly abundant in summer - 180 per sq. m. - but infrequent at other times.

The remaining 5 species belong to the genus Hydrobaenus and not having been separated in the collection will not be referred to.

SUB-FAMILY CHIRONOMINAE. (Figs. 27-33, 67-78).

Members of this sub-family accounted for almost 70% of the 11,555 chironomids collected and therefore constitute the most abundant group in the loch. They fall into the three genera Tanytarsus, Pseudochironomus and Chironomus, which form 34, 6 and 60% respectively of the collection.

The genus Tanytarsus includes at least* the seven species which are dealt with hereafter; and though it is easily the most abundant chironomid genus in June and July (Fig. 33) it is at all other times outnumbered by the genus Chironomus. This and the fact that it is essentially an inhabitant of shallow waters, and is absent from the oxygen-rich profundal zone of the loch, are worthy of note for the physicochemical features of Lomond/

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* Of the 2,729 Tanytarsus larvae collected, 205 have had to be left unidentified.

Lomond are such (see Ch. I) that it should fall within the "Tanytarsus lake-type" of Thienemann (1922) or of Lundbeck (1926).

Tanytarsus (Tanytarsus) holochlorus Edw. is one of the species included in the "Eutanytarsus gregarius group" of Bause (1921). The larva is orange to brownish yellow in colour and its small Lauterborn organs are borne upon stalks which are each about twice as long as the last 4 antennal segments together (cf. T. (T.) glabrescens below).

It is typically an inhabitant of shallow regions in Auchentullich Bay and reaches its maximum concentration at 4 m. (Station 2) where there are generally 350 larvae per sq. m.. Beyond this depth numbers decrease rapidly; for at 7 m. there are seldom more than 20 per sq. m., and none was ever found at the sampling Stations in deeper areas (Fig. 67).

In spite of the large population inshore that of McDougall Bank rarely exceeds 5 per sq. m., and this I believe is because these larvae dwell in tubes and are thus protected from off-shore currents which might wash them away. For if it were due to some special difficulty the gravid females encountered, in reaching and in ovipositing on the bank, there should still be some evidence of the pronounced seasonal maximum in larval population that follows the hatching of eggs inshore, even at a place like Station 3 where the average population density is almost as low as it is on the bank. Like all chironomid larvae T. (T.) holochlorus can swim and the bank is probably reached by this means.[*]

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[*] See Ch. VI for a full discussion.

In the seasonal variation that has just been referred to, a population density of nearly 1,415 per sq. m. was reached in July, 1949 at Station 1 for example, where it had varied during the previous four months between the values 27 and 99 per sq. m., and had averaged 60 per sq. m.. Almost 75% of the larvae making up this July population were ready to pupate,[*] and it was a puzzle therefore where the extra individuals had come from.

A separation of the larvae into three groups (1) the very small and presumably newly hatched ones, 1 to 2 cm. long, (2) the large ones with swollen thoraces ready to pupate, and (3) those of intermediate size, suggests that in Loch Lomond Tanytarsus (T.) holochlorus is bivoltine; and that this accounts for the puzzling feature referred to above. The mature larvae of July are not the final instars of the previous winter's generation, but of a new, a summer generation of larvae.

From the curves in Figures 27 and 28, which indicate the seasonal variation of each of these three size groups of larvae and of all of them together, it will be seen that by the end of winter all larvae have attained intermediate size; none is very small or very large. They continue to grow and are mature by May. Pupation and metamorphosis occur between May and June and result in the complete disappearance of these large larvae. Mating, oviposition and hatching must take place in quick succession there:after/

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[*] This was easily evident in the enlargement of the larval thorax. Besides all those that were reared pupated within a week of collection.

:after for small larvae 1 to 2 mm. long first appear at the beginning of June. These newly hatched larvae which constitute about 90% of the popu-:lation in this month grow very rapidly. By July most of them are ready to pupate; they are the mature larvae the origin of whose large numbers was puzzling at first. Pupation followed by the emergence of a second genera-:tion of imagines and by mating and oviposition, occur in July and August for by September all the mature larvae have disappeared, and the population consists once more almost entirely of small newly hatched larvae. These grow rapidly and by October have reached intermediate size. This genera-:tion of larvae overwinters and gives rise in the succeeding year to the first summer generation of imagines. Figure 27 in particular bears out this interpretation for it shows (a) that there are two seasonal maxima, M and M', for larvae ready to pupate, and two, Y and Y', for small newly hatched larvae; and (b) that these maxima alternate. When mature larvae are at a maximum newly hatched larvae are at a minimum and vice versa.

Tanytarsus (Tanytarsus) glabrescens Edw.. This species is also one of those in Bause's "Eutanytarsus gregarius group", but unlike Tanytarsus (T.) holochlorus the stalks bearing its Lauterborn organs are each about four times as long as the last four antennal segments together; and the larva is greenish in colour.

It is less abundant than T. (T.) holochlorus and seems to extend a little farther out into the bay (Fig. 68) but is in other respects rather similar. Thus the population on McDougall Bank is very small, about 2 per sq./

sq. m., and shows no trace whatsoever of the pronounced increase in summer which characterises the population of the inshore Stations 1 and 2. The significance of this has already been pointed out in connection with T. (T.) holochlorus (q.v.).

Again, the seasonal variation in population density (Fig. 29) suggests that the species is bivoltine. In February and March, 1949 no larvae were taken anywhere along the transect line. Yet in April there were large numbers of them at the inshore Stations, almost 110 per sq. m., at Station 2 for example. These larvae were medium sized but by the end of May they were large and beginning to pupate. And corresponding with the emergence of adults that must occur during the period there is a marked fall in the numbers of larvae caught during May and June (Fig. 29). The density at Station 2 is now 9 per sq. m. - only a twelfth of what it was in April. In the next month, July, the population is very large (Fig. 29); at Station 2 there are 720 larvae per sq. m., eighty times as many as there were a month before. This July population consists of small newly hatched larvae, of large larvae about to pupate, and of ones intermediate in size. Small larvae must have appeared for the first time about the end of June, for they are numerous in July; and they must grow very rapidly for the equally numerous mature and medium sized larvae of July must belong to the same generation and cannot belong to the one which formed the population in April and had disappeared by June. In the very next months, August and September, the/

the population is once more extremely small and contains no small larvae; whilst no larvae at all were found in October, November and December. 1 very small larva was taken in January, 1950 and 2 in February (Fig. 29).

This sequence suggests that the July larvae, some of which had begun to pupate by the end of that month, had all emerged from the loch by September; and that the eggs of the second generation of imagines so produced over-:wintered without hatching or, what is more likely, hatched into first instar larvae which themselves overwintered but were too small to be retained in the sieves used in the investigation.

If this interpretation is incorrect and the species is univoltine, one has the task of explaining what becomes of the medium and large sized larvae of July during the autumn and winter. If these larvae had not yet occupied the whole extent of their habitat, then some lowering of population density might be expected to follow the colonisation of the unoccupied regions. But it is not likely that such regions were of any considerable size for, by July, larvae were very numerous down to 7 m. (Station 3) which is at or near the outer limit of their range in the bay; any fall in density on account of subsequent dispersion must therefore be slight and cannot account for the complete absence of medium sized and large larvae in the autumn and winter collections.

Another possibility is that these larvae pass the autumn and winter, buried so deep in the substratum that they are beyond the reach of the sampler/

sampler I used, i.e. more than 12 cms. beneath the surface. But it is difficult to see why this should be necessary in a loch where winter tempe:ratures are relatively mild; and, in any case, why it should be necessary during the period August to November when water temperatures are higher than in April (Fig. 3) at which time the larvae are once again at the surface of the substratum.

Apropos of my own view that the species is bivoltine and overwinters in a very small sized stage, it is relevant to note that Berg (1938) when discussing the *Eutanytarsus gregarius* group of species in Lake Esrom, has himself suggested that the winter is passed in this manner - though he does not mention the possibility of a second summer generation of imagines.

Of *Tanytarsus (T.) holochlorus* and *T. (T.) glabrescens* in Lake Innaren Brundin (1949) notes that the former occurs at depths of 0 to 3 m., and that the latter is moderately abundant. But no comparison of densities or of bathymetric distribution can be made since he treated these species and at least 7 others including the bathyphilous *T. eminulus* (Walker) and *T. gregarius* Kieffer, together. Similarly in Lake Windermere where Humphries (1936) states that "Tanytarsus gregarius group" larvae are frequent down to 60 m.; and in Lake Esrom, where Berg (1938) states that though they occur down to depths of about 15 m. they are infrequent elsewhere ex:cept at about 2 m., where the average density is about 300 per sq. m..

Tanytarsus (Microspectra) sp. A. Of the two species of larvae in Loch Lomond, which fall within the *Eutanytarsus inermipes* group of Bause (1921) one/

one has the spur on its antennal peduncle very well developed and claw-like; the other has a small, poorly developed spur. Both belong to the subgenus Microspectra and since I have not identified their imagines I shall refer to the former as species A and the latter as species B.

Species A closely resembles Tanytarsus (T.) glabrescens in its frequency, and its bathymetric distribution (Fig. 69); and also in its seasonal varia:tion (Fig. 30). There are, for example, no larvae in collections from October to April; a large population in May; a sharp fall in June followed by a second and very much larger population in July and early August; and a rapid decline to zero in September-October.

None of the May larvae is small, and all the June larvae are large and ready to pupate. In July very small larvae dominate the population in the early part of the month - forming about 80% of the collections - whilst medium and large larvae dominate it in the latter part of the month and in early August. All this is consistent with the view that the species is bivoltine and passes the autumn and winter in the egg stage.

Tanytarsus (Microspectra) sp. B. This species is almost as frequent as species A or T. (T.) glabrescens, which it also resembles in being more or less confined to the margin of the loch down to about 7 or 8 m. (Fig. 70) Within this zone however it shows a greater preference for the deeper silty areas (Stations 2 and 3) than do the other two species; and is very infrequent on the sandy substratum at Station 1. A few specimens were taken at 13 m.; and two only on McDougall Bank.

In/

In its seasonal variation however it differs considerably from them. In the first place the population curve shows only one peak - in June-July - (compare Fig. 31 with Figs. 29 and 30). In the second place only 2 to 3% of this large June-July population consists of small larvae - the rest are large (70 to 85%) or medium sized (12 to 28%). From September to May very few larvae were taken and all those were of rather small size.

This population structure suggests that the species is univoltine, and passes the winter as small larvae - probably first instars, which are not found in the collections because they are too small to be retained in the sieves. Some of them may grow and the small larvae captured during the autumn and winter (Fig. 31) probably represent these. But growth becomes general only about the beginning of summer and results in larger and larger numbers of larvae being captured, the vast majority of them of medium and large size. Larvae ready for pupation, first met with at the end of June, continued to be found till mid-August; and it seems that pupation occurs throughout this long period until the entire larval population has left the loch. Eggs laid by the imagines so produced do hatch, but the majority of the larvae from them pass through the autumn and winter as first instars.

For other lakes there is little information about larvae of this group. <u>T. (Microspectra) monticola ?</u> Edw. is reported to occur at all depths of Lake Innaren (Brundin, 1949); whilst in Windermere and Esrom larvae of this group are reported to be confined to shallow waters (Humphries, 1936, Berg/

Berg, 1938), as they are in Loch Lomond.

Tanytarsus (Tanytarsus) ~~stridersum~~ atridorsum Kieff.. This species falls within Kieffer's genus Cladotanytarsus and also Zavrel's genus Atanytarsus (Zavrel, 1934, Johannsen, 1937b). Its larva, green in colour and with large Lauterborn organs carried upon short stalks, is the most numerous Tanytarsus in the collections and is most abundant in the lower phytal zone (about 4 m. - Station 2) where there are on an average about 500 per sq. m., and where a maximum of about 1,300 per sq. m. was attained in December. Popula:tions both above and below this depth, and upon McDougall Bank are very much smaller. The averages at 2.4 m., 7 m. and on the bank are under 50 per sq. m. (Fig. 71).

At first glance the numbers of larvae collected during each month of the survey seemed to show no evidence of a seasonal variation; only a great increase in the 1949-50 winter such as was found amongst the oligochaetes, or Asellus aquaticus or the nematodes (q.v.), and was attributed to a favourable influence upon reproduction of the fine summer of 1949. Never:theless an analysis of the larvae into three main size groups shows that a very pronounced seasonal variation is present.

Larvae found in February to April 1949, at the beginning of the survey, were all of intermediate sizes and included none that were small nor any that were ready to pupate. With the appearance of the latter in May the propor:tion of middle sized larvae in the population falls steadily to zero by the/

the end of August. In the meantime mature larvae increase steadily to reach a maximum in July after which they disappear. During the whole of this period, May to July, pupation and emergence of adults must occur. Small larvae of the new generation first appear in August, increase greatly in numbers to a maximum in October and then begin to disappear from the collections; for none is found after November. Whilst this happens the medium sized larvae appear once more and by December form 100% of the collections.

This sequence is clearly seen in Fig. 32, where the seasonal variations of mature and of very young larvae are shown. It indicates that <u>T. (T.) atridorsum</u> is univoltine - and that it differs from the other univoltine species, <u>T. (Microspectra)</u> sp. B, in growing during the autumn and winter and in not passing these seasons in the first instar. The uni:modal curves for the populations of mature and of newly hatched larvae of this univoltine species contrast with the bimodal curves of a bivoltine species like <u>T. (T.) holochlorus</u> (Figs. 32 and 27).

In Lake Innaren, <u>T. (T.) atridorsum</u> and two related species <u>mancus</u> (Walker) and difficilis (Brund.) occur. Brundin (1949) treats all three together in the group "<u>Cladotanytarsus</u>" and a full comparison of the con:ditions in the two lakes is not therefore possible; but it does seem that its density and depth distribution are essentially the same in Innaren and in Lomond. Thus in the former at 2 m. there are only about 40 larvae per sq./

sq. m.; at 4 to 5 m. about 600 per sq. m.; and at 7 m. about 60 per sq. m.. Specimens were however taken occasionally even at 19 m. in Lake Innaren.

Tanytarsus (Stempellina) sp. A is a small pink larva with alternate Lauterborn organs carried upon short stalks. It lives in a sub-cylindrical case constructed of very fine sand grains. Empty cases are found in very large numbers in the silt at 13 m. (Station 4) and most have been washed there from the margin of the loch by water currents. For the larvae them:selves were never found at Stations deeper than Station 3 (= 7 m.) and are so infrequent even there that it is unlikely that they occur at depths much greater than about 8 m.. They are most frequent in the upper part of the phytal zone (Station 1, 0.7 to 2.4 m.; average density about 80 per sq. m.) and become rapidly scarcer with increase in depth (Fig. 72). They also occur, but in small numbers, upon McDougall Bank.

Pupation and emergence begin very early in the year, in the first week of March, and continue to about the beginning of July. Small larvae of the new generation were first taken in samples in July. It appears therefore that the species is univoltine in Loch Lomond.

Tanytarsus (Stampellina) sp. B. 10 specimens of this larva were taken in the course of this survey: 5 at Station 1 and 5 on McDougall Bank. The larva has a palmate process upon the inner side of each antennal peduncle and was identified as falling within the larval genus Stempellina Bause (Brundin's key, 1949).

Pseudochironomus prasinatus/

Pseudochironomus prasinatus Staeger. This larva resembles the tanytarsids in having a pair of large, transversely elongate paralabial plates which nearly meet in the middle line. It is pale green when young, orange with a green thorax when older.

The lower phytal zone, where the substratum is mud covered sparsely with Isoetes and Nitella, seems to afford the larva an optimum habitat; for there were on an average about 250 of them per sq. m.. In the sandy upper phytal zone (Station 1) there were seldom more than 3 per sq. m., and lower down upon the bare silts at 7 m. (Station 3), the population was also relatively small, about 50 per sq. m. (Fig. 73). It seems unlikely that the species ranges to depths much greater than about 8 m.. On McDougall Bank the average population consisted of about 5 larvae per sq. m..

Larvae grow through the winter and begin to pupate in April. Emergence occurs during May, June and July and during this period populations are at a minimum. With the appearance of the new generation of small larvae in August populations increase once more and reach a maximum in October.

The genus Chironomus.

15 species of this genus have been found to inhabit Loch Lomond but it is certain there must be many more, some amongst the 270 larvae that I was unable to identify beyond their genus, others amongst the 4,523 which I was able to classify down to sub-genera.

Like Tanytarsus, this genus is best represented in the phytal margin of the/

the loch; C. (Pentapedilum) rubens and C. (Cryptochironomus) spp. being the most conspicuous of those that range widely beyond this zone. Except in June and July it is more numerous than Tanytarsus. It's populations in the 1949-50 winter were much larger than those in the previous one (Fig. 33), most of this increase being due to C. (Chironomus) spp. (= Limnochironomus).

Chironomus (Cryptochironomus) spp.. As will be seen in Appendix I. the imagines collected from the loch include at least three species, but I shall deal with the larvae as a single group as I had not the time to differentiate them in my collection of over 900 individuals.

These larvae are almost equally abundant throughout the phytal zone - 0.7 to 4 m. - inshore, and upon McDougall Bank, the population seldom differing much from the figure 120 per sq. m. except that it was generally a little smaller during the first half of the survey and a little larger during the second half. This increase is probably of the same nature as that which was found amongst the nematodes and in Peloscolex ferox and and Caenis horaria (q.v.) and may have the same explanation - namely an enhanced reproduction due to the fine summer of 1949.

Outside the phytal zone the population becomes rapidly smaller with increase in depth down to about 7 m. (about 30 per sq. m., Fig. 74) after which any decrease is very slight; for there were 12 larvae per sq. m. at 11 m. (Station 8), 10 per sq. m. at 13 m. (Station 4). When the mud at 60 m. from the Luss Station was sampled 2 larvae were found in each of two samples/

samples and the population is probably not much less than that at 13 m. (Fig. 74). In being well represented at great depths and upon McDougall Bank these larvae differ from almost all the chironomids dealt with hitherto. The outstanding exceptions are the larvae of Pentaneura and of Procladius. These are carnivorous and so also are species of the sub-genus Cryptochironomus (Wesenberg-Lund, 1943, pp. 502, 511). I have already argued from the distribution of detritus feeders like the oligochaetes and Asellus aquaticus etc. that the deep areas of the bed of Loch Lomond and the surface of McDougall Bank are poorly provided with nutritive detritus; and that this accounts for their very poor representation in or even their total absence from these areas. A carnivore on the other hand would not be influenced by this factor except indirectly, and its distribution would be restricted only to the extent to which it confined itself to one or the other of the detritus feeding species for its food. If it preyed upon a large number of different species it would be able to exist in considerable numbers in areas where each of these species was itself fairly infrequent. I suspect that the predatory chironomids as well as other predatory insect larvae like many ceratopgonids have this catholicity of taste; and that this accounts for their wide range in the loch and for their large populations on McDougall Bank. In this connection it is perhaps noteworthy that the bathymetric distribution of C. (Cryptochironomus) spp. on the one hand and of total oligochaetes and total benthos on the other parallel each other quite/

quite well (cf. Figs. 74, 43 and 81).

In Lake Innaren, there are eight species of this sub-genus, including two, namely Chironomus (C.) vulneratus and C. (C.) pseudosimplex, of the three I have found in Loch Lomond. These two have a similar bathymetric distribution in Innaren, extending from 0.5 m. down to the deeper parts of the lake (19 m.). Population densities for the sub-genus as a whole are also very much the same there; thus at 4 m. there are about 140 larvae per sq. m. in Innaren and about 130 per sq. m. in Lomond.

Chironomus (Pentapedilum) flavipes Meigen is a red larva about 8 to 9 mm. long when full-grown. It is confined to the phytal zone, in the upper part of which it is most abundant, i.e. 20 per sq. m. at Station 1. Only occasional specimens were taken from McDougall Bank, and the population there is about 3 per sq. m.. It has a similar range in Lake Innaren (Brundin, 1949) but seems to be even less abundant there - about 5 per sq. m. at 1 to 2 m. - than in Lomond.

Chironomus (Pentapedilum) rubens Edw. is a red larva with a distinct greenish tinge; and even when full-grown is small, about 4 mm. long. It is one of the most abundant chironomids in Loch Lomond. On a silty sub-:stratum bearing some Isoetes and Nitella (e.g. Station 2 - 4 m.) it averaged about 450 larvae per sq. m., and formed a little over 13% of all the Chironomidae collected during the survey. In the upper phytal zone where the substratum is sandy and covered with Litorella it is relatively poorly/

poorly represented, about 30 per sq. m.; and outside the phytal zone, the population decreases rapidly in size with increase in depth though even at 13 m. there are generally about 7 larvae present per sq. m. (Fig. 75). On McDougall Bank there are even fewer larvae than in the deep areas round it.

Pupation and emergence begin about the end of May, and continue through:out the summer to August. Small larvae of the new generation appear in the samples about the end of this period. There is however no marked seasonal variation in the population density, a fact which must be due in part to the very long period over which emergence and oviposition are spread and may also indicate that the larval life is longer than one year. The somewhat higher populations in the winter months of 1949-50 than in those of 1948-49 were probably due to the existence of conditions specially favourable for reproduction in the fine summer of 1949. This has already been referred to many times - in connection with C. (Cryptochironomus) spp. (q.v.) for example.

These larvae from Loch Lomond show a remarkably close resemblance in structure to ones found by Brundin (1949) in Lake Innaren and described by him under the name Pagastiella orophila Edw.* (nov. gen. op. cit., pp. 840-845). Yet the imagines I reared from them proved to belong to the species Chironomus (Pentapedilum) rubens Edw.. Brundin himself states that his Pagastiella orophila in both its larval and its pupal characters shows/

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* Equivalent to Chironomus (Lanterborniella) orophilus Edw..

shows a close relationship to the sub-genus Pentapedilum. The bathymetric distribution of P. orophila in Lake Innaren is closely parallel to that of C. (P.) rubens in Loch Lomond, almost the only difference being that at each depth the population density is rather higher in Innaren than in Lomond as it is for most chironomids. Finally P. orophila is one of the most abundant chironomids in Innaren just as C. (P.) rubens is in LochLomond. The possibility cannot be ruled out that Brundin and I are referring to the same animal.

Chironomus (Polypedilum) spp.. Four species of this sub-genus have been identified amongst the imagines captured with funnel traps as they emerged from the loch. I have not however distinguished between them amongst the larvae, which will therefore be treated as a single group.

They live in tubes of mud, are long and slender - about 10 mm. by 0.7 mm. when full-grown - and red in colour. Their optimum habitat seems to be the lower phytal zone (Fig. 76) like other chironomids. A population of about 50 per sq. m. in the Litorella carpet of the sandy upper phytal zone increases to about 160 per sq. m. at 4 m. (Station 2) and then outside the phytal zone falls rapidly to about 40 per sq. m. at 7 m.. Thereafter the decrease is gradual for there were about 10 per sq. m. at 13 m., and probably about the same at 20 m.; for when the mud at this depth was examined on 5/4/49, 6 larvae were taken in 3 samples. None was ever found at the Luss (60 m.) or Tarbet (180 m.) Stations. Populations on McDougall Bank/

Bank are very small and seldom reach 6 per sq. m..

There seems to be a distinct fall in population density in August, more or less coincident with the end of the period of emergence.

The sub-genus Polypedilum is represented by eight species in Lake Innaren (Brundin, 1949); and its abundance and distribution there closely resembles that in Loch Lomond at corresponding depths. It is not possible, however, to say definitely that the very large numbers (about 550 per sq. m.) found in the 0.2 to 0.5 m. belt of the phytal zone in Innaren have no counterpart in Lomond since this area was not quantitatively sampled here.

Chironomus (Microtendipes) spp.. These red larvae will also be treated as a single group as I was unable to separate them into the two species which the examination of imagines captured in emergence traps show they must include. As in Lake Innaren they are here found in the phytal zone, particularly in the upper part of it where there are on an average 90 of them per sq. m. (Fig.77), at Station 1 in 0.7 to 2.4 m. of water, and probably even more at shallower depths. Outside the phytal zone numbers decrease rapidly for at Station 3 (7 m.) only 12 per sq. m. are found and none at all was taken at the deeper sampling Stations.

In Lake Esrom, however, the sub-genus extends down to depths of 15 m., and is most abundant at 8 m.. Berg (1938, p. 112) seems to suggest that the decline in population densities, from 170 per sq. m. at 8 m. to zero below 15 m., in this eutropic lake is due to a tendency these larvae have of avoiding any excessive lack of oxygen.

Admittedly/

Admittedly oxygen may be a controlling factor; for Lang (1931) has shown that lack of it retards the development of *Microtendipes* larvae which he therefore regards as high O stenoxybionts. But it cannot be responsible for their restricted distribution in Loch Lomond, since, in this loch, water at all levels is rich in oxygen even under the thermocline during the summer. I feel, instead, that the controlling factor in Loch Lomond is again the nutritive content of the detritus.

On the other hand, in an eutrophic lake like Esrom, where the autoch:thonous detritus, derived from plankton, may be large enough in quantity completely to override any local differences in the quantity of alloch:thonous matter in the bottom deposit, *Microtendipes* larvae might extend their range outwards to greater and greater depths until some other factor, temperature perhaps, or as Berg suggests, oxygen content of the bottom water in summer, becomes limiting.

Populations on McDougall Bank seldom exceed 6 per sq. m..

Pupation and emergence occur in April and May, whilst small larvae of the new generation were found in June and July but not after that month, when at first medium sized, and later large larvae were the only ones collected. It seems fairly certain, therefore, that in Loch Lomond the subgenus is univoltine and that the two extra generations that Jonassen (in Berg, 1948) found to characterize its populations in Naaby on the River Susaa are absent here.

No marked seasonal variation in density was found but populations were much/

much larger in February-April, 1949, than in subsequent months. (cf. Pentaneura and Procladius).

Chironomus (Chironomus) spp. = Limnochironomus spp.. Green to greenish brown larvae belonging to Kieffer's genus Limnochironomus (Goetghe:buer, 1928, Johannsen, 1937b) are found mainly in the phytal zone in the lower part of which they are especially abundant and form populations of about 220 per sq. m. (Fig. 78) except in May, June and July when there are rarely more than 30 per sq. m.. Outside this zone numbers decrease extremely rapidly to about 6 per sq. m. at 7 m.. A few are still present at 13 m. but none was taken from 20, 60 or 180 m..

Its bathymetric distribution in Lake Innaren is essentially similar, but in Lake Esrom maximum densities are found at 8 to 11 m..

Populations on McDougall Bank are exceptionally large - about 500 per sq. m. - much larger than any inshore Station sampled; this is a rather puzzling feature and one which makes it particularly unfortunate that the 0 to 0.5 m. belt of the phytal zone was not quantitatively sampled.

After the summer of 1949 there were very many more larvae in the loch than before; and as in so many other cases I feel this is due to the fact that reproduction of these species was especially favoured by the 1949 summer.

Chironomus (Chironomus) sp. A. Two specimens of a large, red, tubuli-bearing larva were obtained during the survey, both from a depth of 7 m. (Station 3), one in March, 1949, the other in January, 1950. They belong/

belong to a species of one of the three groups _thummi_, _bathyphilous_ and _percurrens_ into which Lenz (1921) and Goetghebuer (1928) have divided the tubuli-bearing larvae of the subgenus _Chironomus_.

Chironomus (Endochironomus) sp.. About thirty years ago Thienemann (1921) described certain cysts which had been sent to him by Dr. Gunnar Alm from the eutrophic Swedish lake, Yxtasjö. Alm had found them in the late autumn and in the spring just after the ice on the lake had melted; and he referred to them as overwintering capsules. Most of them were in the plant debris on the bottom of the lake at depths of 1 to 2 m. but a few were found amongst leaves of Ceratophylum and other plants. The cysts were completely closed and of a light brownish, transparent, silky material. Each contained a single large chironomid larva which Thienemann identified as belonging to the genus _Endochironomus_ Kieffer. It was bent upon itself at intersegments 2/3 and 8/9 so that it lay with its head and its posterior end in contact, beneath its abdomen.

Since Thienemann's account, Decksbach (1933) has reported the occurrence in autumn and in winter of cysts in the littoral zone of the eutrophic Russian lake, Pereslawskoja. She states that the larvae in the cysts were _Endochironomus dispar_ Meigen; and that Grandilewskaya-Decksbach (1928) gives an account of their ecology. This latter publication is not available in Britain; nor have I been able even to find an abstract or a reference to it.

I have found similar cysts in Loch Lomond; from late summer (30/8/49) to/

to spring (March). They were most frequent at Station 2 (depth 4 m. - scattered clumps of <u>Isoetes</u> and <u>Nitella</u>) where there were on an average 15 per sq. m. during this period. Within each cyst there was a large cream-coloured larva belonging to Kieffer's genus <u>Endochironomus</u>. It tightly fitted the cyst, lying bent upon itself, not in the manner figured by Thienemann (1921), but at intersegment 6/7, so that head and posterior pro-:legs were together at one end of the cyst.

When taken out of the loch, the encysted larva is quite motionless. It does not respond to mechanical stimulation with a needle; nor are there any movements in the heart or gut. But two days at room temperature (16.5°C.), or about four hours at 21°C. is sufficient to activate the larva which ultimately tears its way out of the cyst. A while before this happens, touching the cyst with a needle will cause the larva to move back-:wards. Confined as it is by the cyst, it can only crawl over itself; and often gets into the position figured by Thienemann. This worker had kept his cysts alive for some time and I suspect that his figure does not illustrate the usual position of the larva within the cyst.

Such few experiments as I have made with the cysts indicate that if they function as an overwintering device, it is not by protecting the larva from any direct ill-effects of low temperature. The material of the cyst does not seem to be heat-insulating, for as already indicated heat is readily transmitted to the larva within the cyst, activating it. Moreover, larvae dissected out of their cysts, and those left within their cysts, both survived/

survived 19 days of complete freezing. Berg (1950) reports that C. (Endochironomus) nigricans feeds upon suspended particles of food which it filters out of the water by means of a conical silken net. If the feeding habits of the Loch Lomond species are similar, it might well be that encystment occurs when some particular type of food particle becomes scarce in the plankton of the loch, and that the function of the cyst is to cut down the katabolic rate of the larva, so that it is able to tide over this period. This would be in harmony with the appearance of the cysts as early as August, 1949, when the temperature (16 C.) of the water just above the bottom on which they lay could not have been much below the summer maximum. Besides, Mayenne (1933) has shown that C. (Glyptotendipes) polytomus, a related species, is habitually frozen in the mud of fish-ponds in Moscow which are drained at the beginning of the winter. No cysts were formed and though the winter (1931-32) was severe (-30.2 C. being often recorded) about 70% of the larvae were alive next spring. It seems unlikely that C. (Endochironomus) sp. will require to be protected from the very moderately low temperature of the winter in Loch Lomond by a cyst; particularly as all the other chironomids in the loch survive the winter as active unencysted larvae.

It might be mentioned here that though the three species of Endochironomus which Brundin (1949) found in Lake Innaren, belong to the same group of Endochironomus as does E. dispar Meigen; and although there were over 100 of them per sq. m. at depths of 1 to 3 m., he makes no mention/

mention of these cysts.

BATHYMETRIC AND SEASONAL DISTRIBUTION

These larvae are almost confined to the phytal zone of the loch margin and of McDougall Bank; and are most numerous at Station 2 - 30 per sq. m.. Small unencysted forms occur from July to August.

INSECTA - DIPTERA - OTHER FAMILIES

One tipulid (Tipula) and two limnobiid genera (Dicranota ? and Pentophthera ?) are represented in the benthos of Auchentullich Bay. They are, however, very infrequent both along the transect line and in the shallow zones which were not quantitatively sampled.

CHAPTER IV.

THE BENTHIC COMMUNITY.

Five of the sampling Stations, 1 to 4 and 8, traverse Auchentullich Bay from mouth to apex and from them it is possible to obtain a fairly complete picture of the benthos of the bay as a whole.

Where the bottom deposit is a typical gyttja such as one finds all over the deep parts of the bay, the benthos is rather sparse and consists almost entirely of oligochaetes, chironomids, pisidia and nematodes. The first two of these groups are dominant and account for 55% and 30% respec:tively of the animals. Of the oligochaetes Paranais sp., Peloscolex ferox, and Tubifex tubifex are the commonest and of the chironomids, Procladius spp. and Cryptochironomus spp. both of them carnivorous. The other two groups, pisidia and nematodes, account for about 3% each (Table 8).

Nearer the edge of the loch, where the substratum lies about 4 to 8 m. below the surface, these groups increase greatly in size so that the benthos is now quite abundant. But they do not increase all at the same rate; and as a result the chironomids now outnumber the worms. Certain other groups, too, come into some prominence here, namely the Ephemeroptera, the Trichoptera, the Ceratopogonidae and the Hydracarina (Table 8); but in spite of that the Chironomidae account for as much as 50% and the worms 20%/

20% of the benthos. It is only in very shallow waters where the sub-:stratum is sandy and covered with a carpet of Litorella uniflora (e.g. at Station 1) that the Chironomidae cease to dominate the fauna as completely as they do elsewhere. For here Asellus aquaticus is so numerous that it makes up 16% of the benthos. Limnius tuberculatus larvae make up another 6% and the Chironomidae, though still the most abundant group, account for only 23% (Table 8).

At depths greater than 13 m. (= Station 4) the bottom deposit has not been examined systematically; but such evidence as has been obtained points to its supporting a fauna rather like that at 13 m. in the bay, though almost certainly poorer in individuals and in species. Peloscolex ferox, Tubifex tubifex, Procladius sp. and Pisidium sp. have been found at 180 m. off Tarbet in the "highland" basin of the loch, and the first three are among the four most abundant species in the benthos at 13 m..

One may conclude that the benthos of the whole of Loch Lomond is characterised by the presence of pisidia, nematodes and, especially, of worms and chironomids; and in the margin of the loch, by Asellus aquaticus and Limnius tuberculatus as well.

There are certain deficiencies in the benthos which also serve to characterise it. Snails, for example, are poorly represented and such species as are present are small in size and have but slightly calcified shells.

Of/

Of the Chironomidae the following species are most abundant:- C. (Pentapedilum) nubens, T. (Tanytarsus) atridorsum, T. (Tanytarsus holochlorus, Pseudochironomus prasinatus, and Procladius sp.; and whilst the genus Tanytarsus is more numerous than any other in summer, it is found mainly in the summer (Fig. 33), and seldom on substrata more than 7 m. below the surface of the loch. Of the worms one naid, Paranais sp., and three tubificids, Peloscolex ferox, Tubifex tubifex, and Limnodrilus sp. are the most abundant and characteristic species of the benthos in general, whilst in the phytal margin of the loch Marionina sp. and Lumbriculus variegatus are also important.

Now, the waters of Loch Lomond are oligotypic for Ca, N, P etc., and humic acid; and they are also always well provided with oxygen even in the hypolimnion. Lomond is, in short, an harmonic, oligotypic loch. Such lakes generally possess a benthos very similar to what has just been described as characteristic of Lomond. Some examples are Lake Innaren (Brundin, 1949), Nipigon (Adamstone, 1923, Adamstone and Harkness, 1923), Fiolen (Lang, 1931), Aoki-ko (Miyadi, 1930-1, 1), Motosu-ko, Nisino-umi and Asino-ko (Miyadi, 1932-3, 5), and Inawasiro-ko (Miyadi, 1932-3, 8). The benthos of Innaren closely resembles that of Lomond though it is somewhat richer and contains a fair sized population of Tanytarsus (gregarious group) even at 18 to 19 m. in the deepest area of its bed, and a small but definite population of Corethra. None of the other lakes mentioned has been studied anything like as systematically as these/

these two, and resemblances in details cannot be sought, whilst certain differences are noticeable. Thus the amphipod *Pontoporeia* occurs in Nipigon but not in Lomond, and Inawasiro-ko contains fair numbers of *Chironomus bathophilus* in its shallower areas; whilst in all the Japanese lakes *Tanytarsus* larvae are not more or less confined to the shallow lake margin, but extend to very great depths e.g. to 119 m. in Motosu-ko. The probable zonation of the benthos in the loch is shown in Table 10. p. 146a

Table 10. Faunistic zonation of Loch Lomond.

Zone	Sub-zone	Approx. Depth (m)	Macrophytic Vegetation	Characteristic Fauna
Marginal Edge of loch to Lower limits of aquatic Macrophytes	Stony	0 to 0.5	Fontinalis Lobelia Litorella	Ancylastrum fluviatile, Limnaea pereger, Ephemerella ignita, Ecdyonurus dispar, stonefly larvae, Gammarus pulex, and triclad planarians
	Sandy*	0.5 to 2.5	Litorella (and some Isoetes)	Asellus aquaticus, Limnius tuberculatus, Peloscolex ferox, Marionina sp., Pisidium spp.
	Silty*	2.5 to 4.0	Isoetes (and some Nitella)	Tanytarsus spp., Chironomus (Pentapedilum) nubens, Caenis horaria, Pseudochironomus prasinatus, Peloscolex ferox, Limnochironomus
Transitional Lower limits of aquatic Macrophytes to Average position of thermocline ?	Upper	4.0 to 9.0	-	Transitional - C. (Pentapedilum) nubens, P. prasinatus and C. horaria still form a large part of benthos
	Lower	9.0 to 25.0	-	Transitional - most 'marginal' species absent or scarce; 'profundal' species conspicuous e.g. Tubifex tubifex
Profundal Average position of thermocline ? to Deepest part of loch		Below 25.0		Fauna consists almost entirely of Tubifex tubifex, Peloscolex ferox, Pisidium spp. and Procladius spp.

* Much reduced in the 'highland' part of the loch.

CHAPTER V.

PRODUCTIVITY.

1. THE MARGINAL ZONE.

Whereas the composition of the benthos of Lomond agrees fairly well with what has been found in oligotypic lakes by other workers, its density certainly does not. It is generally accepted that such lakes are very poorly productive (Macan and Worthington, 1951; Berg, 1938; Hutchinson, Deevey and Wollack, 1939; Lang, 1931; Miyadi, 1930-1, I, 1932-3, X; Naumann, 1929, 1929a; Ström, 1928; Carpenter, 1928; Thienemann, 1922, 1922a, 1925, 1931, 1932, etc.). But in Loch Lomond almost 11,000 animals per sq. m. have been found in the phytal zone along the margin of the loch[x]; and the average here over a period of thirteen consecutive months, and including two winters when populations are at a minimum, was between 6,100 and 6,200 per sq. m..[xx] (Table 9). Densities of this sort are of the same/

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[x] At Station 1 in July, 1949 (Table ~~26~~ 9).

[xx] The densities found by Moon (1934-6) in the littoral zone of the oligotypic lake, Windermere, varied from about 100 per sq. m. to about 3,400 per sq. m. according to the nature of the substratum. These figures are based upon single samples and are not really comparable with the figures for Lomond. Besides, well weeded substrata were not sampled.

Adamstone and Harkness (1923) state that the shallow marginal zone of Lake Nipigon contains about 750 animals per sq. m.. They do not, however, state the depths involved, though it seems from their tables to be from about 2 to about 10 m.. Nor do they seem to have sampled amongst weeds.

same order of magnitude as those characteristic of the corresponding area of typically eutrophic lakes. In Esrom Lake, for example, Berg (1938) found an average population density at 0.2 m. of about 5,000 per sq. m., and at 2.0 m. of about 11,000 per sq. m.; and Muttkowski (1918), found about 2,400 animals per sq. m. at 4 m., and less elsewhere, within the phytal zone of Lake Mendota. Thienemann (1925) and Miyadi (1932-3, X) are both of opinion that a benthos of 2,000 or more per sq. m. may be taken as characteristic of the eutrophic state; and one of 1,000 or less per sq. m. as characteristic of oligotrophic state. From all of which it is clear that the margins of the oligotypic Loch Lomond are eutrophic.

