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ECOLOGICAL STUDIES ON THE ZOOPLANKTON OF LOCH LOMOND

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the degree of Doctor of Philosophy, November, 1965.

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INTRODUCTION

'...studies of energy flow at the population level must be based on a firm foundation of descriptive ecology and life history.' Odum et al 1962

The most fundamental objective of the ecologist lies in the defining of the processes involved in the transfer of energy from the sun through the ecosystem. He wishes to know exactly how this energy is utilised, with what efficiency, and how much organic matter is produced as a result of these processes. In studying this flow of energy the inter-relationships between the organisms on different trophic levels and those between the species on each separate level are of great importance, since they determine not only the pattern of this flow, but also the stability of the community, and, on a long term basis, the production.

An analysis of the seasonal changes in the pathways of energy transfer therefore requires a detailed knowledge of the relationships of the various species of the community to each other, and, furthermore, of the factors controlling the seasonal cycles of each species. This study is largely concerned with one of the species in the aquatic community in Loch Lomond, the most abundant zooplankter, Diaptomus gracilis Sars. The annual cycle is described, and the varying balance between mortality and reproduction is analysed in an attempt to contribute towards an eventual understanding of all the interactions within the community. The other species of zooplankton are not considered in such detail but particular attention is also paid to the life cycles of the two cyclopoid species, Mesocyclops leuckarti (Claus) and Cyclops strennus abyssorum Sars, and the causes underlying the fluctuations in the abundance of the copepods are discussed. In addition, some consideration is given to the spatial distribution of the animals and its relation to their biological cycles.

Much of the available information on the biology of Loch Lomond is summarised in Slack et al. (1957) and since then further work on the bottom fauna by Fedoruk (1964) and Slack (1965) has appeared. Maitland (e.g.1964) has studied the fauna of the major inflowing river, the Endrick. The loch was, of course, included in the work of the Scottish Loch Survey (Murray & Pullar 1910), although its biology is not discussed specifically in the reports. These works, however, provide little data on the zooplankton and the present work is the first full scale study of these animals in Loch Lomond.

METHODS

Sampling was carried out from the Zoology Department's launch 'Fiona', except for much of the summer of 1964 when a dinghy had to be used whilst the launch was out of the water for painting. Sampling was begun in October 1962 and terminated in January 1965, but was greatly handicapped by the severe winter of 1962-63, when ice prevented access to the Strathcashel basin working area, and also by prolonged mechanical difficulties with the launch in the summer of 1963.

Temperatures were measured with a thermistor, constructed by Dr. H. D. Slack after the design of Mortimer & Moore (1953). Samples for chemical analysis and for chlorophyll estimations were collected either in a plastic bottle held below the surface, or, when available, by a Van Doorn sampler of 6 litre capacity. This was also used at times to supplement the standard zooplankton samples. The samples were run into a large plastic container and later through a filter unit, which consisted of two cylinders of perspex, 5 cm. in diameter, each with a flange at one end. A piece of bolting silk (200 meshes per inch) was held between them by clamp screws through the flanges. After filtration the silk was placed in a small jar, the unit rinsed and formalin added. In the laboratory the silk was well washed down and the sample re-concentrated for direct counts of the animals.

The samples for chlorophyll estimation were kept cool and dark on board and at 0°C. in the laboratory until processing, which was almost always on the evening of collection. Triplicate samples, each of two litres, were filtered under vacuum from a water pump through Whatman GF/B glass paper filters (Spencer pers. comm. & 1964). Surplus water from the folded filter was absorbed with blotting paper, and it was placed in a screwtop vial with a little powdered magnesium carbonate. 8 mls. of 90% A.R.acetone were added and the sample left for 24 hours at 2°C. It was then centrifuged to throw down the remains of the filter, and the absorption at 720mμ, 665mμ, 630mμ, 510mμ and 480mμ was read, in a Unicam SP600 spectrophotometer prior to January 1965, and after this in a Hilger-Watts Spectrochem H840, using a 2 cm.cell. The pigment concentrations were calculated from the revised equations given by Parsons & Strickland (1963).

The choice of a routine sampling method for the zooplankton was dictated partly by external circumstances such as the limited time in the field and the available equipment. The method adopted was that of vertical samples taken with a closing net from as many stations as possible. This enabled samples of known size (i.e. vertical distance hauled) to be taken in specific depth ranges. Samples taken with an obliquely or horizontally towed net would have the advantage of covering a larger area and would obviate the need for taking a number of vertical series at different places to allow for uneven horizontal distribution but they do not readily lend themselves to accurate sampling at known depths. The use of a bottle, such as the Van Doorn, or a pump, would be more accurate quantitatively since the volume sampled is known exactly, and the catch is free from errors due to clogging by phytoplankton, partial malfunction of the closing mechanism etc., but the depths of the stations and the densities of plankton were such that an inordinate number of samples would be required for complete coverage of the water column.

The closing net was felt to provide a reasonably quick and accurate means of obtaining samples suitable for both quantitative and qualitative assessment of population sizes and vertical distributions. The latter were considered in broad outline only, i.e. whether the animals were in the surface layers or deeper levels rather than whether they were at 3 metres or 4 metres depth.

In practice it was found that the samples from the upper layers were at times rather large, which in turn necessitated larger sub-samples for the ageing of the animals, whilst the lower ones were at times too small, on occasion having to be counted directly. Comparable disadvantages are found in any method, however, and all sampling involves some compromise between the desirable and the achieved. On the whole it may be concluded that the methods used were satisfactory for the investigation as it was carried out.

The net used was a Nansen (1915) type closing net, based on the modified design of Currie and Foxton (1957). A canvas sleeve of 26 cm. diameter held open by a brass ring at the top, and 48 cm. in length was followed by a straight section of bolting silk of the same diameter and 37 cm. long and then by a conical section of 65 cm. straight length which tapered down to end in a canvas sleeve held by a jubilee clamp over a brass bucket of 7.5 cm. diameter. The bucket was designed for the collection of live samples and was therefore of relatively large capacity to reduce to some extent the density of the animals concentrated together during tows etc. It had an upper straight section of 5 cm. length followed by a 10 cm. conical section tapering into a tube of 4 cm. length and 2 cm. diameter over which a piece of rubber tubing, closed at the bottom by a screw clip, fitted. The silk used had 74 meshes/inch. The mesh retained only the larger nauplii and these stages were not studied in this work. There is a possibility some of the smallest copepodites may have escaped also but this could not be assessed, although the results of the analyses suggest that any such loss was not great.

The net was supported by three bridles from a brass ring at its mouth. These led into a D-ring held in a Friedinger release. The Throttling line ran from the release through rings sewn around the canvas sleeve 25 cm. below the mouth. Weights were suspended below the net from a brass ring at the base of the canvas, the lines running through lugs on the bucket. The net was lowered open and was then hauled vertically upwards for the required distance, depths being read off a metre wheel over which the cable ran. Historical continuity was assured by the fact that the winch and the wheel were originally used by the Challenger Expedition. The net was closed whilst the net was still in motion. On reaching the surface it was well washed down and the contents run into Kilner jars for immediate preservation. Duplicate hauls were taken in each depth range and if time permitted, an extra single sample of the entire water column. The standard series taken (worked from the surface downwards) was from 0-10 metres, 10-20 metres and from 20 metres to the bottom. On occasion the samples were taken at closer intervals. Visual comparison of the duplicates in the field provided some check on the operation of the net, and in the rare event of obvious discrepancies the sample was repeated.

It was intended that sampling should be at intervals of 10-14 days and that stations in as many different parts of the basin as possible should be worked but owing to circumstances beyond the control of the author the sampling programme although adequate (at least in 1964) was not as complete as was desired.

In the laboratory the samples were concentrated by filtration through a small hand net of 200 m.p.i. bolting silk. The animals were washed carefully into small jars for preservation in 10% formalin. Except at times of high density, or for checks of sampling efficiency, the duplicates were combined. Statistically, it would have been desirable always to count them separately but this would have unduly multiplied an already large number of samples.

The primary counts for the numbers of each species were made by taking four (or more if close agreement between each was not obtained) 5 ml. sub-samples from the well shaken bottle of concentrate by a wide mouthed pipette. Counts were made at x25, the numbers being recorded on an electric counter. The volume of the concentrate was adjusted to give about 100-150 animals in each sub-sample. Knowing this volume the total numbers of each species in the sample could be found.

For storage the samples were again filtered and the animals washed into 3" x 1" tubes. This final concentration was done only to reduce the volume occupied by the collections. The figures for the population densities of the animals are quoted in terms of the numbers per standard sample, i.e. either in the duplicates from a specific depth range, or the total in the complete series of duplicates from surface to bottom, according to context. Plankton numbers are often given as numbers per litre but this is not considered desirable since the vertical distribution of the animals is almost always highly irregular and hence such figures have little meaning if based on samples taken over relatively large distances. This is particularly so in Loch Lomond where differences in density of up to 1000 times could be found between the surface and deep samples. A more appropriate unit for the present work would be the numbers found under

TABLE 1

Results of Replicate Samples
(S.VI, 15.1.64)

Depth(m.)	Diaptomus	Mesocyclops	Daphnia	Bosmina	Total
0-10	440	220	110	110	880
	594	306	144	252	1296
	611	208	208	312	1339
	544	187	170	289	1190
10-20	272	176	192	320	960
	544	221	204	272	1241
	490	252	98	266	1106
	403	156	117	221	897
20-42	500	380	220	380	1480
	504	420	210	609	1743
	481	169	195	338	1183
	504	182	112	238	1036
Total Nbr.	1212	776	555	810	3320
	1642	947	558	1133	4280
	1582	629	501	916	3623
	1451	525	399	748	3123
Mean total	1472	719	495	902	3588
Standard deviation	190	183	68	169	506
Coeff. of variation	13%	25½%	13½%	18½%	14%

a square metre of surface but since the absolute accuracy of the sampling technique was not assessed the figures are considered comparable only in so far as the same net was used by the same person. If desired the densities quoted may be multiplied by 127.4 to give numbers under a square metre, and by 0.530 times the length of haul for the numbers in the volume sampled.

Identification of the animals was made from the keys of Scourfield & Harding (1958) and Harding & Smith (1960).

The testing of the accuracy of sampling poses some difficulty, as in any set of figures three variables are involved: the efficiency of the net itself, of the counting process, and the natural variation induced by the non-random distribution of the animals. This latter aspect is a particularly complex one (recently reviewed by Cassie 1963). Elaborate analyses of the variance in large numbers of replicates are therefore necessary, but an approximate indication of range of variability encountered in the sampling is given by Pearson's coefficient of variation (100.standard deviation/mean). This has been calculated for a typical set of data in Table 1, which shows that the variability is not great. The values obtained compare well with the typical range of 20-50% quoted by Cassie (loc. cit.).

The major sources of error are likely to be clogging of the net by phytoplankton, and losses on closure (Barnes & Marshall, 1951). The former would be lessened by the fact that the length of haul was relatively short. Although at no time was the net seen to be heavily coated with algae, clogging remains a possibility as on occasion a smaller total number of animals were caught in direct hauls from the bottom to the surface than in the divided series. The high ratio of total filtering surface to the mouth area of the net will give good filtering efficiency, and will reduce losses from the entrance due to back pressure when the net is closed. Currie & Foxton (1956) found 80-90% efficiency with their net, which was of similar proportions, and the 14% coefficient for the total numbers caught (Table 1) suggests an equivalent value for my net. There was no tendency for a higher catch in the straight samples as against the divided series and boundary losses on closure are not considered to be significant in the routine sampling.