2. THE PROFUNDAL ZONE.

However, the benthos of the loch bed at depths greater than 8 m. - that is over the greater part of the loch - is very poor and quite in keeping with its oligotypic nature (Fig. 81). At 10 to 13 m. it comprises about 400 animals per sq. m., and below that it gradually becomes scantier with increasing depth so that in the deepest parts of the loch (180 to 192 m.) there are probably less than 25 per sq. m.. In an eutrophic lake on the other hand benthic densities remain high far beyond the shallow marginal zone and, often even in the deepest parts of the lake, are of comparable size. Taking Esrom Lake once again as a typical example one finds that at 8 to 9 m. the population density is about 9,300 per sq. m.; at 14 to 15 m. it is 7,000 per sq. m.; at 17 to 18 m., 5,800 per sq. m.; and/

and at 20 m. which is very nearly the maximum depth of the lake 4,000 per sq. m. (Berg, 1938). In Mendota (Juday, 1922) it is about 15,200 in the deepest parts of the lake - 20 to 23 m..

But though unusual, Loch Lomond is not unique in this respect; for another oligotypic lake, Innaren, has recently been reported to possess a very rich benthos in its marginal zone. Brundin (1949) found in it about 18,500 animals per sq. m. at 0.2 to 0.5 m.; 10,000 per sq. m. at 1 to 2 m.; 8,700 at 4 m.; but only about 1,000 at 12 to 13 m.. He has suggested an explanation for these extraordinarily high densities and I shall comment on it later. In the meantime I wish to refer once more to the fauna of McDougall Bank.

3. McDOUGALL BANK.

The environmental conditions on the bank resemble fairly closely those of the margin of the loch at Stations 1 and 2. Thus it has a vegetation cover of Isoetes and some Nitella like Station 2; its bottom deposit is a coarse sand like that at Station 1; it lies at 2.4 to 4 m. below the surface of the loch as does Station 2; the C/N ratio of its bottom deposit, the oxygen, phosphate, temperature and pH values of the water in contact with it, are all similar to those at Stations 1 and 2 (Tables 6 and 7). In fact, the only noteworthy difference detected was the smaller amount of organic matter in the deposit on the bank. This difference, evident upon any casual comparison of the sediments dredged up/

up from the bank and from Stations 1 or 2, has been confirmed by the results of chemical analysis (Table 6). For the carbon and the nitrogen contents of the deposit on the bank are one quarter to one fourteenth what they are along the margin of the loch. In addition to this difference, the bank is probably much less disturbed by the action of waves than Station 1 - but this is a factor which should tend to raise population, not lower it. For though the composition of the benthos shows many resemblances to that of Station 1, there are on an average 2,400 animals per sq. m. on it (Table 9), or only a third as much as at either of the Stations 1 and 2, in the loch margin.

This relative poverty must be due, in part at least, to the smaller amount of detritus on the bank; for the detritus serves (both directly and indirectly) as food for many members of the benthos, both stenotopic and heterotopic.[*] There is no doubt, of course, that other factors too must operate to reduce the density of the benthos in the bank. The very fact that about 25 of the species[**] found at Station 1 are absent from the bank (Table 11) suggests that this must be so. Greater distance of the bank/

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[*] These terms are due to Enderlein (1908) and refer to animals which do (stenotopic) and which do not (heterotopic) pass their whole life cycle within the lake or stream.

[**] All the absentees are insects, except H. stagnalis and G. pulex.

bank than of Stations 1 and 2 from dry land is probably the most potent of such factors. For it is here, upon the trees and other plants of the land, that the imaginal instars of heterotopic members of the benthos rest after they have emerged from the loch; and it is from here that they fly out to the loch to lay their eggs. Therefore, whatever be the method by which a new generation of larvae reaches its habitat, the bank will always be less accessible than Stations 1 and 2, precisely because it is more distant than they are from the resting places of the gravid female adults. Hence the heterotopic benthos of the bank will be poorer than that of the loch margin.

But however important this factor of accessibility is, it can account for a part only of the decrease in benthis density, since in this decrease the stenotopic species are involved to as great an extent as are the heterotopic. These stenotopic species do not leave the bank to complete their life cycles; their reproductive stages, be they sexual or asexual, are attained upon the bank and reproduction occurs thereon. Their populations here should therefore be of much the same size as those of the loch margin; but in fact most of them are much smaller.

There are, for example, 950 Asellus aquaticus per sq. m. at Station 1 and only one fifth as many, that is 190 per sq. m. on the bank; and A. aquaticus feeds upon decaying vegetable matter (Cooper, 1925, Collinge, 1946, 20). Most of the oligochaetes show the same sort of reduction in population/

population and are also detritus feeders. Thus Marionina sp. occurs to the extent of 140 per sq. m. at Station 1 and only 35 per sq. m. on the bank; Eiseniella tetraedra is only one twentieth as frequent on the bank as at Station 1; Peloscolex ferox, one thirteenth; Paranais sp., one fifth; Lumbriculus variegatus, one eighteenth; Tubifex tubifex and Limnodrilus sp., one half. The Pisidia, also detritus feeders, are three times more numerous at Station 1 than on the bank; the mites, six times; and Alona affinis, about nineteen times. There is little to be gained by adding to this list; it would merely make tedious reading; for the phenomenon is widespread amongst the stenotopic species.

If the detritus factor is mainly responsible for these reduced popu:lations of detritus feeding stenotopic species, it must also be respon:sible for a part at least of the reduction in the case of detritus feeding heterotopic species. It is significant that whilst only four of the chironomids of the marginal zone continue to be well represented on McDougall Bank three of these, namely Cryptochironomus, Procladius and Pentaneura are carnivorous and the fourth, Limnochironomus may also be carnivorous (see p. 29). For a carnivore will not be affected directly, but only indirectly and through the intermediacy of its prey, by a reduc:tion in the amount of nutritive detritus in the substratum; and the more various its prey the smaller will be this indirect effect. On non-carnivores the effect will be direct and unmitigated, and one therefore finds/

finds that C. (Microtendipes), C. (Polypedilum), C. (Pentapedilum) nubens and Tanytarsus spp. are extremely scarce on the bank, though well represented at Stations 1 and 2.

In the two areas we have been comparing, the loch bed receives its organic detritus from three main sources: 1) the plankton, both animal and plant, above it; 2) the phytobenthos upon it; and 3) allochthonous debris which falls or is washed or blown into the loch from outside.

At Station 2 the quantity of Isoetes and Nitella is only slightly greater than on the bank, and, since both places have the same depth of water over them, the quantity of dead plankton reaching the one will be almost the same as that reaching the other. As for Station 1, whereas it has more phytobenthos it has almost half as much water and therefore almost half as much plankton over it as has the bank. It is likely, therefore, that the amounts contributed by the first two of the sources together, to bank and to margin of loch are much the same; and that most of the difference between detritus content of these two regions is due to the third source, allochthonous debris. One region, the marginal, lies very close to the land from which this allochthonous debris comes; the other, McDougall Bank, is on all sides very far from land, never closer than 750 m. to it. It seems reasonable to suppose that less allochthonous debris, probably much less, reaches the bank than the loch margin; and that this is one of the main ultimate causes of the difference in productivity/

productivity between these two rather similar regions.*

4. EUTROPHISM IN OLIGOTYPIC LAKES.

Returning to the phenomenon of eutrophism in the marginal regions of certain oligotypic lakes, we are now in a position to see that Brundin's suggestion that it follows from the scarcity of the macrophytic vegetation in these regions is not likely to be correct. He says (1949, p. 867), "the fact that the littoral region of an oligotypic oligohumic lake is so rich in species and in individuals is probably due to its poor vegetation, which leaves enough space, and secures the most favourable oxygen condi:tions. In the dense vegetation of the eutrophic lake conditions of existence are not so favourable in this respect".** But we have just seen that the benthos of the McDougall Bank is much poorer than that of the phytal margin of the loch, though its vegetation is sparser and not denser, and though the oxygen content of the water layers in contact with it are no higher. And we have also seen that this relative poverty seems to be due mainly to the small amount of allochthonous debris that reaches the bank.

This same factor is, I believe, responsible for the anomalous eutro:phism we are now considering. For if the drainage basin of an oligotypic lake/

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* The other main cause being the difference in accessibility already referred to.

** Translated from the German original.

lake is well wooded, particularly along its shores, then allochthonous debris may reach its marginal zone in quantities large enough to counter-:balance its oligotypic nature, even to the extent of producing eutrophism. Little of this allochthonous matter will reach regions of the lake bed distant from the shores - as conditions on Mc Dougall Bank have suggested - and their main source of detritus will therefore be plankton. Hence these regions will correctly reflect the oligotypy of the lake waters and will be oligotrophic.

The bathymetric distribution in Loch Lomond of detritus feeding species like _Asellus aquaticus_, _Peloscolex ferox_, _Caenis horaria_, _Ephemera danica_ and _Culicoides cubitalis_ (q.v.) for example indicates that there is a rapid decline in the nutritive value of the bottom deposit with increase in distance from the loch margin, and fits in well with the view expressed above regarding the part played by allochthonous matter. It is there-:fore particularly significant that the drainage basin of Lomond includes extensive woodlands and that much of its shore line is wooded; and also that Brundin (1949) states that Lake Innaren lies in well forested country. Both lakes exhibit this phenomenon of anomalous eutrophism.

5. CONCLUSION.

If the hypothesis postulated above proves correct, then the abundance, and possibly the nature, of the plant cover on the drainage basin of a lake/

lake is of greater importance in determining the richness of its benthic fauna than has hitherto been recognised. And other anomalous cases which have been discovered in the course of studies on lake productivity may be due to the disturbing effect of this factor. Lake Simcoe in Canada is an example. Its temperature, dissolved O_2 and other chemical features point to eutrophy; its benthos which contains much Corethra and is dominated by the chironomid C. plumosus, also points to eutrophy. Yet it contains only about 800 animals per sq. m. in its profundal zone (Rawson, 1930). Others are certain Japanese lakes, like Saino and Mara, which ought similarly to be eutrophic but contain such sparse faunas that Miyadi (1930-1, I, 1932-3, X) has had to create a special lake type - the oligotrophic-plumosus - to include them.

And it may be found that a sure and cheap way of increasing the productivity of a lake - especially an oligotypic one - is to introduce large quantities of dead plant matter into it.

Table 11. Distribution of heterotopic species.

	A	B	C	D
	Marginal (-Phytal) Zone of Loch	Upper Transitional Zone	Lower Transitional Zone	Phytal Area of Bank
Depth in metres	0-4	c. 7	9-13	2-4
No. of Petersen samples examined in 13 months	39	39	78	78
Group (i)				
<u>Plecoptera</u>				
Amphinemoura cinerea	+	-	-	-
Nemurella inconspicua	+	-	-	-
Leuctra fusciventris	+	-	-	-
L. hippopus	+	-	-(1)	-(1)
L. (moseleyi ?)	+	-	-(1)	-
L. nigra	+	-	-	-
Nemoura avicularis	+	-	-	-
Chloroperla torrentium	+	-	-	-
<u>Odonata</u>				
Enallagma cythigerum	+	-	-	-(1)
<u>Ephemeroptera</u>				
Ecdyonurus dispar	+	-	-	-
Ephemerella ignita	+	-	-	-
Cloeon simile	+	-	-	-
Centroptilum luteolum	+	-	-	-(4)
Leptophlebia sp.	+	-(1)	-	-(3)

Table 11 (contd.)

	A	B	C	D
Trichoptera				
Phryganea sp.	+	-	-	-(1)
Limnophilus marmoratus	+	-	-	-
Halesus digitatus	+	-	-	-
Chaetopteryx villosa	+	-	-	-
Sericostoma personata	+	-	-	-(1)
Goera pilosa	+	-	-	-
Tinodes waeneri	+	-	-	-
Lype phaeopa	+	-	-	-
Hydroptila femoralis	+	-	-	-
Diptera				
Hemerodromia sp.	+	-(8)	-	-(3)
Tipula sp.	+	-	-	-
Limnobiid (2 species)	+	-(1)	-(1)	-
Dasyhelea sp.	+	-	-	-
Stilobezzia	+	-	-	-
Anatopyma (M.) goetghebueri	+	-	-	-(2)
Orthocladiines (about 5 species)	+	-	-	-
Prodiamesa olivacea	+	-	-	-
Diamesa (P.) lacteipennis	+	-	-	-
Group (ii)				
Ephemeroptera				
Ephemera danica	+	+	-	-
Diptera				
Culicoides cubitalis	+	+	-	-(3)
Orthocladiines (about 5 species)	+	+	-	-

Table 11 (contd.)

	A	B	C	D
Group (iii)				
<u>Diptera</u>				
Palpomyia sp.	+	+	+	+
Dicrobezzia venusta Johannsenomyia nitida	+	+	+	+
Bezzia sp.	+	+	+	+
Pentaneura spp. (4 species)	+	+	+	+
Procladius spp. (2 species)	+	+	+	+
Anatopymia (M.) trifascipennis	+	+	+	+
Tanytarsus (T.) glabrescens	+	+	+	+
T. (Mocrospectra) sp.B	+	+	+	+
Chironomus (Cryptochironomus) spp. (3 species)	+	+	+	+
C. (Pentapedilum) nubens	+	+	+	+
C. (Polypedilum) spp. (3 species)	+	+	+	+
C. (Chironomus) sp.	+	+	+	+
Orthocladiines (about 2 species)	+	+	+	+
Group (iv)				
<u>Ephemeroptera</u>				
Caenis horaria	+	+	-(2)	+
<u>Trichoptera</u>				
Leptocerus spp.	+	+	-	+
Mystacides azurea	+	+	-	+
M. longicornis	+	+	-	+
Oecetis lacustris	+	+	-	+
O. ochracea	+	+	-	+
<u>Diptera</u>				
Tanytarsus (T.) holochlorus	+	+	-	+
T. (T.) atridersum	+	+	-	+
T. (Microspectra) sp.A	+	+	-	+
T. (Stempellina sp.A	+	+	-	+
Chironomus (Microtendipes) spp. (2 species)	+	+	-	+
Pseudochironomus prasinatus	+	+	-	+

Table 11 (contd.)

	A	B	C	D
Group (v)				
<u>Trichoptera</u>				
Lepidostoma hirta	+	-(1)	-	+
Cyrnus trimaculatis Cyrnus flavidus	+	-(2)	-	+
Oxyethira simplex	+	-(1)	-	+
<u>Diptera</u>				
Tanytarsus (Stempellina) sp.B	+	-	-	+
Chironomus (Pentapedilum) flavipes	+	-	-	+
C. (Endochironomus) sp.	+	-	-	+

CHAPTER VI

REPOPULATION OF MCDOUGALL BANK WITH HETEROTOPIC BENTHOS

INTRODUCTION

It has already been pointed out that Mc Dougall Bank is an oval platform-like elevation of the loch floor, lying in the mouth of Auchen-:tullich Bay. About 250 m. long and 70 m. wide, it lies 750 m. or more from dry land, except to the west and north-west. Here it is somewhat closer, but even so the distance is over 500 m. (Map 3).

Upon the bank is found macrophytic vegetation consisting mainly of Nitella opaca Ag. and Isoetes lacustris L.. This patch of vegetation is separated from the vegetation zone of the loch margin and of the islands, by an aphytal zone of the loch floor, which is over 700 m. wide except to the north-west, where a shallows along the shore reduces the distance between the vegetation zones of the bank and loch margin to about 450 m. (Map 3).

Collections made before this investigation was begun had suggested that most of the heterotopic species found in the benthos of the inshore vegetation zone were also found on McDougall Bank but were absent from the aphytal zone between them. Heterotopic species periodically leave the water and spend part of their lives as non-aquatic insects, before returning to the water generally in the egg-stage. McDougall Bank, will therefore be periodically depopulated of these species.

THE SPECIES INVOLVED/

THE SPECIES INVOLVED

The results of the quantitative benthic survey of February, 1949 to February, 1950, show that the number of insect larvae which are restricted to the bank and the loch margin and absent from the zone between them, is much smaller than was originally supposed.

From the list, in Table 11, of heterotopic species found in the survey, I have excluded all those in which the sexually mature adult is aquatic, even though a part of its life-cycle is still spent outside water. For the adults of such species will not find the water of the loch a barrier separating them from the larval habitat, or from the place where the eggs have to be laid. They will have no difficulty in reaching McDougall Bank and in laying thereon. Examples of these species are Limnius tuberculatus, Corixa distincta and Micronecta poweri.

Of the species remaining in the list, it will be seen that the great majority (over 75%) consists of (i) species which are confined to the vegetation zone of the loch margin, (ii) species which do extend somewhat beyond the vegetation zone of the loch margin, down to about 7 m., but are not found beyond that, nor on McDougall Bank, and (iii) species which are found all the way from the shore to McDougall Bank and even beyond it. All these have a continuous distribution[x] upon the loch floor; and whatever/

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x A larva was sometimes captured outside its normal habitat (see bracketed figures in Table 11), but these instances are too infrequent to be indicative of a wider range for the species. The animal was probably washed out of its habitat by off-shore currents.

whatever the means by which this distribution is achieved, the presence of certain of them (group iii) on McDougall Bank presents us with no special problem.

Just about 25% of the species in the list have that sort of disconti:nuous distribution that makes it necessary to ask how they return periodi:cally to McDougall Bank. Some of them (group v) are confined to the vegeta:tion zones of bank and loch margin; others (group iv) seem to extend a little beyond these zones; but all of them are absent from the deep aphytal loch floor which completely surrounds the bank.

They consist of:- the ephemeropteran Caenis horaria; the trichopterans Mystacides azurea and M. longicornis, Leptocerus spp., Oecetis lacustris and O. ochracea, Lepidostoma hirta, Cyrnus trimaculatus and C. flavidus, and Oxyethira simplex, the chironomids, six species of Tanytarsus, Pseudochironomus prasinatus, Chironomus (Microtendipes) spp., C. (Pentape:dilum) flavipes and C. (Endochironomus) sp..

Attention during this investigation was directed mainly at the trichopterans, but where information has been obtained about the other species it will be included in the discussion below.

POSSIBLE METHODS

The method by which the bank is repopulated by each of these species will depend upon the way its eggs are laid. Oxyethira simplex enters the water and attaches its string of eggs to a submerged water plant, and

Cyrnus/

Cyrnus flavidus deposits its eggs as a flat plate cemented to the under-:surface of the floating leaf of an aquatic plant (Siltala, 1906).

In _Mystacides azurea_, _M. longicornis_, _Oecetis lacustris_ and _Lepidostoma hirta_ oviposition is of a different type. A small spherical mass of eggs is extruded from the tip of the insect's abdomen and dropped into the water. The mass sinks to the bottom and sticks firmly to it. Oviposition in the remaining species, namely _O. ochracea_ and _Leptocerus_ spp. is very probably the same for Siltala (1906) reports that it is typical of the leptocerid genera _Oecetis_, _Mystacides_ and _Leptocerus_. Oviposition in the mayfly _Caenis horaria_ is much the same but the mass of eggs disintegrates as it sinks through the water.

McDougall Bank may receive its population of these species by one or perhaps more of the following methods:-

a) transport of egg-masses or eggs by water currents, from loch margin to bank except in the cases of _O. simplex_ and _Cyrnus_ spp.;

b) active migration of larvae from loch margin to bank;

c) detection of, and oviposition on the bank by gravid females;

d) indiscriminate laying all over the loch, and therefore on the bank by gravid females.

Each of these methods will be considered below.

TRANSPORT OF EGGS

When/

When oviposition occurs, i.e. in the summer, the water level of the loch is low and McDougall Bank is never covered by more than 3.2 m. of water. On an average the depth of water is about 2.8 m., though it is sometimes as little as 2.0 m.. (See Fig. 7).

One may therefore safely assume that the maximum vertical distance through which an egg-mass laid in inshore waters may fall, as it is being carried across to McDougall Bank, is 3.2 m.. Whilst falling through this distance, it has to traverse a horizontal distance of 450 m. at the very least; this being the shortest distance separating the vegetation zone of the loch margin, over which it is presumed oviposition occurs, from that of the bank (Map 3).

I have measured the rate at which egg-masses of the following insects sink through undisturbed loch water in the summer:- Mystacides azurea, M. longicornis, Oecetis lacustris, Lepidostoma hirta, and Sericostoma personata amongst the caddis flies; Ephemerella ignita amongst the mayflies. The timing method used was not very accurate but showed quite definitely that it took these egg-masses, which varied in diameter from about 1.5 to about 2.5 mm., approximately 10 seconds to fall through a column of water 20 cms. high.

I have not measured the sinking rate of Caenis horaria eggs, but Percival and Whitehead (1926) have done so for those of E. danica and found it to be 0.5 cms. per second. The eggs of C. horaria are smaller than those of E. danica, but not much smaller, and it is probable that their rate/

rate of sinking is much the same. To be on the safe side, however, I shall assume that they sink twice as slowly, namely at a rate of 0.25 cms. per second.

It only requires a simple calculation now, to show that a current with a minimum speed of 280 cms. per second will be necessary to carry egg-masses of the caddis species from the loch margin to the surface of McDougall Bank. In the case of Caenis horaria eggs the minimum speed though much less is still quite large, namely 35 cms. per second. Even currents of this sort of speed (35 cms. per second) could be produced in Loch Lomond only by strong winds (cf. Wedderburn's observations on Loch Garry, 1909); and these winds will have to reach gale strengths before currents with anything like the speed of 280 cms. per second are produced.

It is important therefore that the observations I made during the summers of 1949 and 1950 upon the swarming and oviposition of caddis flies have shown that the oviposition and indeed flight of any sort is impossible except during periods of calm or of very light breeze. This applies to mayflies and to chironomids as well.

A number of attempts were made by me during the summer of 1949 to measure water-current speeds when wind conditions were suitable for laying. The Ekman current meter did not on any of these occasions register a measu:rable current. But I have, by timing objects on the water surface as they floated past the anchored boat, detected currents which were sometimes as fast as 5 cms. per second. Generally, however, they were much slower. These/

These s peeds are quite insufficient to carry to the bank eggs or egg-masses deposited along the loch margin.

Nor are those laid under calm conditions available for transport later on, should strong winds subsequently set in. For the egg-masses of these caddis flies adhere firmly to the substratum they settle on, by a sticky cementing substance borne upon their surfaces; and the eggs of C. horaria by adhesive threads. I have upon two occasions subjected egg-masses of Lepidostoma hirta and Sericostoma personata, adherent to the bottom of a glass breffit jar, to water currents of speeds of about 100 cms. per second. These were produced by violently whirling around the water in the jar. In neither case was the egg-mass detached. It is therefore improbable that an egg-mass which has come to rest upon the bottom of the loch, will be washed away, even by the currents produced by very strong winds. Admittedly, waves raised by heavy on-shore gales - which it should be noted are themselves not very frequent in Auchentullich Bay - do tear off vegetation and portions of the loch bottom; and with these, of course, must come any adherent egg-masses. But such material is not carried out to McDougall Bank. On the contrary, it is thrown up upon the shore.

These considerations alone make it very unlikely that water currents are responsible for the carriage to McDougall Bank of eggs or egg-masses of the species referred to. But there are also other facts which point to the same conclusion.

Thus though caddis egg-masses were recovered from samples taken with the/

the Petersen grab from Stations 1 and 2 in the summer of 1949 during the benthic survey, they were never found in similar samples taken from Stations 6 and 6B on McDougall Bank.

Furthermore, in *Caenis horaria*, Figure 20 shows that immediately following the period of emergence, which is indicated by an absence of larvae in June and July, there is a sudden and very pronounced rise in popu:lation density at Station 1* in August. This is made up entirely of very small sized larvae - the smallest found throughout the year and, undoubtedly, members of the new generation. These larvae are presumably quickly dis:persed over their habitat in the loch margin for the peak has disappeared by September. Since this peak is sharply circumscribed in time, it follows that the eggs, from which are derived the larvae producing the peak, must also have been laid within a short period of time. If some of these eggs were carried to the bank by currents, immediately upon their being laid, then the population density of McDougall Bank should show a similar sharp rise of short duration. In fact, however, it shows no such rise (Fig. 20), an absence which is rendered all the more striking by the coincidence on the bank and the loch margin of the fall in population which marks therperiod of emergence. This difference in the seasonal variation of population density is therefore a very important indication that

Caenis/

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* The same phenomenon occurs at Station 2, and has not been graphed.

Caenis horaria eggs are not transported to McDougall Bank by water currents.[x]

Similar differences between bank and loch margin have been found in the seasonal variation of leptocerid caddis worms (Fig. 21), Pentaneura populations (q.v.) (Fig. 26) and T. (T.) holochlorus (q.v.) populations; and point to the same conclusion, namely the egg-masses of these species are not carried to the bank by water currents.[x]

ACTIVE MIGRATION OF LARVAE

The differences which have just been discussed, in the seasonal variation of population density between bank and loch margin, are what one should expect if eggs are laid near the shore only, and if the larvae hatching from these eggs make their way actively to the bank, the migration being spread over a fairly long period of time. Unfortunately for this hypothesis, none of the larvae concerned is capable of movement that is both rapid and sustained. Caenis horaria, for example, is a very clumsy swimmer, and does so in short and infrequent bursts, preferring to spend its time crawling over weeds or over the bottom deposits. This it does at speeds that seldom exceed 1 cm. per second. Of the caddises, larvae of Lepidostoma hirta, Leptocerus spp., Mystacides spp. and Oecetis spp. are all crawlers and very slow at that. They seldom move faster than 0.5 cm. per second/

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[x] These differences also indicate, of course, that eggs and egg-masses of these species are not carried to the bank by the imagines.

second. Oxyethira simplex is even slower, covering a centimetre of ground in about 3 seconds. Cyrnus flavidus and C. trimaculatus are the only ones that can swim, but as with C. horaria, this swimming is in short bursts; it seems to be an escape mechanism more than a method of moving from place to place. These larvae spend most of their time in their silken nests, and when they crawl do so at about 1 cm. per second.

In these circumstances C. horaria will take at least 8 hours to cover the minimum distance of 300 m. separating its home on the loch margin from that on the bank (i.e. between the 7 m. contour lines - see Map 3). Cyrnus spp. will take 12½ hours to cover the 450 m. separating the outer limit of its range on loch margin from McDougall Bank. Leptocerus spp., Mystacides spp. and Oecetis spp. will take at least 16½ hours (for 300 m.); Lepidostoma hirta at least 25 hours;(for 450 m.); and Oxythira simplex at least 37½ hours (for 450 m.).

These figures have been calculated on the assumption that movement is continuous. This,is, in fact, not so, all these larvae interspersing periods of quiet between periods of movement. It has also been assumed that migrating larvae will cross over to the bank where the aphytal zone around it is narrowest; that is, north-west of the bank (Map 3). But if migration does indeed occur there is no reason to suppose that larvae will not make for the bank from the loch margin all round it. The distances they will have to travel will generally be twice as great as have/

have been assumed.

If therefore one multiplies the calculated migration times by a fairly large factor, say 4, one will obtain a much closer approximation to the real migration times. Thus Caenis horaria will probably take at least 32 hours to reach McDougall Bank; Cyrnus spp., 50 hours; Leptocerus spp., Mystacides spp. and Oecetis spp., 66 hours; Lepidostoma hirta, 100 hours; and Oxyethira simplex, 150 hours.

In each of these cases the larva has to spend a relatively long period of time in a habitat in which it does not normally live; a habitat which may lack some essential environmental factor, food for example, or a firm substratum for the migrants to crawl upon; or which may contain some deleterious factor, a very fine sediment for example which will impede the functioning of larval gills, or into which the larvae themselves may sink.

This being so, a very powerful stimulus, of which there is no evidence, will be necessary to induce larvae already living in a suitable habitat, to leave that habitat and to enter such an unsuitable one, merely in order to cross it and reach a new habitat (McDougall Bank) which is in no way more suitable than the one they left.

Furthermore, in 1950 samples were taken, with a dredge, of the surface mud from the loch-bed near Station 4 (Map 3). The area sampled reached a total of 7 sq. m.. The period when these samples were taken extended from July to August, when if migration did occur, migrating larvae should have been found. Yet no larvae of these species were ever found in the samples.

Chironomid/

Chironomid larvae are generally capable of swimming for fairly long periods and it is probable that none of the species we are concerned with is an exception to this. It should therefore be possible for them to make their way across to the bank quite quickly, provided there is a suitable stimulus to attract them, and of this again there is no evidence.

DETECTION OF BANK BY OVIPOSITING FEMALES

This third alternative was examined in two main ways - by observation of the behaviour of those caddis flies in the field and by trapping them quantitatively.

From mid-June to mid-September, 1949, I spent much time, not only on the shore of Auchentullich Bay but also over McDougall Bank and over the deep waters between bank and shore, observing the insects and noting at regular intervals, light intensity, wind strength and direction, cloud cover, air and surface water temperatures, etc.. It became apparent, soon after these observations had begun, that though the bank had previously to be found by sounding, it was in summer covered by so shallow a layer of water (2.3 to 3.2 m. deep) as to be visible to a human observer in a boat over it. Light had of course to be good, and the water surface undisturbed by ripples. In these circumstances the bank reflected sufficient light back into the air for it to be visible as late as 9 p.m. GMT in June-July, 8.00 p.m. in mid-August, and 7.30 p.m. at the end of August.

Here, it seemed at first, was an obvious means, reflected light, by which/

which laying females might be guided to Mc^{D}ougall Bank. Further observa-:tions, however, soon showed that laying occurred in the dark, or at best in very poor light, even in the case of those species like M. azurea, whose swarming is a diurnal phenomenon (See Ch. III).

It next seemed possible that the bank might be sufficiently heated during the day to maintain by means of convection a patch of relatively warm surface-water over itself at night. Such a patch, surrounded as it would be by relatively cooler water, might well serve as an indicator of a suitable area for laying. Measurements of surface-water temperatures were made on many occasions; and disproved this possibility completely.

Furthermore, measurements of O_2 content, pH and temperature of the water within 0.5 m. of the bottom, where any differences due to different natures of the bottom deposit and of bottom vegetation should be most marked, showed that no such differences existed between the bank and the deep areas around it (Table 2).

This left me with one other of the more obvious factors that might produce a difference between surface-waters over bank and elsewhere that would be detectable by gravid female insects. That factor was scent. For it was possible that the vegetation of the bank gave out into the waters above it some chemical substance which, carried by convection currents to the surface, was there detectable by the gravid female. Walker and Hasler (1949) found that the blunt-nosed minnow Hyborhynchus notatus, was able to detect at extremely great dilutions (1 in 10,000 or more) water that/

that had been in contact with aquatic vegetation. Gravid insects might be equally sensitive. I was unable to test this possibility in the summer of 1949, and by the next year the results of my trapping experiments had rendered it unnecessary to pursue the matter. Besides, certain instances of aberrant laying in caddis flies and mayflies suggested that it was unlikely that scent played a part in guiding them to their laying sites. Thus Verrier (1941), Lestage (1937) and Denis, Paris and Pillon (1936) have found various mayflies laying on wet motor-car hoods, on soil and even on dry, tarred roads. *Caenis horaria* L. has been observed laying upon wet leaves of *Glyceria* plants growing many metres from the nearest stream (Lestage, 1937). I have found egg-masses of the caddis flies *Mystacides azurea*, *Oecetis lacustris* and *Seriocostoma personata* laid upon a rain-moistened wooden pole, on which they later perished by drying (see Ch. III). In view of this it seemed highly improbable that *Caenis horaria* and the species of caddis flies concerned were attracted to McDougall Bank by any scent emanating from it.

My observations on the caddis flies (Ch. III) gave me the impression that the bank was not detected by them. The diurnal forms - males of the species *M. azurea* for example - were never found swarming over McDougall Bank or anywhere else except over a narrow zone near the shore. Crepuscular species and the crepuscular sex (♀) of diurnal species did range all over Auchentullich Bay, including McDougall Bank. Numbers were everywhere much smaller than along the shore, but as between the bank and the deep areas/

areas around it there seemed to be no difference. This impression was confirmed by the results of the quantitative trapping of caddis flies under-:taken to test it.

Three double-traps were placed near each of my transect Stations 2, 4 and 6. Each set of three traps was arranged in alline parallel to the shore, the central trap being about 50 m. from the traps on either side of it. Each double-trap consisted of a rectangular float anchored to the bottom of the loch. The float (Fig. 12) was of vulcanised sponge-rubber, 30 cms. x 60 cms. x 3 cms. in size. At one end it carried a vertical cotton net, (dark green in colour, mesh 1 cm., area 0.1 sq. m. approximately) supported upon a wire frame. The two legs of this frame were slipped into holes in the float, and the net stretched so as to allow one of the meshes on its lower edge to be looped over a screw in the edge of the float. This served to hold the net-trap firmly in position and at the same time allowed it to be removed with ease for changing. The second trap on the float consisted of a thin transparent rectangular sheet of celluloid, 30 cms. x 45 cms. in area, held to the float by means of a nail at each of its corners. The consistency of the float was such that these nails were easily pressed in by hand and could be as easily drawn out when the sheet-trap had to be changed. The float itself was painted an orange colour, since preliminary tests had showed that more insects seemed to settle upon this than upon boards painted white or black. Sheet and net were both coated with "Stopmoth", a proprietary tree-banding grease.[x]
They/

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x Supplied by Joseph Bentley Ltd., Barrow-on-Humber, Lincs..

They were replaced by fresh sheets and nets at the end of each week.

It was found impossible to pick the caddis flies off the nets without seriously damaging them, and the first week's net-trappings were thus lost. Thereafter instead of attempting to remove the insects from the trap before treating them with a mixture of ethyl acetate and acetic acid (1:1) to dissolve away the "Stopmoth" (see Broadbent et al., 1948, for details of the technique) I slipped the whole net off its frame and heated it in a beakerful of the mixture, and was able to recover all the caddis flies undamaged. They were preserved in 70% alcohol; and examined in the following April, i.e. as soon as time permitted.

Most of the caddis flies on the sheet-traps had legs, wings, antennae and even heads detached from their bodies by waves having broken over the float. If they were to be preserved it would have been necessary to remove, degrease and bottle each specimen separately; a procedure that would have left me little time for the field observations and the faunistic survey then in progress. These caddis flies were therefore not removed from the sheets. They were examined through a hand-lens and the numbers recorded, of the males and the females, gravid and empty, of each species caught.

Trapping began in the first week of August, 1949, and had to be stopped after the first week of September, 1949, because of bad weather in which the celluloid sheets were torn away and sometimes even entire floats.

In/

In all very nearly 1,000 caddis flies were captured, 215[x] of them being gravid females (Tables 12, p173a 13, p173b 14, 173c). Both virgin and fecundated females have been included in the category 'gravid'.

Figure 37 shows that as far as the nets are concerned, the curves for <u>Oecetis lacustris</u>, for all Leptoceridae, and for all species together, indicate that gravid female caddis flies do not detect the bank. If they did, the number of gravid females caught over the bank (Station 6) would have been distinctly larger than that caught over Station 4. It was not.

In the case of the sheet-traps, however, it was (Fig. 37). But a statistical examination of the figures by an analysis of the variance due to trap, week and Station (see Appendix 2) showed that whilst the difference in numbers caught at Stations 2 and 4, or at Stations 2 and 6, was signi:ficant, that between numbers caught at Stations 4 and 6 was not significant.[xx]

One must therefore conclude that the distribution of gravid female caddis flies over the loch affords no evidence in support of the possibility that they detect McDougall Bank and lay their egg- masses on it.

There is other evidence which also indicates that the oviposition does not occur on McDougall Bank.

In the first place, though the spherical egg-masses typical of the Seriocostomids/

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[x] This figure does not include the results of the first week's trapping.

[xx] The difference in numbers caught by net-traps at Stations 4 and 6 was also not significant (see Appendix 2).

TRAPPING RESULTS

Table 12. Numbers of caddis flies of both sexes and all species captured by traps.

Week No.	Trap No.	SHEET TRAPS Station No. 2	4	6	8		NET TRAPS Station No. 2	4	6	8
1	1	34	3	12	-		-	-	-	-
	2	29	4	15	-		-	-	-	-
	3	27	4	14	-		-	-	-	-
2	1	62	7	23	-		6	3	15	-
	2	41	21	19	-		4	3	2	-
	3	19	22	29	-		7	3	5	-
3	1	94	23	13	-		20	7	9	-
	2	68	14	23	-		13	17	9	-
	3	71	22	22	-		25	5	11	-
4	1	-	9	4	-		-	-	1	1
	2	-	6	-	-		-	4	-	1
	3	-	5	2	-		-	2	2	0
Total (W_{1-4})		445	140	176	-	W_{2-4}	75	44	54	2
Total (W_{1-3})		445	120	170	-	W_{2-3}	75	38	51	

Note: 1. In week 4 traps were set at Station 8 instead of Station 2. Bad weather resulted in loss of all these sheets.

Note: 2. In week 1 all caddises caught by nets had to be discarded as technique for recovering them proved inappropriate.

Table 13. Numbers of female caddis flies of all species caught on traps.

Week No.	Trap No.	SHEET TRAPS Station No. 2	4	6	8		NET TRAPS Station No. 2	4	6	8
2	1	19	1	9			4	1	7	
	2	13	3	5			3	1	0	
	3	6	9	10			4	2	3	
3	1	21	3	3			5	3	5	
	2	14	0	3			6	8	2	
	3	14	3	4			10	3	3	
Total (W_{2+3})		87	19	34	-		32	18	20	-
4	1	-	1	0	-		-	-	0	1
	2	-	1	-	-		-	0	-	0
	3	-	0	0	-		-	1	1	0
Total W_4		-	2	0	-		-	1	1	1

Note: In the case of the sheet traps empty females have been omitted from the figures.

Table 14. Numbers of <u>Oecetis lacustris</u> and leptocerid females captured by traps.

Week No.	Trap No.	Oecetis lacustris: Sheet Traps, Station No. 2	4	6	8	Net Traps, Station No. 2	4	6	8	Net Traps, Station No. 2	4	6	8
2	1	16	1	7		3	1	2		3	1	7	
	2	9	3	2		2	1	0		3	1	0	
	3	6	7	9		4	2	2		4	2	2	
3	1	18	2	2		2	1	1		4	2	5	
	2	11	0	3		6	6	0		6	7	2	
	3	12	2	2		7	2	1		8	3	2	
Total (W_{2+3})		72	15	25	-	24	13	6		28	16	18	
4	1	-	1	0	-	-	-	0	0	-	0	0	1
	2	-	1	-	-	-	0	-	0	-	0	-	0
	3	-	0	0	-	-	1	0	0	-	1	1	0
Total W_4		-	2	0	-	-	1	0	0	-	1	1	1

Note: 1. In the case of sheet traps empty females have been excluded from the figures.