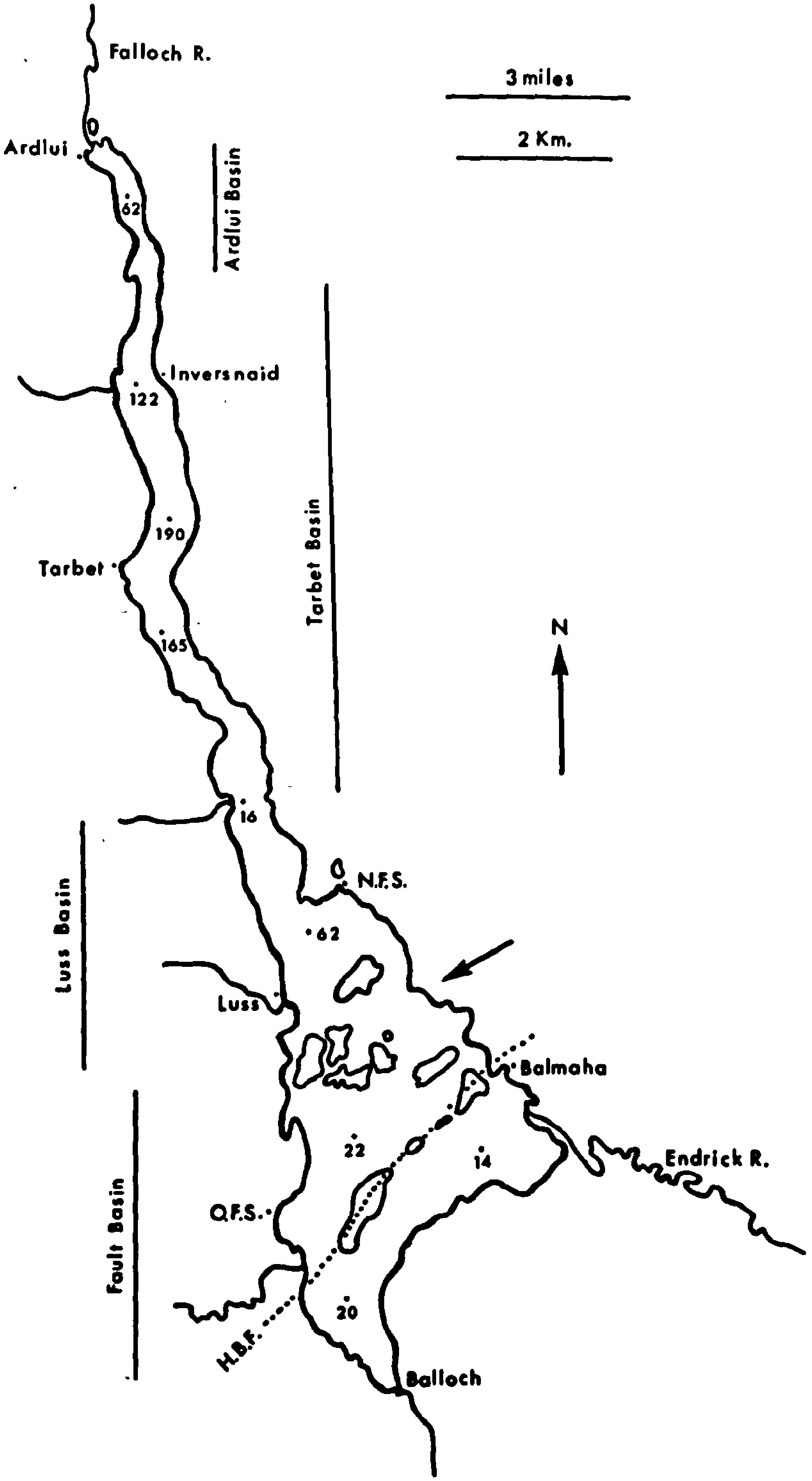
The copepod species were further analysed, the animals being aged and sexed. For <u>Diaptomus gracilis</u> a well mixed portion of the final concentrate was placed in a 5 ml. petri dish and the animals in randomly chosen fields were assessed under the binocular at a magnification of x50. The concentration was such that about 10-15 animals were found per field, and between about 100-200 animals were aged, representing roughly 5-10% of the whole sample. This number gave good agreement between replicates. The facts that the samples from each depth range were analysed separately, as were samples from other stations, was a further check, since samples could be re-assessed in the rare event of obvious discrepancies. The choice of females for measurement of the metasomal length, and of egg sacs for counts of clutch size was made similarly, taking the animals found in randomly chosen fields.

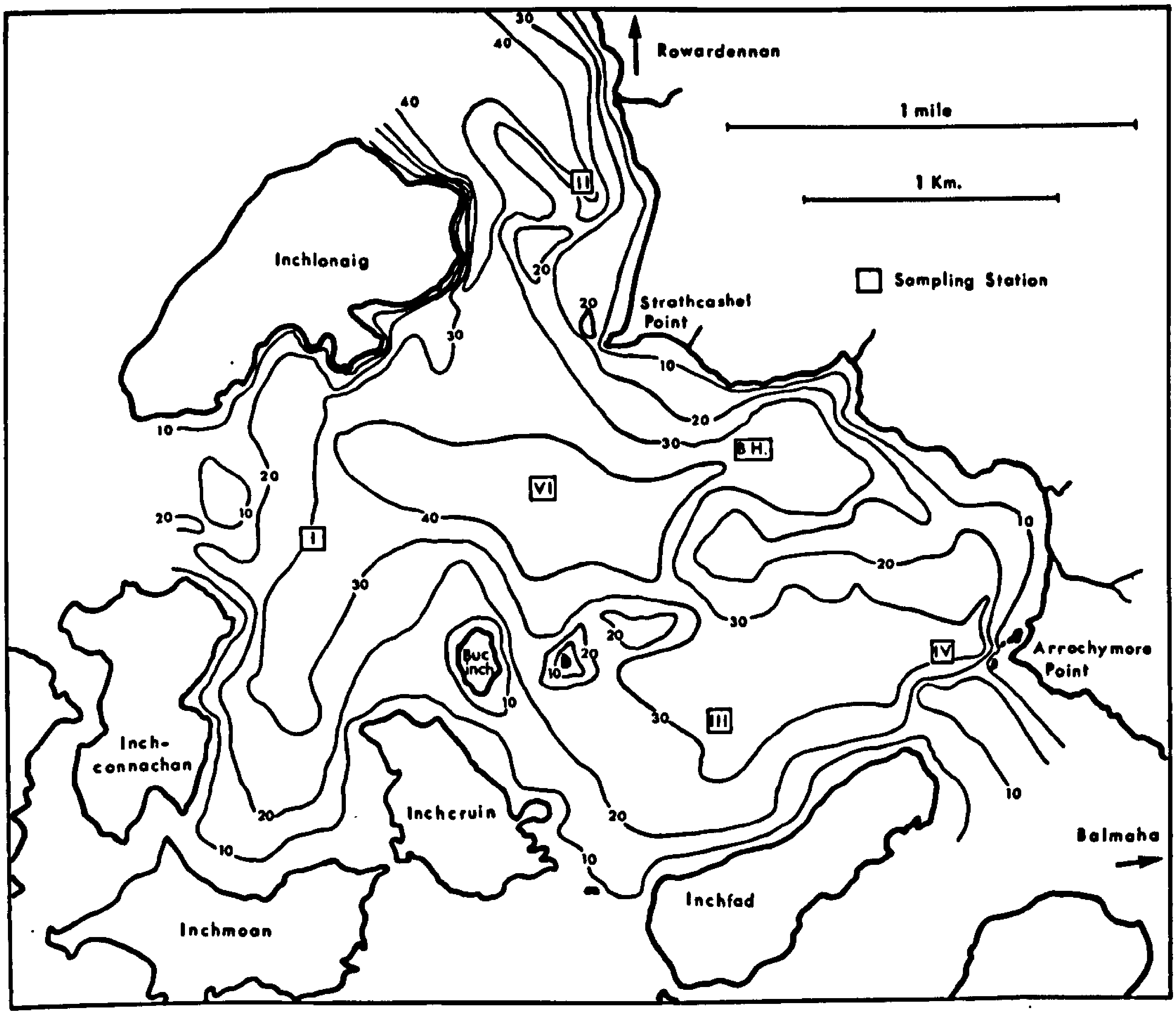
With *Mesocyclops leuckarti* and *Cyclops strenuus abyssorum* whose copepodites were smaller than those of *D. gracilis*, it was found to be easier to pick out by pipette about 50-100 of them (except for the late copepodites and the adults of *Cyclops strenuus abyssorum*, whose numbers were recorded directly) from random fields as above, and to use a Zeiss inverted microscope for their identification. The two species were distinguished with the aid of the figures of Ravera (1953) and also by size. The stage V copepodites of *M. leuckarti* were sexed by the differences in the genital segment (Andreae 1955, Smyly 1961).

The percentages of each stage found in the sub-samples from each depth range were used to determine the total number of each stage, and the totals in the various depth ranges were then added to give the composition of the population in the whole water column. It is shown later that differences could exist in the composition found in each depth range, as well as in the total numbers found, hence the need for analysis of all samples.

Fig. 1: Map of Loch Lomond, showing the hydrographic basins. Strathcashel basin is indicated by the arrow.

Fig. 1a: (facing). Map of Strathcashel basin, showing depths and sampling stations (after Fedoruk, 1964).


Falloch R.
3 miles
2 Km.
Ardlui
62
Ardlui Basin
Inversnaid
122
Tarbet Basin
190
Tarbet
165
N
16
N.F.S.
62
Luss Basin
Luss
Balmaha
22
14
Endrick R.
Q.F.S.
Fault Basin
20
H.B.F.
Balloch



Rowardennan
1 mile
1 Km.
Sampling Station
Inchlonaig
Strathcashel Point
II
B.H.
VI
I
IV
III
Arrochymore Point
Buc Inch
Inch-connachan
Inchcruin
Inchmoan
Inchfad
Balmaha
10
20
30
40

THE PHYSICAL CHARACTERISTICS OF LOCH LOMOND

Physiography

Loch Lomond lies just north of Glasgow, at 56°05'N., and 4°35'W., and has the largest surface area, 7112.5 ha., of any of the British (excluding Ireland) lakes. It is of glacial origin and this is clearly indicated by the steep-sided, narrow, and deep upper part (fig. 1). Below Luss the loch widens and becomes more shallow, and there are a number of closely spaced islands separated only by narrow passages. The physiography of the loch is described more fully elsewhere (Murray & Pullar 1910, Slack 1954) and will be only briefly outlined here.

There are three major basins. The long upper basin, Tarbet, has a maximum depth of 198 metres; it is separated by the Inverbeg bar from the Luss basin (maximum depth 67 metres), which has a south-easterly extension into the subsidiary Strathcashel basin. The remainder of the loch, below the first island groups, lies in the shallower Fault basin (maximum depth 23 metres) across which the Highland Boundary Fault runs. Above the fault the bed rock is of old Dalradian rock, but below it is of the more recent Old Red Sandstone.

The work described in this thesis was carried out in the Strathcashel basin, an area originally chosen for a study of the bottom fauna by Dr. A. N. Fedoruk as being the nearest deep basin to the old University Field Station. It had the added advantage of being relatively more sheltered from the prevailing northerly and westerly winds than the upper basins.

Strathcashel is bounded to the east by the mainland, and on the remaining perimeter is circled by a number of islands (fig.1a). The narrow gaps in this ring of land are all shallow, of about 10 metres depth, except at the northerly end between Inchlonaig and Strathcashel Point, where a deep channel of 40 metres depth leads into the Luss basin. The maximum depth is 46 metres, but the mean depth is only 22.8 metres. It is approximately circular in shape, with a diameter of 3-3½ km., and has a surface area of approximately 673 ha. (Fedoruk 1964, to whom I am indebted for permission to quote these figures and also to reproduce fig.1a).

Much of the earlier work in this study was carried out concurrently with that of Dr. Fedoruk, and of necessity, due to the limited time available in the field, the same sampling stations were used. The major station, S.VI, which lay in the centre of the basin, had a depth of 44.3 metres and was marked for part of the time by a

TABLE 2

Chemical Analyses of Loch Lomond Waters

Date	Alkalinity		SiO_2		Total Phosphorus	
	Creinch	Luss	Creinch	Luss	Creinch	Luss
30.5.55	6.4	8.8	0.97	0.86	0.009	0.007
1.7.55	8.8	6.8	0.77	0.92	0.008	0.012
31.7.55	8.8	7.6	0.44	0.37	0.007	0.006
5.9.55	8.2	6.8	0.58	0.37	0.005	0.006
8.10.55	8.6	6.2	0.61	0.54	0.009	0.005
5.11.55	8.4	6.0	0.82	0.77	0.008	0.005
23.1.56	7.4	6.0	1.13	0.72	0.003	0.004

(Figures in mg./litre)

buoy. Constant interference by the public prevented permanent marking of all the stations but their position was known from cross-bearings to the shore. The westerly station, S.1 (or C_1), was 30 metres deep, the southerly S.III 28 metres, the southeasterly S.IV 30 metres, the eastern B.H. (not often visited) 35 metres, and the northerly S.II 42 metres. The water level of the loch can vary up to 2 metres (Hunter 1953); the depths quoted are based on the mean level.

Chemical Conditions

It was originally intended to carry out routine determinations of the important nutrient salts but this programme proved impossible to maintain owing to the elaborate and time consuming methods required for the small amounts present.

The loch is oligotrophic and therefore is not rich in dissolved salts, although there is a slight tendency for the lower basins to have higher concentrations due to the softer nature of the rocks of the watershed, and to the more cultivated country (Slack 1957). The water is slightly acid (generally around pH 6.8). The figures in Table 2 have been extracted from analyses made by A. V. Holden (pers. comm. to H. D. Slack, 1955) to show the probable range in Strathcashel. (Creinch is an area lying within the lower Fault basin).

Slack (loc.cit.) found that no marked reduction in the oxygen content of the water occurred at any time. Dr. Fedoruk and I made occasional analyses in Strathcashel but even in midsummer the lowest value recorded for the water immediately above the bottom 11.4 ppm. or 85% saturation.

Transparency

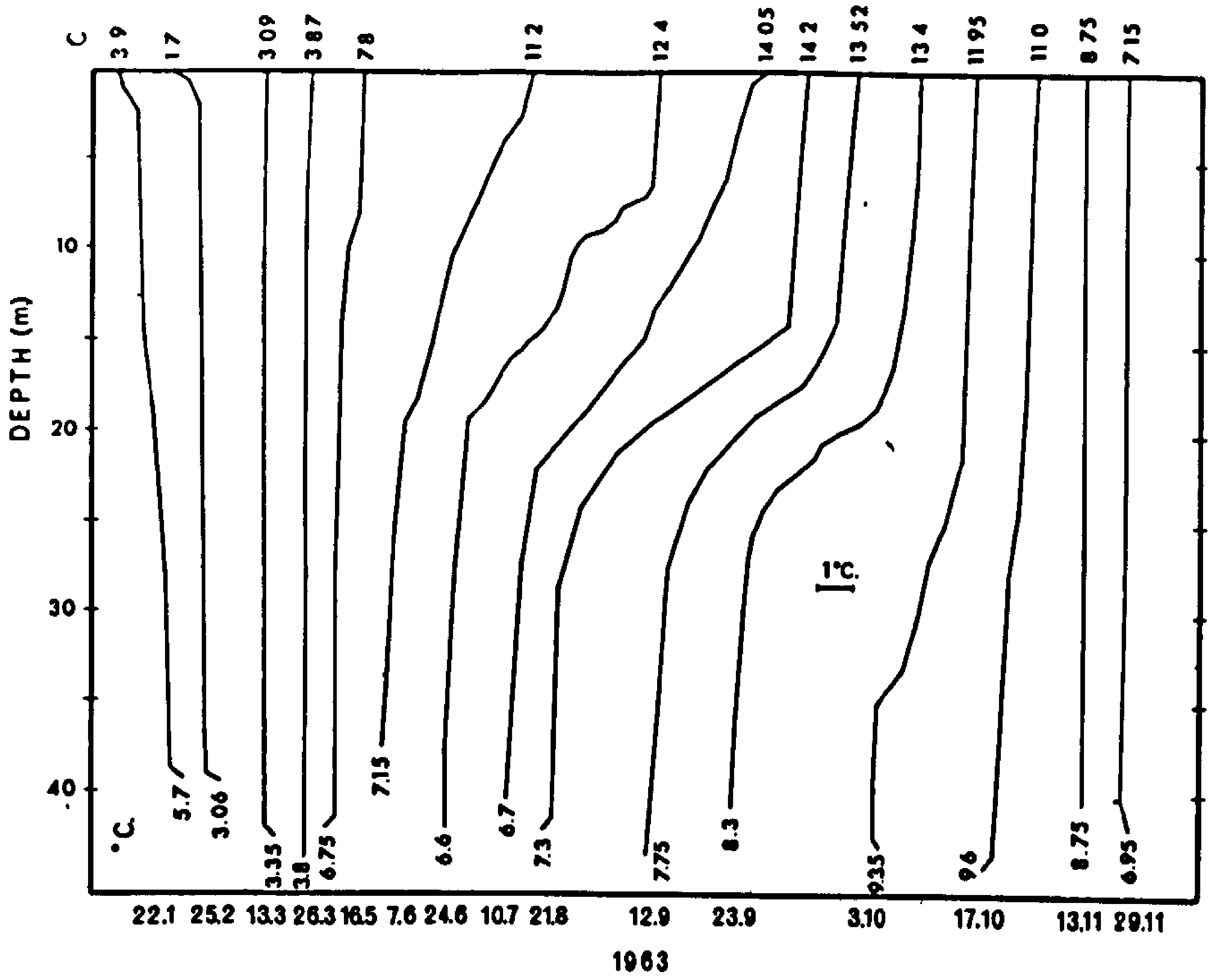
A very general indication of the transparency of the water, which was a dark green-brown colour, is given by the depth at which a white Secchi disc of 20 cm. diameter disappeared from sight (App. Table 1). The readings varied between 3 and 7½ metres, the most usual being 5½ metres, but they showed no distinct seasonal pattern of changes. Measurements of the transmission of light of different wave lengths would have been desirable but equipment for this was not available.

Temperatures

Loch Lomond may be said to hold an honoured place in the history of our knowledge of thermal conditions in lakes, some observations being made as early as 1812 (Buchan 1871), whilst the records of stratification at Inversnaid of Buchanan (1886) are among the earliest made in any lake. An outline of this early work,

Fig. 2: Temperatures in Strathcashel basin in 1963 and 1964.

The surface and bottom water temperatures are indicated; on some dates the mud temperature is also graphed. The curves are for S.VI, except on 22.1.63 & 26.3.63 (both Luss basin), 25.2.63 (S.I.) and 13.3.63 (S.II).


C
3.9
17
3.09
3.87
7.8
11.2
12.4
14.05
14.2
13.52
13.4
11.95
11.0
8.75
7.15
DEPTH (m)
10
20
30
40
1°C.
°C.
5.7
3.06
3.35
3.8
6.75
7.15
6.6
6.7
7.3
7.75
8.3
9.35
9.6
8.75
6.95
22.1
25.2
13.3
26.3
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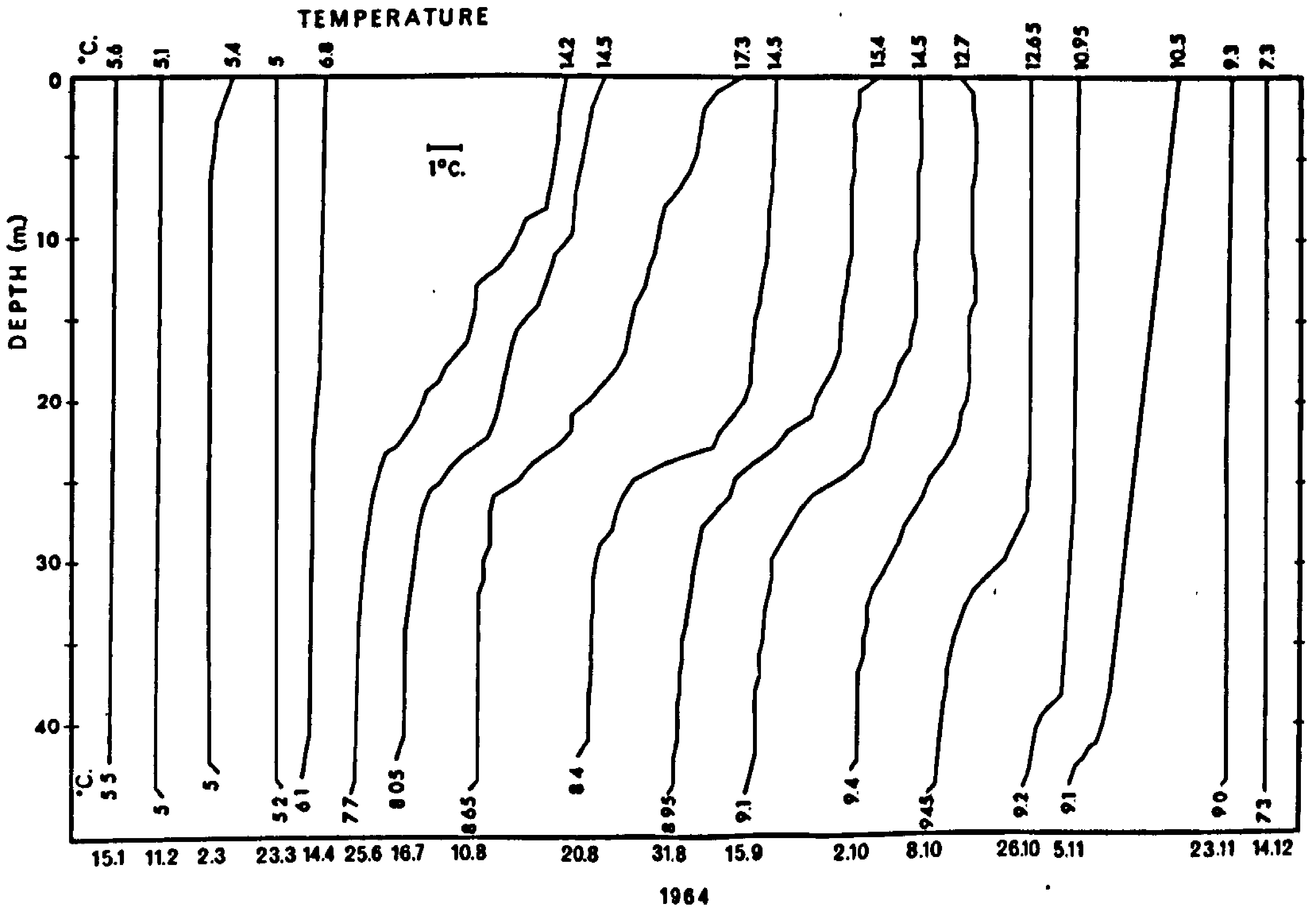
3.10
17.10
13.11
29.11
1963


TEMPERATURE
°C.
5.6
5.1
5.4
5
6.8
14.2
14.5
17.3
14.5
15.4
14.5
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10.95
10.5
9.3
7.3
0
10
20
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DEPTH (m)
1°C.
°C.
5.5
5
5
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7.7
8.05
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8.95
9.1
9.4
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9.2
9.1
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7.3
15.1
11.2
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23.3
14.4
25.6
16.7
10.8
20.8
31.8
15.9
2.10
8.10
26.10
5.11
23.11
14.12
1964

together with the results of the Scottish Loch Survey may be found in Murray and Pullar (1910). Further information on thermal conditions in the various basins is given in Slack (1957).

Temperatures in the Strathcashel Basin were measured routinely in this study and are graphed in fig. 2. The effects of the severe winter of 1962-63 are apparent in the low temperatures recorded in the first months of 1963 when considerable areas were covered by ice and the reversed stratification in January and February may be noted. Although sheltered bays often freeze in winter, it is exceptional for the open water of the loch to do so.

Although the water was in general warmer in 1964 the development of stratification followed a similar course in both years. Temperatures began to rise in April and May from the minimal values found in February and March, and by June stratification had begun. Maximal temperatures were not recorded until early August but by the end of this month mixing of the upper layers had begun, and in September and October the thermocline sank lower until by early November little slope remained in the temperature curve. In both years the basin was virtually completely homothermal by the end of November.

The mean temperatures in the upper 10 metres during 1964 are graphed in fig. 4, but require no comment. Fedoruk (1964) discusses the bottom temperatures of the basin.

TABLE 3

Results of chlorophyll analyses.

Date	Chlorophyll (mg./m^3) a	b	c	Plant Carotenoids M.S.P.U./m^3
1.11.63	3.61	1.01	3.17	4.0
9.12.63	1.62	0.74	1.30	2.4
15.1.64	1.39	0.69	3.04	2.5
11.2.64	1.01	1.24	2.85	3.0
23.3.64	0.87	0.30	1.17	1.0
14.4.64	2.21	0.52	1.06	0.24
10.5.64	1.23	0.05	0.10	1.15
18.6.64	1.33	0.13	0.99	2.2
20.8.64	1.96	0.64	1.90	2.8
31.8.64	1.95	0.32	1.22	3.04
8.10.64	1.77	0.29	1.47	2.36

PHYTOPLANKTON

It was not possible to deal adequately with the phytoplankton of the loch in this study and information on the seasonal cycles of abundance is largely confined to the results of some chlorophyll analyses (Table 3). They may be regarded as giving only a very generalised picture of the temporal fluctuations, which may be much more pronounced than these scattered figures suggest. The values obtained for chlorophyll are comparable to the mean level found in Windermere (J. Talling, pers. comm.).

Examination of net samples showed that the flora had a mainly diatom-cyanophycean aspect and that desmids and green algae were neither varied nor abundant, at least amongst the larger algae. During the autumn and winter *Oscillatoria* and *Asterionella* were dominant. In the spring *Melosira* was abundant but after about April was displaced by *Asterionella*, *Staurastrum*, *Tabellaria* and *Dinobryon*. Later in the summer *Asterionella* and *Oscillatoria* were prominent. At this time and in the autumn clumps of *Coelosphaerium* were readily visible in the water. It is probably the spring burst of *Melosira* which is reflected in the chlorophyll a peak in April, and similarly the higher values in autumn are presumably due to the increasing amounts of the blue-green algae. Most of these species are filamentous and had considerable nuisance value during the sorting of the zooplankton owing to the entanglement of the animals in the threads.

It may be noted that a study of the nannoplankton or μ-algae is likely to prove rewarding in considering the relationship between phytoplankton and zooplankton abundance since these small species form an important part of the diets of the animals, notably of *Diaptomus gracilis* (Naumann 1923, Storch & Pfisterer 1925). Bacteria and organic detritus may also be of importance (Nauwerck 1962).

THE ZOOPLANKTON

PART I : THE BIOLOGY OF THE ENTOMOSTRACA

INTRODUCTION

The biology of limnetic plankton species has received little attention in Britain, with the notable exception of Smyly's work on Mesocyclops leuckarti. A number of general surveys have been made of various lakes (Dakin & Latarche 1913, Southern & Gardner 1926, Wailes 1939, Thomas 1949) but they were largely concerned with the composition of the zooplankton community and the annual fluctuations in numbers rather than with detailed studies of the life cycles of the various species. Gurney's (1931-33) important systematic work on the British Copepoda includes some biological data.

Within Scotland the work of the Scottish Loch Survey (Murray & Pullar 1910) provided a large body of general information of great value on the physical features of the habitats, and on the distribution of the various species within the region, but again was not concerned with the biology of the plankton. No close studies of the zooplankton have been made on any of the Scottish lochs, although a certain amount of incidental information is available in the reports of the Brown Trout Research Association.

The Fauna of Loch Lomond

It is often difficult to make a distinction between littoral and limnetic species, but taking consistent presence in the samples as a standard it can be said that the truly limnetic species of Loch Lomond are:

Diaptomus gracilis Sars
Mesocyclops leuckarti (Claus)
Cyclops strenuus abyssorum Sars
Daphnia hyalina var. *lacustris* Sars
Bosmina coregoni var. *obtusirostris* (Sars)
Leptodora kindtii (Focke)
Bythotrephes longimanus Leydig

The limnetic fauna is thus rather limited, the lack of diversity amongst the Cladocera being a particularly noticeable feature.