Note: 2. <u>Oecetis lacustris</u> generally formed about 75% of all caddis flies caught.

sericostomatids and the leptocerids were taken, at the rate of 1 per Petersen grab sample,* from Station 1 in the loch margin in July and August, 1949, none of them was ever taken from McDougall Bank. Admittedly, there are about a third as many of these larvae per sq. m. on the bank as at Station 1, and one cannto therefore expect the same number of eggs at the two places. But twice as many samples were taken during this period from the bank as from Station 1 - there being two Stations on it, 6 and 6B - and if egg-masses were laid on the bank some should have been found in these samples. But none were.

In the second place, the sharp and pronounced rise in population density of Caenis horaria, of the Leptoceridae and of Pentaneura (Figs. 20, 21, 26) which occurs at Station 1 in the loch margin is absent on McDougall Bank. I have already shown (p163-175) that this difference indicates that eggs are not transported from the loch margin to the bank by water currents. It likewise indicates that eggs are not laid on McDougall Bank.

Besides, in species where the first stage of the new generation be it egg, larva, or bud is liberated by the parent upon the bank itself, that is, in stenotopic species, any marked seasonal variation of population densities in the margin of the loch is paralleled by a similar variation on/

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* This is equivalent to a density of about 27 egg-masses per sq. m. of substratum.

on McDougall Bank. Outstanding examples are Stylaria lacustris (Fig. 15); Eurycercus lamellatus (Fig. 18), Sida crystallina (q.v.) and Asellus aquaticus (Fig. 19). Peloscolex ferox constitutes an apparent exception but an explanation of its behaviour has been suggested earlier (p. 49).

INDISCRIMINATE OVIPOSITION

The field observations referred to on p. 170 and the trapping results (p. 173 are both consistent with the possibility that gravid females (except those of Oxyethira simplex and Cyrnus spp.) drop their eggs indiscriminately into the water all over the loch; and that only those that fall upon a suitable substratum, e.g. loch margin or McDougall Bank, will develop and hatch; while the others falling upon an unsuitable substratum will perish.

But two sets of facts already referred to are very definitely against it; namely, the absence from the bank of leptocerid and Lepidostoma egg-masses, and of the pronounced seasonal rise in population densities of C. horaria, the Leptoceridae, and Pentaneura (q.v.). For egg-masses should be present and the seasonal rise should take place whether oviposition on the bank is deliberate or merely unintentional.

Besides, a careful search was made in the summer of 1950 for egg-masses of Lepidostoma hirta and of the leptocerids in an area of Auchentullich Bay, which these larvae do not inhabit, namely, around Station 4, between loch/

loch margin and bank. Egg-masses should have been present here if egg-laying were indiscriminate. The collections were made at short intervals of two or three days, during the months July and August, when oviposition occurs and when egg-masses had been found in the previous year at Station 1. A small dredge was used to collect surface mud and a total area equivalent to that covered by about 180 Petersen grabs (roughly 7 sq. m.) was ultimately sampled. The samples were examined by the technique developed for the faunistic survey, 1949-50 (see Ch. II), and known to recover any caddis egg-masses present. Yet not one egg-mass was found.

RESUME

Having set out to discover how certain heterotopic larvae reach McDougall Bank, I have succeeded in showing that their eggs are not laid on the bank either by accident or by design; that those laid inshore are not carried to the bank by water currents; and that the larvae themselves do not actively migrate to the bank from the loch margin. Yet these larvae are present each year on McDougall Bank.

HYPOTHESIS: CURRENT CARRIAGE OF PLANKTONIC LARVAE

In the summer of 1949 I happened to place in a large beaker of water an egg-mass of Phryganea sp. collected from the loch. When I next looked at the beaker, many days later, I was surprised to see large numbers of some small planktonic animal swimming about in the water. Closer examination/

examination disclosed that these were not, as I had first believed, a species of cladoceran; they were first instar larvae of Phryganea sp.. Each had a tiny case made of material from the envelope of the egg-mass. It maintained itself almost vertically in the water, with head uppermost, and swam about by a rhythmical beating of its legs. Though very surprised to find these planktonic caddis larvae I soon forgot them in the great press of work. It was not until the winter of 1950-51 that I remembered them and realised their possible significance. I had to leave Scotland before the following summer, and was unable to investigate this possibility experimentally.

Day and Wilson in 1934, and Wilson in 1937 and 1948 have shown how the discontinuous distribution of certain benthic marine worms* follows from the habit their planktonic larvae have of selecting a suitable substratum for metamorphosis. When ready for metamorphosis they settle on and crawl over the substratum. But metamorphosis does not follow unless this substratum is suitable. If it is not, the larvae swim up into the water and resume their planktonic existence. This process of testing the substratum is presumably repeated until a suitable one is found, metamor-:phosis being postponed for several weeks if necessary.

The/

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* The polychaetes Scolecolepis fuliginosa Clap., Notomastus latericeus Sars and Ophelia bicornis Sav..

The possible significance of the planktonic Phryganea larvae should now be apparent. For, if a normally benthic insect larva has a planktonic instar or phase in which it behaves in much the same way as do the worm-larvae then its discontinuous distribution on loch margin and bank will be readily explainable. Since all that would now be required to enable such larvae to reach the bank is the existence of currents in the water above the loch-bed. Such currents need not be at all fast, but they should flow from the loch margin to, and over McDougall Bank.

I have not looked for such currents in Auchentullich Bay, but there is little doubt that they do exist. For when wind blows over the surface of a lake it produces a consequent current in a relatively shallow layer of water at the surface, and return currents of opposite direction and smaller velocity in the waters below it, right down to the bottom of the lake if it is not thermally stratified; or, if it is, then down to the bottom of the epilimnion (Wedderburn, 1907, 1909, 1910; Wedderburn and Watson, 1909; Alaterberg, 1930; Mortimer, 1942, 1951).* Water in the southern/

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* Few direct measurements of the speeds of such return currents are available. Wedderburn (1909) found an easterly current of 3.3 cms. per second at a depth of 60 m. just over the bottom of Loch Garry on 28/3/08, the wind being moderate and due west. On 31/3/08 a strong west wind produced a westerly surface current of 28 cms. per second and an easterly return current at 60 m. of 3.1 cms. per second. The loch was unstratified at the time. Wedderburn and Watson (1909) worked on Loch Ness after thermal stratification had set in, and found that strong winds (strength 3-4) gave rise to return currents varying from 1 to 15 cms. per second, in the epilimnion; fastest currents were near the bottom of the epilimnion, i.e. at about 37 m., speeds decreasing with decrease in depth.

southern basin of Loch Lomond does not become thermally stratified, and its entire mass will circulate under the influence of wind. Therefore except during rare periods of flat calm there should be off-shore currents close to the loch bed. And whatever the direction of the wind some of these currents will move from a part of the loch margin towards and over McDougall Bank.

It is perhaps worth recalling here the discovery of a small stonefly larva on silt at a depth of 13 m. (Station 4) and another at a depth of 11 m. (Station 8). For the presence here of these inhabitants of the stony edge of the loch is an almost certain indication that such currents exist and may sometimes be strong enough to carry away forms adapted to clinging to stones. James Murray's discovery (reported by Wesenberg-Lund, 1905) of a few stonefly, mayfly and beetle larvae at a depth of 100 m. in Loch Ness has a similar significance.

As for the planktonic habit, it is well known that larvae of most Chironomidae and of the mayfly Caenis horaria can swim. I have noticed also that the very young Caenis horaria larvae collected in August spend much more time swimming than do the larger larvae collected at other times. Once a larva is washed away by off-shore currents it is reasonable to suppose that it will persist in swimming off the unsuitable substratum it finds itself on, again and again. Each time it swims up it will be carried further by the current and ultimately to a suitable environment on McDougall Bank or the opposite shore unless failure of the current leaves it to perish on the deep water substrate. The few larvae of Leptophlebia and/

and Centroptilum found on the bank could represent the fraction of the smaller shore population carried there in the same way.

Ability to swim seems to be wide-spread amongst caddis larvae. Handlirsch (1933-36, p. 1531) states that the young stages of most species are relatively good swimmers, some using movements of the abdomen (e.g. polycentropids), others those of the limbs (e.g. phryganeids). Siltala (1907) shows that it is generally the first instar larva that swims and reports that its claws, tarsi, tibiae and many of its bristles are relatively longer than in later instars. He suggests "that these long appendages are possibly a means to hinder sinking through the water" etc..

It is quite possible therefore that each of the species (p. 159) with which this investigation has been concerned has a planktonic phase during which it is distributed by water currents and during which it selects a suitable substratum for permanent settlement.

It is worth pointing out that if this hypothesis of the current-carriage of a planktonic phase is shown to be the correct explanation of the particular instance of discontinuous distribution that I have attempted to investigate, then it will also be strong evidence that this method plays an important part in the distribution of heterotopic benthos in general. For it is usually assumed today that when oviposition in such species occurs at or near the edge of the loch and the larvae are found some distance away, then these larvae have migrated actively to their future habitats. This may, of course, happen in some cases. But it is very probable that in others the larvae are carried about passively over the loch-bed by water/

water currents, which they leave and enter at will until they have found a suitable substratum to settle upon permanently. And though Berg has suggested that currents are responsible for the distribution of *Corethra flavicans* (1937) and of *Sialis lutaria* and various ceratopogonid larvae (1938), he seems to think of them as surface currents and furthermore he does not suggest how the larvae happen to leave these currents at the correct places.

SUMMARY

1. A quantitative survey has been made of the benthos in a wide bay of the southern basin of Loch Lomond.

2. The loch is oligotypic and oligohumic, and its bed is divisible into three faunistic zones, marginal, transitional and profundal.

3. The marginal zone is eutrophic, the profundal zone oligotrophic; and it is shown that the eutrophy of the marginal zone is probably due, in the main, to a large quantity of allochthonous vegetable matter entering it.

4. The composition of the benthos is typical of oligotypic, oligohumic lakes. In the eutrophic margins it is dominated by various Chironomidae, Oligochaeta, Pidisium and Nematoda. In the profundal zone it consists almost entirely of Peloscolex ferox, Tubifex tubifex, Pisidium sp. and Procladius sp.. Asellus aquaticus and Limnius tuberculatus also are very numerous in the upper part of the marginal zone.

5. Of the Chironomidae the genus Tanytarsus is the most abundant - in summer and in the marginal zone. At other times of the year it is less numerous than the genus Chironomus, and it does not occur in the profundal zone.

6. Tubuli-bearing larvae of the genus Chironomus, and larvae of Corethra are both exceedingly rare.

7. Of the oligochaetes the family Tubificidae is the most prominent at all depths, the most abundant species being Peloscolex ferox and Tubifex tubifex./

Tubifex tubifex.

8. 171 species and 115 genera have been identified in the benthos; and the distribution, both seasonal and bathymetric, of most of them has been discussed.

9. The benthic community characteristic of each of the sampling Stations has been described and an account given of seasonal changes in its composition.

10. The benthos of the permanently submerged McDougall Bank is essentially the same as that of the marginal zone, though it is poorer both in species and in individuals.

11. As the bank is separated by wide stretches of deep water from the marginal zone, attempts were made to discover how heterotopic species reach it each year. It is suggested that they are carried thence, in the larval stage, by water currents; and that the possession by many trichopteran larvae of a planktonic first instar is an adaptation for dispersal by this means.

12. A rapid method of recovering nearly all the animals from a sample of bottom deposit or of aquatic weeds was evolved and is described. It includes a modification of Ladell's floatation technique.

APPENDIX I.

CHECK LISTS.

THE CHIRONOMIDAE OF AUCHENTULLICH BAY, LOCH LOMOND.

The imagines listed below were, with one exception, all of them reared from larvae taken out of the loch, or captured in traps as they emerged from the loch. The single exception is Chironomus (Stenochironomus) gibbus Fabr., which I have felt justified in including in the list because a specimen was found ovipositing on the loch. The trap used was the same as that described by Brundin (1949).

My determinations of the imagines of all species, except those marked with an asterisk, have been checked by Dr. Paul Freeman of the British Museum (Natural Hiatory), London. All the larval types except those marked thus ⁂ have been examined by Mr. W.W. MacDonald, who confirms my determi:nations of the genera and subgenera.

The Chironomidae are a family with a complex and often obscure synonymy, both for the imagines as well as for the larvae. The latter have often been assigned to genera independently of the imagines into which subsequent investigation has shown them to develop. Wherever possible I have given the larvae in this list the same names as their imagines, but in order to avoid confusion I have, wherever necessary, included at least one of the larval generic names in common use. For the imagines I have adopted the names used by Kloet & Hincks (1945) in their "Check List of British Insects".

SUBFAMILY TANYPODINAE

	Imagines		Larvae
1.	Anatopynia (Macropelopia) goetghebueri Kieffer	-	A. (M.) goetghebueri Kieffer = Macropelopia.
2.	A. (Psectrotanypus) trifascipennis Zett.	-	A. (P.) trifascipennis Zett. = Psectrotanypus.
3.	Procladius (Procladius) crassinervis Zett.	-	Procladius spp.
4.	P. (Psilotanypus) rufovittatus (v.d. Wulp		
5.	Pentaneura (Isoplastus) monilis L.	-	Pentaneura spp. = Ablabesmyia.
6.	P. (I.) carnea Fabr. var. festive Meigen		
7.	P. (Pentaneura) binotata Wiedemann		
8.	P. (P.) nigropunctata Staeger		

SUBFAMILY DIAMESINAE

	Imagines		Larvae
9.	Diamesa (Psilodianesa) lacteipennis Zett.	-	D. (P.) lacteipennis Zett. ※
10.	Prodiamesa olivacea Meigen	-	P. olivacea Meigen.

SUBFAMILY ORTHOCLADIINAE/

SUBFAMILY ORTHOCLADIINAE

	Imagines		Larvae
11.	Cricotopus lacuum Edw.	)	
		) -	Spaniotoma sp. 2.
12.	Cricotopus sylvestris Fabr.	)	
13.	Metriocnemus (Heterotrissocladius) marcidus Walker *	-	M. (H.) marcidus Walker = Heterotrissocladius.
14.	Hydrobaenus (Bryophaenocladius) semivirens Kieffer	-	?
15.	?	-	Metriocnemus apicalis Kieffer.
16.	?	-	Pseudorthocladius curtistylatus Goetghebuer.
17.	H. (Psectrocladius) sordidellus Zett.	-	H. (P.) sordidellus Zett. = Spamotoma sp. = Psectrocladius sp.
18.	?	-	Trichocladius tendipedellus Kieffer. *
19.	H. (Smittia) cheethami Edw.	) -	
20.	H. (Orthocladius) oblidans Walker	)	
		) -	Spaniotoma spp.
21.	Corynoneura (Conynoneura) acutellata Winnertz	)	
22.	C. (Eucorynoneura) lacustris Edw.	)	

SUBFAMILY CHIRONOMINAE

SUBFAMILY CHIRONOMINAE

	Imagines		Larvae
23.	Pseudochironomus prasinatus Staeger	-	P. prasinatus Staeger.
24.	Chironomus (Chironomus) vulneratus Zett.	)	
25.	C. (C.) pseudosimplex Goetghebuer	) -	Chironomus (Cryptochironomus) spp. = Cryptochironomus spp.
26.	C. (C.) falcatus Kieffer	)	
27.	C. (Microtendipes) pedellus Degeer	)	
28.	C. (M.) nitidus Meigen ⁂	) -	Chironomus (Microtendipes) spp. = Microtendipes spp.
29.	C. (Polypedilum) prolixitarsis Lundstr.	)	
30.	C. (P.) albicornis Meigen	)	
31.	C. (P.) acutus Kieffer	) -	Chironomus (Polypedilum) spp. = Polypedilum spp.
32.	C. (P.) convictus Walker	)	
33.	C. (Pentapedilum) nubens Edw.	-	C. (P.) nubens Edw. = Pagastiella sp. ⁂
34.	C. (P.) flavipes Meigen	-	C. (P.) flavipes Meigen = Lenzia sp. ⁂
35.	C. (Chironomus) longipes Staeger ⁂	-	Limnochironomus sp.
36.	C. (Stenochironomus) gibbus Fabr.	-	?

37./

SUBFAMILY CHIRONOMINAE (contd.)

	Imagines		Larvae
37.	?	-	Chironomus (Endochironomus) sp. = Endochironomus sp. ⋇
38.	?	-	Synchironomus sp.
39.	?	-	Chironomus (Chironomus) sp. = Chironomus thusmi-bathophilus group. ⋇
40.	Tanytarsus (Tanytarsus) holochlorus Edw.	-	T. (T.) holochlorus Edw. = Eutanytarsus gregarius group.
41.	T. (T.) glabrescens Edw.	-	T. (T.) glabrescens Edw. = Eutanytarsus gregarius group.
42.	?	-	T. (Microspectra) sp. A. = Eutanytarsus inermipes group. ⋇
43.	?	-	T. (Microspectra) sp. B. = Eutanytarsus inermipes group. ⋇
44.	T. (T.) atridorsum Kieffer	-	T. (T.) stridorsum Kieffer = Cladotanytarsus sp. = Atanytarsus sp.
45.	T. (Stempellina) brevis Edw. ⋇	-	T. (Stempellina) sp. A. Stempellinella sp.
46.	?	--	T. (Stempellina) sp. B. Stempellina sp. ⋇

APPENDIX 2.

STATISTICAL TREATMENT OF THE RESULTS OF TRAPPING.

The variance in numbers of gravid female caddis flies caught (Tables ~~A~~ 11, ~~B~~ 12 and ~~C~~ 13) was analysed in order to find out whether significantly more of them were caught over McDougall Bank (Station 6) than over the deep waters around it. A summary of the statistical treatment and its results is given below.

I. SHEET TRAPS.

(i) <u>Gravid females of all species</u> (Table ~~B~~ 12 - 2nd and 3rd weeks only).

Note: logarithmic conversion has been applied.

Source of Variation S.V.	Degrees of Freedom N	Sum of Squares S.S.	Mean Square S.S./N	Variance Ratio	Probability	Significance
Total	17	2.7200				
Stations (2, 4, 6)	2	1.6289	0.8144	10.53	0.01-0.001	highly sig.
Stations (2, 4)	1	1.6131	1.6131	20.86	<0.001	highly sig.
Stations (2, 6)	1	0.5504	0.5504	7.12	0.05-0.01	sig.
Stations (4, 6)	1	0.2760	0.2760	3.58	0.2-0.05	not sig.
Weeks (2, 3)	1	0.0710	0.0710	0.91	>0.2	not sig.
Traps (1, 2, 3)	2	0.0915	0.0457	0.59	>0.2	not sig.
Error	12	0.9286	0.0773			

(ii) Gravid females of *Oecetis lacustris* (Table 13 - 2nd and 3rd weeks only).
Note: logarithmic conversion has been applied.

Source of Variation S.V.	Degrees of Freedom N	Sum of Squares S.S.	Mean Square S.S./N	Variance Ratio	Probability	Significance
Total	17	2.3967				
Stations (2, 4, 6)	2	1.7028	0.8514	19.93	<0.001	highly sig.
Stations (2, 4)	1	1.6045	1.6045	37.57	<0.001	do
Stations (2, 6)	1	0.8164	0.8164	19.11	<0.001	do
Stations (4, 6)	1	0.1313	0.1313	3.07	0.2-0.05	not sig.
Weeks (2, 3)	1	0.0942	0.0942	2.21	0.2-0.05	do
Traps (1, 2, 3)	2	0.0872	0.0436	1.02	>0.2	do
Error	12	0.5125	0.0427			

II. NET TRAPS.

(i) Females of all species (Table 13 - 1st-3rd weeks).

Source of Variation S.V.	Degrees of Freedom N	Sum of Squares S.S.	Mean Square S.S./N	Variance Ratio	Probability	Significance
Total	17	113.78				
Stations (2, 4, 6)	2	19.11	9.55	1.64	>0.2	not sig.
Stations (2, 4)	1	18.33	18.33	3.16	0.2-0.05	do
Stations (2, 6)	1	12.00	12.00	2.06	0.2-0.05	do
Stations (4, 6)	1	0.33	0.33	0.056	>0.2	do
Weeks (1, 2, 3)	2	22.22	11.11	1.91	0.2-0.05	do
Traps (1, 2, 3)	2	2.78	1.39	0.23	>0.2	do
Error	12	69.67	5.80			

(ii) Females of Oecetis lacustris (Table ~~6~~ 13 - 2nd and 3rd weeks only)

Source of Variation S.V.	Degrees of Freedom N	Sum of Squares S.S.	Mean Square S.S./N	Variance Ratio	Probability	Significance
Total	17	72.28				
Stations (2, 4, 6)	2	27.44	13.72	4.73	0.05-0.01	sig.
Stations (2, 4)	1	10.08	10.08	3.47	0.2-0.05	not sig.
Stations (2, 6)	1	27.00	27.00	9.31	0.05-0.01	sig.
Stations (4, 6)	1	4.08	4.08	1.40	>0.2	not sig.
Weeks (2, 3)	1	4.50	4.50	1.55	>0.2	not sig.
Traps (1, 2, 3)	2	5.44	2.72	0.93	>0.2	not sig.
Error	12	34.90	2.90			

(iii) <u>Females - all Leptoceridae</u> (Table 13 - 2nd and 3rd weeks only).

Source of Variation S.V.	Degrees of Freedom N	Sum of Squares S.S.	Mean Square S.S./N	Variance Ratio	Probability	Significance
Total	17	90.45				
Stations (2, 4, 6)	2	13.78	6.89	1.34	> 0.2	not sig.
Stations (2, 4)	1	12.00	12.00	2.33	0.2-0.05	do
Stations (2, 6)	1	8.33	8.33	1.62	> 0.2	do
Stations (4, 6)	1	0.33	0.33	0.064	> 0.2	do
Weeks (2, 3)	1	14.22	14.22	2.77	0.2-0.05	do
Traps (1, 2, 3)	2	0.78	0.39	0.076	> 0.2	do
Error	12	61.67	5.13			

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STUDIES ON THE BOTTOM FAUNA OF LOCH LOMOND.

by

A. C. J. Weerekoon.

Volume II.

(Figures)

Presented to the University of Glasgow as a thesis for the degree of Ph.D. February, 1953.

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40. do do Sphaeridae.

41. do do Gastropoda.

42. do do Hellobdella stagnalis.

43. do do Oligochaeta.

44. do do Paranais.

45. do do Arcteonais lomondi.

46. do do Tubifex tubifex.

47. do do Peloscloex ferox.

48. do do Limnodrilus.

49. do do Marionina.

50. do do Lumbriculus variegatus.

51. do do Stylodrilus heringianus.

52. do do Hydracarina.

53. do do Copepoda.

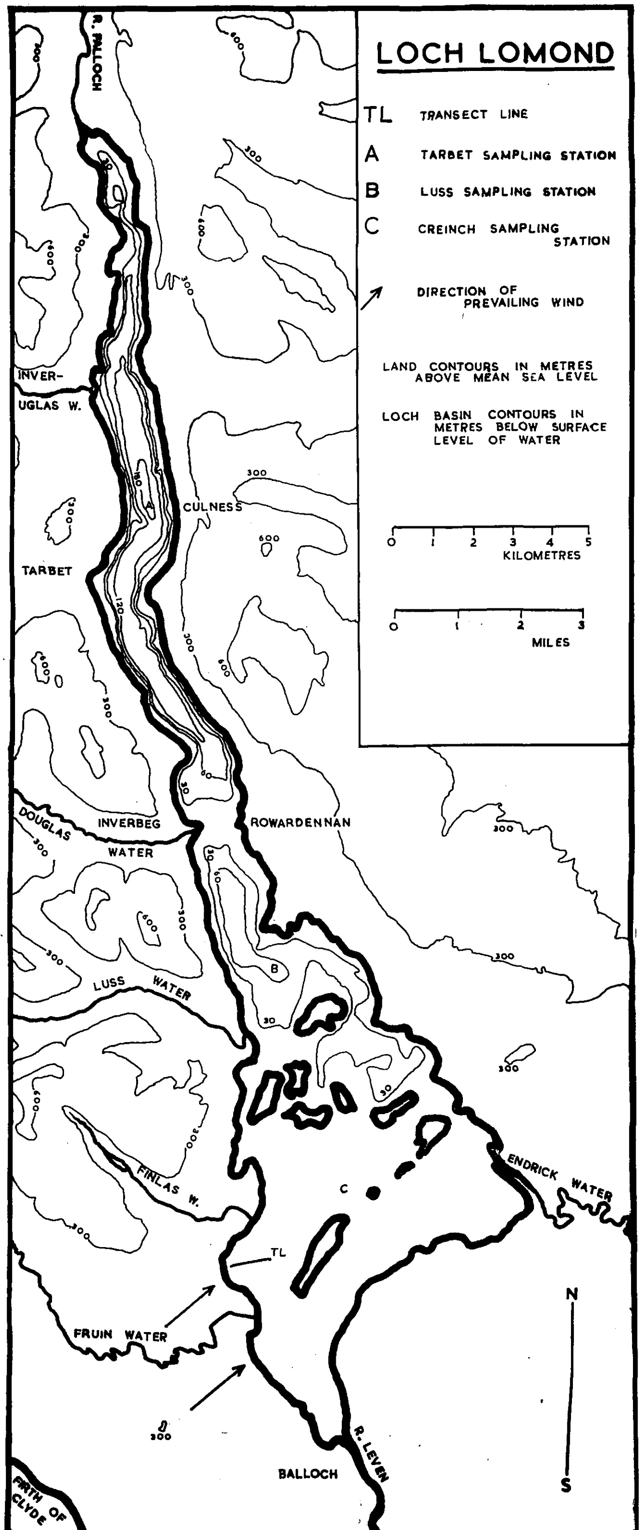
54. do do Ostracoda.

55.	Bathymetric distribution of Cladocera.		
56.	do	do	*Asellus aquaticus*.
57.	do	do	Plecoptera.
58.	do	do	Ephemeroptera.
59.	do	do	*Caenis horaria*.
60.	do	do	Trichoptera.
61.	do	do	*Limnius tuberculatus* (larvae and adults).
62.	do	do	*Hemerodromia*.
63.	do	do	Ceratopogonidae.
64.	do	do	*Bezzia* and *Culicoides cubitalis*.
65.	do	do	*Palpomyia*.
66.	do	do	Chironomidae.
67.	do	do	*Tanytarsus holochlorus*.
68.	do	do	*Tanytarsus glabrescens*.
69.	do	do	*Tanytarsus (Microspectra)* sp. A.
70.	do	do	*Tanytarsus (Microspectra)* sp. B.
71.	do	do	*Tanytarsus atridorsom*.
72.	do	do	*Tanytarsus (Stempellina)* sp. A.
73.	do	do	*Pseudochironomus prasinatus*.
74.	do	do	*C. (Cryptochironomus)*.
75.	do	do	*C. (Pentapedilum) nubens*.
76.	do	do	*C. (Polypedilum)*.
77.	do	do	*C. (Microtendipes)*.
78.	do	do	*C. (Limnochironomus)*.

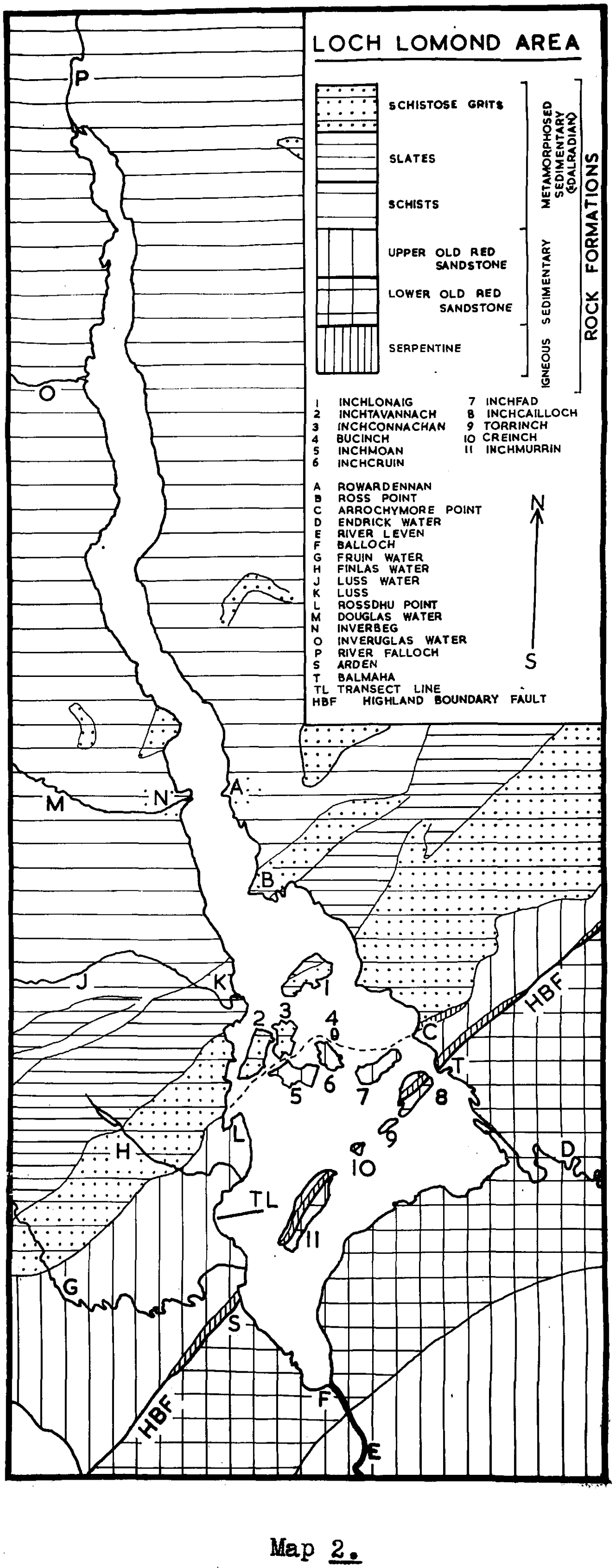
79. Bathymetric distribution of *Pentaneura*.

80. do do *Procladius*.

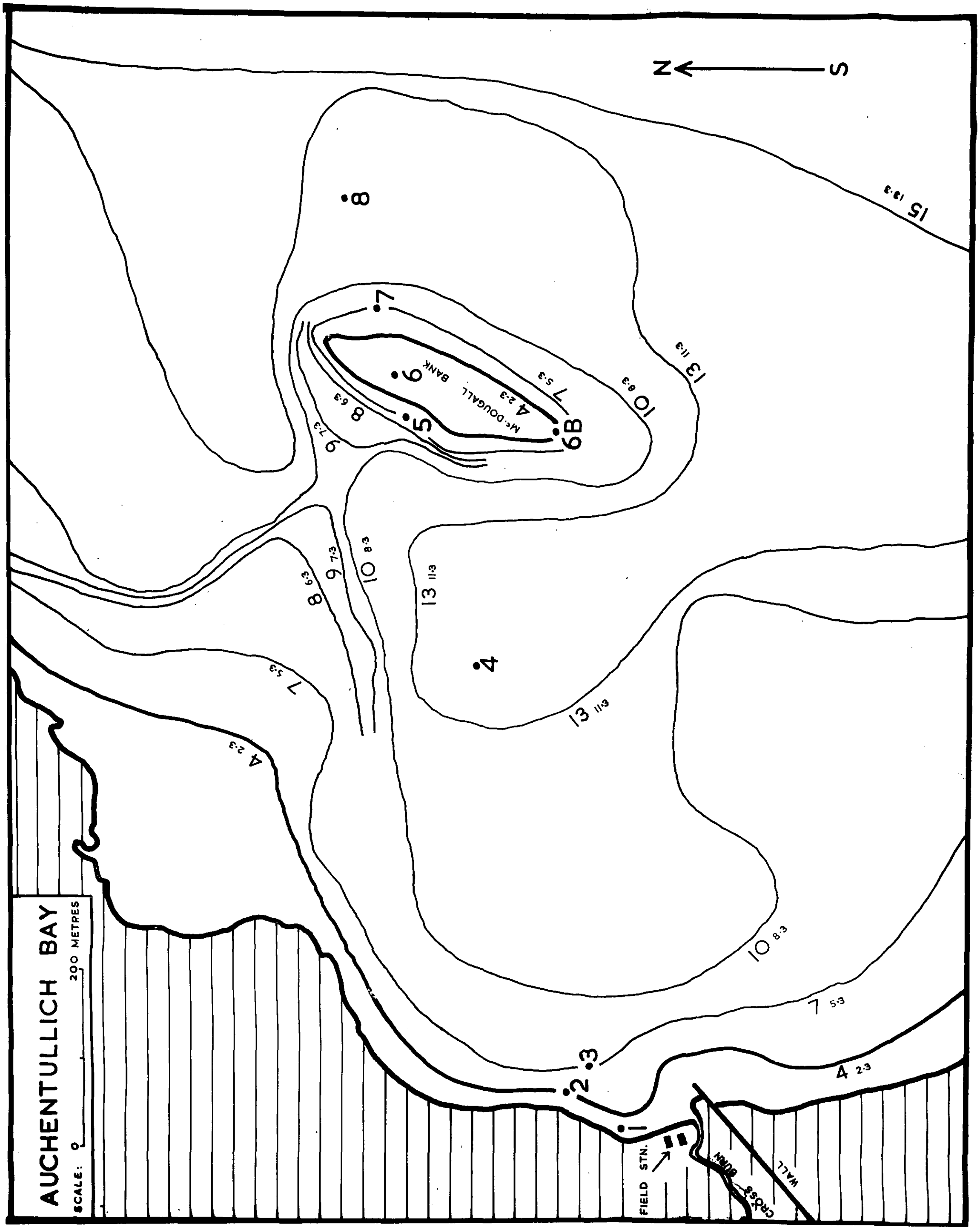
81. do do total Benthos.


LOCH LOMOND
TL TRANSECT LINE
A TARBET SAMPLING STATION
B LUSS SAMPLING STATION
C CREINCH SAMPLING STATION
DIRECTION OF PREVAILING WIND
LAND CONTOURS IN METRES ABOVE MEAN SEA LEVEL
LOCH BASIN CONTOURS IN METRES BELOW SURFACE LEVEL OF WATER
0 1 2 3 4 5
KILOMETRES
0 1 2 3
MILES
R. FALLOCH
INVER-
UGLAS W.
TARBET
CULNESS
DOUGLAS WATER
INVERBEG
ROWARDENNAN
LUSS WATER
FINLAS W.
ENDRICK WATER
FRUIN WATER
BALLOCH
R. LEVEN
FIRTH OF CLYDE
N
S

Map 1.


LOCH LOMOND AREA
SCHISTOSE GRITS
SLATES
SCHISTS
UPPER OLD RED SANDSTONE
LOWER OLD RED SANDSTONE
SERPENTINE
METAMORPHOSED SEDIMENTARY (DALRADIAN)
SEDIMENTARY
IGNEOUS
ROCK FORMATIONS
1 INCHLONAIG
2 INCHTAVANNACH
3 INCHCONNACHAN
4 BUCINCH
5 INCHMOAN
6 INCHCRUIN
7 INCHFAD
8 INCHCAILLOCH
9 TORRINCH
10 CREINCH
11 INCHMURRIN
A ROWARDENNAN
B ROSS POINT
C ARROCHYMORE POINT
D ENDRICK WATER
E RIVER LEVEN
F BALLOCH
G FRUIN WATER
H FINLAS WATER
J LUSS WATER
K LUSS
L ROSSDHU POINT
M DOUGLAS WATER
N INVERBEG
O INVERUGLAS WATER
P RIVER FALLOCH
S ARDEN
T BALMAHA
TL TRANSECT LINE
HBF HIGHLAND BOUNDARY FAULT
N
S
HBF
TL
HBF

Map 2.


AUCHENTULLICH BAY
SCALE: 0
200 METRES
N
S
Mc.DOUGALL BANK
FIELD STN.
CROSS BURN
WALL
1
2
3
4
5
6
6B
7
8
4 2·3
7 5·3
8 6·3
9 7·3
10 8·3
13 11·3
15 13·3

Map 3.

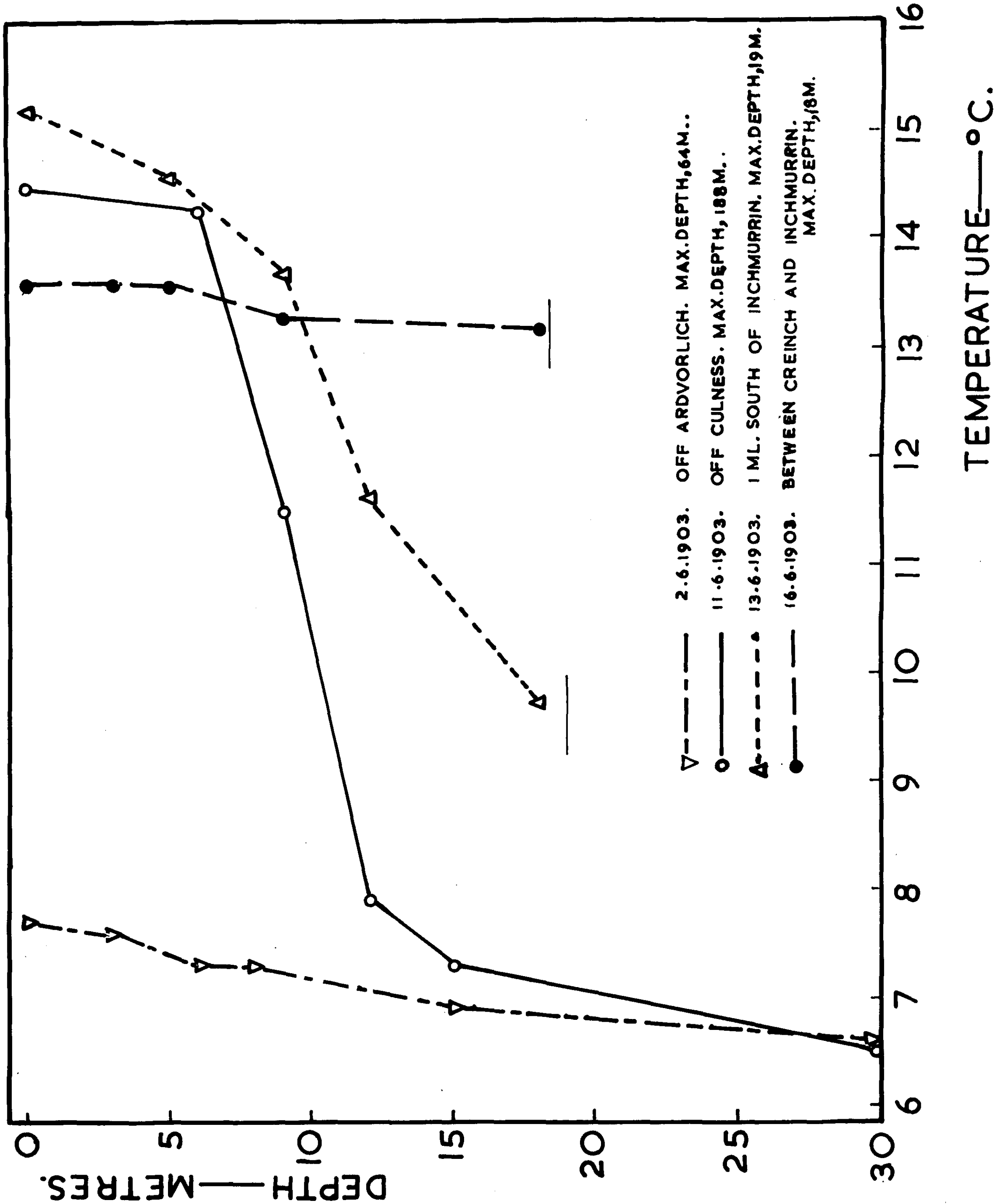


Fig.1. Temperature curves from the data of Murray and Pullar (1910).