A number of other species were also found but these occurred only occasionally in the samples and could be regarded as more properly belonging to the littoral or profundal fauna. They are listed in the subsequent sections.

The species are all common British, and indeed European, animals. Their precise distribution within Britain is discussed by Murray & Pullar (1910), Gurney (1923), and Gurney (1931-33), and need not be further considered here, except to note that *M. leuckarti* is not common in Scottish lochs (Scourfield 1908).

The percentage composition of the Entomostracan zooplankton in 1964 in Strathcashel basin is shown in

Fig. 3: The percentage composition of the Entomostracan zooplankton in 1964, and (upper graph) the mean total numbers.

D.g. = *Diaptomus gracilis*; C. = Cyclopoids;

D.h. = *Daphnia hyalina*; B. = *Bosmina coregoni*.

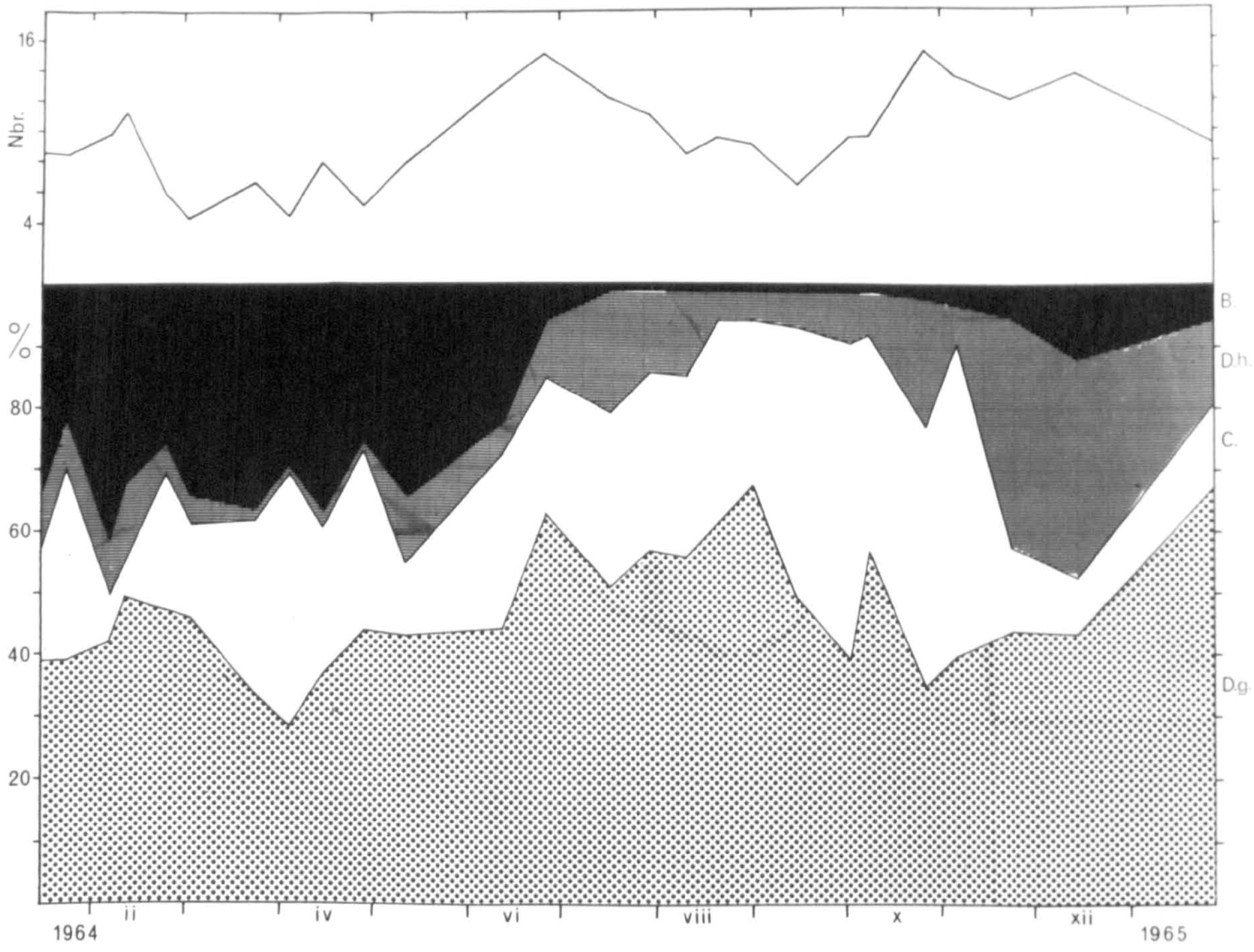

16
Nbr.
4
%
80
60
40
20
B.
D.h.
C.
D.g.
1964
ii
iv
vi
viii
x
xii
1965

fig. 3; since Bythotrephes and Leptodora occurred only in the summer and were not present in large numbers they have been omitted. The predominance of copepods, and above all, of Diaptomus gracilis, is characteristic of many British lakes (Wailes 1939, Murray & Pullar loc. cit.), although in the more eutrophic Lough Derg (Southern & Gardner 1926) Cladocera, particularly Daphnia, are more important. In Loch Lomond the Cladocera comprise a significant fraction of the zooplankton only in the winter months.

Fig. 3 also shows the total numbers of the zooplankton. The annual curve has two pronounced rises, in late spring-early summer and in autumn. It will be seen in the following sections that the former is due to the increased copepod populations, and the latter to the large cladoceran populations developing at that time.

The annual cycles of each species must now be considered separately, before attempting to discuss the inter-relationships between them.

CALANOID COPEPODA

Although Murray & Pullar (1910) mention the presence of *Diaptomus laciniatus* in Loch Lomond this has not been confirmed (Gurney 1931), and *D. gracilis* was the sole calanoid species found in the course of this work.

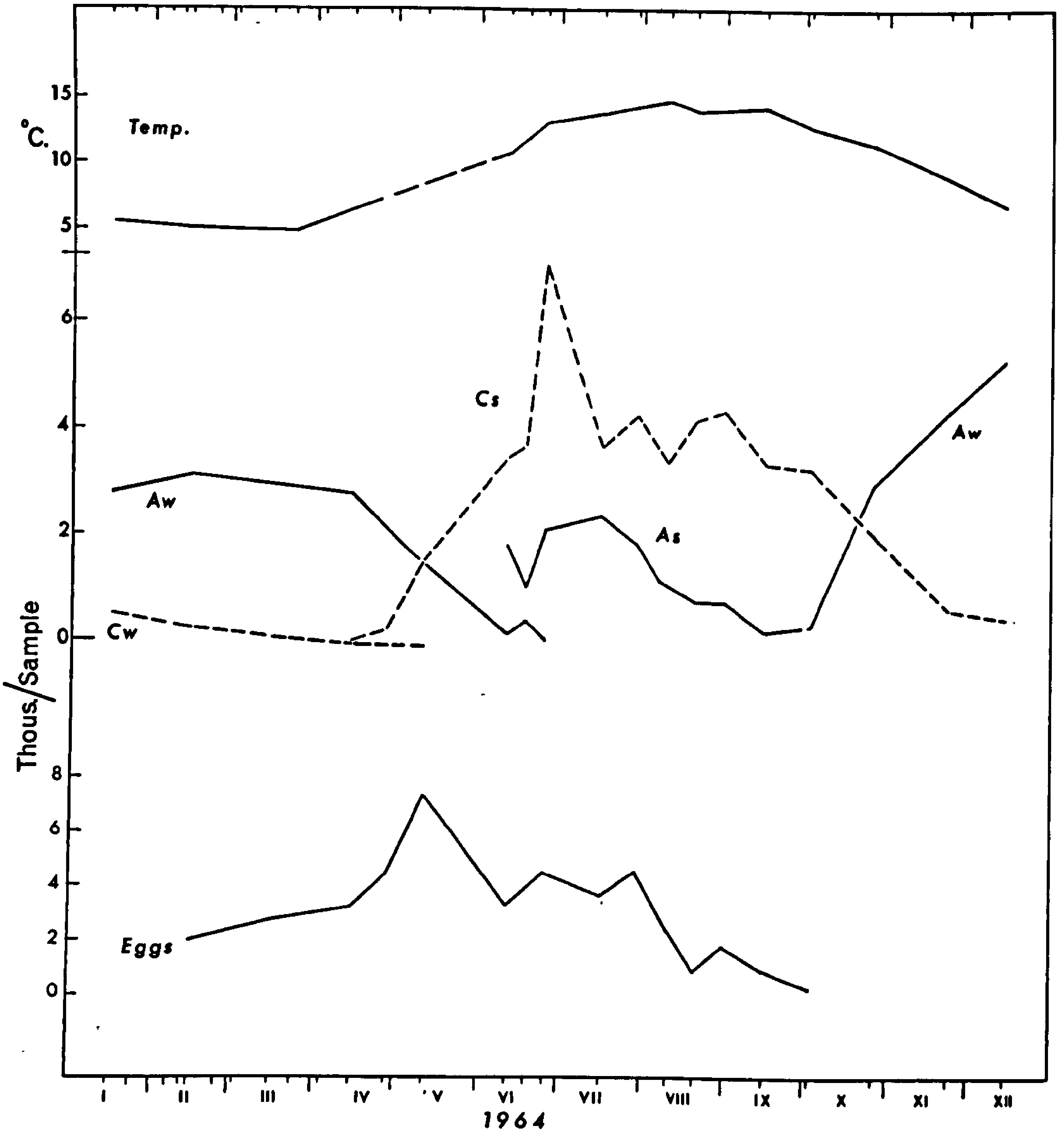
DIAPTOMUS GRACILIS Sars

The Annual Cycle

The discussion of the annual cycle of this species is based largely on the 1964 results, when a more complete and extensive coverage of the Strathcashel Basin was obtained. The results of the investigations of both years are given in full in App. Table 2. The animals were aged and sexed at approximately monthly intervals for the 1963 samples, but in 1964 this was done for the samples from at least one station on virtually every sampling date, i.e. at intervals of two to three weeks. Between April and November the samples from all the stations were analysed but during the winter months this was not felt to be necessary, as the composition of the population showed little change during that time, whilst the vertical distribution of each developmental stage was similar and hence horizontal differences in distribution of the plankton would not lead to differences in the composition of the population at different stations (see

Fig. 4: The standing stock of stages of *D. gracilis*, and the mean temperature for the upper 10 metres.

A_w = overwintering adults; A_s = summer adults; C_w = overwintering copepodites; C_s = summer copepodites.


Temp.
°C.
15
10
5
6
4
2
0
Cs
Aw
Cw
As
Aw
Thous./Sample
8
6
4
2
0
Eggs
I
II
III
IV
V
VI
VII
VIII
IX
X
XI
XII
1964

Part II(a)), so that the proportions of each stage found at the analysed station could be applied without introducing large errors to the mean total numbers for that date or even to the mean total for the month. At other times the mean figures were derived directly from the individual totals found at each station. The derivation of the means is indicated in App. Table 2.

The results are conveniently described in terms of the calendar year, although as willbecome apparent, this does not fully correspond to the developmental sequence of the animals. The terms 'winter' and 'summer' populations are used in their most general sense to separate the phases of developmental activity.

The Winter Population.

The overwintering population, whose origin in autumn is discussed later, consisted largely of adults (over 90% in January), with a few copepodites IV and V which were slowly maturing until by May only an occasional one was found (fig. 4).

The total numbers caught were very similar in January, February and early April, but they were very much lower in March. There was no biological reason for this decline and it must be regarded as a sampling anomaly. The samples of 2.3.64 were from one station only, and whilst four stations were sampled on 23.3.64, there had been several days of strong easterly gales immediately prior to this, which probably greatly affected the horizontal distribution so that a true value for the population density in the basin was not obtained. Accordingly, it is considered that the population remained relatively constant until the adults began to die off in late April after breeding. The numbers fell rapidly in May and few of the overwintering generation were left by June. The first summer adults were present by that time, but, as is shown below, it was possible to separate the two generations by virtue of the considerable size difference that existed between them.

The Summer Population.

The annual cycle started with the production of the first eggs by the overwintering animals at the beginning of February. The egg stock from these animals was at its maximum in May (fig. 4). Nauplii were not studied in this work but the earliest copepodites were found in April and by early June there were already many new adults, the size of their population at that time suggesting that they must have first matured in mid-May. The numbers of copepodites rose rapidly to a pronounced peak at the end of June, and then fell to a more or less constant level at which they remained before finally declining to the low overwintering level during October and November. The adult population rose slightly to reach an ill-defined peak at the end of July, but then steadily decreased in size, being at a minimum in September, after which time it again increased to the high overwintering level. The changes in the egg numbers during the summer were similar to those of the adults, but breeding ceased in October.

The variations in the standing stock of the animals do not provide much information in themselves and an interpretation of the course of events during the summer must be based on a knowledge of the causes underlying the changes, or apparent lack of change, in the stock. Accordingly, these will be considered in more detail in the following sections, starting with certain aspects of the adult populations of both winter and summer origin, which provide useful evidence for interpreting the changes in the composition of the copepodite population.

Egg Production.