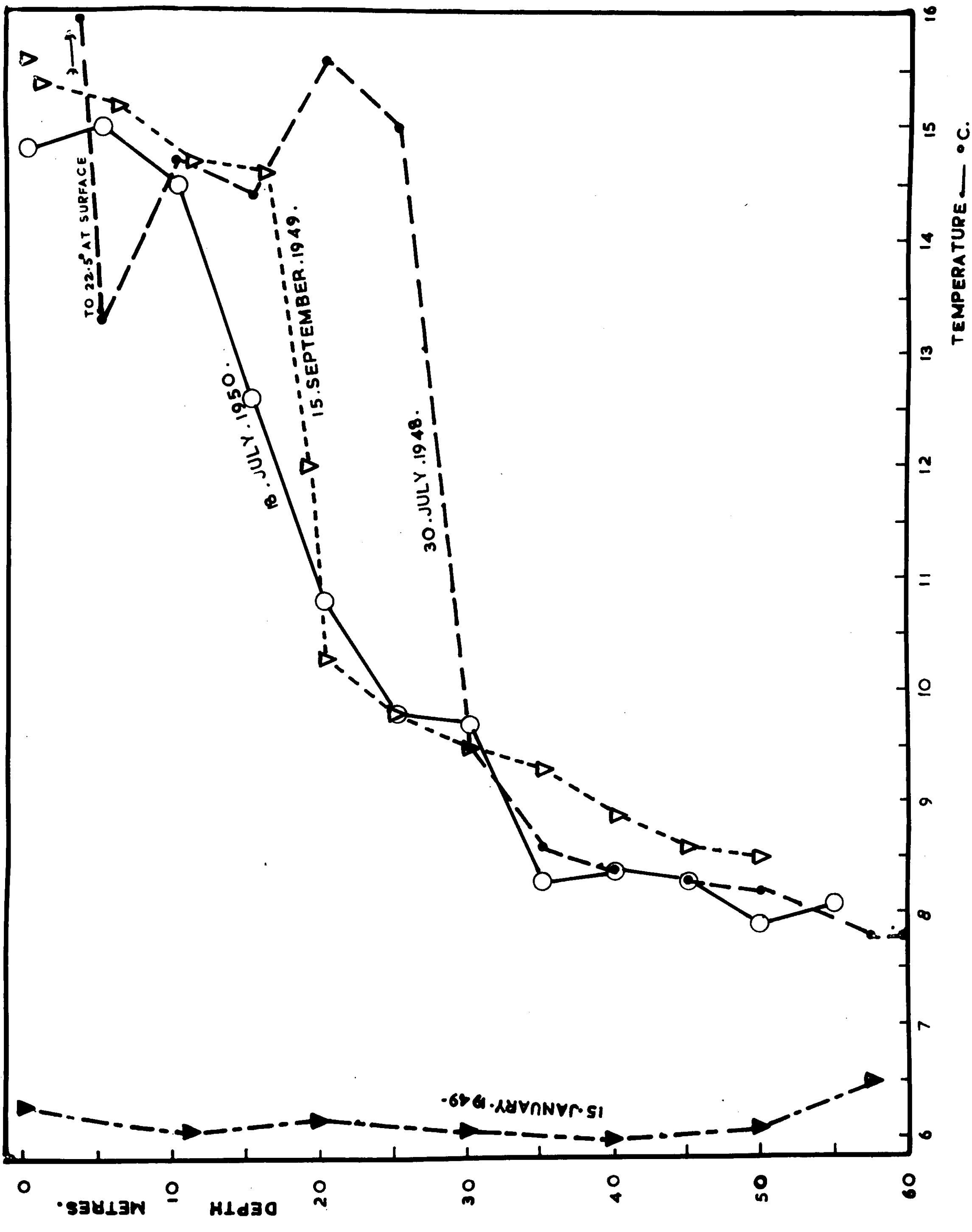


Fig.2. Temperature curves for the "highland" region

from data of the present survey.

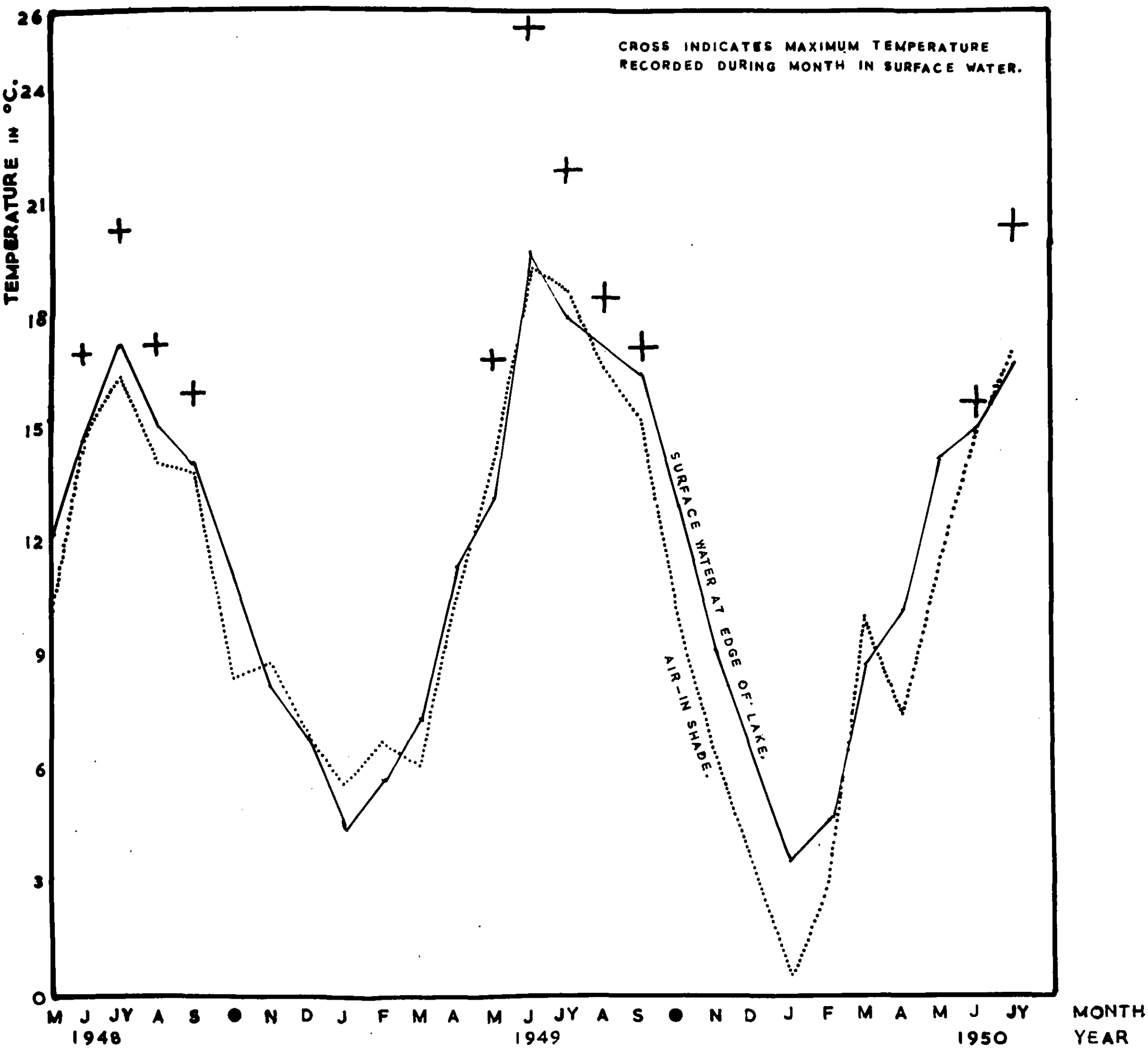


FIG.3. AVERAGE MONTHLY TEMPERATURES; FIELD STATION, AUCHENTULLICH BAY, LOCH LOMOND.

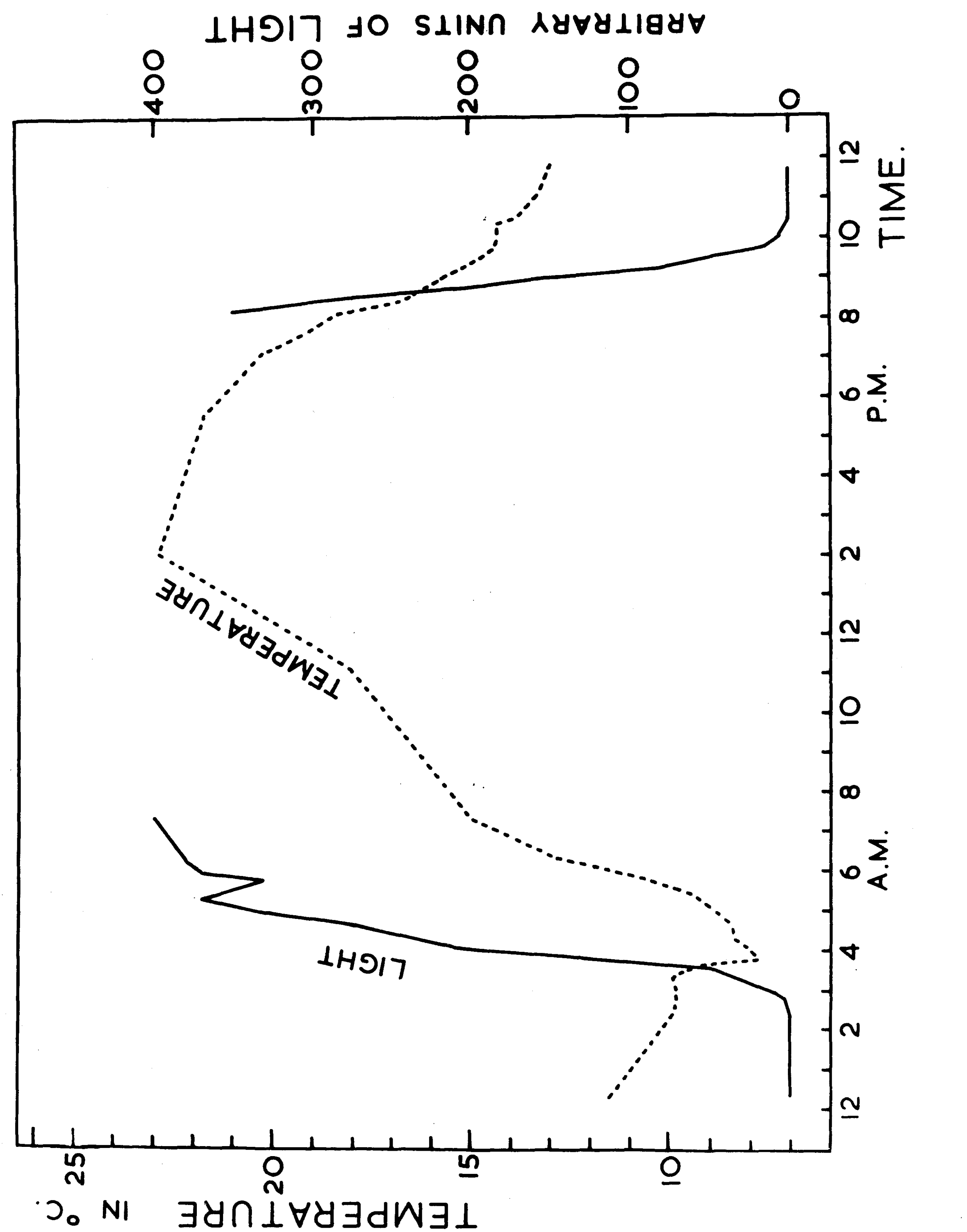


Fig. 4. Diurnal variation in air temperature (shade) and light on 7/7/49.

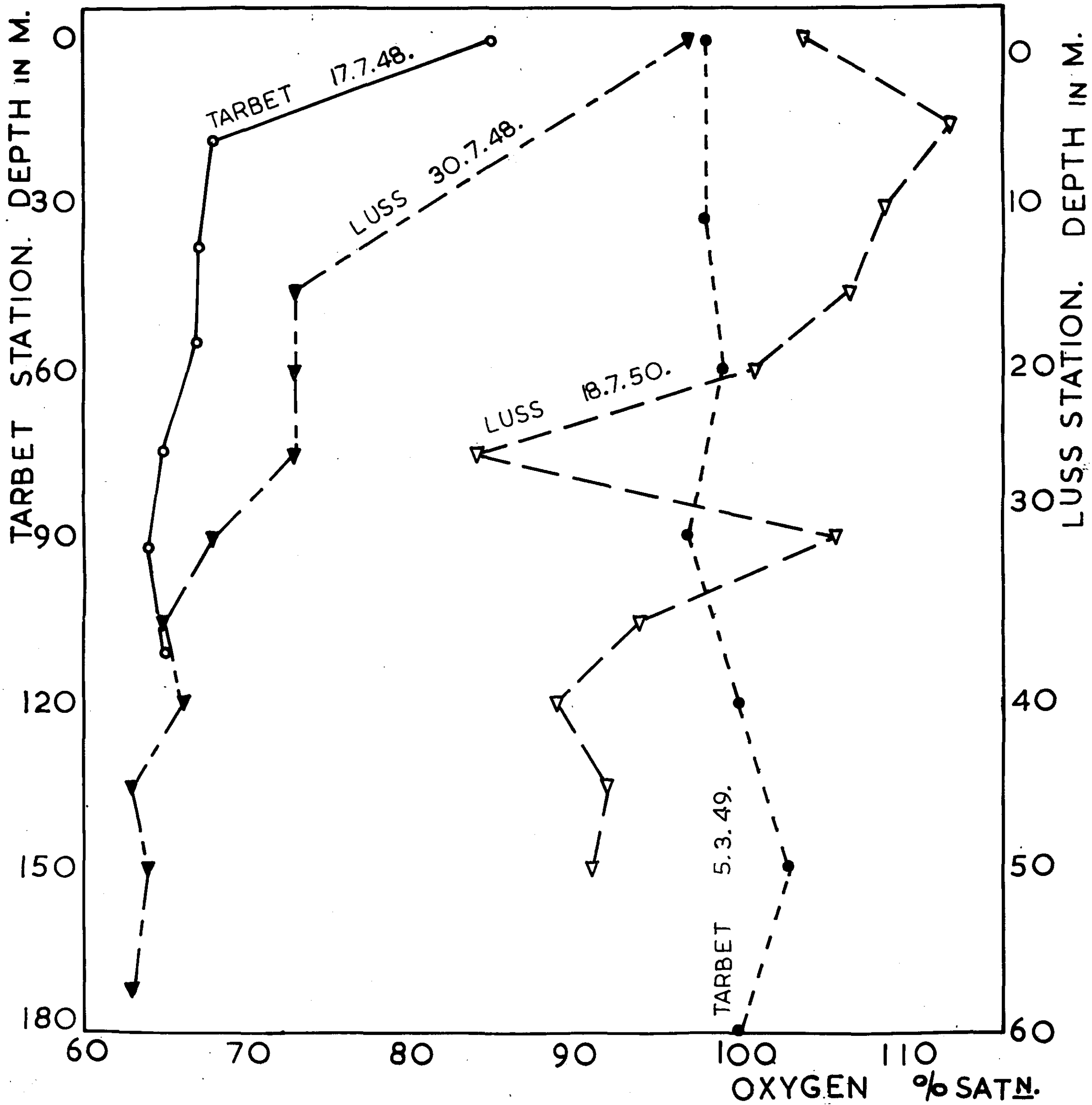


Fig.5. Dissolved oxygen at the Luss and Tarbet Stations.

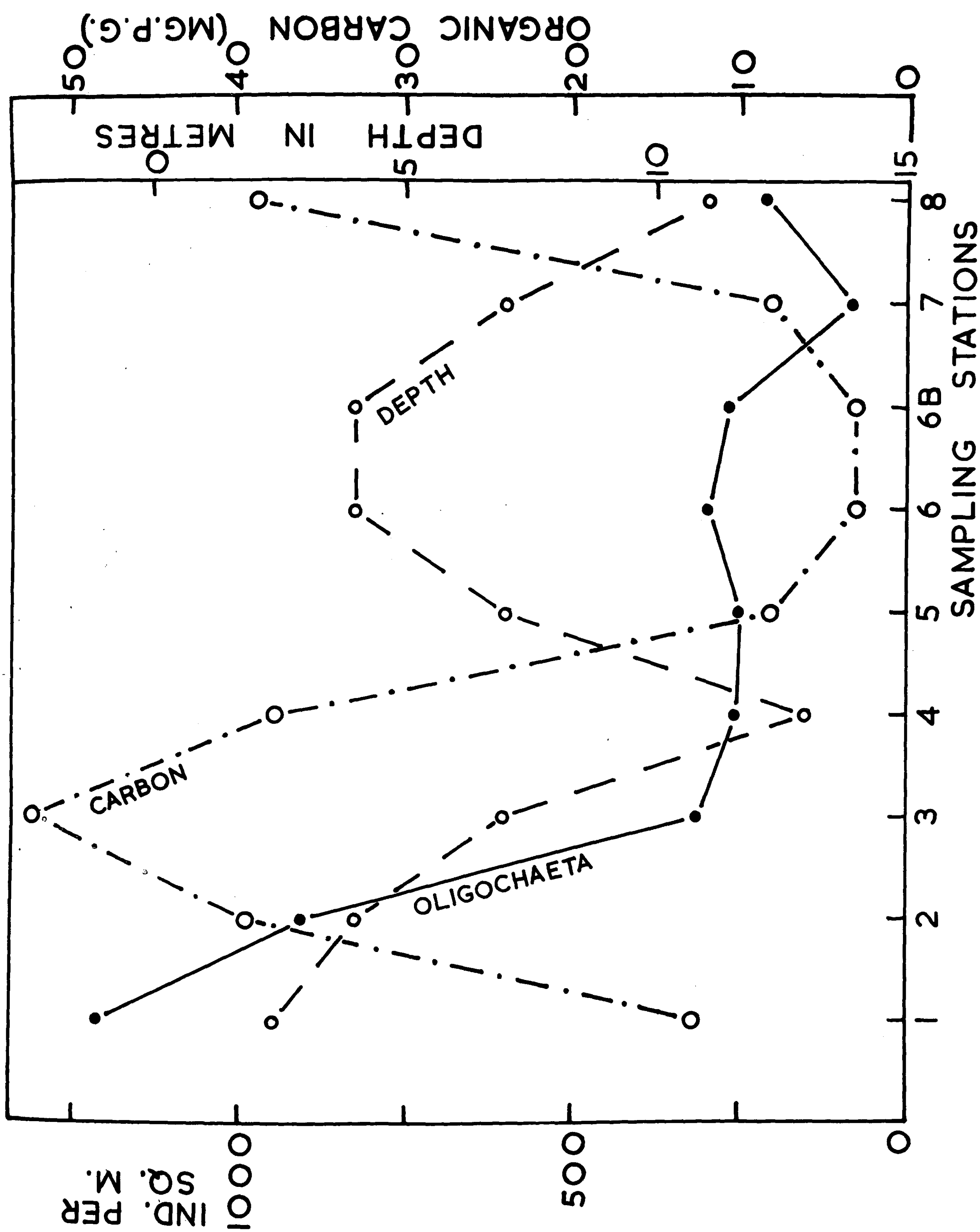


Fig.6. Variation of organic carbon in the bottom deposits and of the oligochaete population along the transect.

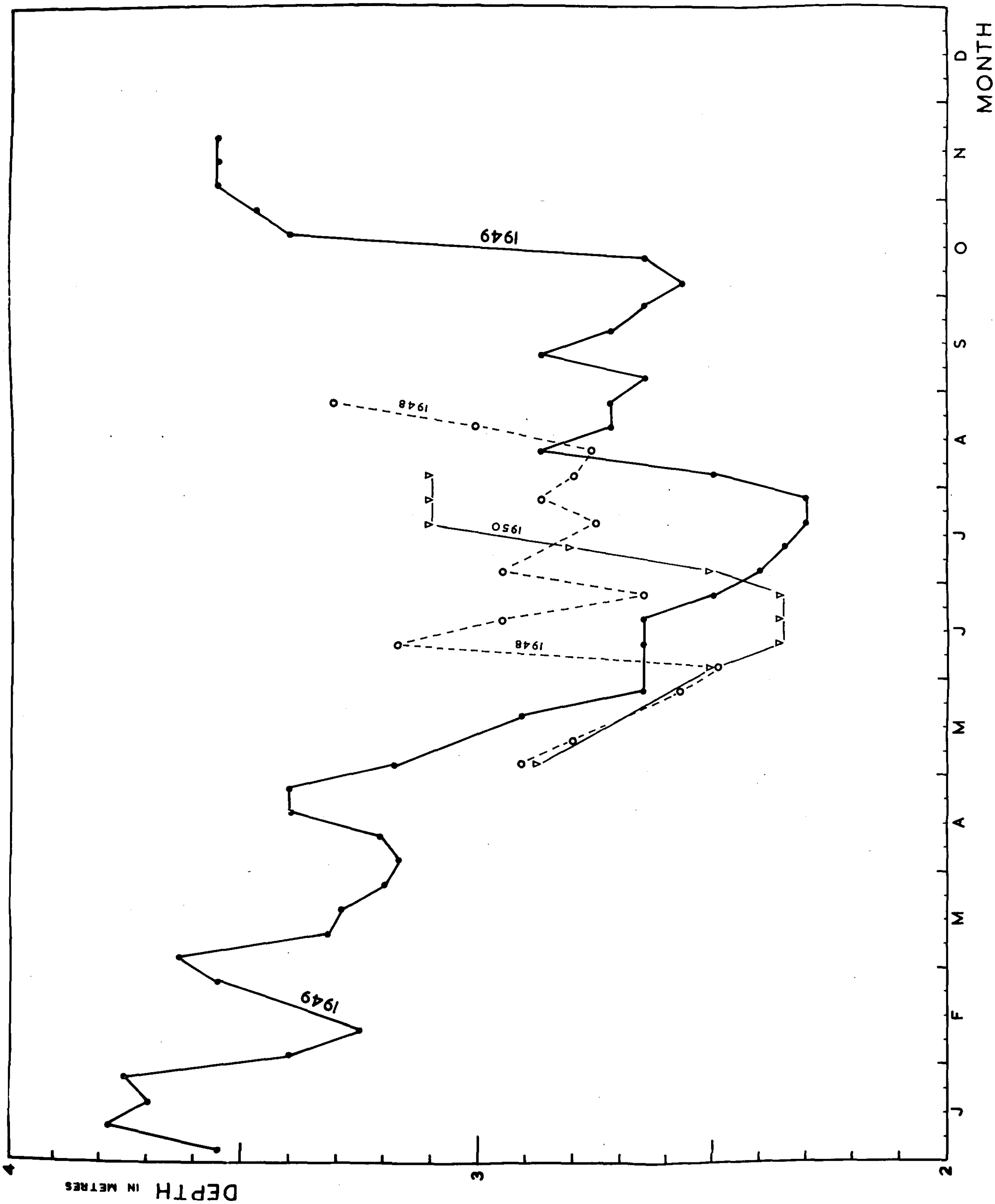


Fig.7. Variation in depth of water over McDougall Bank (St.6.)

- weekly averages, 1948 - 50.

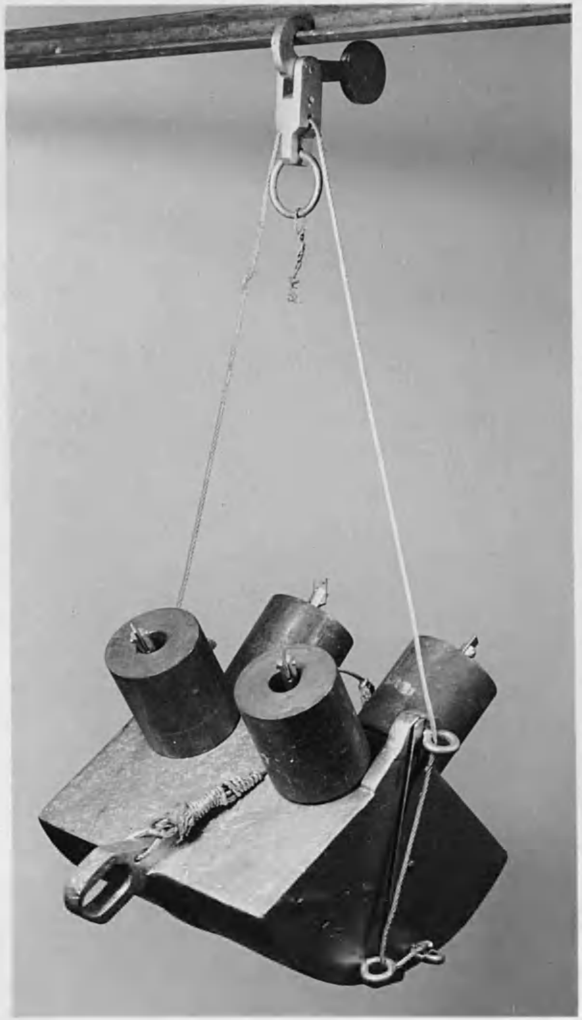


Fig.8. The Petersen grab - with extra weights.

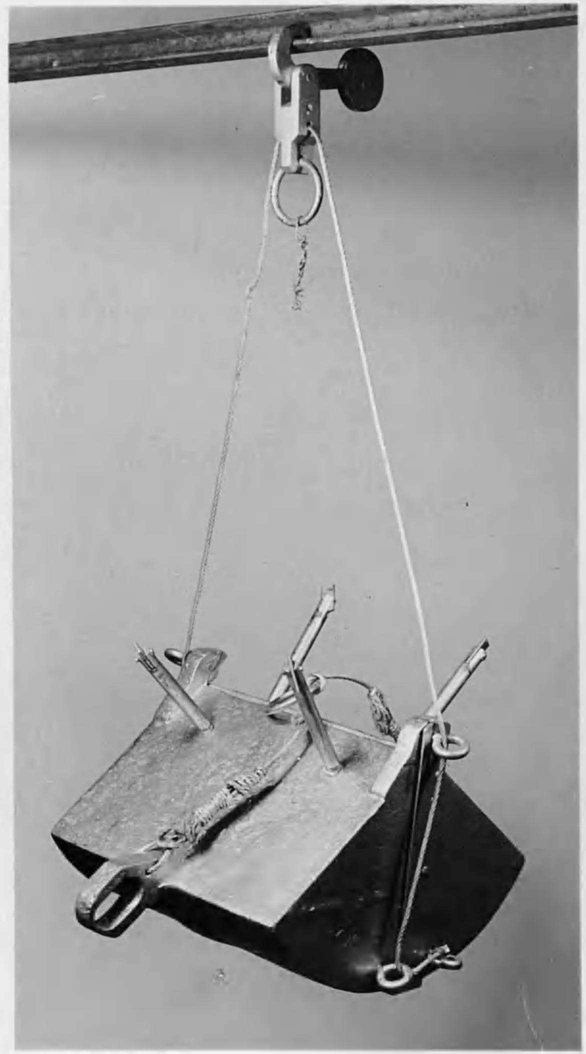


Fig.9. The Petersen grab - without extra weights.

Fig.10. The grab in use (sampling station marked with buoy)

Fig.11. The floating sieve.

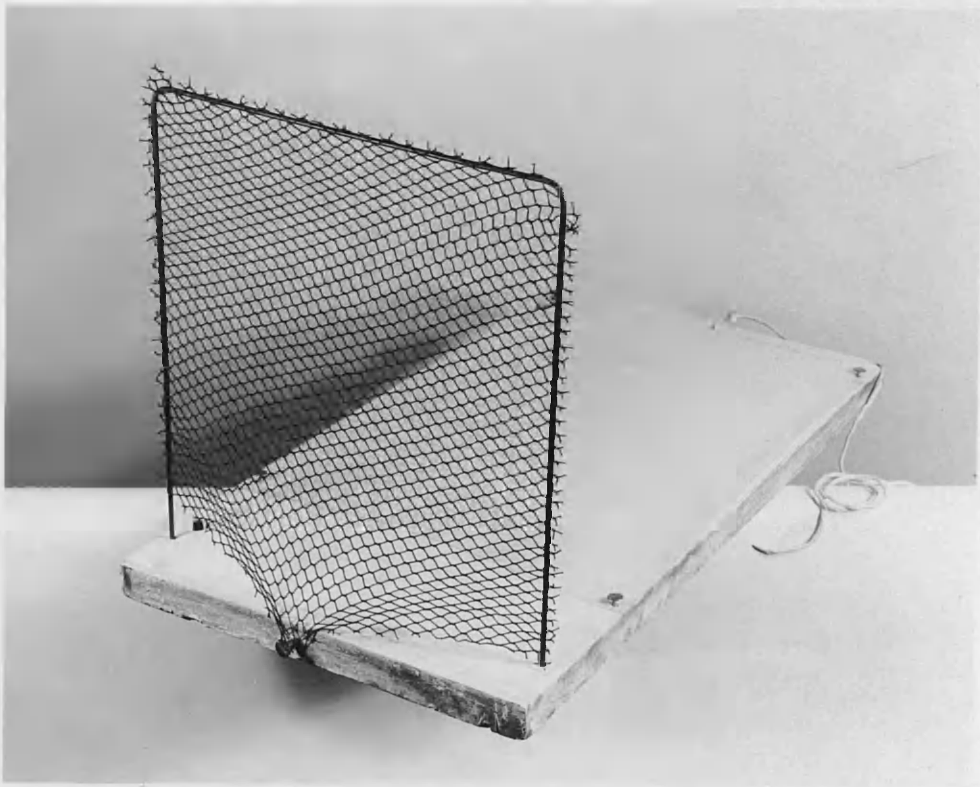


Fig.12. A floating sticky trap.

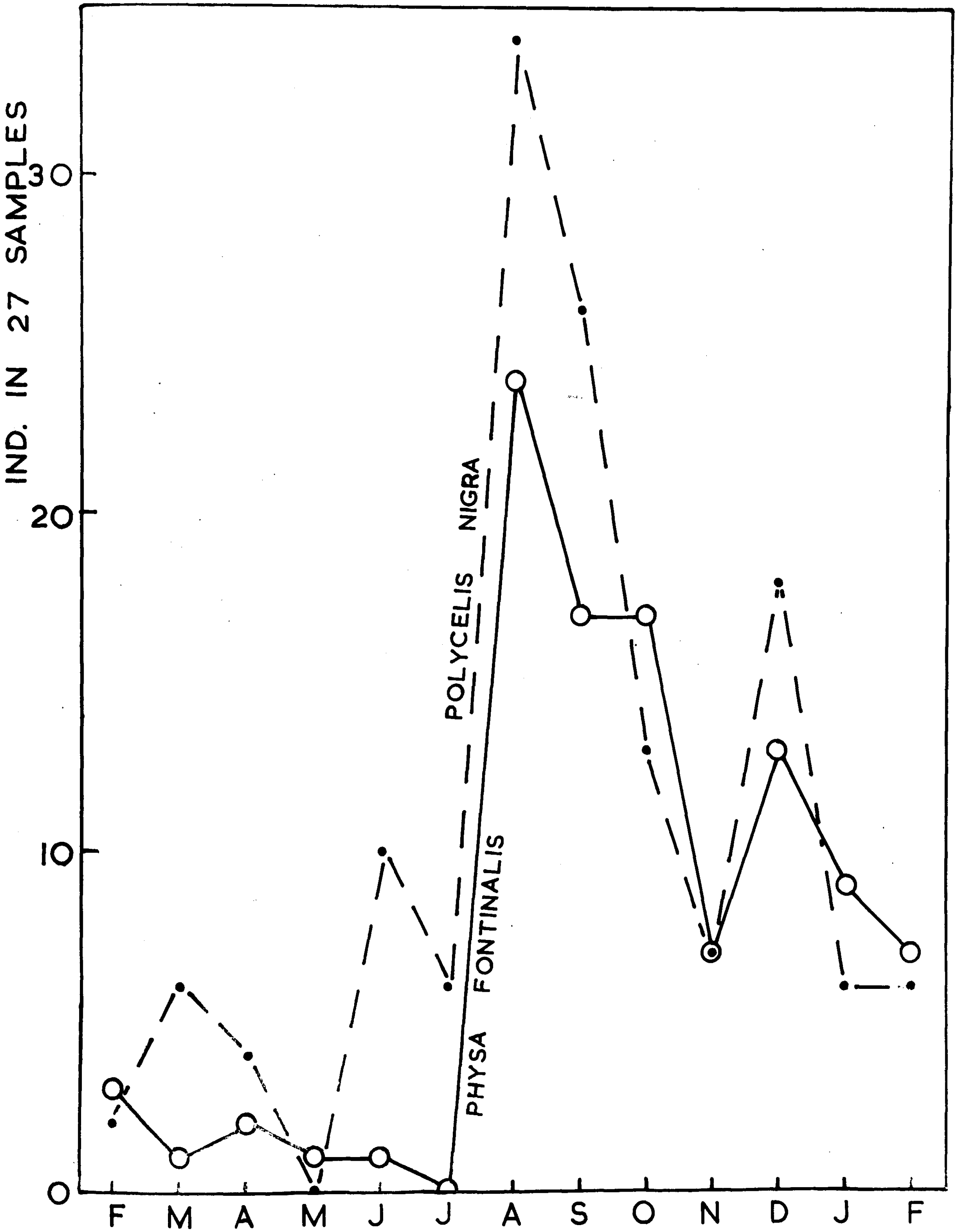


Fig.13. Seasonal variation in numbers caught along the transect - Polycelis nigra and Physa fontinalis.

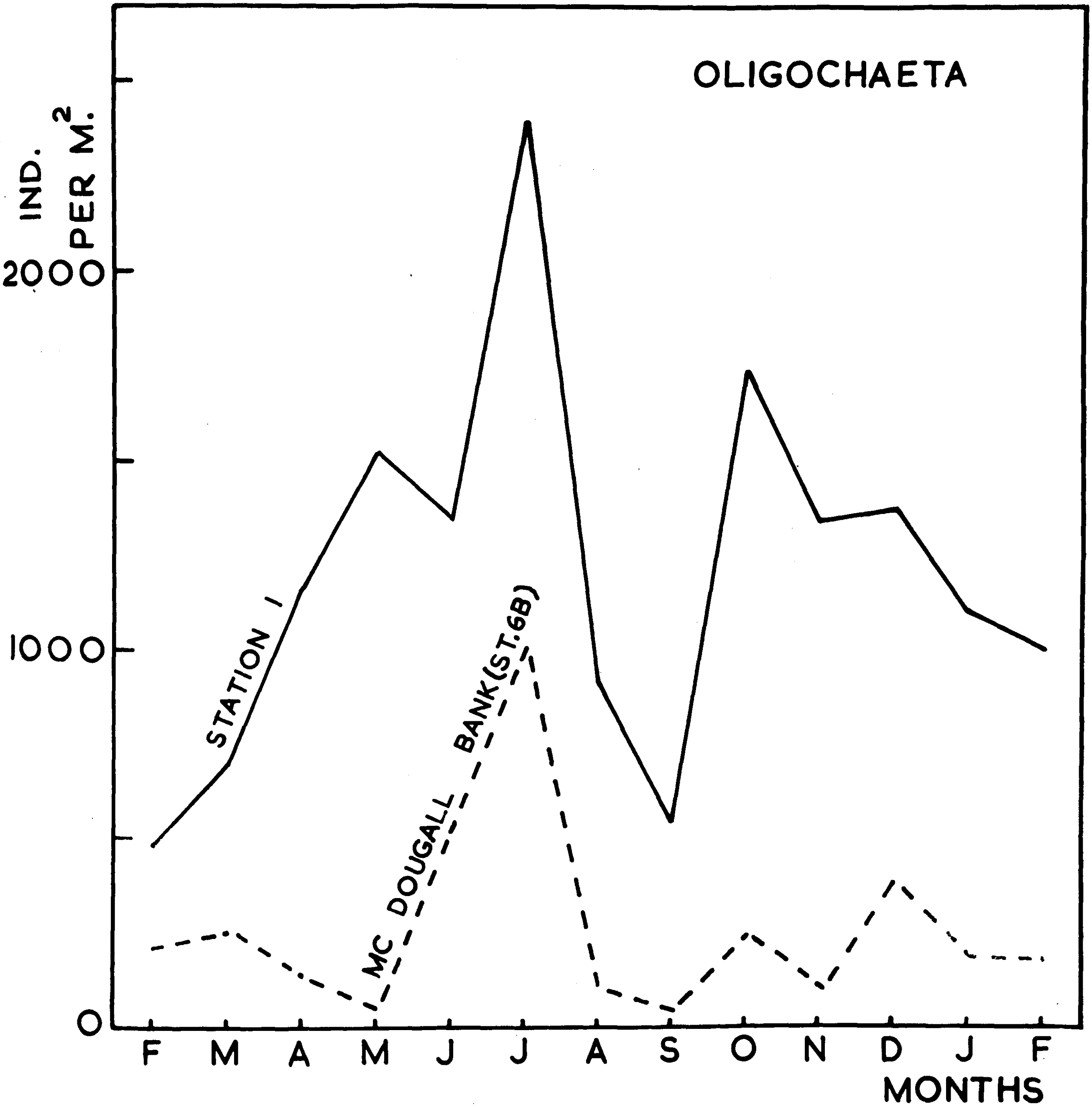


Fig.14. Seasonal population density at St.1. and on McDougall Bank - Oligochaeta.

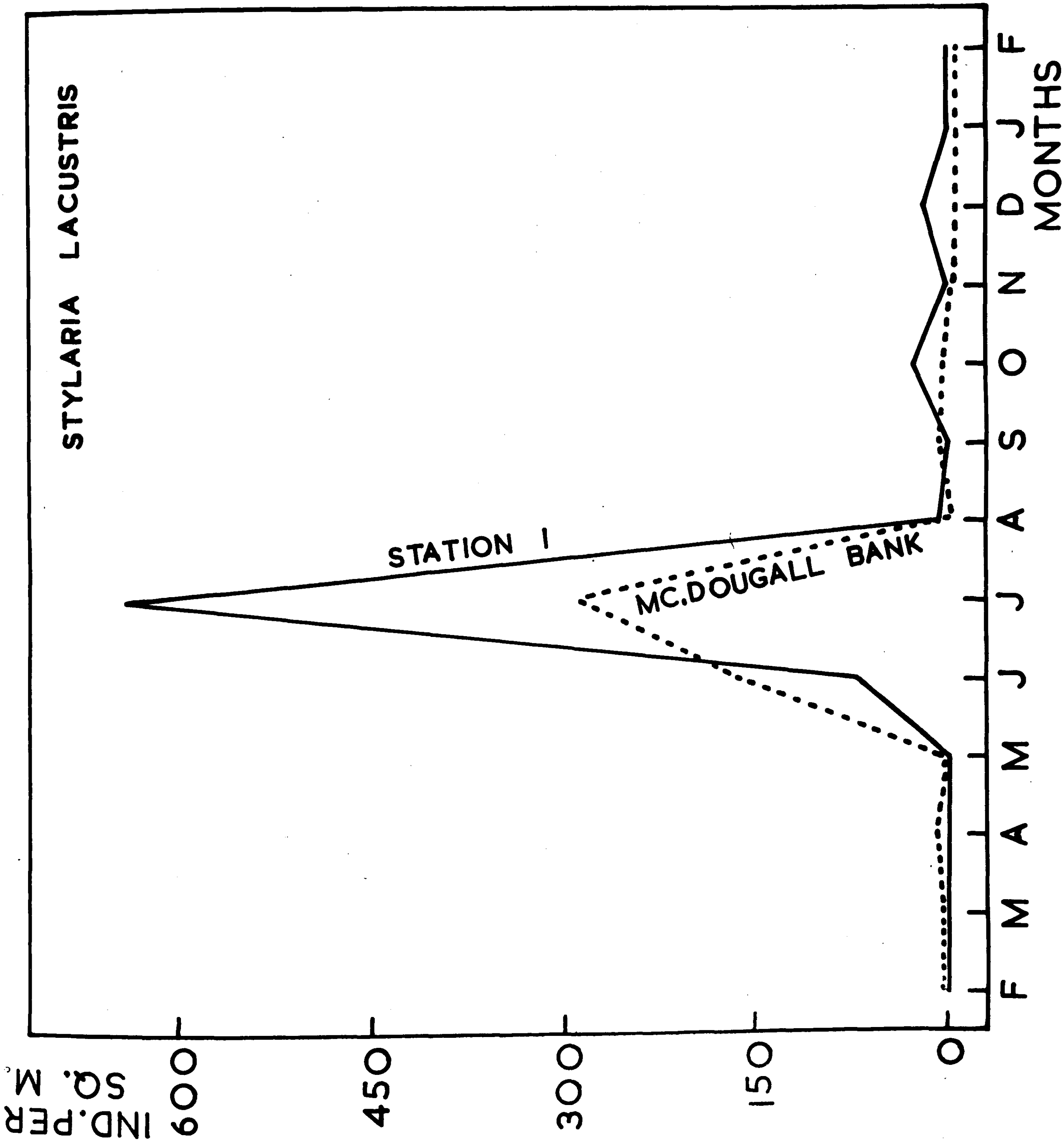


Fig.15. Seasonal population density at St.1. and on McDougall Bank - Stylaria lacustris.

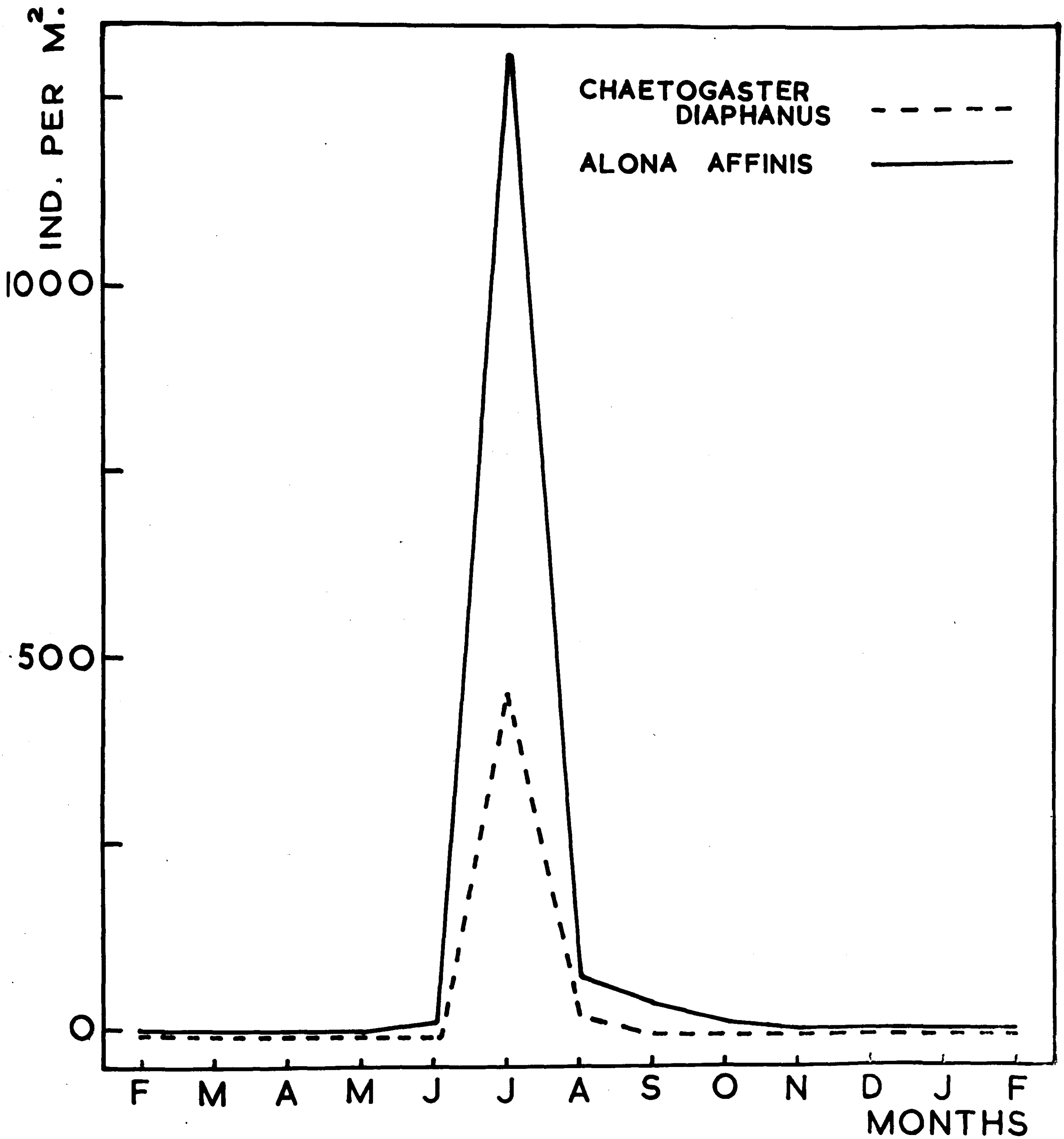


Fig. 16. Seasonal population density at St.1. - Chaetogaster diaphanus and Alona affinis.

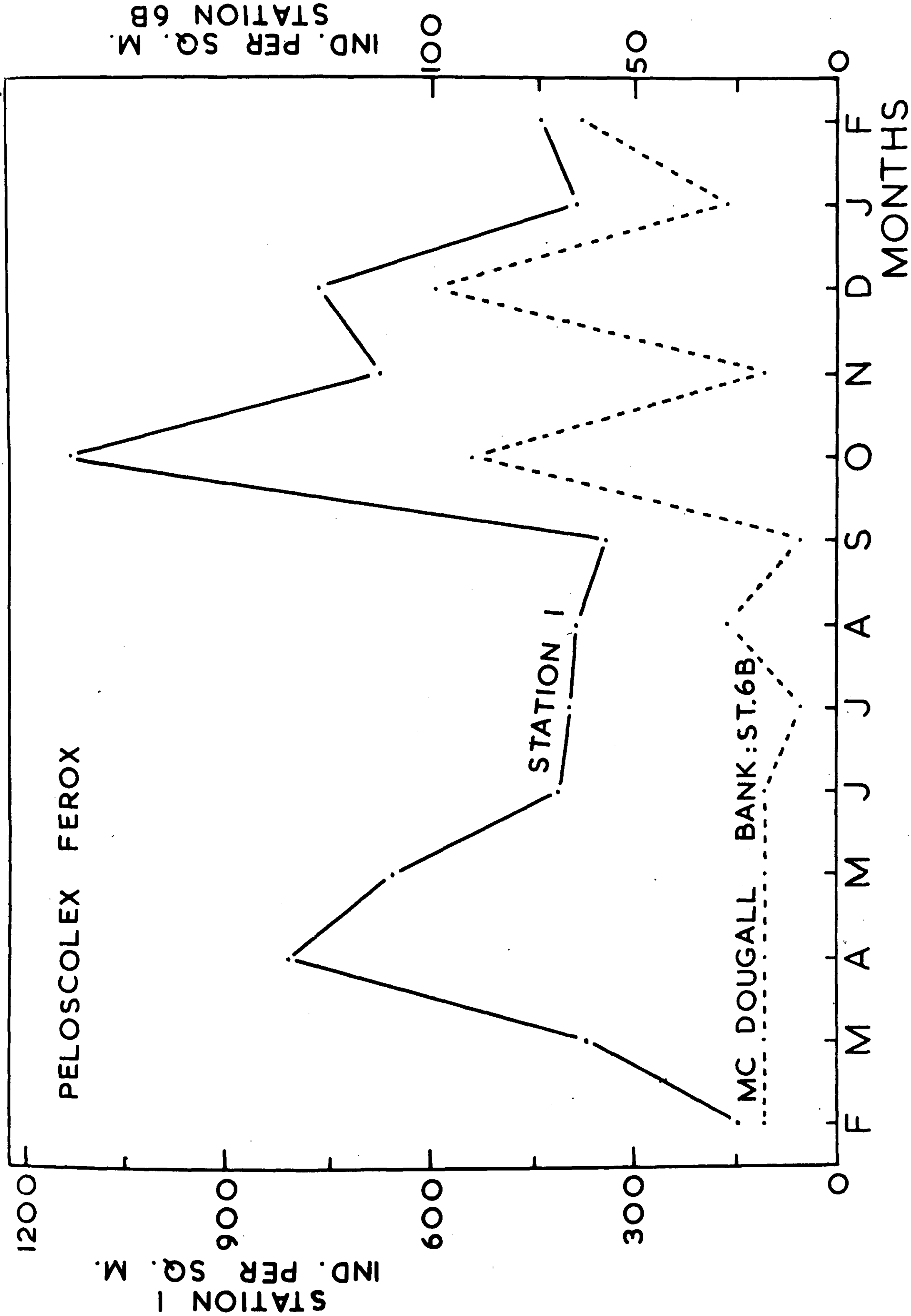


Fig.17. Seasonal population density at St.1. and on McDougall Bank - Peloscolex ferox.

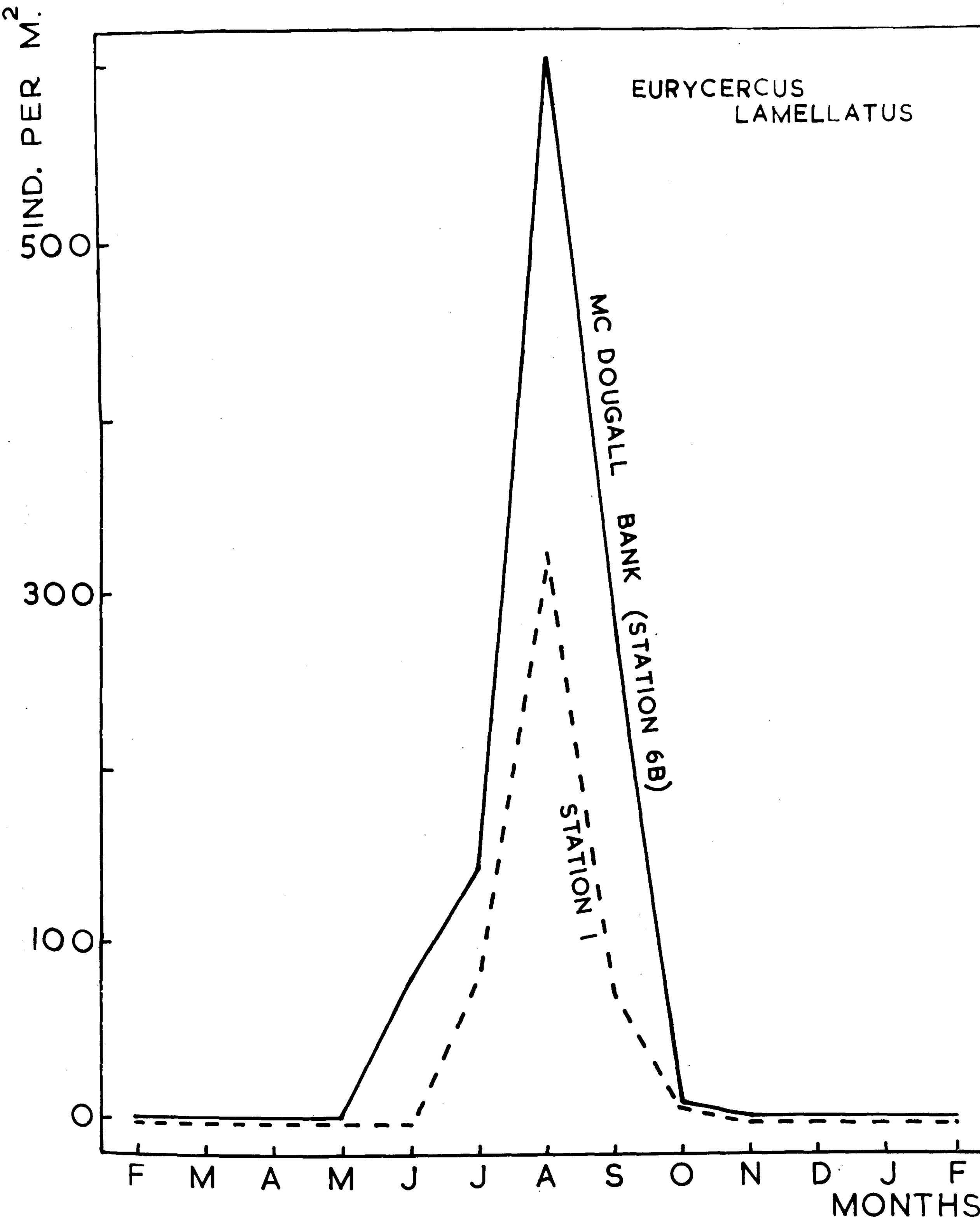


Fig.18. Seasonal population density at St.1. and on McDougall bank - Eurycercus lamellatus.

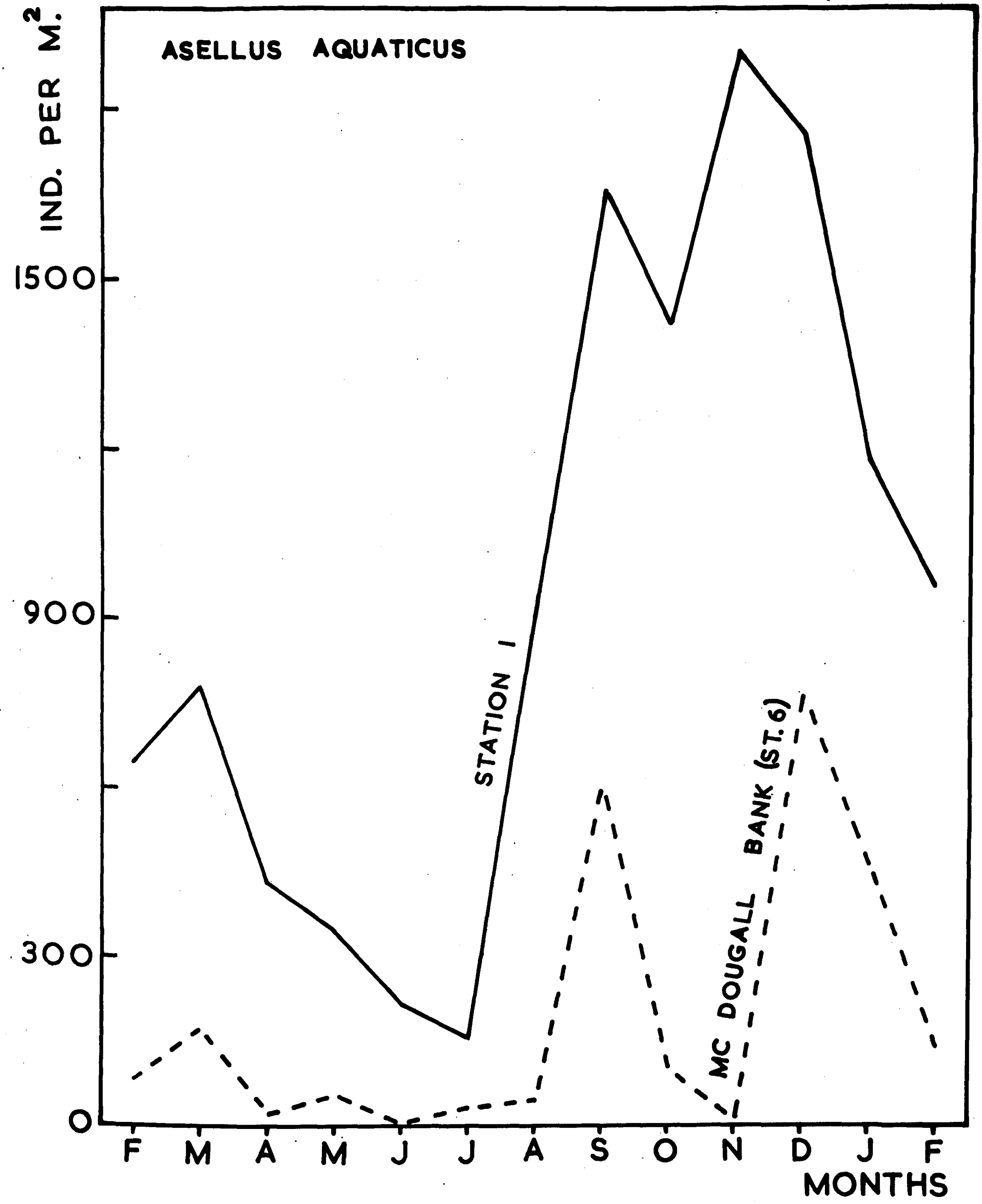


Fig.19. Seasonal population density at St.1. and on McDougall Bank - Asellus aquaticus

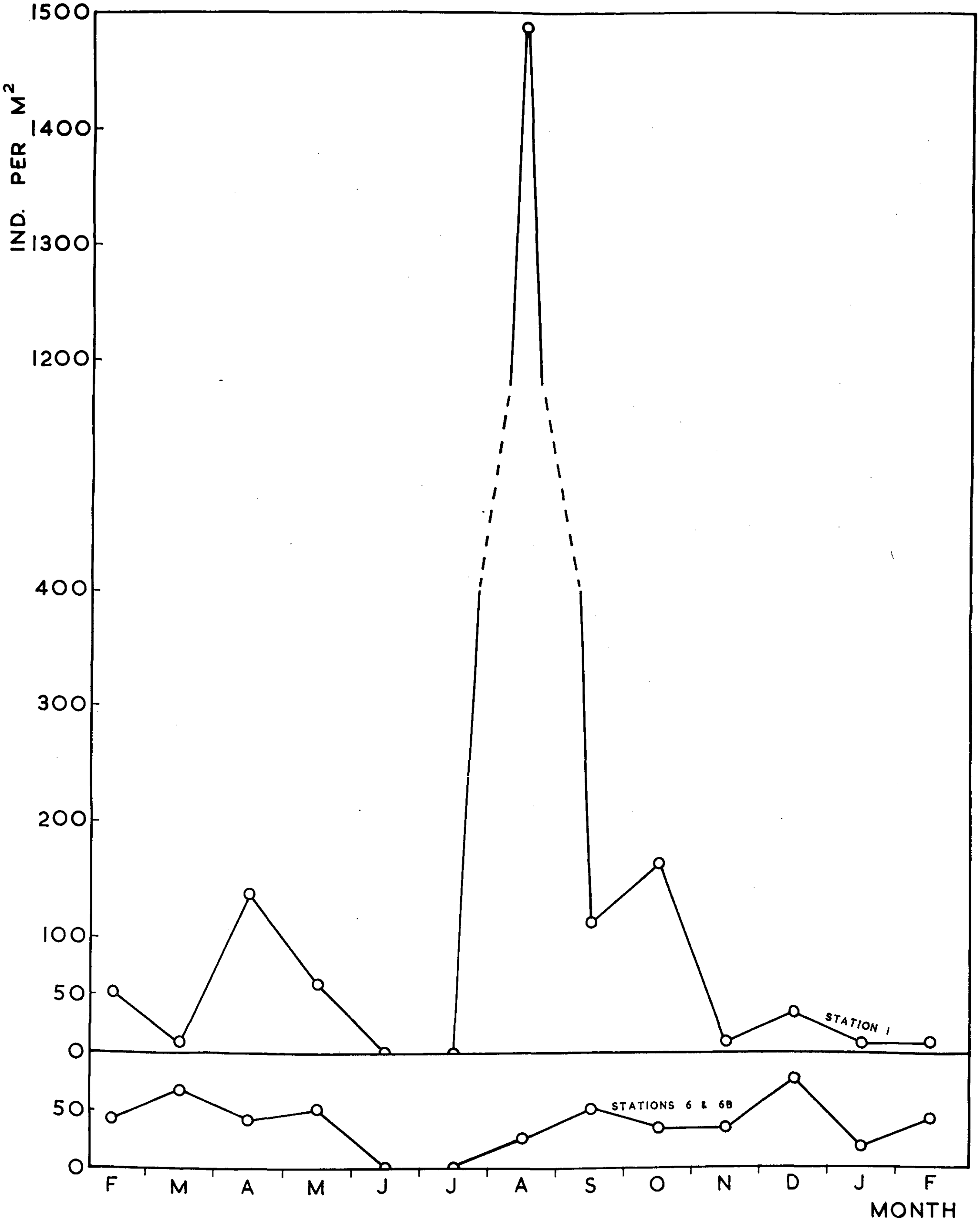


Fig.20. Seasonal population density at St.1. and on McDougall Bank - Coenis horaria.

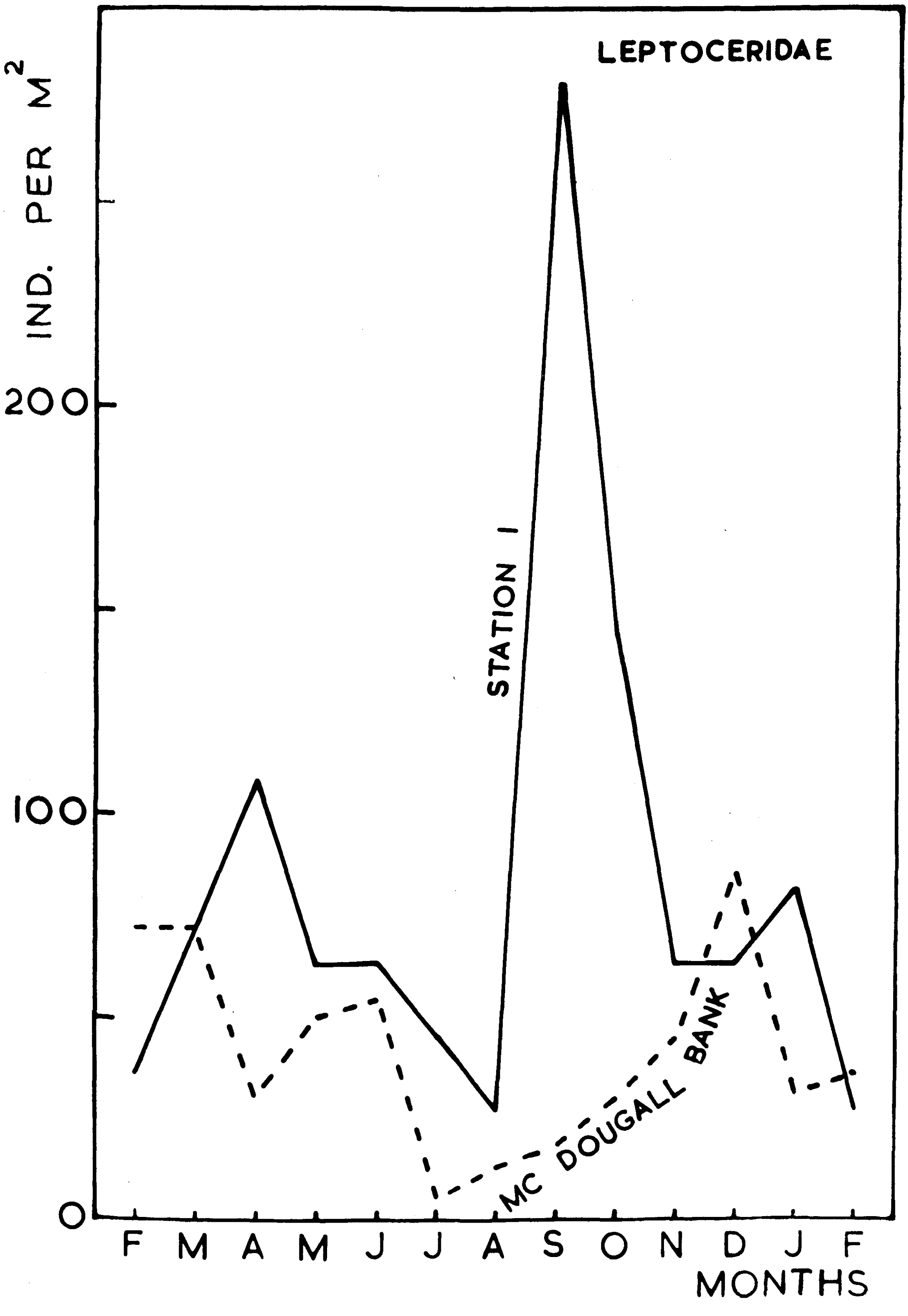


Fig.21. Seasonal population density at St.1. and on McDougall Bank - Leptoceridae.

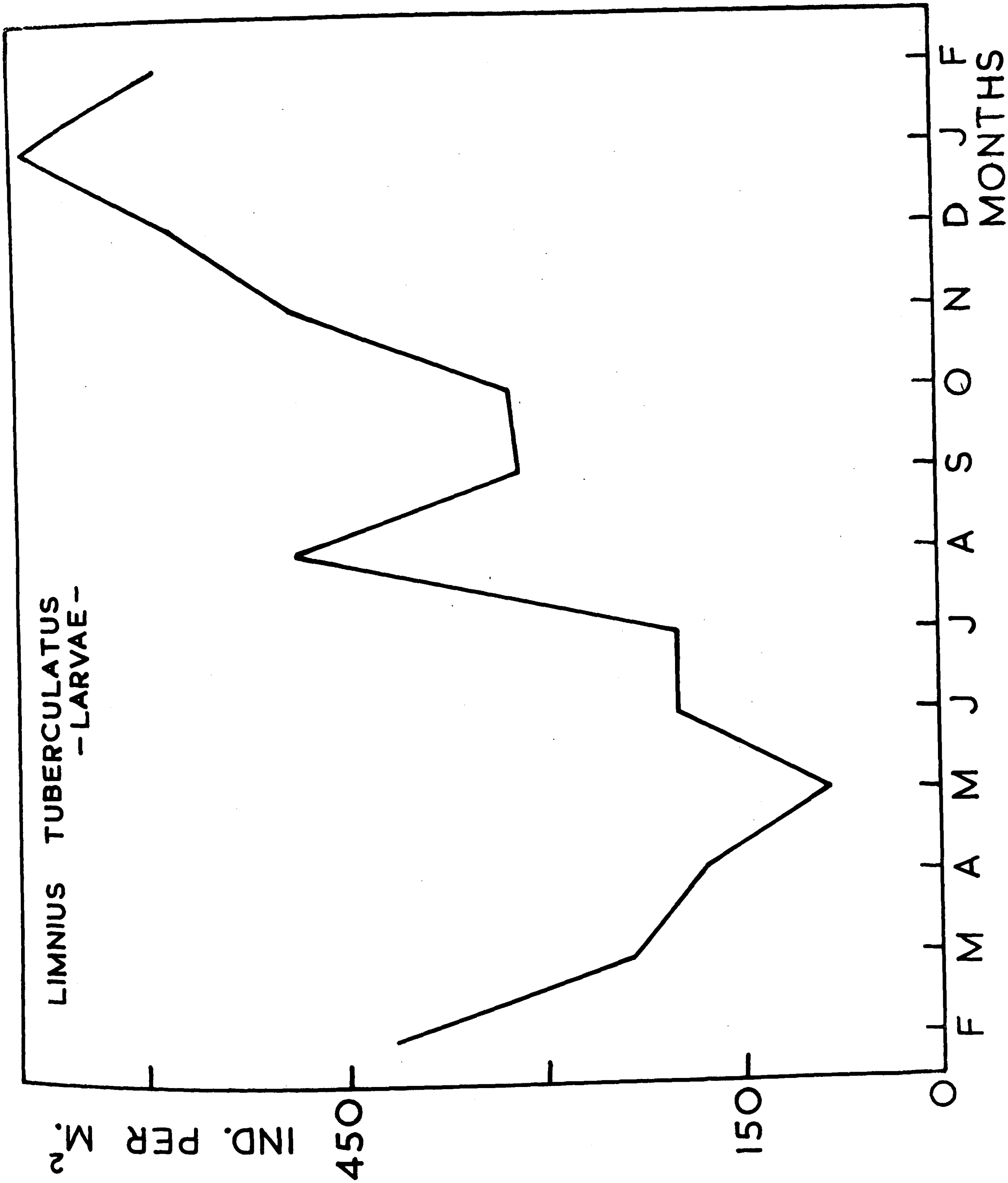


Fig.22. Seasonal population density at St.1. - Limnius tuberculatus.

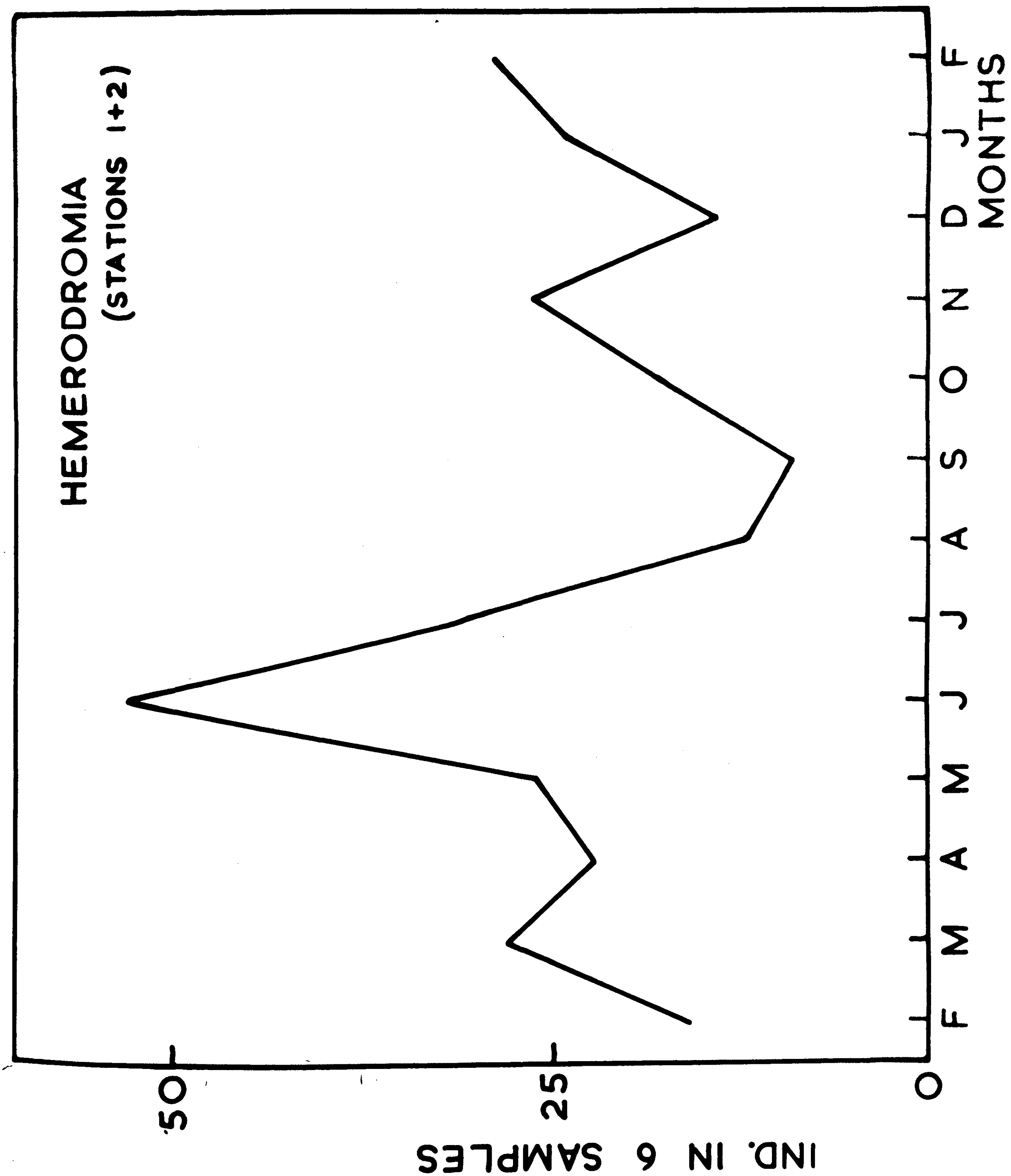


Fig.23. Seasonal variation in numbers at Sts.1. and 2. together -
Hemerodromia sp.

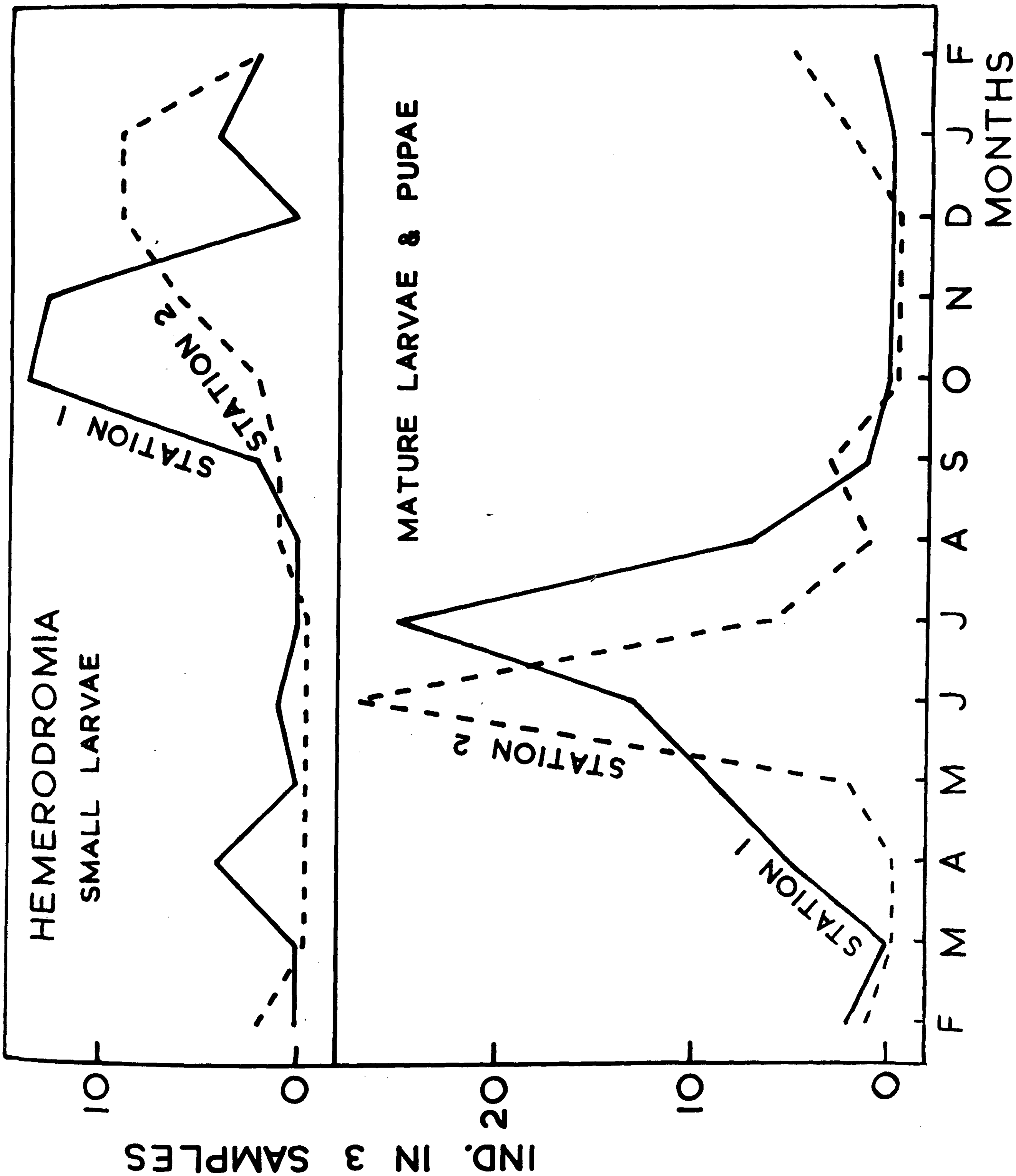


Fig.24. Seasonal variation in numbers caught at St.1. and at St.2. separately.
Hemerodromia sp.

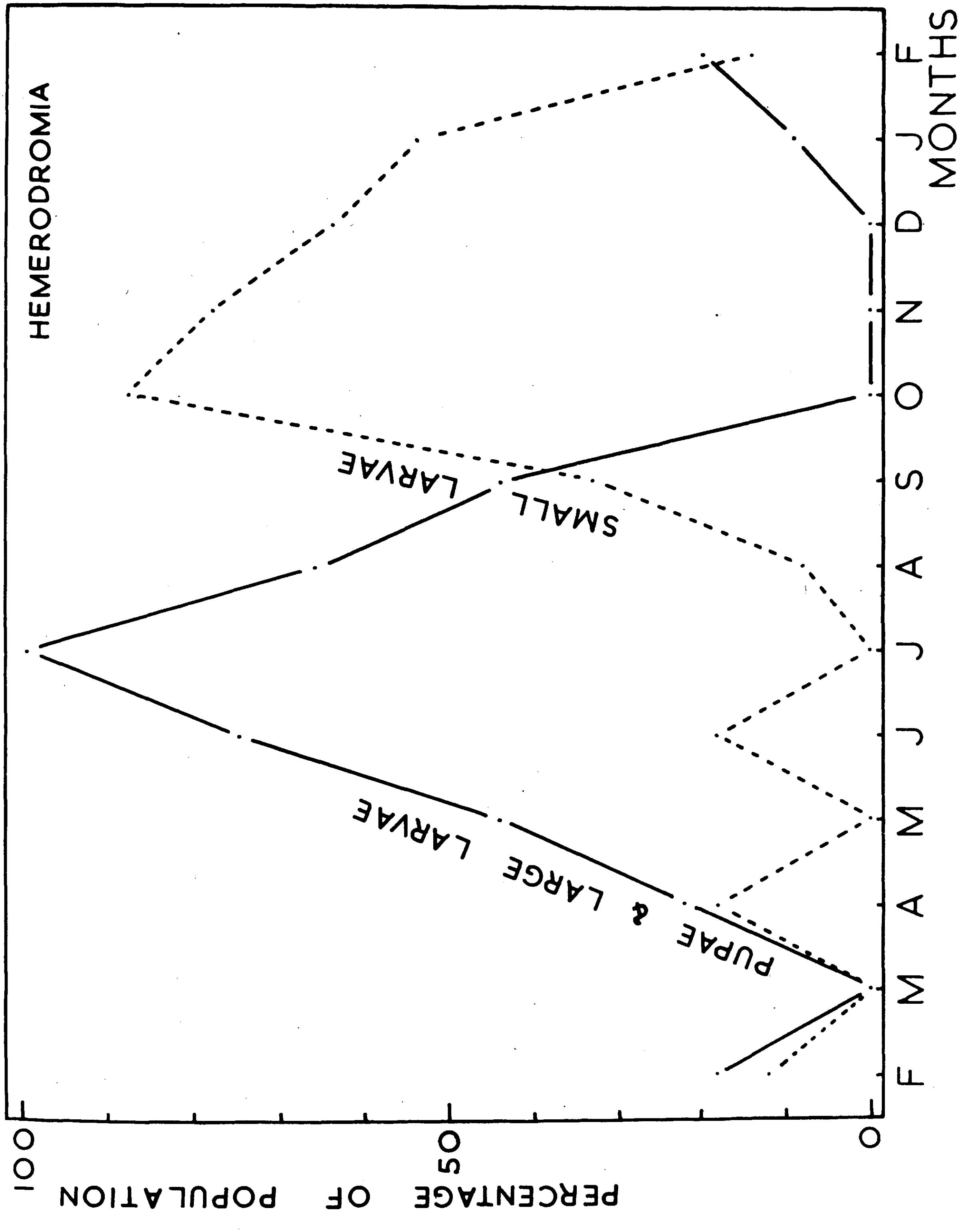


Fig.25. Seasonal variation in percentage of large and of small larvae at Sts.1. and 2. - Hemerodromia sp.