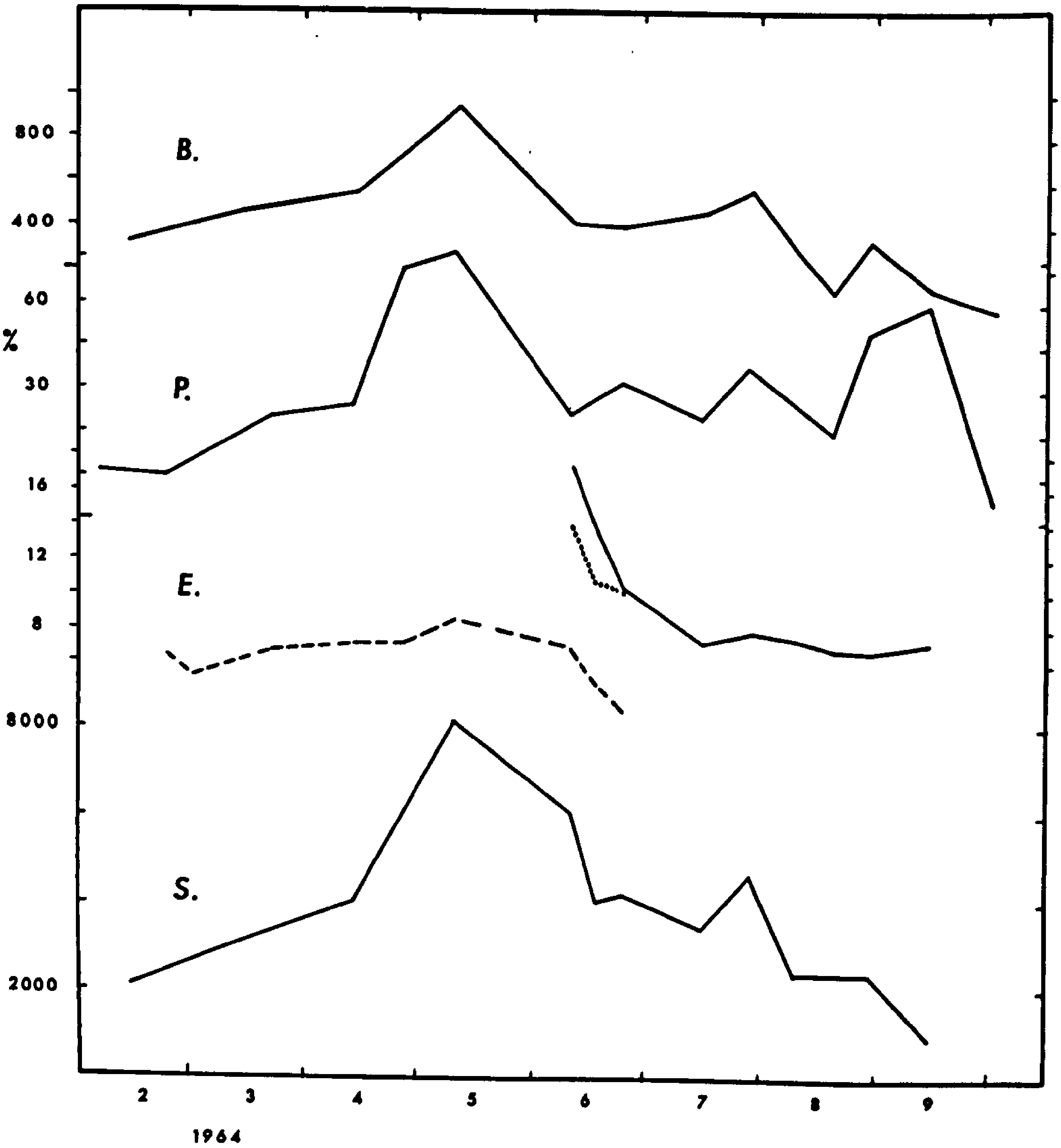
The size of the egg stock is controlled both by the number of eggs carried by each female and by the total number of breeding females, both of which varied during the year.

(a) The Breeding Population.

The size of the breeding population was found by recording the number of loose and attached egg sacs together with the total number of females seen during the analysing of the samples, or, occasionally, during the primary counts. There were usually more loose sacs as they became detached in the processing of the samples.

Both the absolute numbers and the percentage of ovigerous females are shown in fig. 5, and it can be seen that these parameters follow similar courses throughout the breeding season. There were at first few animals carrying eggs when the overwintering population started to breed in February, but the numbers steadily rose, particularly after mid-April, and the peak was reached in May, when a very high proportion (72% on 11.5.64) of the females were ovigerous. Comparison with fig. 4 shows that it was in April that temperatures began to rise, and it was also at that time that a peak in the amount of chlorophyll was recorded (p. 20). It may be noted that during the first part of the breeding season there was little relationship between the total number of females within the population and the size of the breeding population, and that in the winter generation the breeding maximum was reached at a time when the

Fig. 5: Parameters of breeding intensity of *D. gracilis*. The number of egg bearing females (B); the percentage of egg bearing females in the total female population (P); the mean number of eggs per sac (E) - dashed line for the overwintering females, continuous line for the summer females, dotted line for the mixed population in June; the egg stock (S).


800
400
60
%
30
16
12
8
8000
2000
B.
P.
E.
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2
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7
8
9
1964

population as a whole was rapidly declining in size.

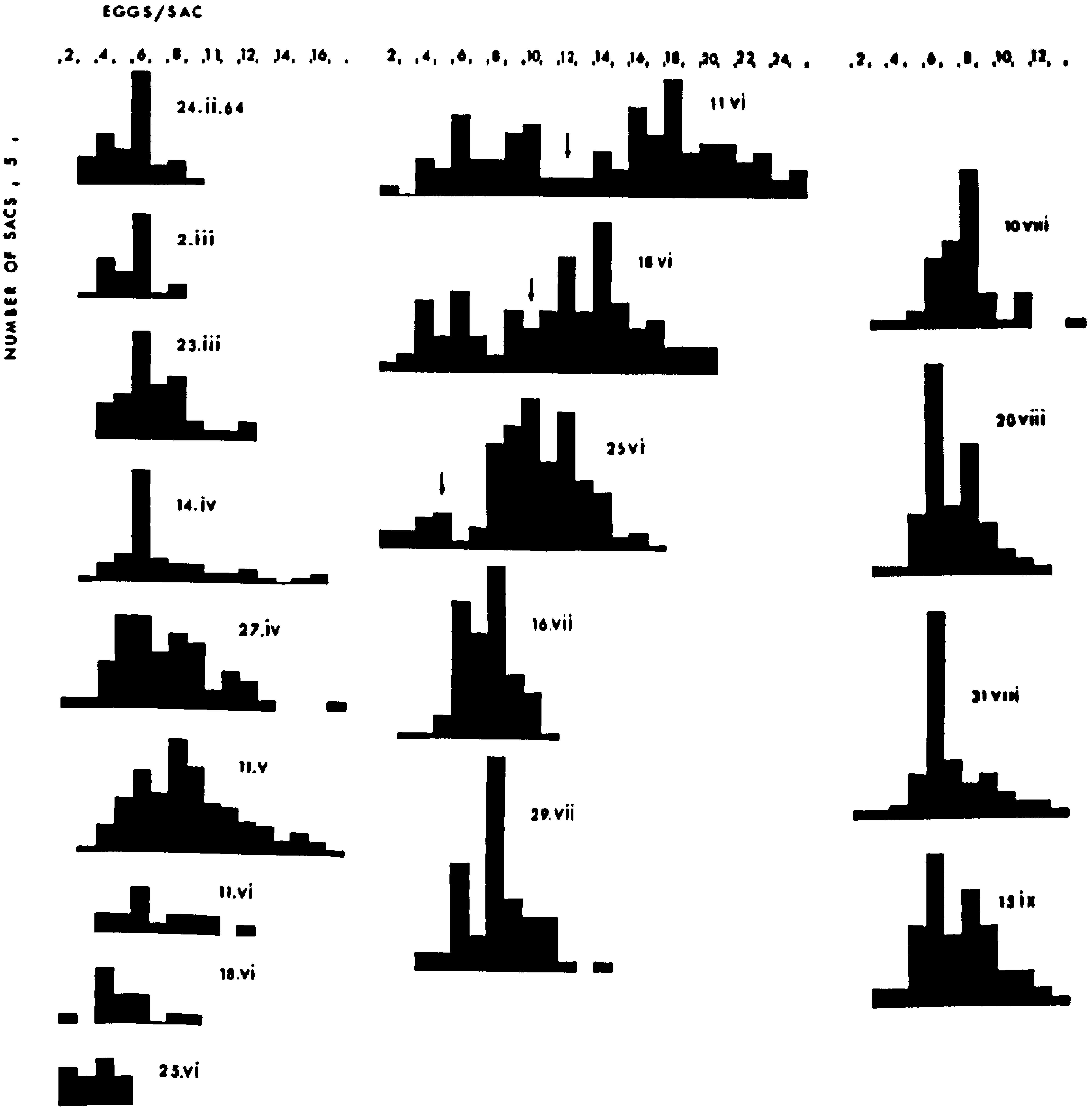
By the time the first summer females were sampled in early June both the percentage and the actual number of ovigerous females had fallen to a lower level, about 40% carrying eggs, although the total population was increasing somewhat at this time. The breeding population remained at a relatively constant level until the end of July, when it declined, as the total population became reduced. There was, however, an increase in the percentage of egg bearing animals at the end of August and in mid-September, when it rose to about 60% again before falling sharply as breeding finished for the year in October. This increase may perhaps represent a response to greater phytoplankton amounts at the end of summer, (the chlorophyll figures were slightly higher at this time).

(b) Clutch Size.

The number of eggs carried by each female varied greatly. This was studied by counting the eggs in at least 60 sacs, where possible taking 20 from each depth range sampled, although there were at times too few in the lower ranges for this to be done. The results are given in full in Appendix Table 3, and they are shown as frequency histograms in fig. 6.

The left hand column shows the results for the

Fig. 6: The clutch size of *D. gracilis*.


EGGS/SAC
2 4 6 8 10 12 14 16
2 4 6 8 10 12 14 16 18 20 22 24
2 4 6 8 10 12
NUMBER OF SACS, 5
24.ii.64
2.iii
23.iii
14.iv
27.iv
11.v
11.vi
18.vi
25.vi
11 vi
18 vi
25 vi
16.vii
29.vii
10 viii
20 viii
31 viii
15 ix

overwintering females, and it will be seen that although there was little change in the modal number of eggs per sac there was a marked increase in the range of variation. During February and early March the range was not great (2-9) and there was a very distinct central mode at 6 eggs/sac. However, from late March until early June the distribution was markedly skew, with the modal frequency becoming less distinct. During this time the range of variation extended from 2-17. Figures from June are rather sparse owing to the small number of females left by that time but amongst these last survivors the range had contracted and the mode had fallen to 4 eggs/sac. These last 3 histograms are for the eggs in attached sacs only, whose origin from winter females could be determined by the size of the animal.

In the June figures in the next column all records from both loose and attached sacs are included, but the arrows indicate the limits above which no eggs attached to winter females were found to occur. Similarly, they mark the lower limit of the number of eggs known to be borne by summer adults. There was therefore a striking difference in the egg production at this time of the animals of the two generations, the mean for the winter animals being 7.1, and for the summer animals 17.6.

Turning now to the summer generations, the maximum numbers of eggs/sac were recorded in early June, when the mode lay at 18, and up to 25 eggs/sac were found. Later in this month there was a rapid decline, together with a decrease in the range of variation, to a more or less constant level from July to September (modes of 6-8), after which virtually no ovigerous animals were found.

The ovaries are paired in copepods and this will account for the fact that the modes were always even numbers, and for the bimodal appearance of many of the histograms, as for example on 15.9.64, when there were not a great many more sacs containing 6 eggs than there were those with 8.

It has been shown experimentally that the number of eggs produced by a copepod is greatly affected by the amount of food available (Marshall & Orr 1952, Elster 1954, Eckstein 1964) and Marshall & Orr (1961) demonstrated that <u>Calanus finmarchicus</u> laid freely only when well fed and able to obtain the large amounts of phosphorus which are present in the eggs. This dependance on the food supply is reflected in the differences between the numbers of eggs found at the same time in lakes of different trophic levels (Czeguga 1959). Eckstein (loc. cit.) quoted as an example of this the finding of a mean number of

TABLE 4

Comparison of Clutch Size in various lakes

Month	Lomond	Schluchsee (Eckstein 1964)	Lunzer (Ruttner 1930)	Schleinsee (v. Klein 1938)
Jan.	-	14.5	5	1.2
Feb.	6.5	9.5		2.5
March	6.85	11	8	7
April	7.3	18.5		10.5
May	8.72	26		8.5
June	14.3-9.8	18	6	4.5
July	7.3-8	10.9	7-8	4
Aug.	7.6-6.9	15		3.5
Sept.	7.3	23.5	Generally no breeding during this period	4
Oct.	-	22.5		6
Nov.	-	8.8		7
Dec.	-	8.8		5
Range	2-25	2-35	2-16	?

eggs/sac of 6-10 in the oligotrophic Bodensee-Obersee as compared with the mean of 20-40 in the eutrophic Bodensee-Untersee. Similarly, Wolf (1905) found an inverse relation between egg number and the size of the lake basin, and Ravera & Tonolli (1956) obtained a direct correlation between egg numbers and the rate of water renewal (expressed as ratio of area of lake to area of drainage basin), all these being factors which affect the nutrient level and hence the primary productivity.