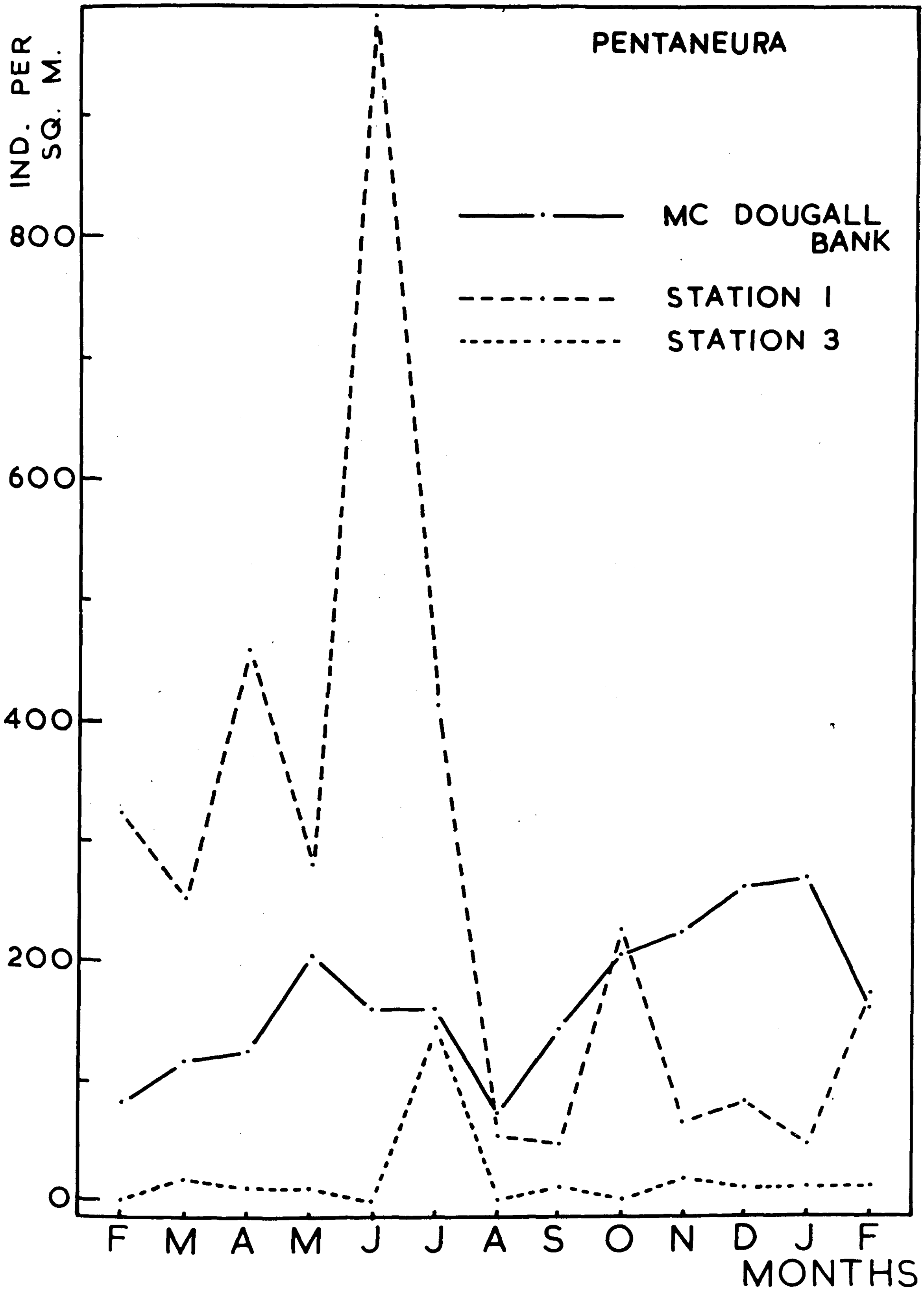


Fig.26. Seasonal population density at Sts.1,& 3. and on McDougall Bank - Pentaneura spp.

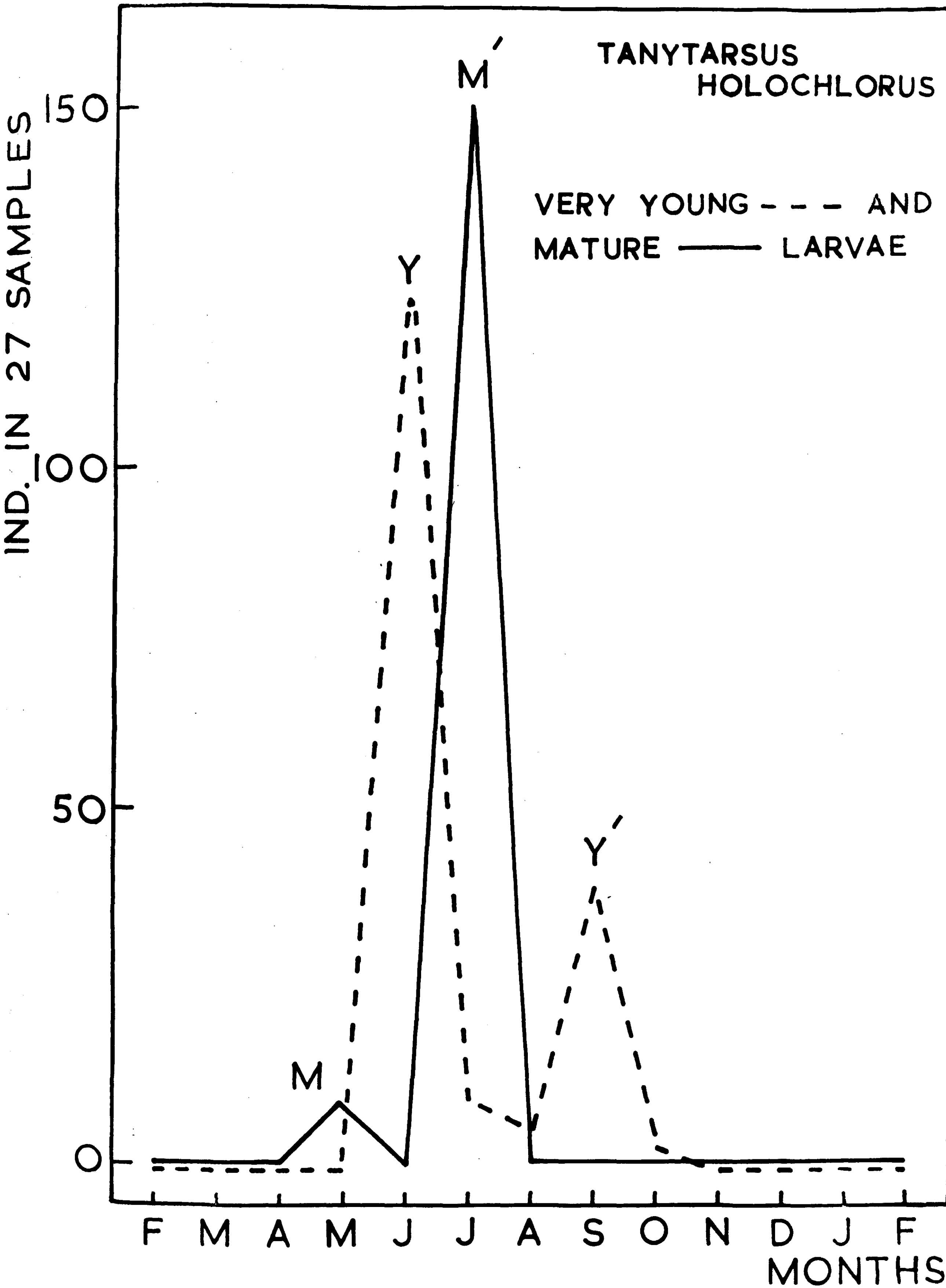


Fig. 27 Seasonal variation in numbers along the transect of very small and of mature larvae - Tanytarsus holochlorus.

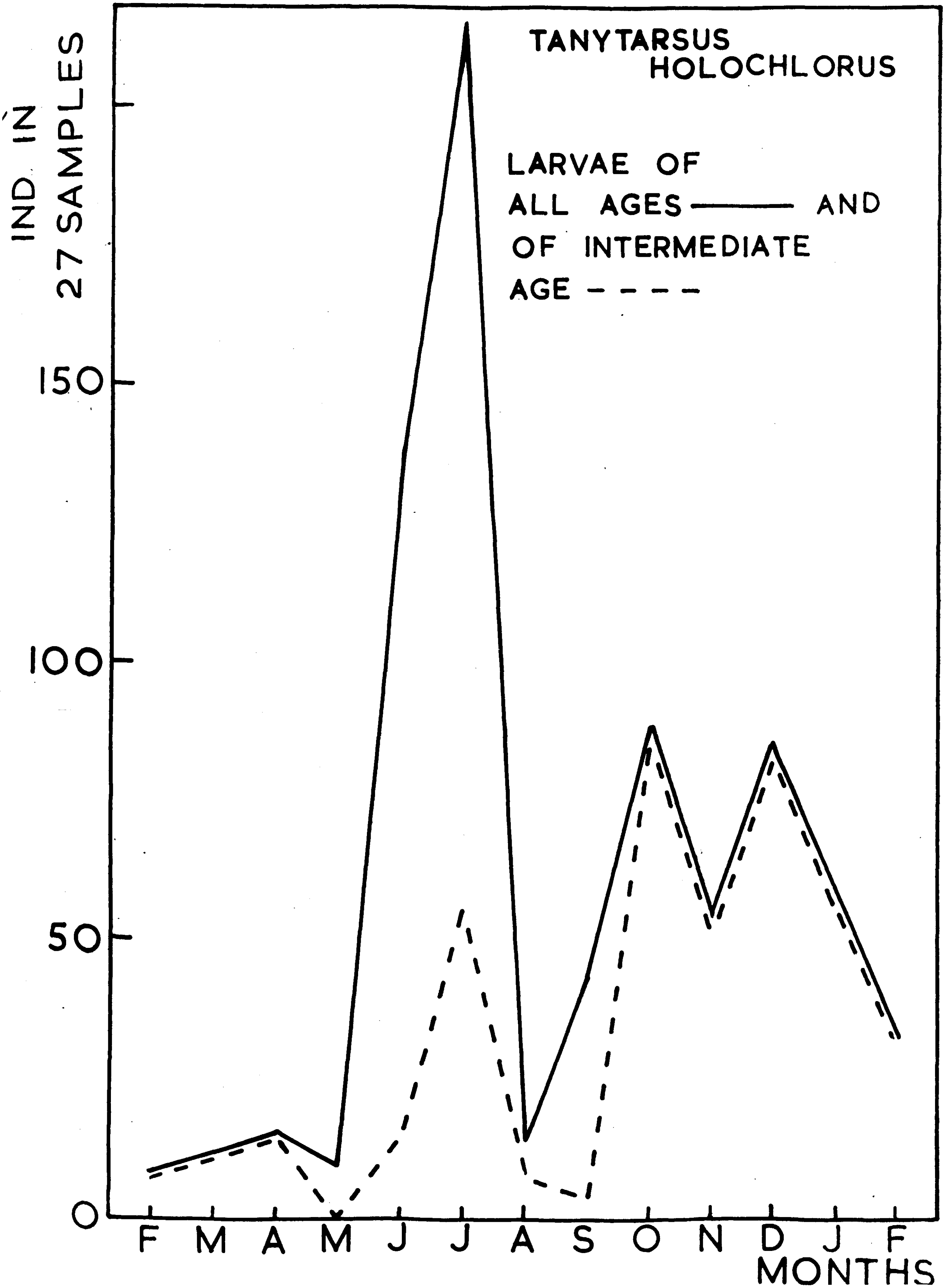


Fig.28. Seasonal variation in numbers along the transect of larvae of all sizes and of intermediate sizes - Tanytarsus holochlorus.

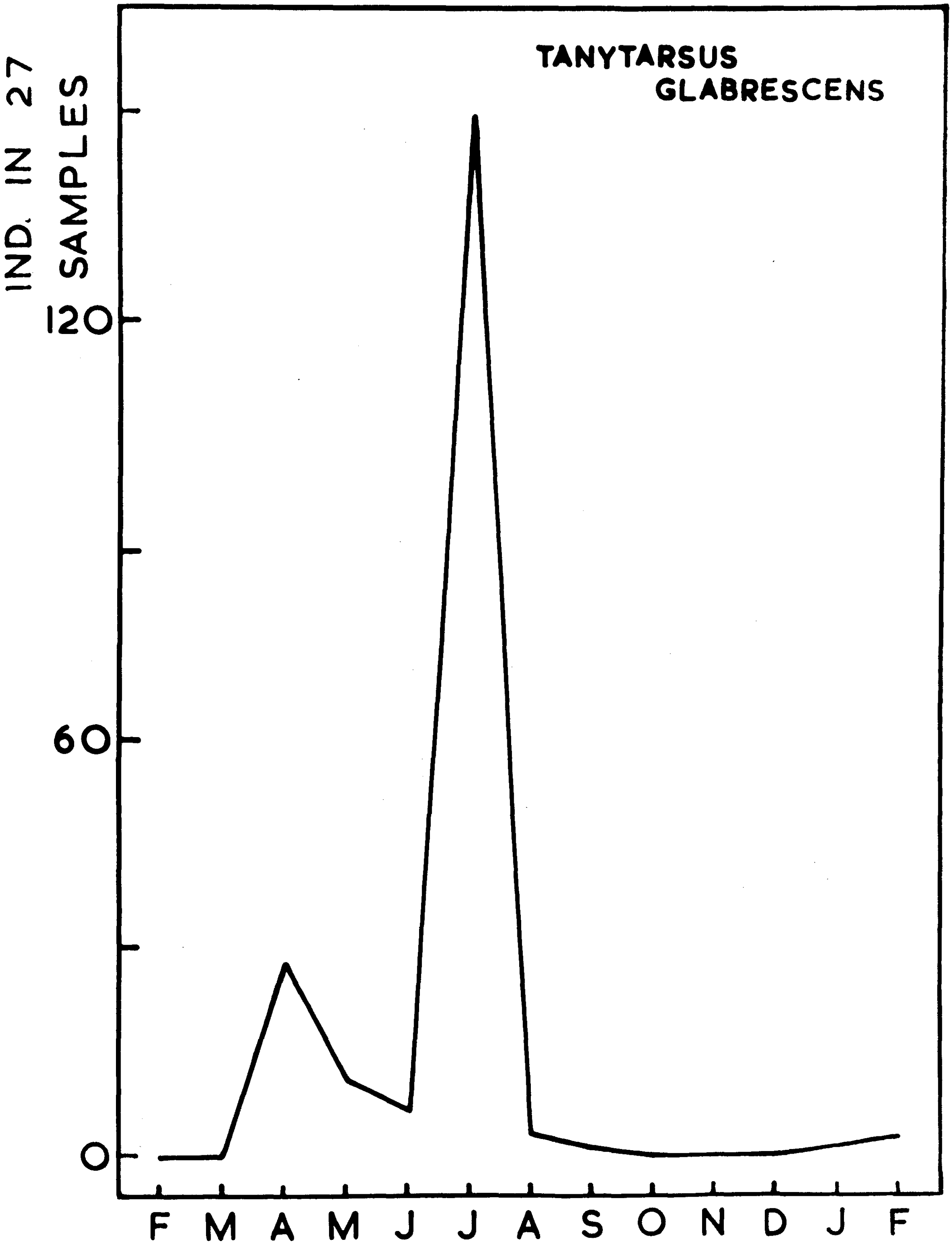


Fig.29. Seasonal variation in numbers caught along the transect - Tanytarsus glabrescens.

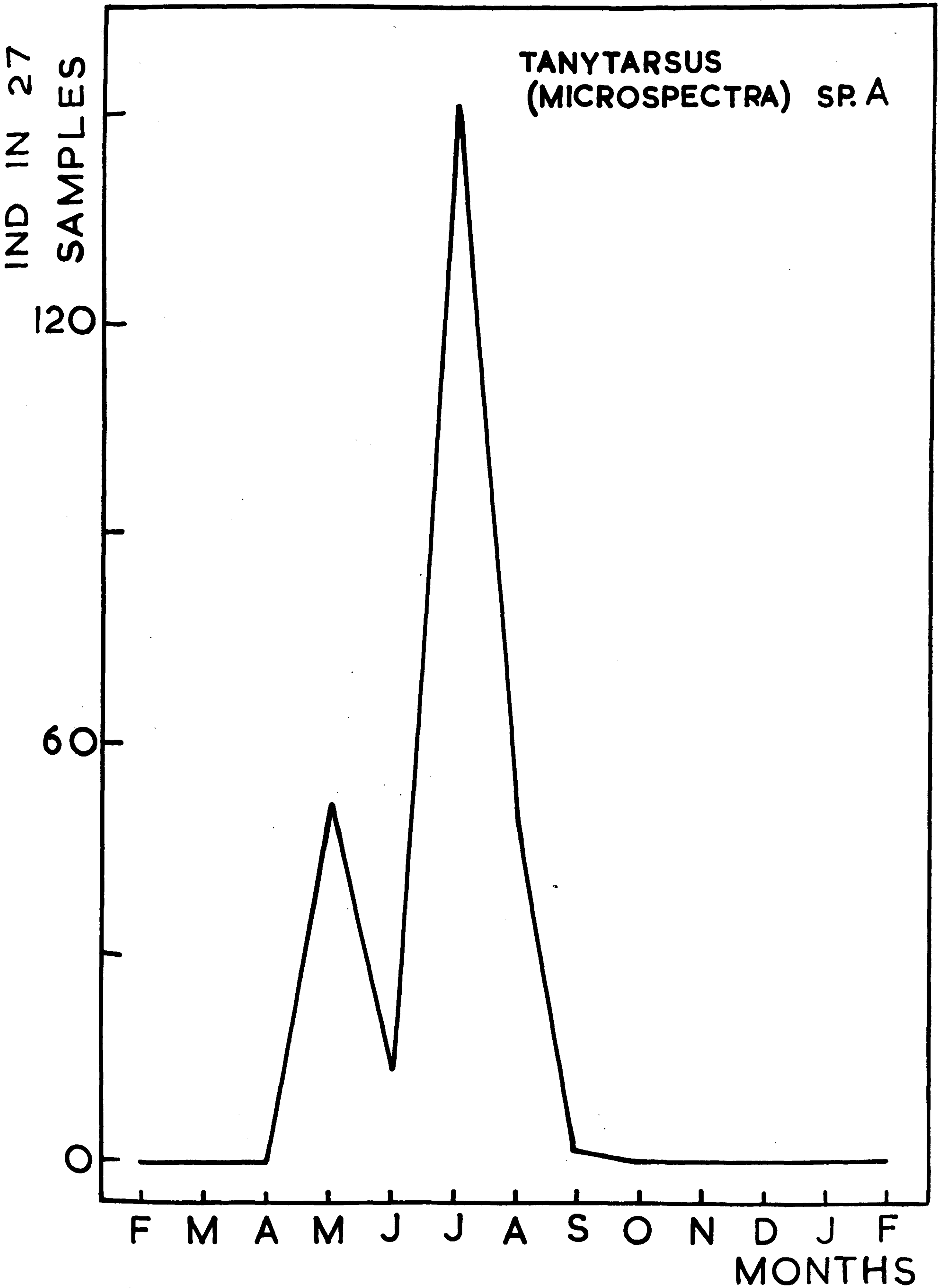


Fig.30. Seasonal variation in numbers caught along the transect - T.(Microspectra) sp.A.

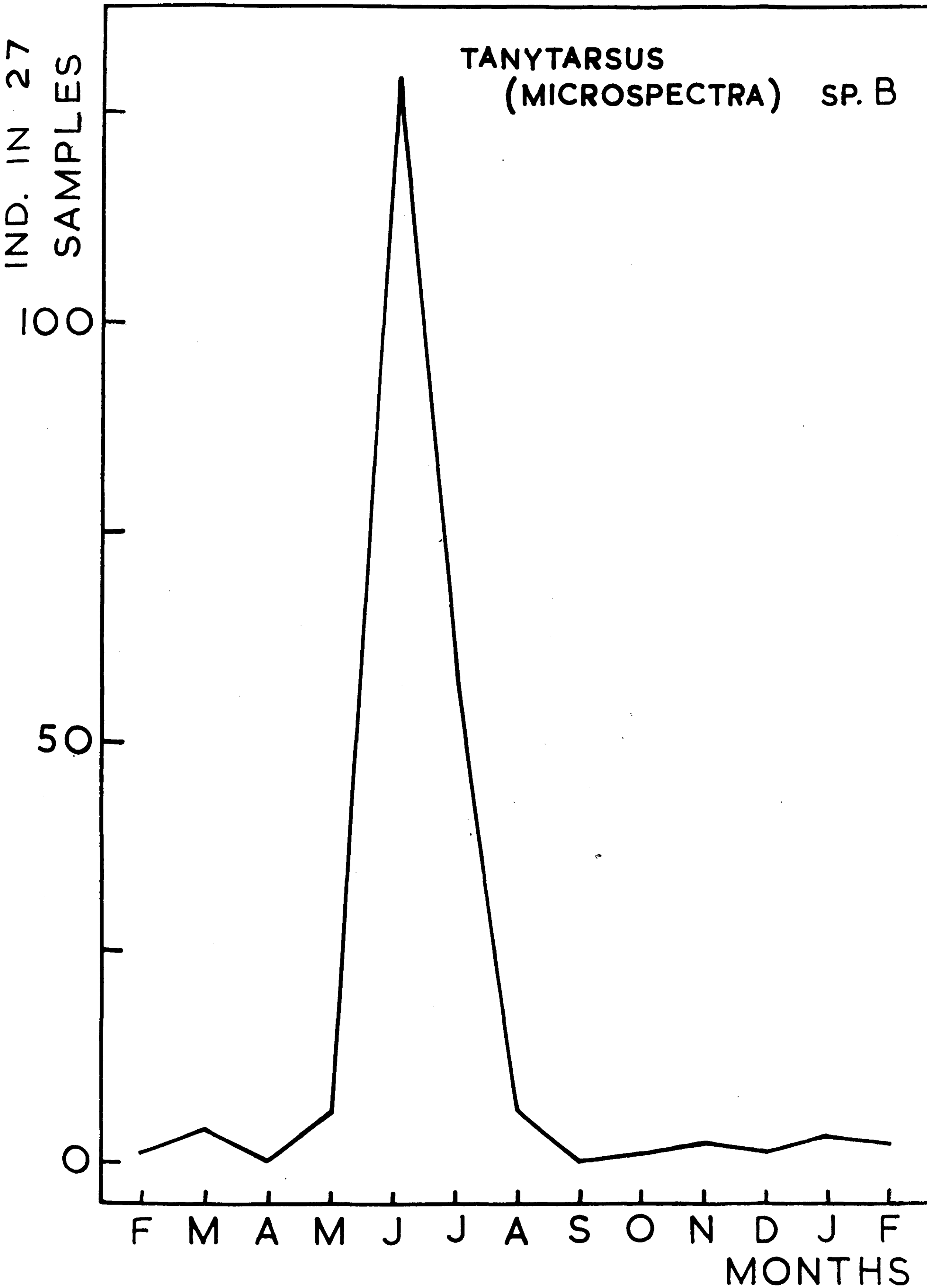


Fig.31. Seasonal variation in numbers caught along the transect - T.(Microspectra) sp.B.

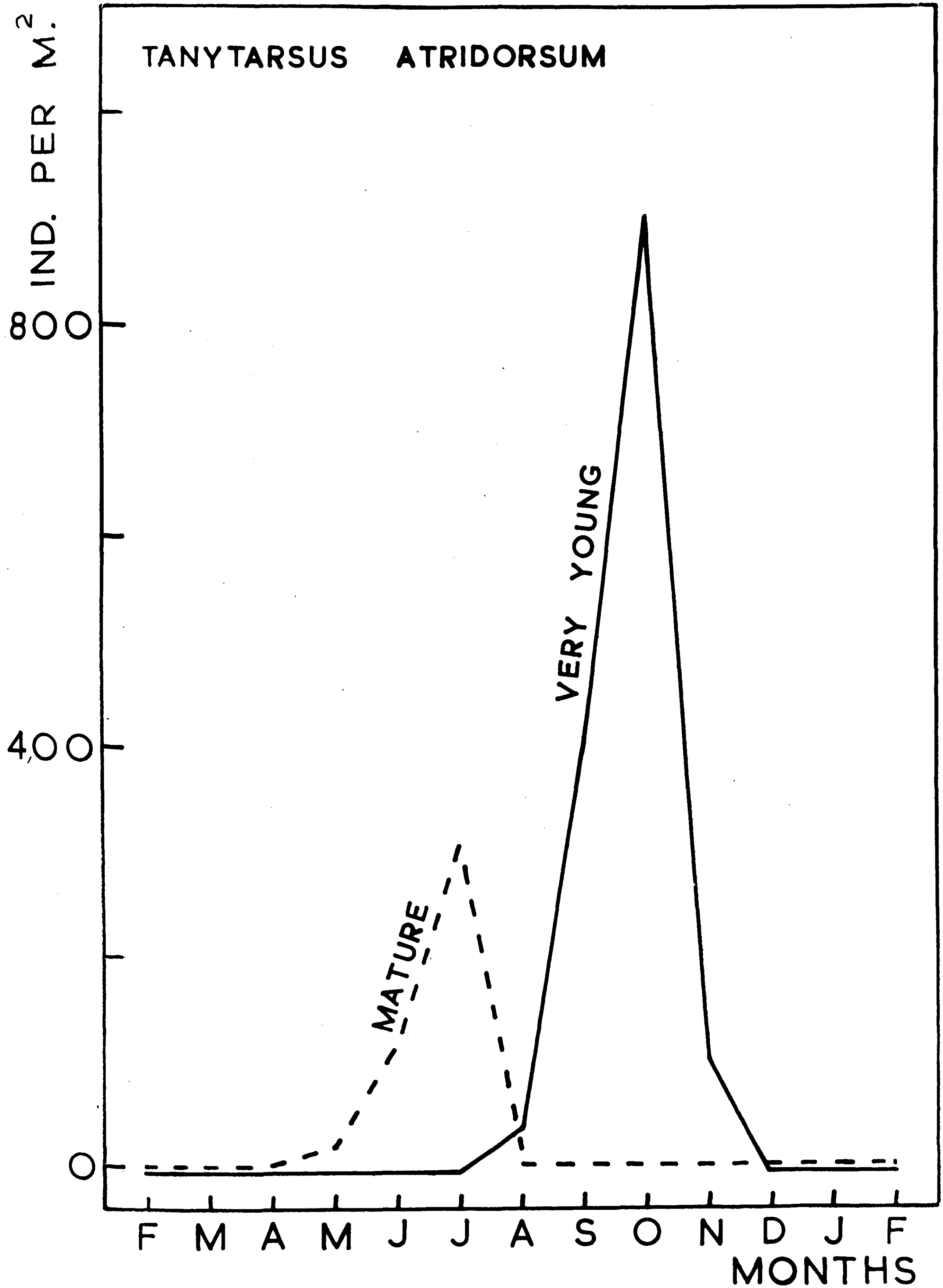


Fig.32. Seasonal population densities of very small and of mature larvae at St.2. - Tanytarsus atridorsum.

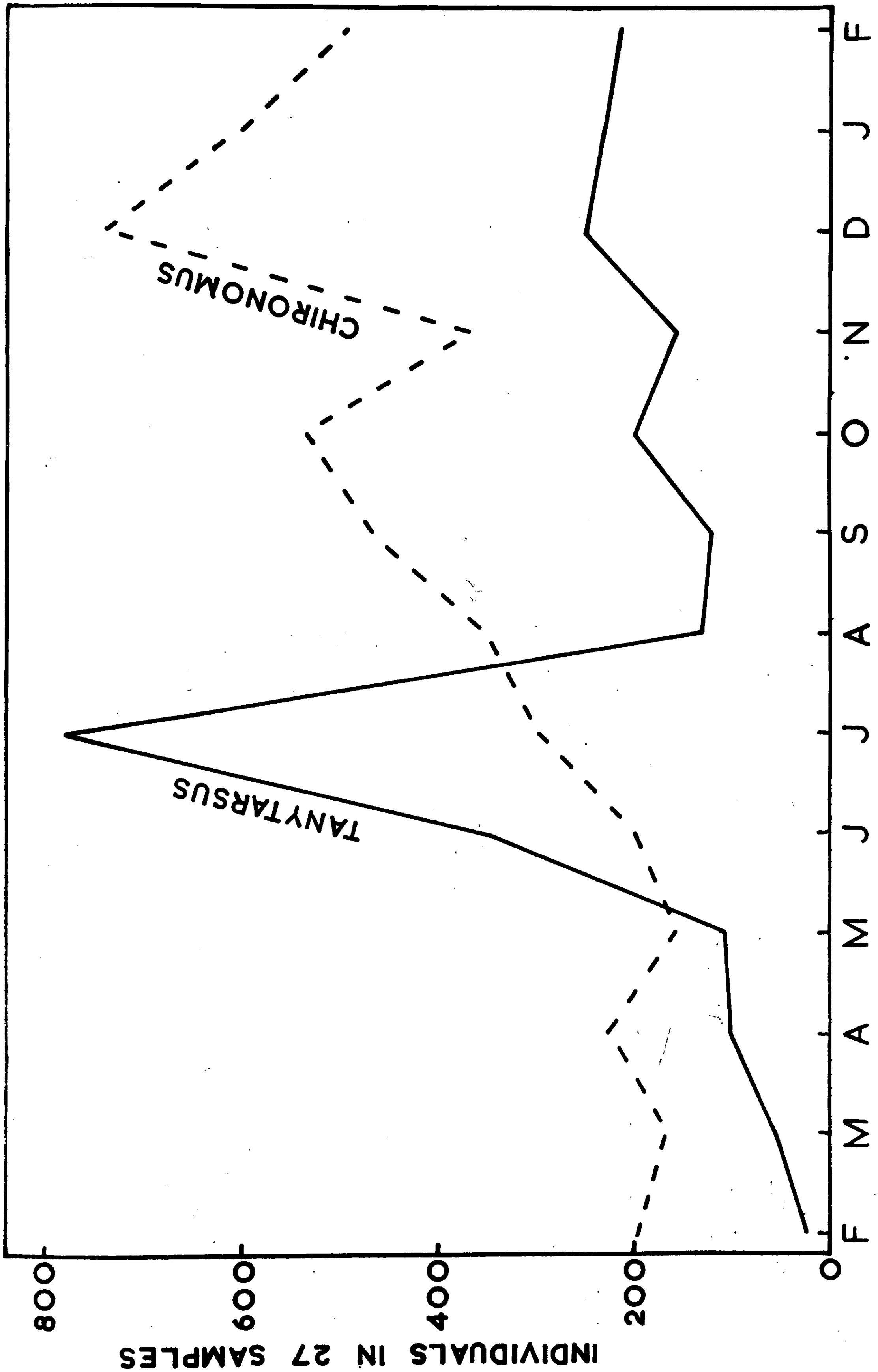


Fig.33. Seasonal variation in numbers caught along the transect - Chironomus and Tanytarsus.

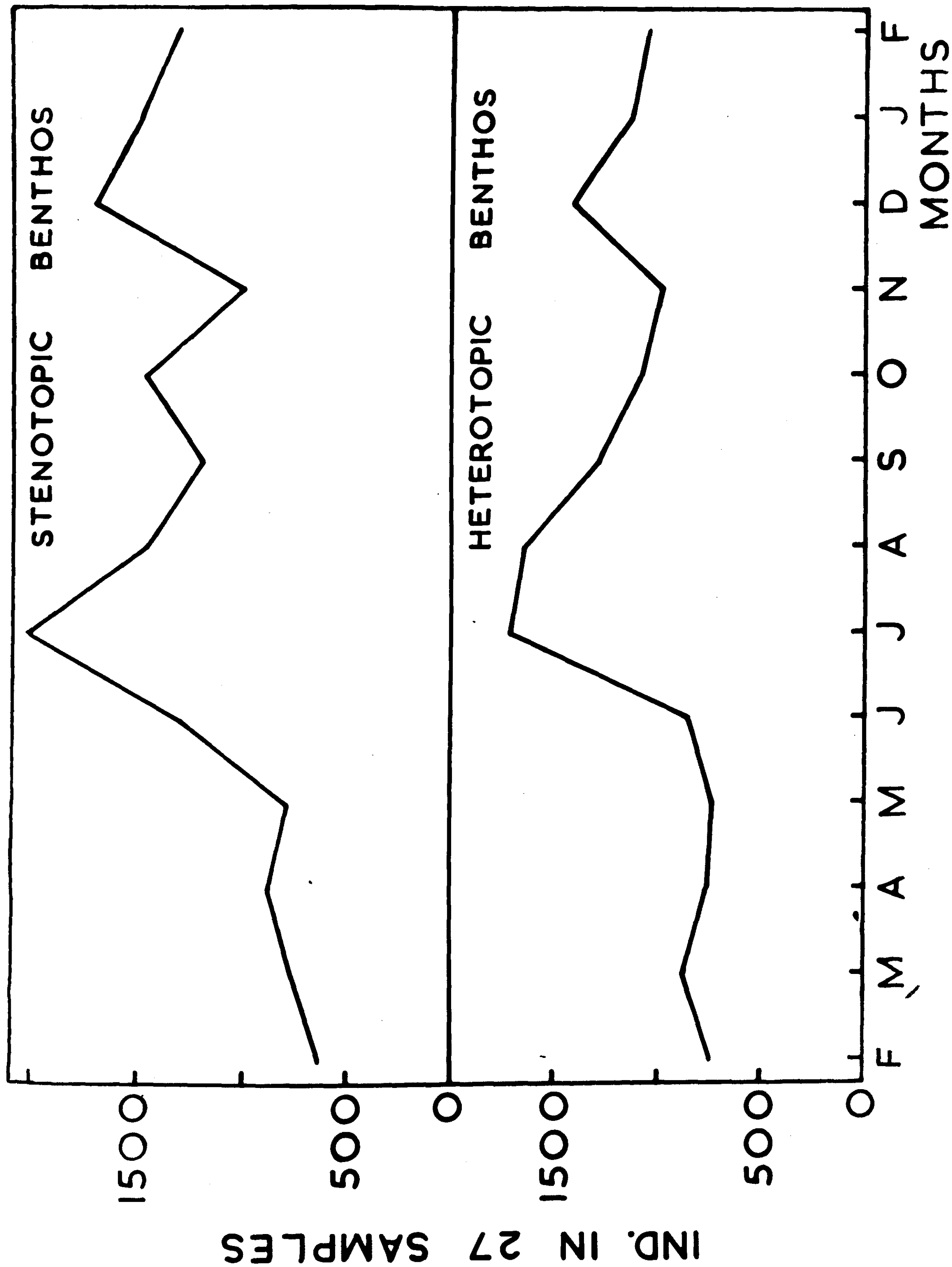


Fig.34 Seasonal variation in numbers caught along the transect - Stenotopic and Heterotopic Benthos.

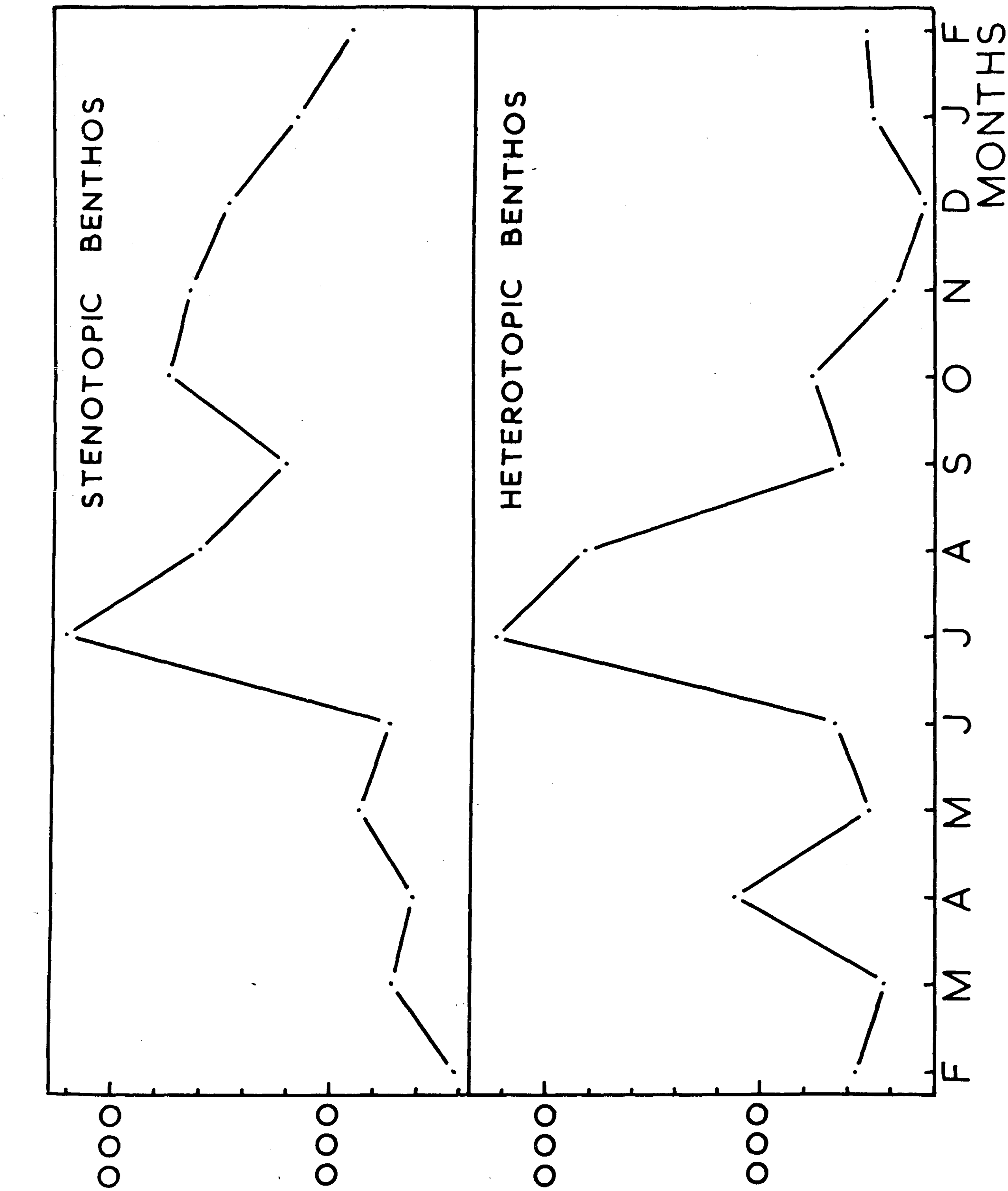


Fig.35. Seasonal population density at St.l. -
Stenotopic and Heterotopic Benthos.

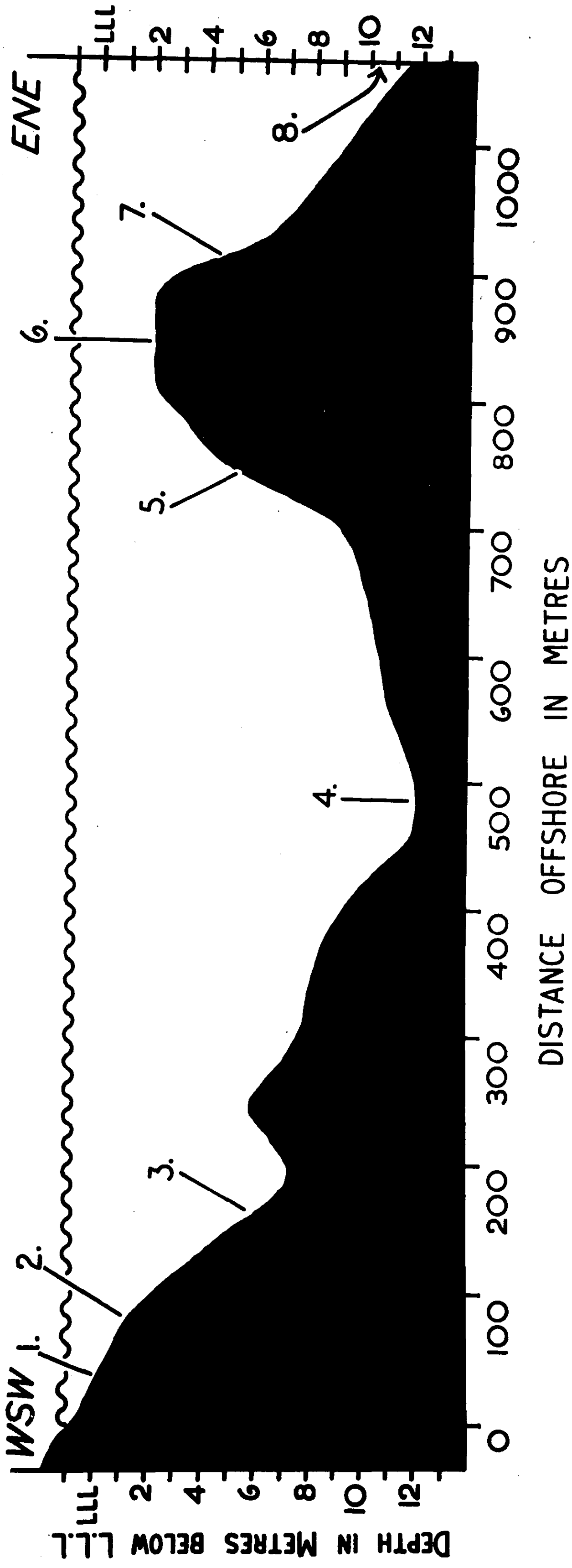


Fig.36 Profile of the transect showing positions of stations.

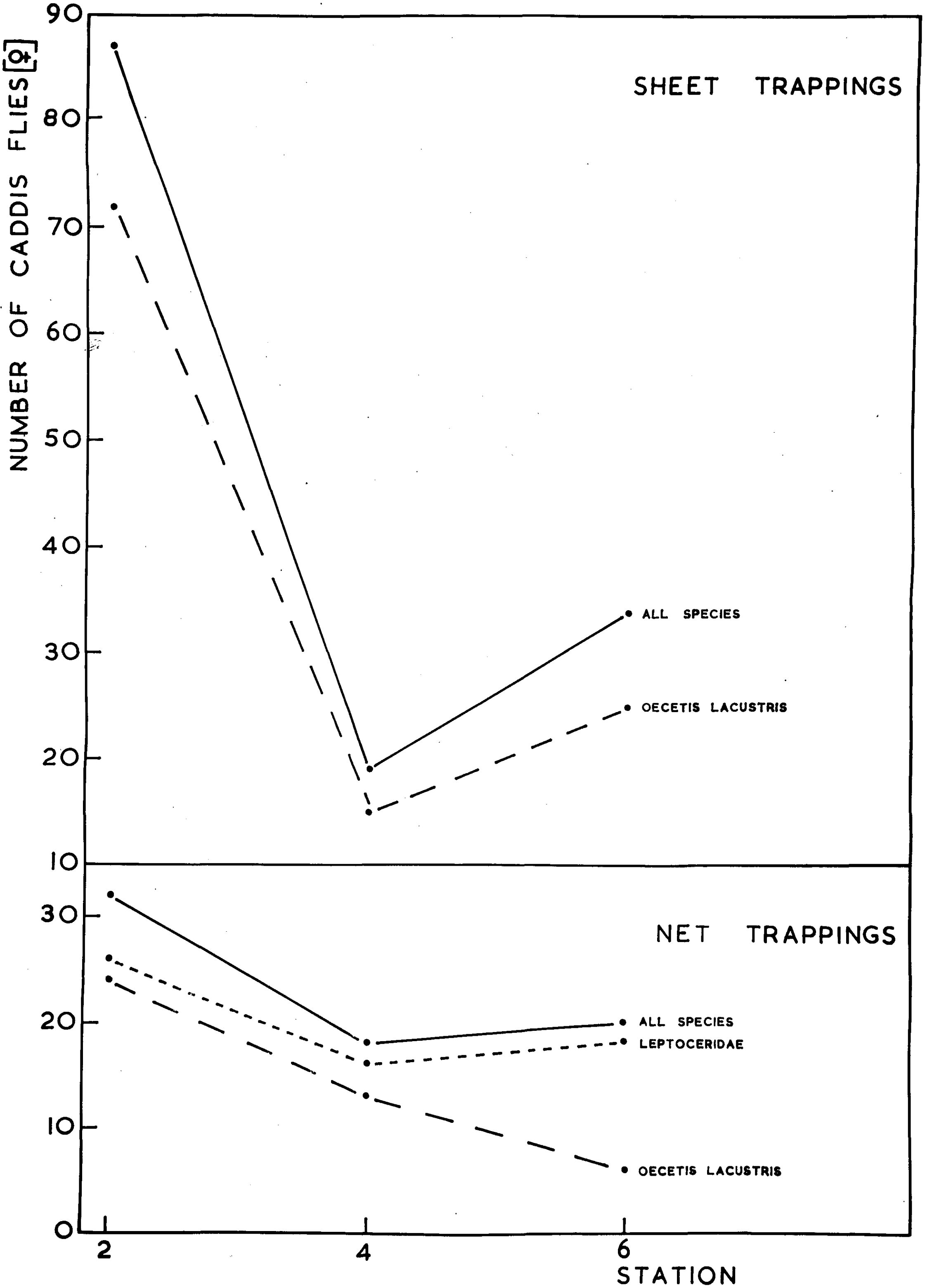


Fig.37. Variation in numbers of female caddis-flies caught at Sts. 2.,4. & 6. by floating sticky traps.

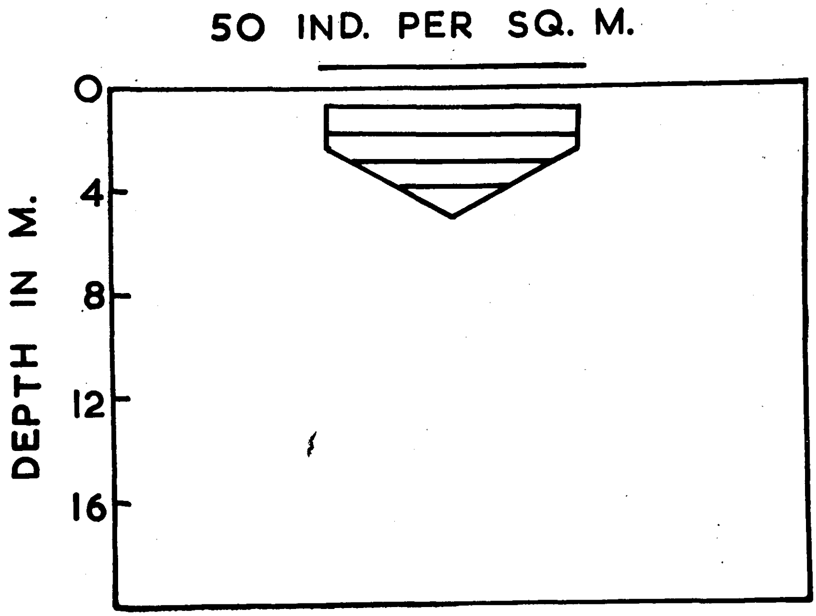


Fig.38. Bathymetric distribution of Turbellaria.

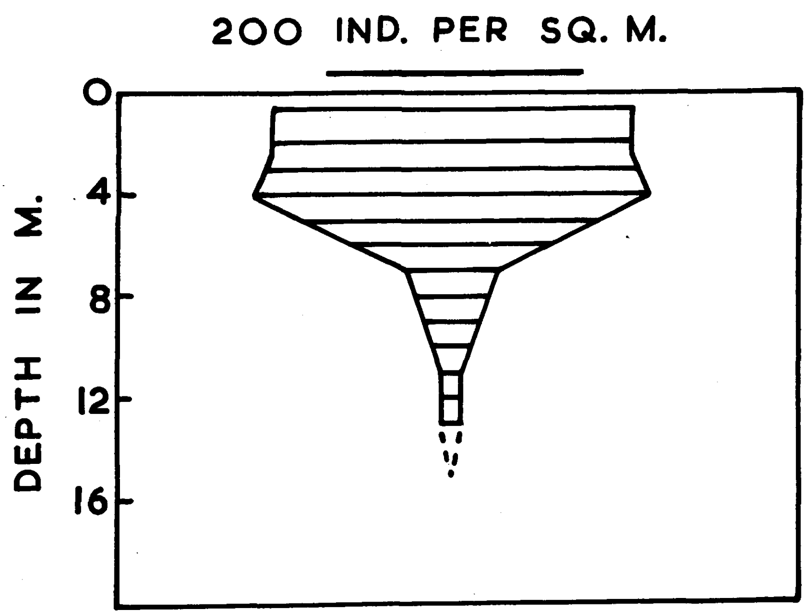


Fig.39. Bathymetric distribution of Nematoda.

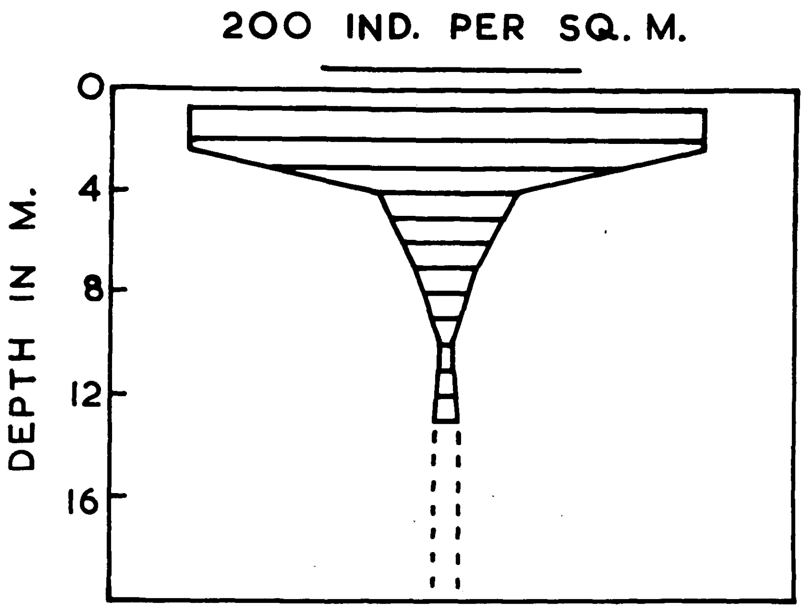


Fig.40. Bathymetric distribution of Sphaeridae.

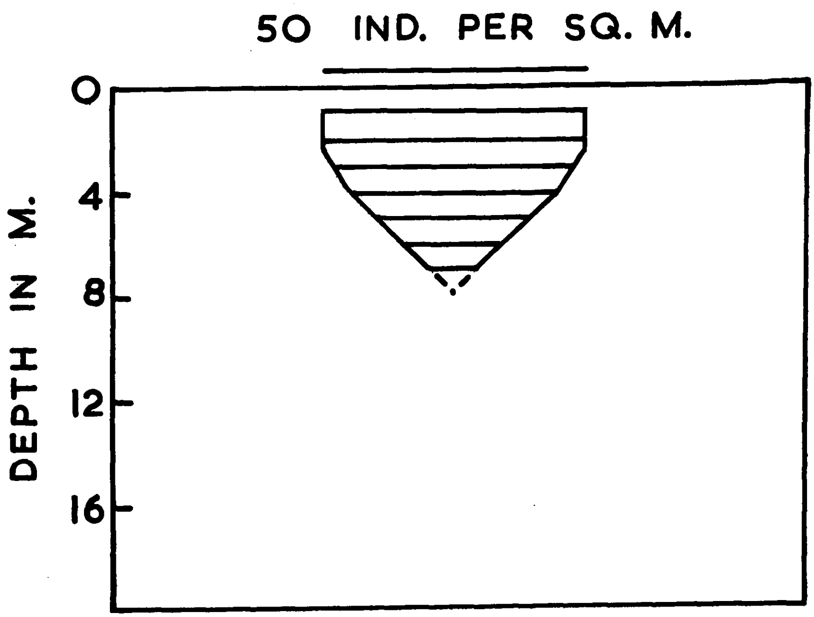


Fig.41. Bathymetric distribution of Gastropoda

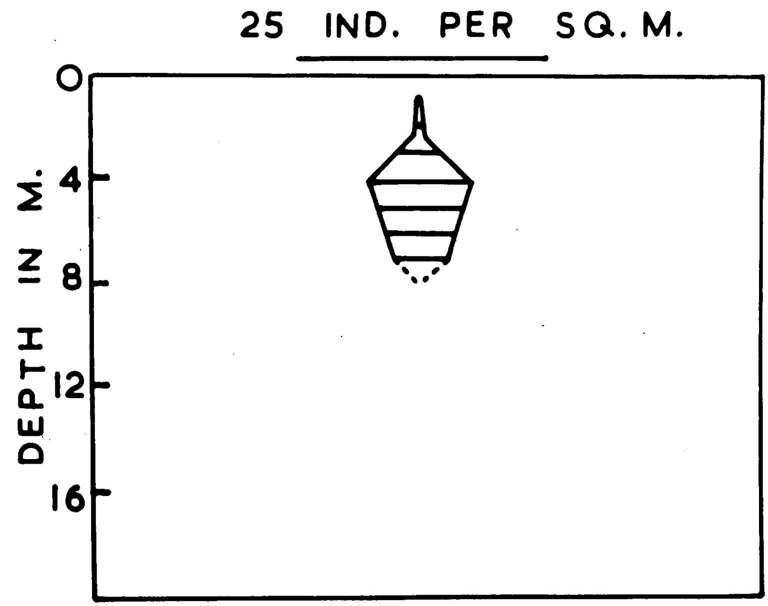


Fig.42. Bathymetric distribution of Helobdella stagnalis.

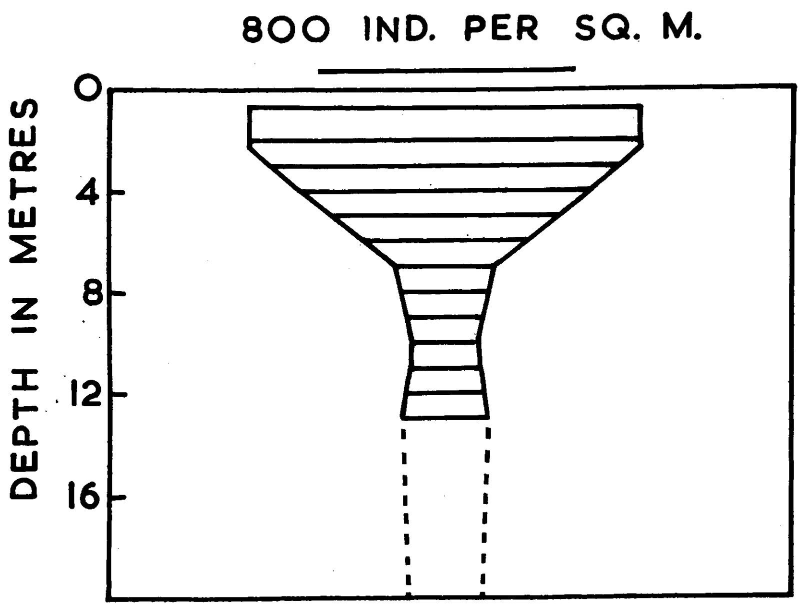


Fig.43. Bathymetric distribution of Oligochaeta

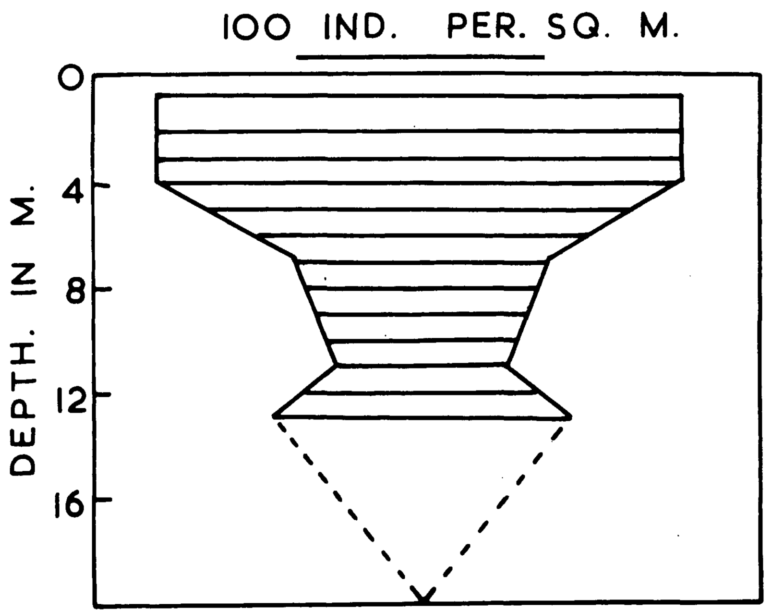


Fig.44. Bathymetric distribution of Paranais.

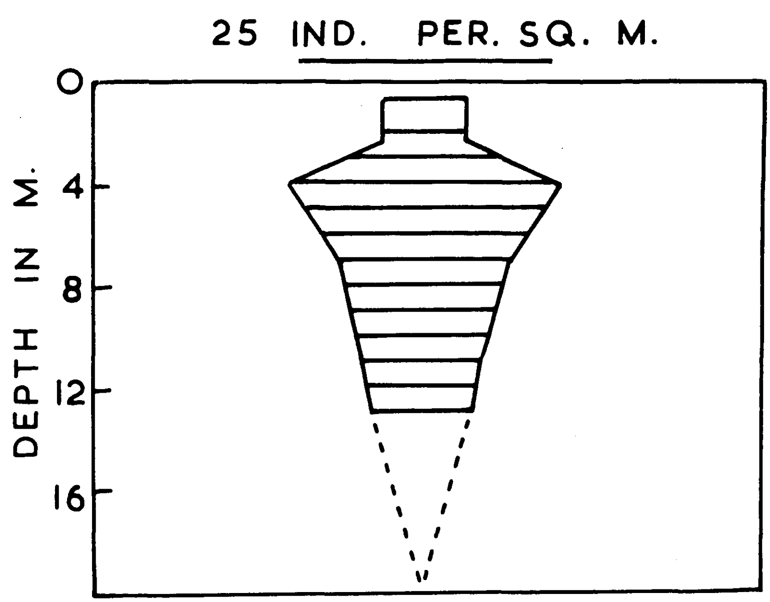


Fig. 45. Bathymetric distribution of Arcteonais lomondi.

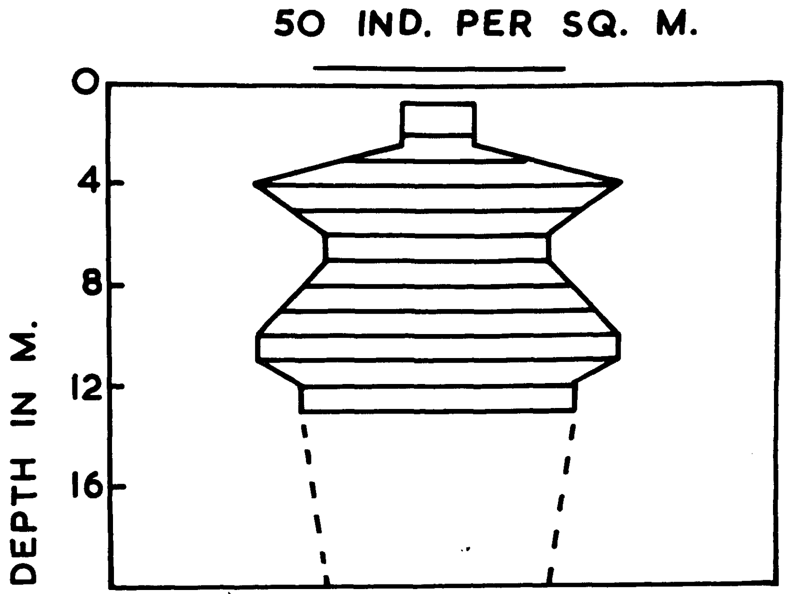


Fig.46. Bathymetric distribution of Tubifex tubifex.

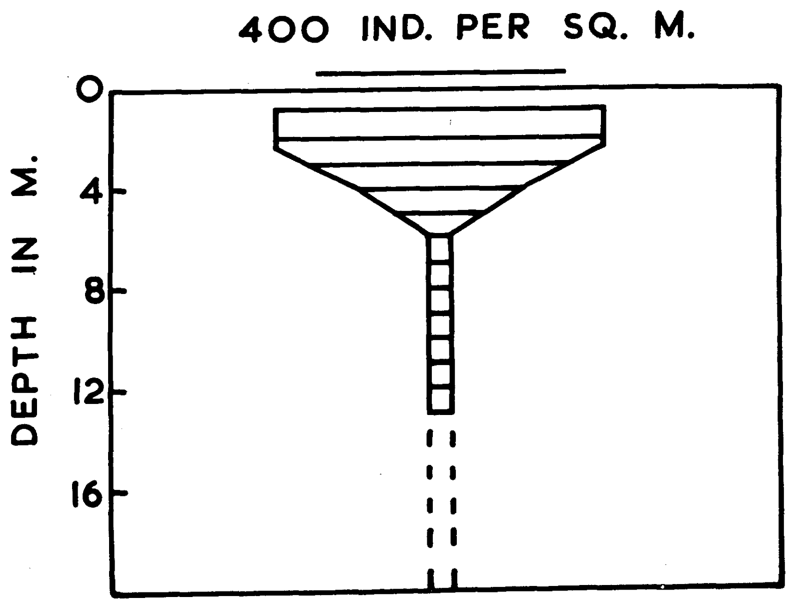


Fig.47. Bathymetric distribution of Peloscolex ferox.

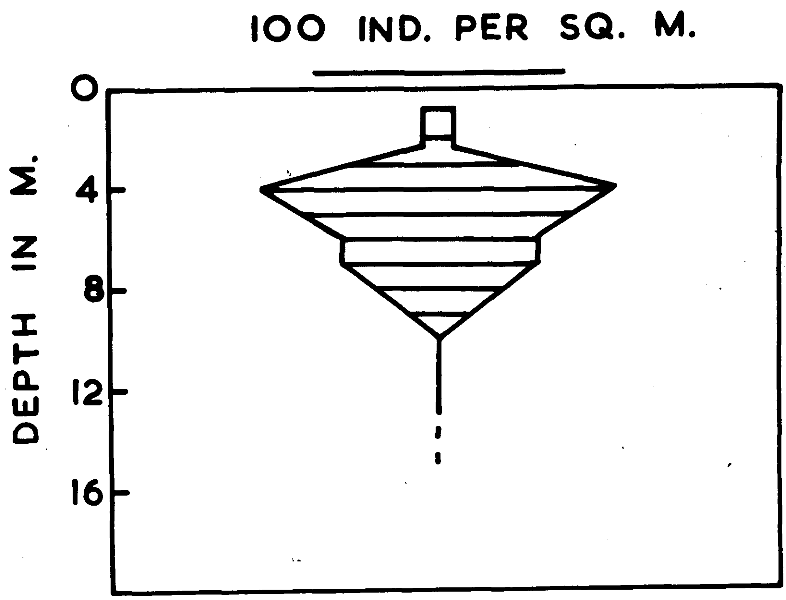


Fig.48. Bathymetric distribution of Limnodrilus.

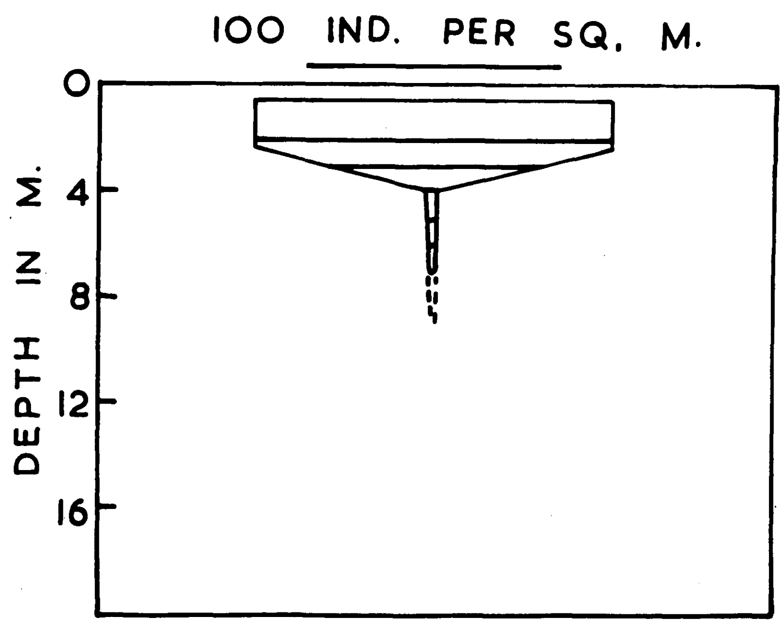


Fig.49. Bathymetric distribution of Marionina.

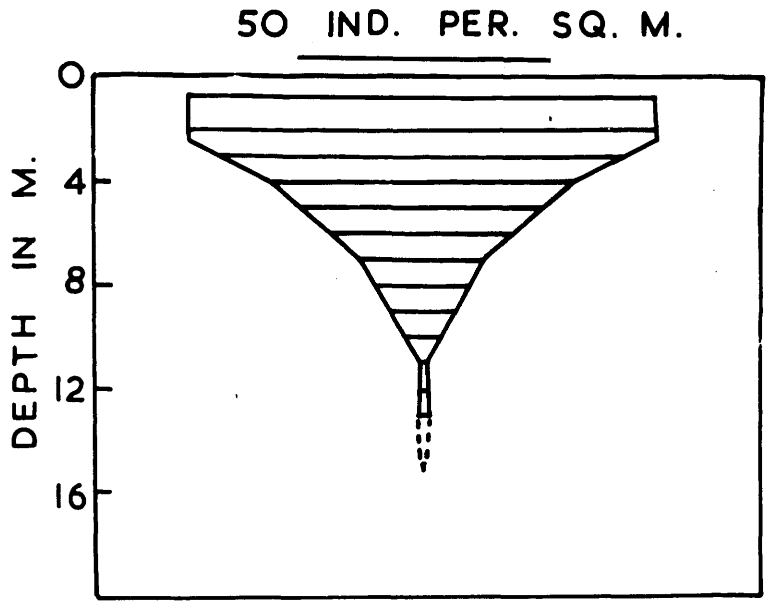


Fig.50. Bathymetric distribution of Lumbriculus variegatus.

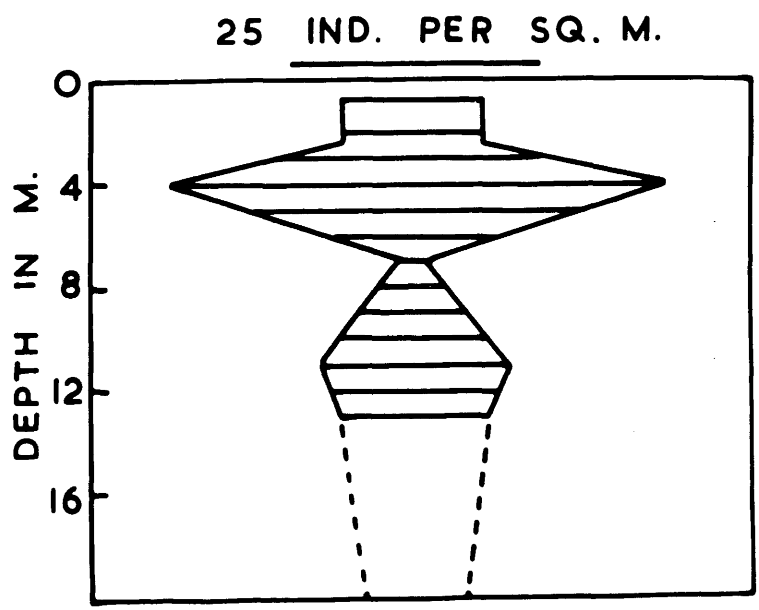


Fig.51. Bathymetric distribution of Stylodrilus heringianus.

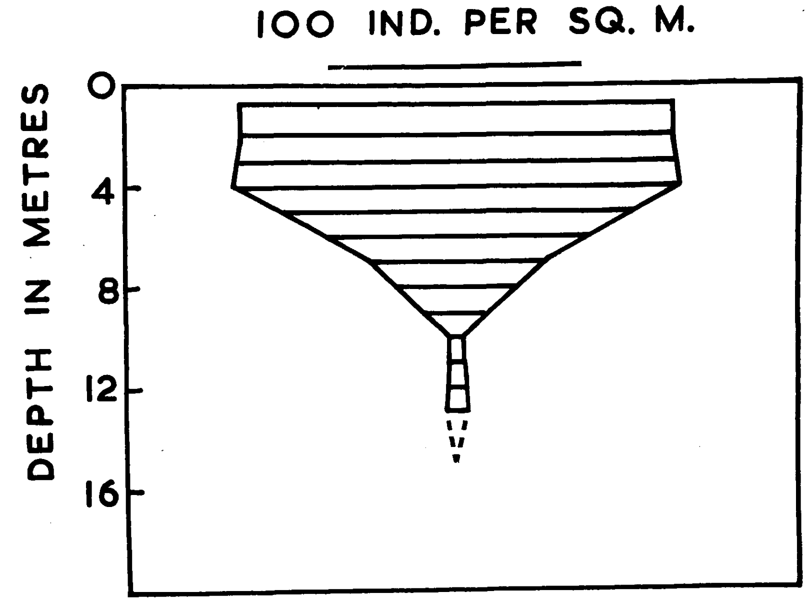


Fig.52. Bathymetric distribution of Hydracarina.

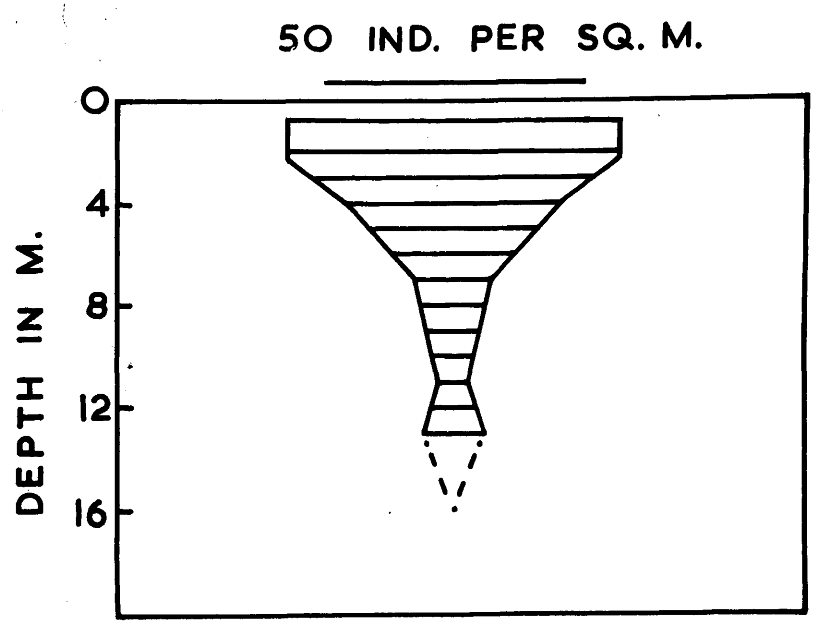


Fig.53. Bathymetric distribution of Copepoda.

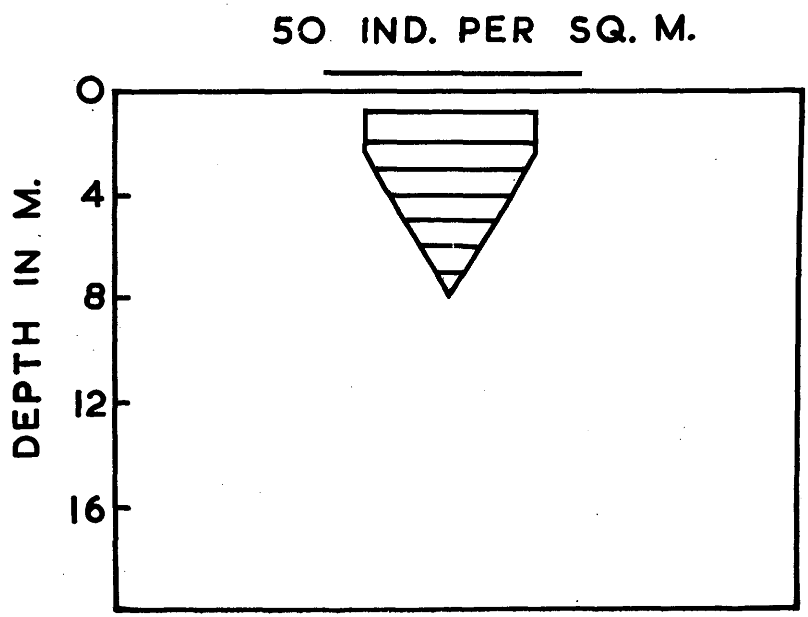


Fig.54. Bathymetric distribution of Ostracoda.

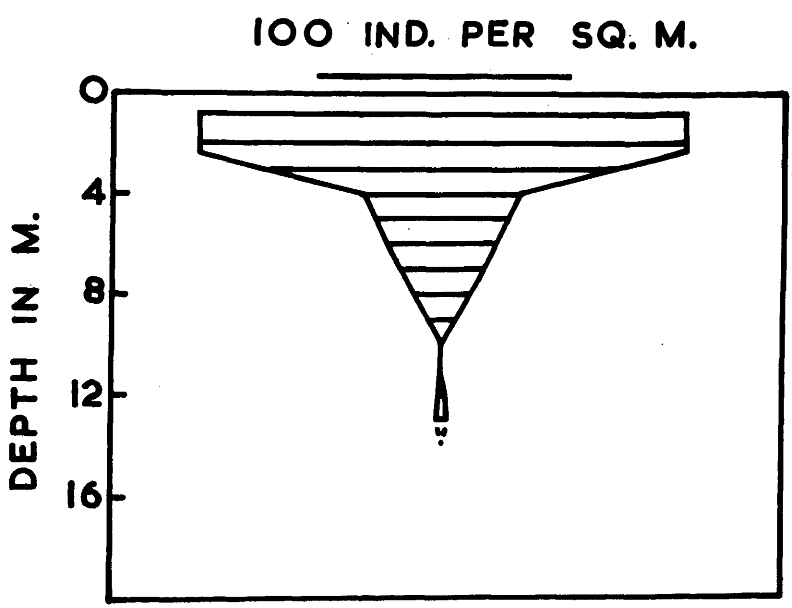


Fig.55. Bathymetric distribution of Cladocera.

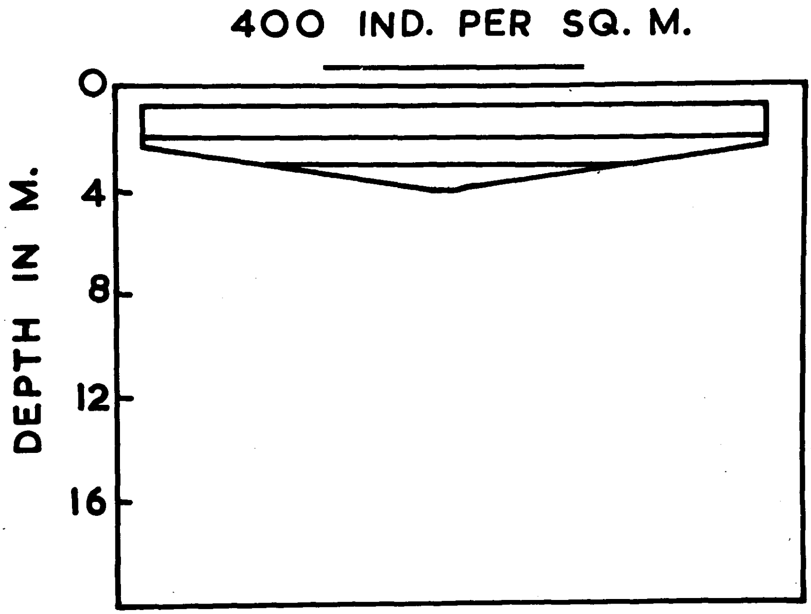


Fig.56. Bathymetric distribution of Asellus aquaticus.