It is of interest to compare the egg numbers found in Loch Lomond with those found elsewhere and in Table 4 the means for the loch are contrasted with those found in some European lakes. The differences are obvious and need not be commented upon, apart from drawing attention to the autumn increases in these lakes. None of these authors give the derivation of their data, which is in the form of monthly values (? means), nor the variation encountered.

Few other authors appear to have made detailed examinations of the egg numbers at all times of the year, although Aurich (1933) gives some comparative data on the differences between lakes in the Chiemgaus region of Germany.

It must be emphasised that in view of the rapid

TABLE 5

Breeding parameters of *D. gracilis*

Date	Total Nbr. of ♀♀	% ovigerous	Nbr. ovigerous	Mean Nbr. of eggs/sac	Total egg stock
6.2.64	1986	21	417		
24.2.64	1324	20	265	6.5	
February	1655	20½	339		2203
2.3.64	(893)	33			
23.3.64	(741)	34		6.85	
March	1400*	33½	469		3212
14.4.64	1558	36	561	7.33	4095
27.4.64	1102	68	749	7.35	5505
11.5.64	1313	72	945	8.72	8240
Mean of 27.4 & 11.5.64	1208	70	845	8.03	6872
11.6.64	1234	35	432	14.3	6177
18.6.64	967	39	377	10.9	4109
25.6.64	1234	36	444	9.8	4351
16.7.64	1416	34	481	7.3	3511
29.7.64	1275	46	586	8.0	4688
10.8.64	850	38	323	7.6	2455
20.8.64	432	30½	132	7.0	924
31.8.64	596	59	351	6.9	2422
15.9.64	222	60	133	7.3	971
2.10.64	290	15	43	?	?

* Estimated number.

changes and the wide range of variation which can occur, as for example in June in Loch Lomond, that considerable care must be taken in the presentation of data on egg numbers and in comparing these in different lakes - a point which Thomas (1961) neglected in attempting to relate egg numbers to the size of the lake basin by means of isolated samples from various British lakes.

(c) Egg Stock.

The data on egg numbers and the size of the breeding population is summarised in Table 5, and can now be used to derive an approximate value for the size of the egg stock on each sampling date (fig. 5) by multiplying the mean number of eggs per sac by the number of egg bearing females. It will be seen that the seasonal course of this curve is similar to those for the percentages and numbers of breeding females, but that it differs from that for the mean number of eggs/sac, since the effect of the high mean in June is cancelled out by the smaller number of ovigerous females, whereas in May, when the peak stock was found, the breeding population was also at its peak, thus compensating for the lower mean.

As was the case with the annual cycle of changes in the egg numbers per sac there is not a great deal of information on the fluctuations in the egg stock in other lakes with which to compare the Loch Lomond findings. In the Bodensee-Obersee (Elster loc. cit.) and the Schluchsee (Eckstein loc. cit.) there were three peaks - in the mid-winter (maximum in the Bodensee), in late spring-early summer (maximum in the Schluchsee), and in the early autumn. In the Schleinsee in 1934 von Klein (loc. cit.) recorded a pronounced spring peak and a smaller autumn one but in 1935 Kuntze (1938) found several smaller peaks during the year. The population of Diaptomus gracilis in Loch Lomond is therefore rather different from some other European lakes in the lack of any autumn increase. The most notable difference, of course, is the complete cessation of breeding between autumn and late-winter, and in this it resembles the species in Lake Krasavitska in N. Siberia (Ivanova 1960).

(d) The number of Clutches per Female.

It is possible to use the above data to estimate the numbers of clutches produced by the animals of the overwintering generation, since their extended period of egg production, lasting from February until June, suggests that individuals must be laying more than once. Since the eggs remain in the sacs until the nauplii hatch, the number of egg bearing females found in the samples

TABLE 6

Number of Clutches Produced by the Overwintering Generation.

Date (1964)	Nbr. of ♀♀	% ovigerous ♀♀	Nbr. of ovigerous ♀♀	Temp. (^{o}C)	Development Time of Eggs (Days)	♀♀ producing eggs		Clutches per female.
						per day	per month	
Feb.	1655	20%	339	5.1	13	26	754	
March	(1600)*	33½%	566	5	13	44	1364	
Feb-March							2118	1.3
April (14.4.64)	1558	36%	561	6.3	11½	48	1440	1
May (27.4.64 -11.5.64)	1208	68% 70% 72%	845	8	9	94	2914	2.4

* Estimated figure. See p.27

may be divided by the development time for the eggs at the prevailing temperatures (using the mean temperature in the upper 10 metres where most of the animals were found) to give an estimate of the number producing eggs per day, and hence by extension per month (Table 6). Elster (1954) showed that the development of the eggs is almost solely controlled by the temperature; small variations in pH, dissolved salts etc. having little effect. Eckstein (1964) found that eggs from the Schluchsee developed at slightly different rates than did those from the Bodensee studied by Elster, but for conformity with a later use of his data for copepodite development Eckstein's rates are used here. It is not clear whether the differences were due to variations in experimental techniques, chemical content of the water or whether they are of genetic origin, but it is unlikely that any great discrepancy will exist between these and the rates of Loch Lomond eggs.

The number of females which produced eggs during the month is divided by the total female population at that time to find the number of clutches these animals could have produced. The table shows that by the end of March each animals could have produced one clutch and that by May a further two to three could have been laid. At least one more could have been produced in early June. Thus, some animals could have laid up to 5 clutches.

The same figure was arrived at by direct calculation starting with a female producing its first clutch at the beginning of February, and working out the time each clutch would take to develop. A period of 10 days was allowed for the time between clutches. This may be taken as a reasonable approximation as Eckstein (loc. cit.) showed that the time between each clutch was more or less constant at any one temperature, but varied from about 5.5 days at 20°C. to more than 10 days at 4°C.

There is little field or experimental evidence on clutch production by individuals. Some of Eckstein's experimental animals produced 4 clutches in 3-4 weeks at 16°C. and 20°C., and Marshall & Orr (1955) have shown that <u>Calanus finmarchicus</u> in laboratory cultures can continue to produce eggs, generally in a series of batches (this species does not have an egg sac), for up to 80 days. Nichols (1933) considered that the same species in the Clyde produced 3-4 batches each in the spring period. Rylov (1948) quoted Walter (1922) and Manfredi (1923) as finding that up to 14 pairs of sacs were produced by <u>Cyclops</u> species. It is therefore quite feasible that some of the Loch Lomond animals do produce 5 or 6 clutches, and further support for this is provided by the changes in the range of variation in the numbers of eggs/sac and the frequency distribution within this range. The absence of a definite mode and the increased variation from March onwards (fig. 6) suggest that, as forecast in Table 6, the animals were by then producing their later clutches, and that whilst the mean number of eggs per sac was in general increasing due to the higher phytoplankton levels, the individual variation in a population always present had become more apparent amongst the older or weaker animals.

Size of the Adults.

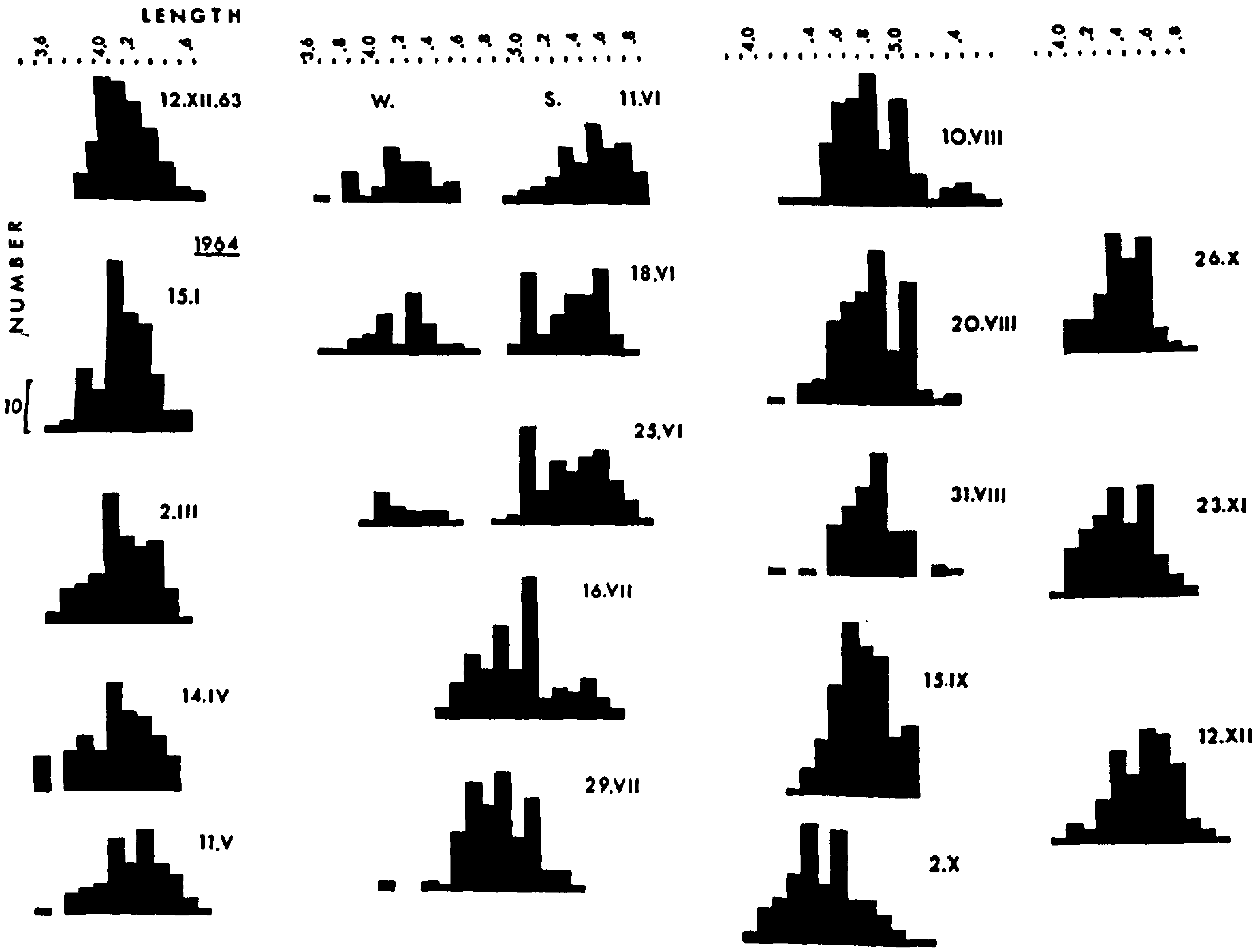
A temporal variation in size, and in other biometric characteristics, is a well known phenomenon in plankton populations (e.g. Wolf 1905, Hartman 1917, Rzoska 1927, Tonolli 1949, 1961, Einsle 1964 etc.). The influence of temperature on size was investigated experimentally by Coker (1934), who found an inverse correlation between size and temperature in the presence of abundant food, a relationship expressed in mathematical terms by McLaren (1963). The inter-relationship between size, food and temperature was analysed more fully by Deevey (1960) in a comparative survey of data on marine copepods from a wide range of localities, and she showed that at temperatures below 14°C there is a direct correlation between size and the amount of phytoplankton, but that above 14°C there is an inverse correlation between size and temperature.

These two environmental factors are constantly changing and their differing levels will likewise be reflected in the varying sizes of the animals developing at different times. By analysing the changes in size or other biometric characteristics occurring in a population over a period of time it is possible to gain some idea of the number of individuals entering the population, and also of their length of life (Tonolli 1964).

Only the adult females were examined in detail in this study. The length of the metasome of 40 animals was measured from each depth range in the S.VI samples (although at times it was not possible to measure the full complement from the samples in the lower depth ranges owing to the very small number present). The results are given in full in App. Table 4, and they are graphed as frequency diagrams in fig. 7. For convenience they are discussed in terms of the micrometer units, which may be expressed as millimetres by dividing by 5.

The overwintering population measured in the

Fig. 7: Metasomal lengths of adult female *D. gracilis*.


LENGTH
3.6
4.0
.2
.6
3.6
.8
4.0
.2
.4
.6
.8
5.0
.2
.4
.6
.8
4.0
.4
.6
.8
5.0
.4
4.0
.2
.4
.6
.8
NUMBER
10
12.XII.63
W.
S.
11.VI
10.VIII
1964
15.I
18.VI
20.VIII
26.X
25.VI
2.III
31.VIII
23.XI
16.VII
14.IV
15.IX
12.XII
29.VII
11.V
2.X

first part of the year had all matured at much the same time in the preceding autumn and early winter, and this is reflected in the normal distribution of their lengths about a mode of 4. From 11.5.64 to 18.6.64 animals of 4.2 became more prominent than previously, which is perhaps due to the maturation of the later copepodites in low temperatures and with the high spring phytoplankton.

The striking size difference between the winter and summer animals, which has already been referred to, is very apparent in the June figures. The largest animals found during the year occurred at this time, with a prominent peak at 5.5 and a maximum of 5.8. These are the females which reached maturity in late May, having developed in the relatively low temperatures of 6-9°C. (fig. 4), whilst the phytoplankton was still at a higher level. However, the size of the animals rapidly fell and even on 11.6.64 many had lengths within the 4.9 - 5.2 range, and by 25.6.64 these animals dominated the population. In the three weeks between this date and the next sample on 16.7.64 the last of the winter females died off, and the new adults which appeared were centred on 4.8 - 4.6. The peak at 5 on 16.7.64 (and probably that at 5.3 on 11.6.64) may be attributed to overlapping of the ranges of the two fractions of the summer population.