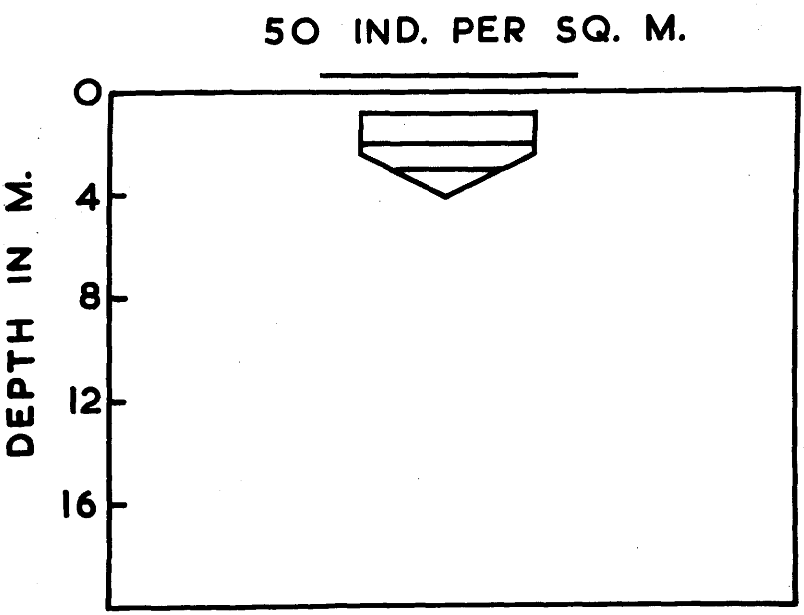


Fig.57. Bathymetric distribution of Plecoptera.

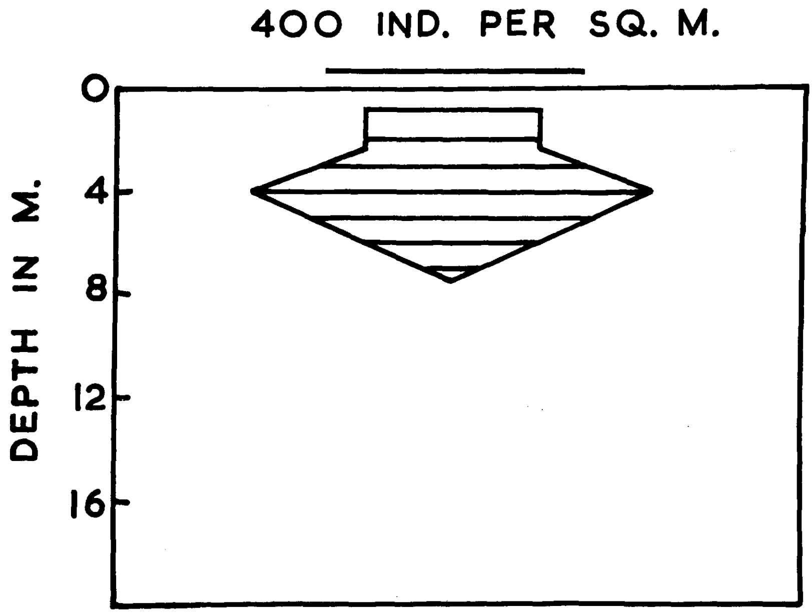


Fig.58. Bathymetric distribution of Ephemeroptera

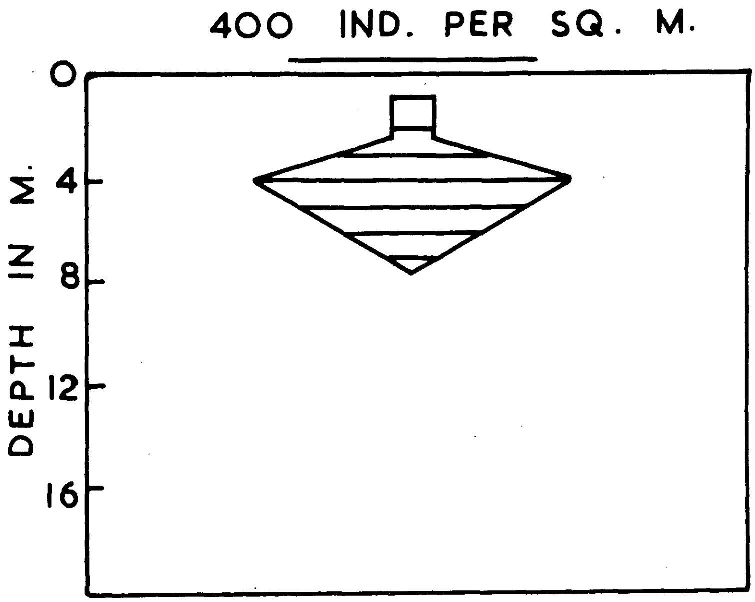


Fig.59. Bathymetric distribution of Caenis horaria.

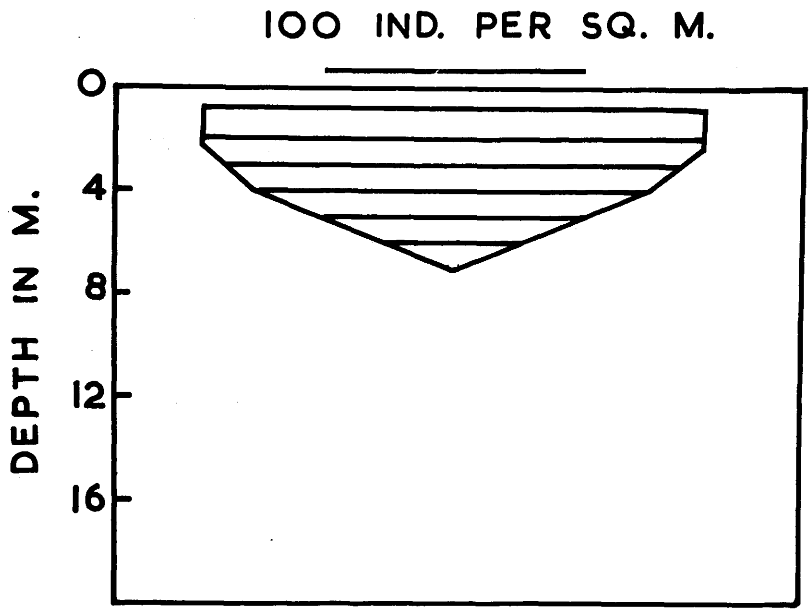


Fig.60. Bathymetric distribution of Trichoptera.

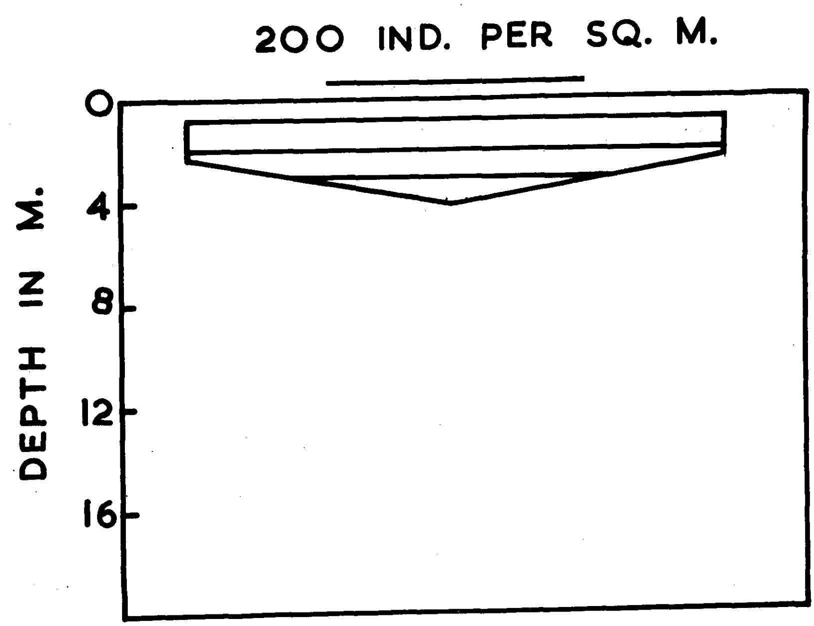


Fig.61. Bathymetric distribution of Limnius tuberculatus (larvae & adults).

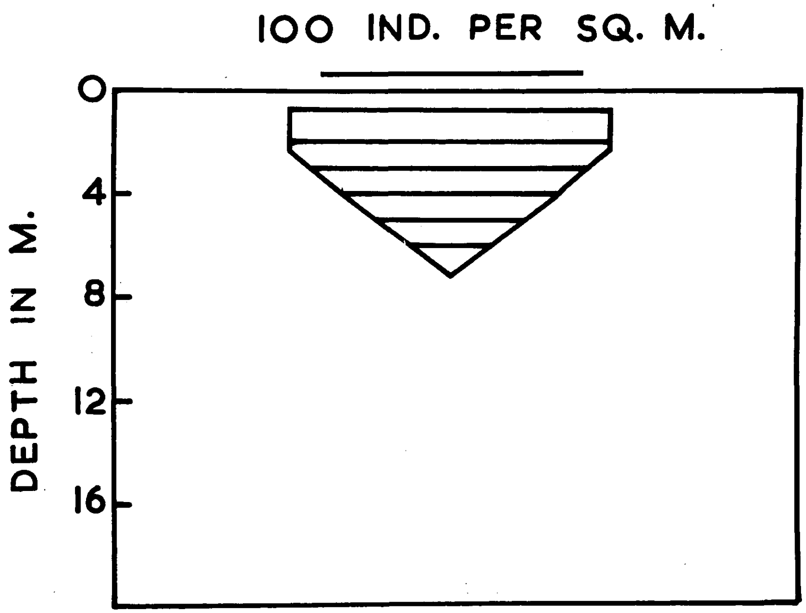


Fig.62. Bathymetric distribution of Hemerodromia.

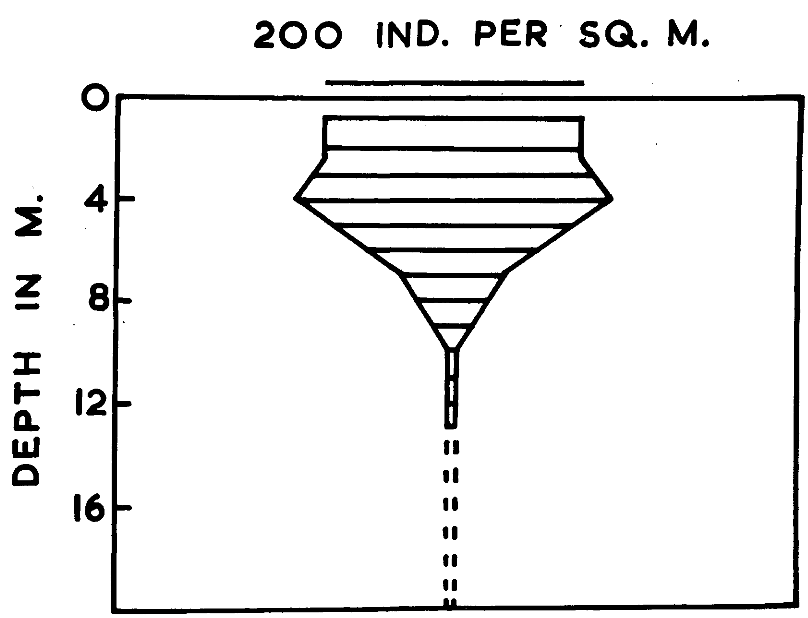


Fig.63. Bathymetric distribution of Ceratopogonidae

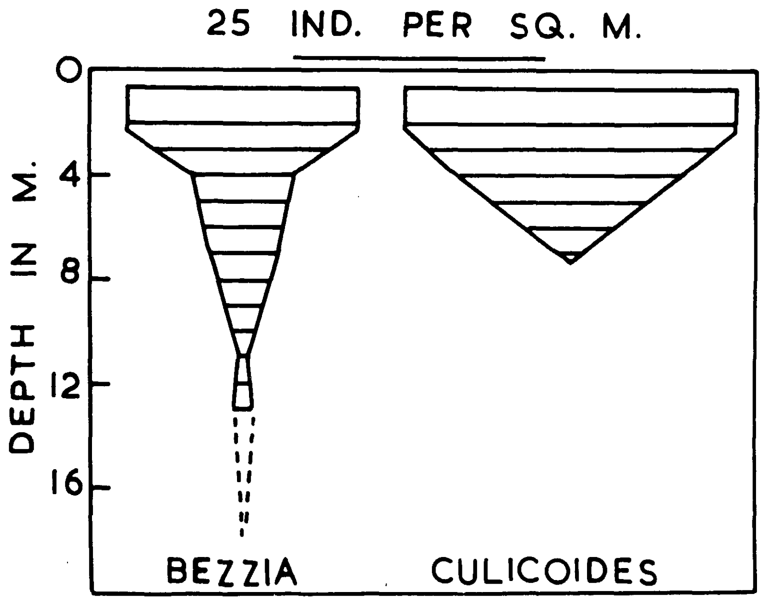


Fig.64. Bathymetric distribution of Bezzia and Culicoides cubitalis.

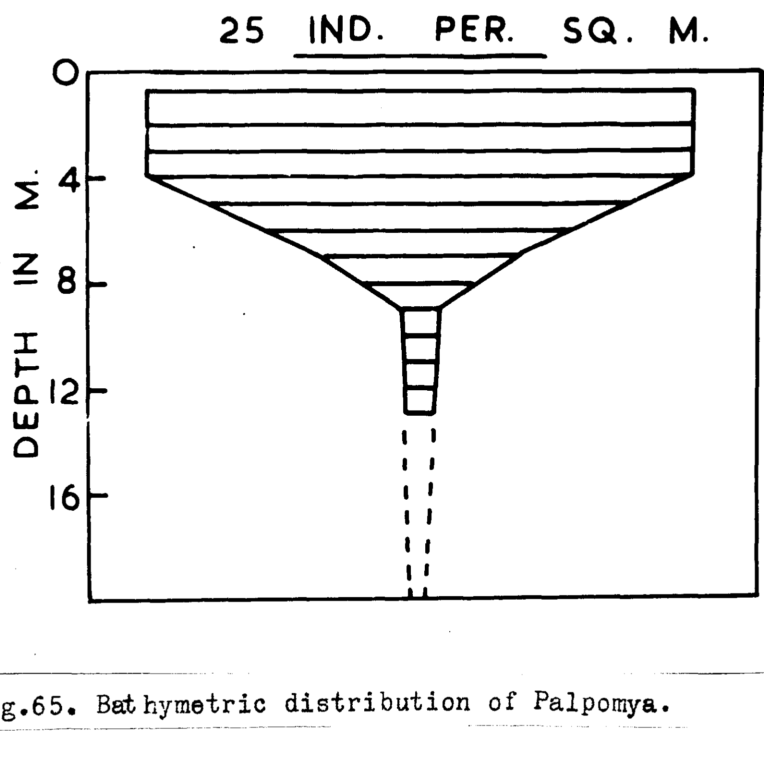


Fig.65. Bathymetric distribution of Palpomya.

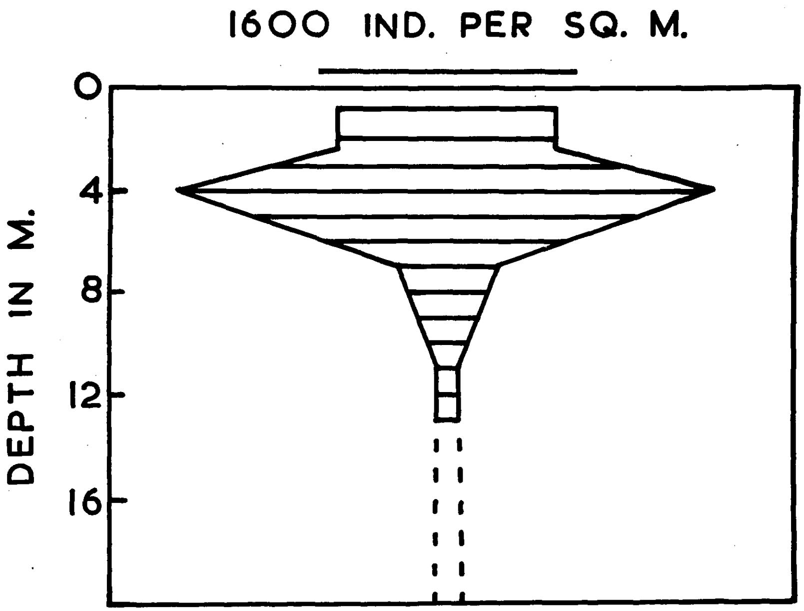


Fig.66. Bathymetric distribution of Chironomidae.

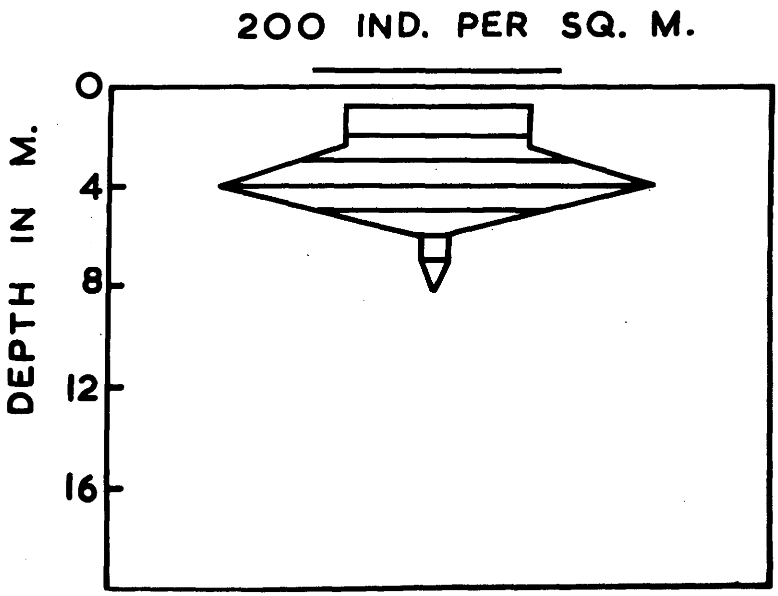


Fig.67. Bathymetric distribution of Tanytarsus holochlorus.

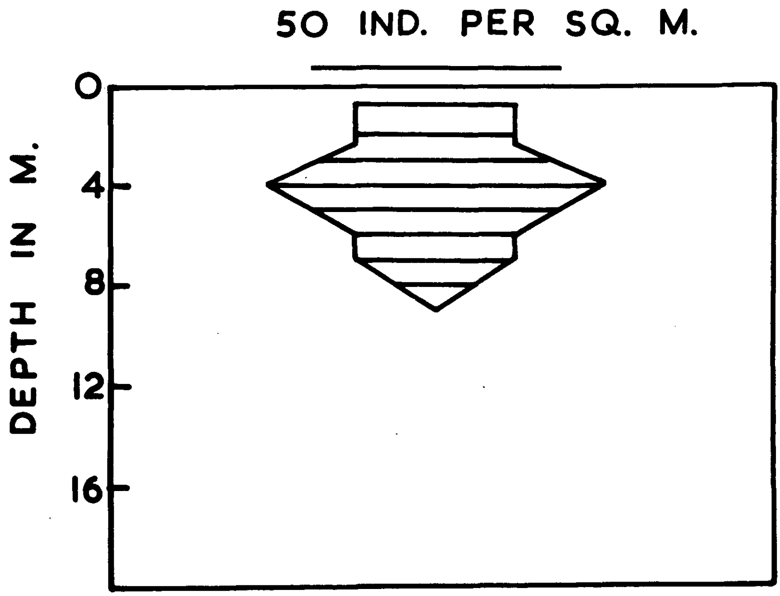


Fig.68. Bathymetric distribution of Tanytarsus glabrescens.

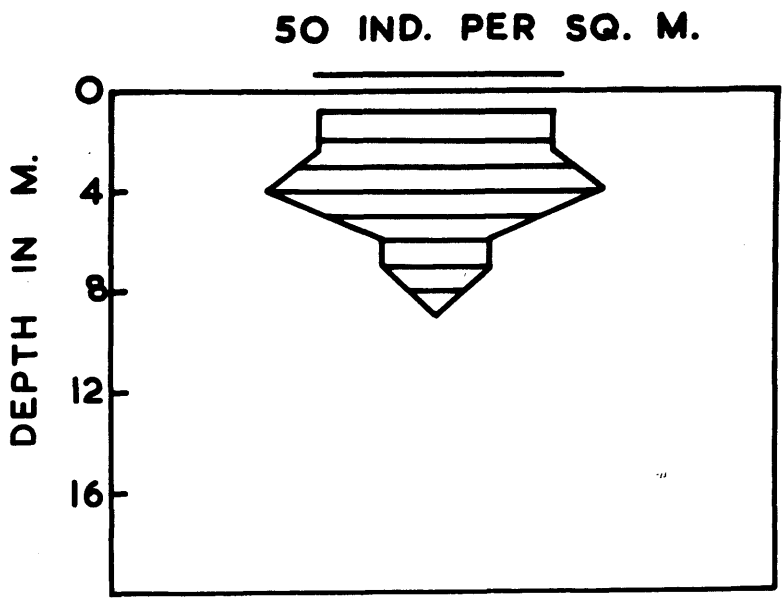


Fig.69. Bathymetric distribution of T.(Microspectra) sp.A.

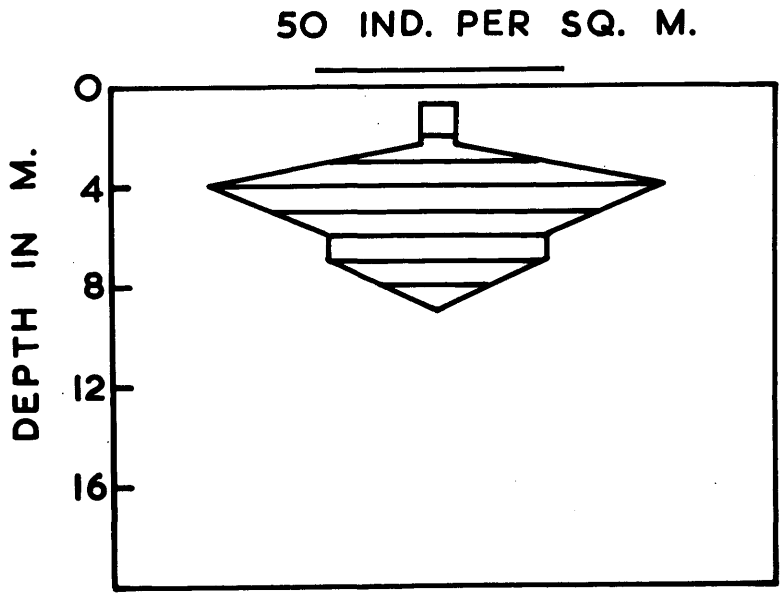


Fig.70. Bathymetric distribution of T.(Microspectra) sp.B.

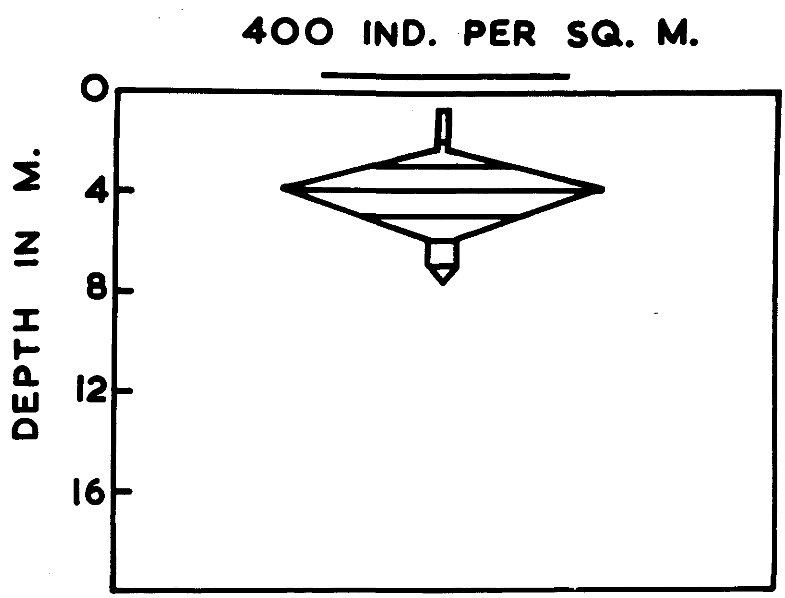


Fig.71. Bathymetric distribution of Tanytarsus atridorsum.

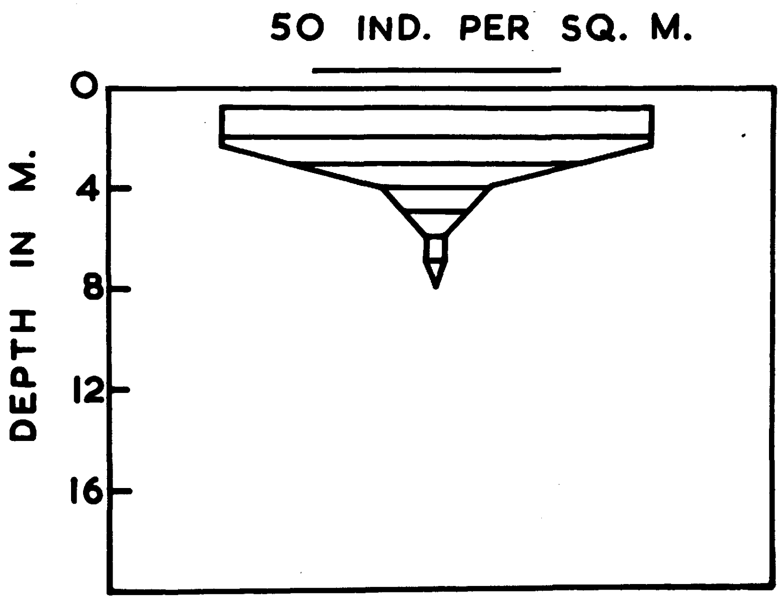


Fig.72. Bathymetric distribution of T.(Stempellina) sp.A.

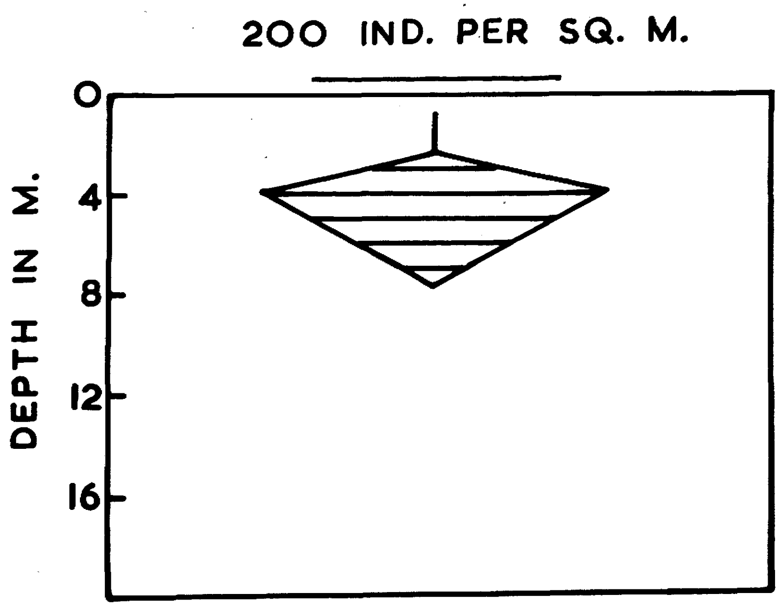


Fig.73. Bathymetric distribution of Pseudochironomus prasinatus.

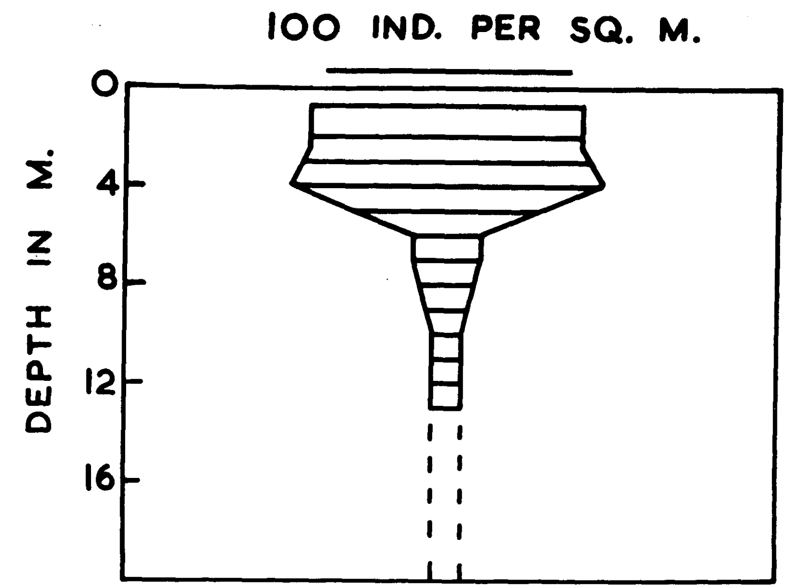


Fig.74. Bathymetric distribution of C.(Cryptochironomus).

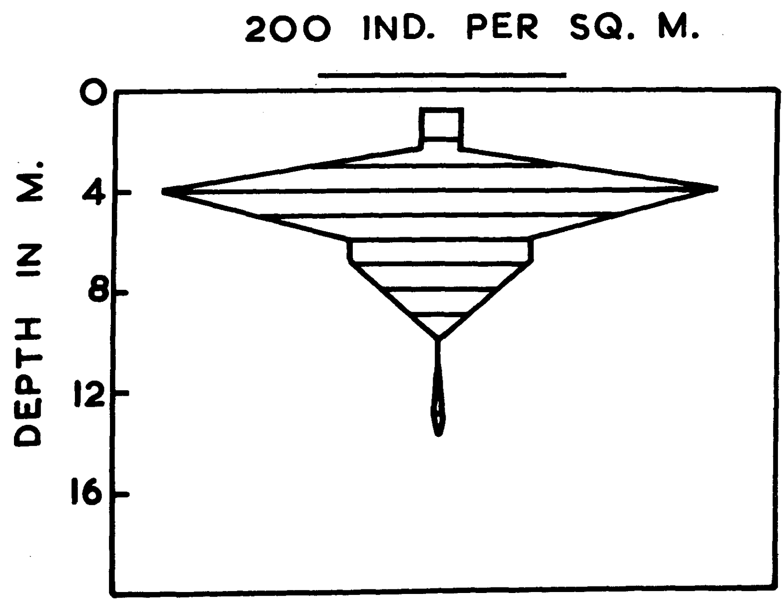


Fig.75. Bathymetric distribution of C.(Pentapedilum)nubens.

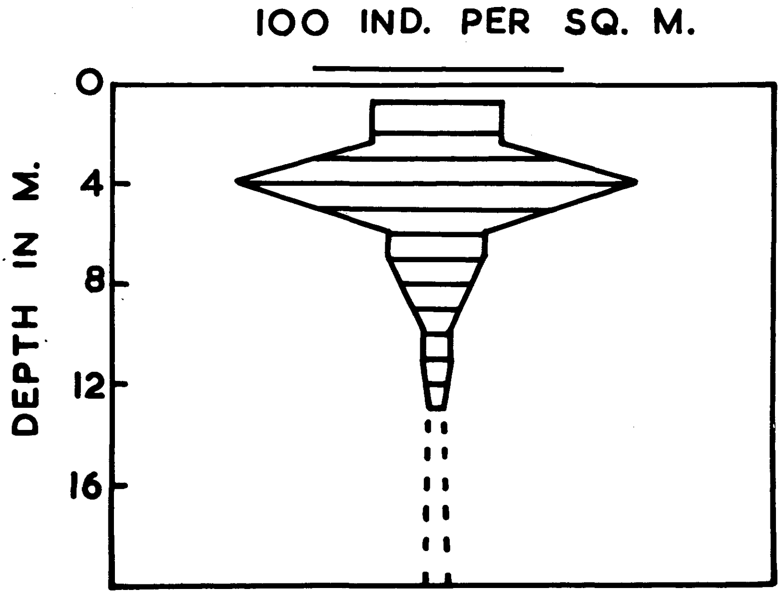


Fig.76. Bathymetric distribution of C.(Polypedilum).

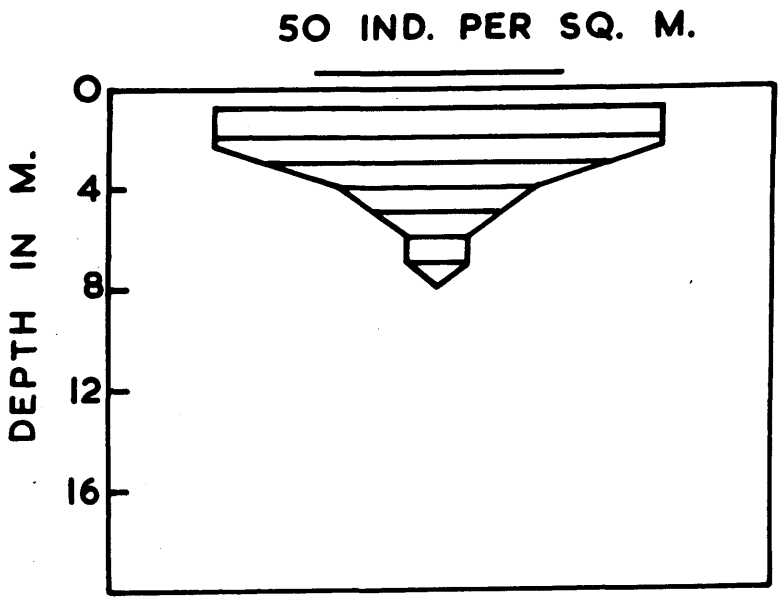


Fig.77. Bathymetric distribution of C.(Microtendipes).

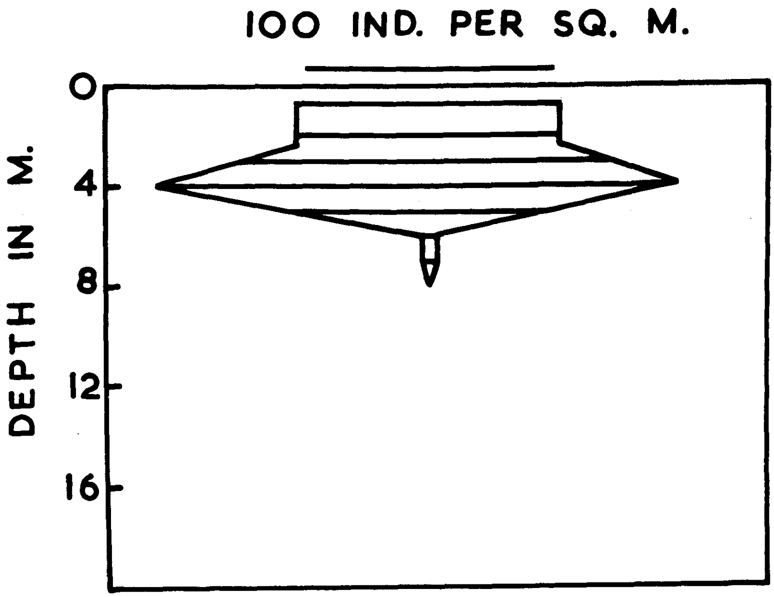


Fig.78. Bathymetric distribution of C.(Limnochironomus).

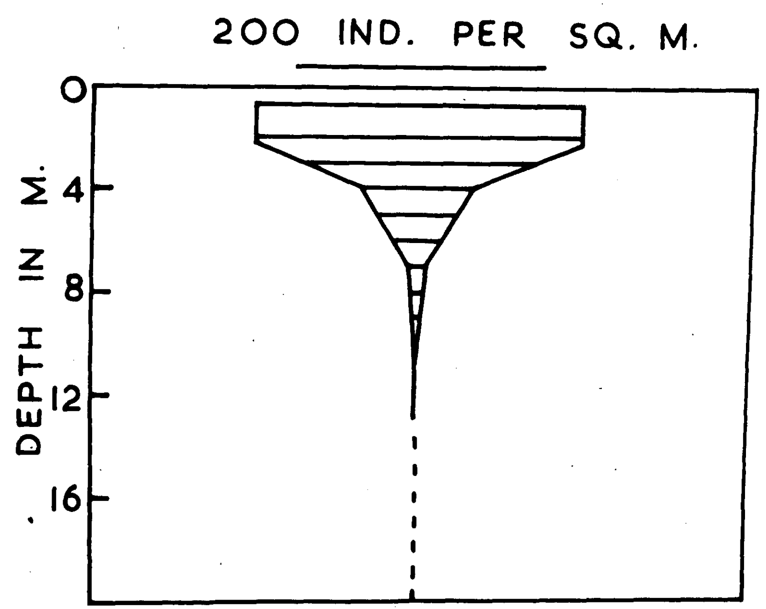


Fig.79. Bathymetric distribution of Pentaneura.

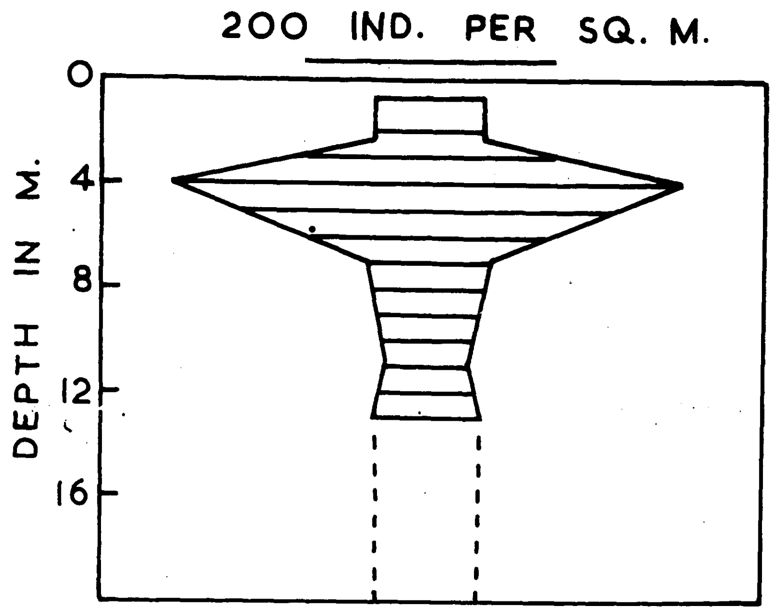


Fig.80. Bathymetric distribution of Procladius.

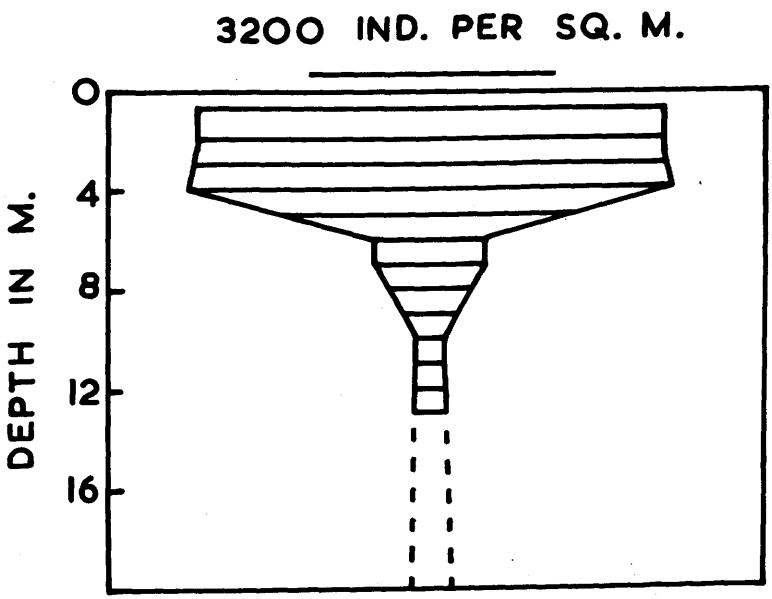


Fig.81. Bathymetric distribution of total benthos.