During July and August there was a decrease in the occurrence of larger animals - thus in July the 5.5 peak had almost gone and during August that at 5 diminished. Apart from these changes there was virtually no alteration in the distribution of the lengths during August and September. In October a distinct shift occurred in the range of variation, and in the peaks, which now lay at 4.3 and 4.5. This change marked the maturation of the overwintering generation and the distribution did not alter significantly in the last months of the year. It is noticeable that the overwintering generation of 1964-65 was rather larger than that of 1963-64.

The summer adults can be divided into three size groups : of 5.8-5.3 (A), 5.2-4.8 (B) and 4.7-4.4 (C), and from the percentage of the measured animals falling into these groups on each sampling date the numbers in each in the whole female population can be calculated (Table 8). It must be emphasised that the use of the terms 'group' and 'influx' in the following discussion do not imply that there were three distinct bursts of maturation of adults. This would be a continuous process, with a progressive slight decrease in size with time, but the intervals between samples are sufficient

TABLE 7

Distribution of Females in June at S.VI

Depth (m.)		11.6.64	18.6.64	25.6.64
0-10	Total Nbr.	986	868	846
	% winter ♀♀	7%	22%	5%
	Nbr. of winter ♀♀	69	191	42
10-20	Total Nbr.	126	88	74
	% winter ♀♀	52%	32%	12%
	Nbr. of winter ♀♀	65	28	9
20-42	Total Nbr.	122	49	117
	% winter ♀♀	52%	50%	37%
	Nbr. of winter ♀♀	13	25	43
Total Nbrs. of winter ♀♀		197	244	94
% of total population		16%	24%	7½%
% derived from summed length frequencies		37½%	37%	17%

to obscure the nature of this change and so it appears to occur in discrete steps.

For the June samples the number of winter animals was calculated separately for each depth and these figures were subtracted from the total before working out the abundance of the summer animals from the sum of the frequency of each size group in the separate depth ranges. The female population as a whole was strongly stratified at this time - as indeed it was throughout the season - with the bulk of the animals in the upper 10 metres. Table 7 shows that although the percentage of winter animals differed greatly at each depth range the animals were in fact distributed relatively uniformly, in contrast to the summer adults. Similar clearcut differences in the distribution of the summer females were not found (App. Table 4) and so the direct use of the summed frequencies from each depth range is considered justified (hence percentages derived in this way can be applied to the mean totals), although if any fractions were more prominent in the lower depths, where fewer animals were usually found, their numbers would be somewhat overestimated. This is demonstrated in the last row of figures in Table 7, where the percentage of winter females derived from the summed frequencies is given for comparison.

TABLE 8

Summer Population of Females.

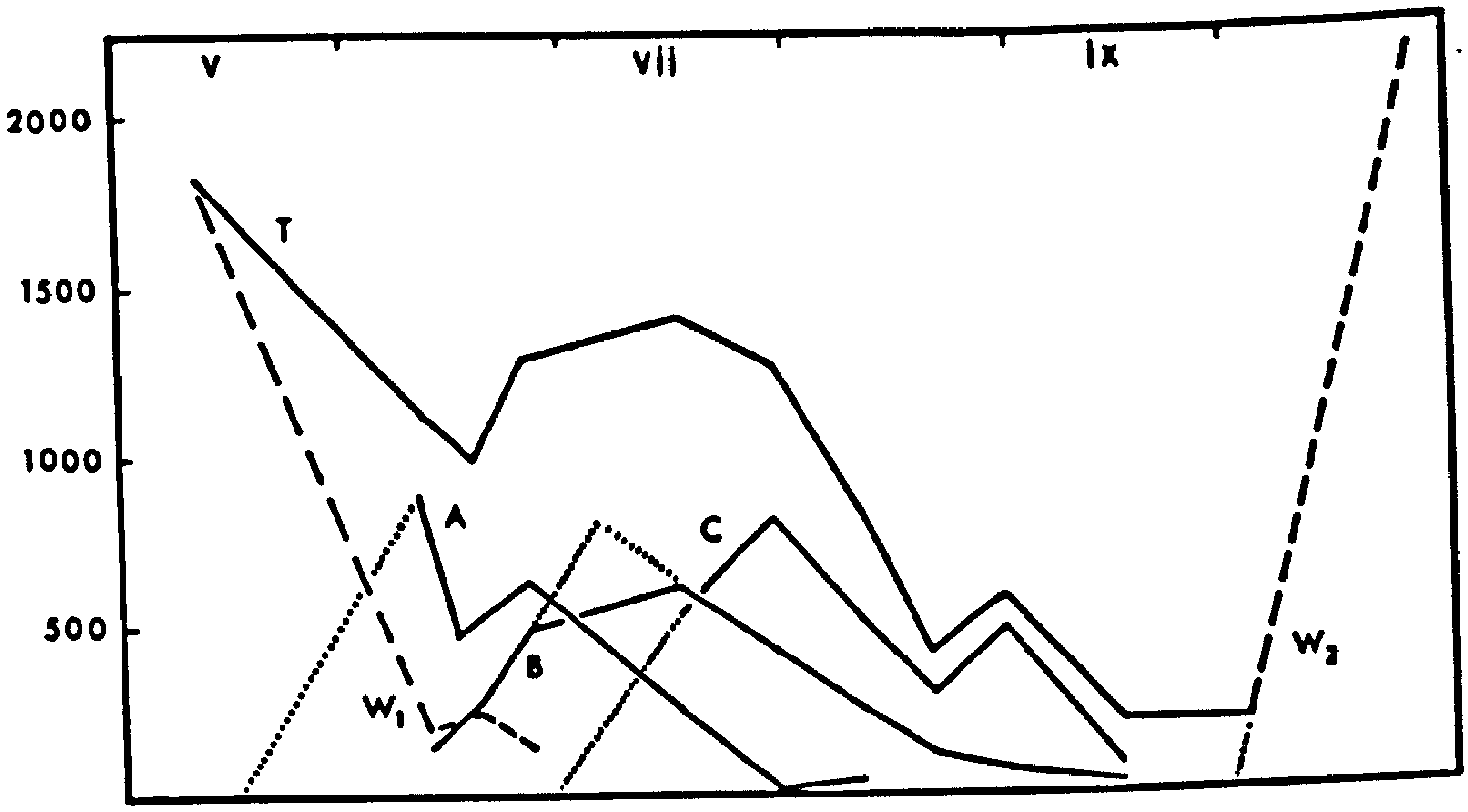
Date	Total Nbr.	Generation				
		Winter (3.6-4.6)	A (5.8-5.3)	B (5.2-4.8)	C (4.7-4.4)	Autumn (4.8-3.9)
11.6.64	1234	197	882	155		
18.6.64	(1005)	(244)	(476)	(285)		
25.6.64	1294	154	638	502		
16.7.64	1416		255	630	531	
29.7.64	1275		20	420	835	
10.8.64	850		63	250	535	
20.8.64	432			127	304	
31.8.64	592			83	509	
15.9.64	222			35	186	
2.10.64	224					224
26.10.64	2226					2226

The percentages of winter and summer animals found at S.VI in June were used to find the mean numbers for the basin and it is these figures for the summer animals that are given in Table 8. Reference has already been made to the fact that the numbers caught at S.VI on 18.6.64 were lower than the means for the 11th and the 25th of June, and it was unexpected to find a higher number of winter females on this date (Table 7). This sample must therefore be regarded as anomalous.

It can be seen from Table 8, showing the mean numbers found in each size group, that there was a constantly changing balance between new animals entering the population and older animals dying off, and this is shown in fig. 8 in relation to the changes in the total female population during the season. This figure shows clearly how little relation there may be between fluctuations in the standing stock and the changes that are actually occurring. Thus, in June the dying off of the winter adults was obscured by the maturation of the new animals. The summer adult maximum in mid-July, occurred when considerable numbers of the three summer influxes were present together - group B at its peak, many of group A still present and group C starting to increase. By the end of July there had been a decrease in the total numbers with groups A

Fig. 8: The adult female population of _D. gracilis_ in summer.

T = total number; W_1 & W_2 = the overwintering generations; A, B & C = the summer size groups (dotted lines show probable times of origin and of peak numbers).


V
VII
IX
2000
1500
1000
500
T
A
B
C
W1
W2

and B dying off, but further new animals in group C had matured. During August and September this decline continued, so that by the end of August group B had entirely gone. Although the total numbers were still low on 2.10.64 the marked change in the length frequency distribution (fig. 7) can be taken to indicate that group C had been replaced by the first of the overwintering generation, although it is not until 26.10.64 that the increase in the numbers of the latter becomes apparent.

The lack of change in the size of the August animals, together with the continued decline in total numbers, strongly suggest that virtually no new animals mature between the end of July and the beginning of October. On the other hand, during this time the temperatures were relatively uniform, lying between 14° and 15°C, and as fig. 6 shows, there was no marked change in the number of eggs per sac, such as would be expected if the phytoplankton was varying to any marked extent. Thus environmental conditions were relatively uniform and the apparent lack of change in size may conceal a renewal of the female population. However, an analysis of the structure of the copepodite population at this time bears out the first suggestion that few, if any, new animals would appear in late summer.

Between August and September the mode shifted from 4.8 to 4.6, the difference between the mean lengths on 31.8.64 and 15.9.64 being significant at P = 0.002. However, it is probable that by that time the first overwintering adults were beginning to appear and so caused this shift.

The Length of Life of the Animals

It is apparent that at least some individuals in each influx are able to survive for long periods. The longest lived were of course the animals of the overwintering generations. These matured in October and November and there was no significant mortality until April - May, so that many lived for 5-7 months. Those that were found in June could have survived up to 8 months, although the last members of this generation may have been later in coming to maturity, having overwintered as copepodites. In this case they will still have lived for 3-4 months at least. Members of the summer population do not survive as long but still show considerable longevity. Thus the very early summer adults (Group A), originating first in early May, are still apparent up to early August, a span of two to three months, whilst animals of group B (mid-June-late August) and group C (early July-September) can also live for a similar length of time. Each of these groups follows a comparable course, taking about one month to reach peak density, but then taking two months before the last animals disappear, although mortality is increasing with age.

These are of course maximal estimates of longevity. The mean length of life can be taken as half the time between successive peaks, which probably occurred at the end of May for group A, at the end of June for B and the end of July for C (fig. 8), so the mean longevity is about two weeks. This estimate may be compared with that of 22.5 days for *D. vulgaris* in Lago Maggiore in July (Tonolli 1964), found by a similar analysis of temporal changes in size, and that of 11.5 days (found indirectly) for *D. laciniatus* in Erken See (Nauwerck 1963) and also with Conovers' (1956) suggestion of a maximum longevity of one month for *Acartia clausi* in the spring.

A number of authors have commented on temporal differences in the size of *D. gracilis*, the most complete information being given by Eckstein (1964). His results are, however, expressed in terms of the mean length found, and as the percentage of 'large' animals in the population, and so much of their value is lost. It is apparent from the Loch Lomond analysis that such data must be considered as a whole in order to understand the changes in the mean.

TABLE 9

(a) Comparison of the lengths of the egg-bearing females (E.) with those of the female population as a whole (T.), in the summer generation of D. gracilis

Date		Numbers found of each length*																			
		4.0	.1	.2	.3	.4	.5	.6	.7	.8	.9	5.0	.1	.2	.3	.4	.5	.6	.7	.8	Total
11.6.64	E.										1	-	2	2	4	5	17	4	5		40
	T.										1	2	3	5	11	8	16	11	12	6	75
18.6.64	E.										1	5	2	8	8	4	8	3	1		40
	T.										2	16	4	5	12	12	17	4			120
25.6.64	E.											20	7	13	9	5	18	10	8		90
	T.								1	6	1	26	11	12	15	17	22	12	9	2	120
16.7.64	E.						1	10	7	11	7	14	4	6	3	-	4	1			68
	T.					2	7	13	10	19	10	29	4	6	5	8	4	2	1		120
29.7.64	E.				1	4	10	11	10	14	6	14	1	1							72
	T.	2	-	-	2	1	12	22	17	24	11	19	4	4	1	-	1				120
10.8.64	E.					1	1	6	7	14	6	12	1	1	1						50
	T.			1	1	1	12	20	23	26	13	21	6	3	3	4	2				136
20.8.64	E.					1	1	7	8	9	3	8	1	-	1	-	1				40
	T.		1	-	4	5	17	21	23	31	11	25	3	1	2						144
31.8.64	E.				2	-	6	19	19	9	3	2									60
	T.		1	-	1	-	10	14	18	25	9	9	1	2	1						91
15.9.64	E.					1	7	7	11	11	5	3									45
	T.			1	5	11	22	35	30	28	12	14									159

* Lengths are of the metasomes, quoted in micrometer units.

<u>TABLE 9</u>

(b) The percentages of the total female population (T.) and of the egg bearing females (E.) in each size group.

Date	Size Group					
	A(5.3-5.8)		B(4.9-5.2)		C(4.8-3.9)	
	E.	T.	E.	T.	E.	T.
11.6.64		85		15		-
18.6.64		62½		37½		-
25.6.64		56		44		-
16.7.64	13½	18	46	44½	40½	37½
29.7.64	2½	1½	29	33	68½	65½
10.8.64	2	7½	40	29½	58	63
20.8.64	5	1½	30	28	65	70½
31.8.64		-	18½	14	81½	86
15.9.64		-	17½	16	82½	84

Eckstein related the changes to the population density, having found that smaller animals resulted from the high production peak in June, and larger ones from the smaller peak in October. Such a relationship would be better explained in terms of the high temperatures and lower phytoplankton levels of the autumn.

Egg Production and Age.

During the counting of the egg numbers in the sacs the females were also measured in anattempt to determine whether age affected the egg production of the animals. The resulting information can be set out in two ways.

Firstly, the sizes of the breeding animals can be compared with those of the total female population to see if any particular size group is more prominent amongst the egg bearing population. Table 9a shows that the peak lengths of both the breeding population and the total populations closely correspond. Table 9b expresses the same figures as percentages in each of the size groups used to separate the animals of different ages (p.42), and again there is a striking agreement. It may be concluded that the percentage of animals carrying eggs is much the same in all age groups.

Secondly, the numbers of eggs carried by the animals of each size group may be compared (Table 10).

TABLE 10

Clutch size in the summer generations of D. *gracilis*

Date	Size Group	The numbers of animals carrying clutches of each size																								Total
		2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	
11.6.64	A									1				3	1	4	5	7	2	3	1	1	2	1	2	33
	B								1	2	1	-	3	-	2	-	1	-	-	-	1					11
18.6.64	A								2	-	3	5	2	12	4	1	2	3	1							35
	B								3	4	3	3	3	3	2	1										22
25.6.64	A					1	1	6	6	12	8	9	2	5	-	1	1									52
	B				1	-	2	7	10	12	4	8	6	5	1	3										59
16.7.64	A					3	4	5	1																	13
	B				1	3	8	9	10	6	7															44
	C					15	6	14	4																	39
29.7.64	B				1	1	2	6	5	5																20
	C			1	1	11	2	18	5	2	2	-	-	1												43
10.8.64	B		1	4	5	7	1	-	1																	19
	C		1	2	3	5	11	3	1	3																29
20.8.64	B			3	-	5	-	3	1	-	-	1														13
	C				2	13	1	3	2	2	1															24
31.8.64	B			1	-	2																				3
	C	2	1	1	4	17	1	3	2																	31
15.9.64	B				2	5	1																			8
	C		2	1	7	10	4	6	4	2	1															37

The data is not extensive because of the difficulties of examining sufficient numbers in samples in which breeding animals are not abundant, but it does show that there is little difference between the modal numbers of eggs per sac in each size group.

Thus, it appears that the effects of size and age, if any, are obscured by the more important effect of food in controlling egg production during the summer. The striking differences between the clutches of the summer and winter females in June have already been referred to but here the comparison is an extreme one, being between animals of great age at the end of their prolonged breeding season, and recently matured animals.

Egg number and size are often correlated (e.g. Ravera & Tonolli 1956, Davis 1961) and such a relationship could be established with the results from Loch Lomond, as the largest clutches were found on the largest animals, in June. However, it is more appropriate to relate both these parameters to the seasonal cycles of phytoplankton and temperature since, as the largest animals are found at times of high food levels and cooler temperatures, and high egg numbers per sac at times of high food levels also, it is not surprising that in temperate lakes the maxima of both should coincide, i.e.

in spring and autumn. On the other hand, when higher temperatures are limiting the size of the animals the egg numbers may fluctuate with variations in the phytoplankton quantities without these fluctuations bearing any relationship to the size, as Eckstein (1964) noted in the Schluchsee.

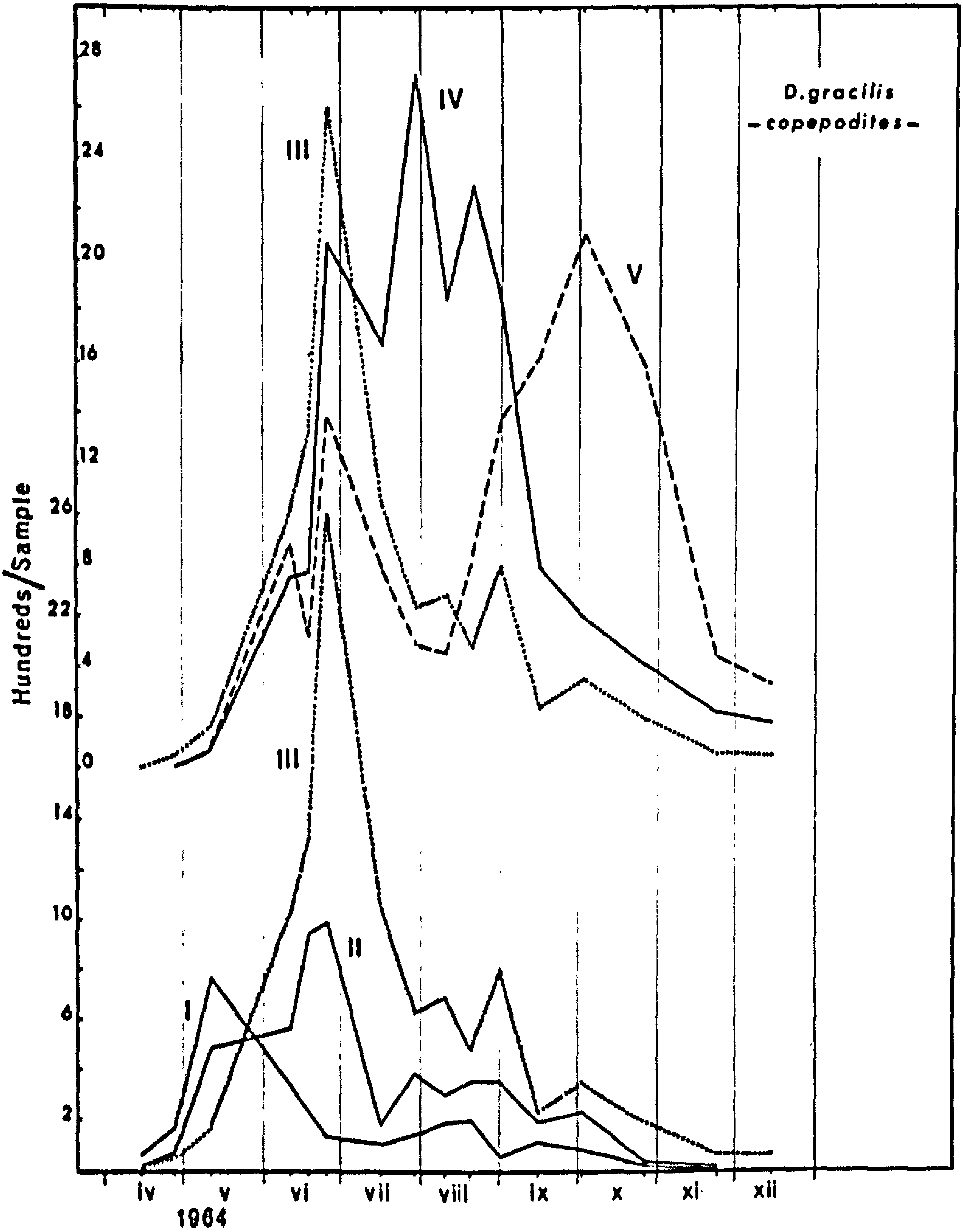
The Sex Ratio.

Throughout the year there was a slight preponderance of males amongst the stage V copepodites, but amongst the adults females were more common. The percentage of females was greater in the spring towards the end of the breeding season of the overwintering generation and again in late summer, indicating a shorter length of life for the males.

The Copepodite Population.

The first copepodites to result from the eggs of the overwintering adults appeared in early April, when small numbers of the first three stages were found (fig. 9). By the end of the month stage IVs were present, and stage Vs by early May. Unfortunately no samples were taken during the latter part of this month but by early June considerable numbers of all stages were found, including adults (fig. 4). There was a further large increase, of all copepodite stages except the Is, between

Fig. 9: Numbers of each copepodite stage of D. gracilis in summer.


D.gracilis
-copepodites-
IV
III
V
III
II
I
Hundreds/Sample
28
24
20
16
12
8
4
0
26
22
18
14
10
6
2
iv
v
vi
vii
viii
ix
x
xi
xii
1964

11.6.64 and 25.6.64, but the numbers had again fallen sharply by 16.7.64, to remain at a relatively constant level until the autumn.

Stage I were at first the most abundant (maximum recorded on 11.5.64), closely followed by stage II (which probably reached their true maximum later in May, although the peak found was on 25.6.64). Throughout June the IIIs were dominant, reaching a well defined peak on 25.6.64. During the rest of the summer the numbers of these young stages declined, the last I and IIs being found at the end of November, although even in December some IIIs remained. The numbers of IVs fell only slightly in early July, and they then rose as this stage replaced the IIIs as the dominant stage, their maximum being recorded on 29.7.64. The population of Vs dropped sharply from the initial June peak but began to rise again as they in turn replaced the IVs, reaching a high peak at the beginning of October, after which they matured into adults. As has already been indicated small numbers of IVs and Vs remained in the population over the winter, and do not mature until the next spring.

The changes in the copepodite population may be summarised then as indicating an early period when there are broadly similar numbers of each stage without a pro-

TABLE 11a.

Times for development (in days) of *D. gracilis**

Temp. (°C)	Eggs	Nauplii	Copepodites	Egg - Adult
5	13	49	53	115
6	12	40	50	102
7	10½	32	43	85½
8	9	24	40	73
9	8	22	36	66
10	7	20	33	60
11	6	18	28	52
12	5	16	25	46
13	5	15	23	43
14	4	14	21	39
15	4	14	20	38

TABLE 11b.

Duration of Development (in days) in Loch Lomond.

Month	Temp. Range in 0-10m.	Eggs	Nauplii	Copepodites
Feb.	5.2-5	13	47-49	53
March	5.05-5	13	48-49	53
April	5.5-8	12½-9	45-24	51½-40
May	8-10.2	9-7	24-20	40-32
June	10.2-13.4	7-5	20-14½	32-22
July	13.4-15	5-4	14½-14	22-20
Aug.	14.6-15	4	14	20
Sept.	14.6-13.2	4-5	14-15	20-23
Oct.	13.2-9.9	5-7	15-20	23-33
Nov.	9.9-8.4	7-8½	20-23	33-38

* Data from Eckstein 1964.

nounced or prolonged dominance by any one stage as in June. In the earlier samples taken between 14.4.64 and 11.5.64 the development of the summer generations was only just beginning but later in May a picture similar to that found in June could be expected. This period gives way to one in which the bulk of the population are found in one or two consecutive stages, when their development can be followed from stage III at the end of June until maturity in October.

Some consideration of the factors controlling the rate of growth of the animals is now necessary. Temperature is known to be of great importance and Eckstein (1964) has made a detailed study of its effect on the growth rate of the developmental stages of D. gracilis. Table 11a is based on his work and shows the rates in otherwise favourable conditions for the range of temperatures found in Loch Lomond. As would be expected, the higher the temperature the faster development will be. Both the quantity and the quality of food are known to affect the rate of growth also, slowing it down very greatly at unfavourable levels (Coker 1933, Eckstein loc. cit.) but no detailed experimental work has been done on this aspect. Eckstein also showed that the pH and the content of dissolved salts may exert some influence, and it is probable that a low content of dissolved oxygen will also affect the rate, as it does in the Cladocera (Green 1956). The variation of these latter factors is not great in Loch Lomond, and food and temperature may be regarded as the two fundamental influences on growth of the animals.

It can be seen from fig. 4 that a particularly rapid increase in the numbers of copepodites took place between 11.6.64 and 25.6.64. An increase would be expected to some extent in June anyway because (a) development times of the egg and naupliar stages were being continually shortened by rising temperatures (table 11b), and hence there would be a more rapid entry into the copepodite population, and (b) the rising egg production of the females as spring advanced means that there would be more animals entering the copepodite population than were leaving it (other things being equal).

However, the increase was very sudden and was followed by an equally rapid decline together with a pronounced change in the structure of the population. Furthermore, during this period in June it was shown above that there was a distinct decrease in the size of the females, and also in the mean number of eggs per sac, which are both indicative of food shortage. It is therefore suggested that food became limiting for the rate of development at this time, when the spring burst of phytoplankton ended. The increase in the standing stock on 25.6.64 would result because the fast temperature-dependant progress from egg to adult had become greatly retarded, and the animals would then spend a very much longer time in each individual naupliar or copepodite stage. Thus, to use Elster's (1954) appropriate phrase, the 'developmental sluice' has become blocked.

If the animals were developing at temperature-dependant rates they would spend only 4-5 days in each copepodite stage during the summer (Table 11b) and, as eggs were produced throughout this period, the population should be constantly renewed. One would then expect that the numbers in each stage would remain relatively similar (as in the early period of development of the copepodite population), without any prolonged dominance by any one stage, and since the samples were taken at two to three week intervals a consecutive pattern of gradual transition from one stage to another would not be found. The fact that the development of the animals 'held back' in stage III in late June can be followed through the later stages until they reach maturity in October can only be explained in the light of a retardation in their growth rate.

Considerable mortality must have been caused by the sudden food shortage before an equilibrium level was reached. The decline in numbers between 25.6.64 and 16.7.64 was least among the IVs but here the losses would be obscured by the simultaneous emergence of some of the IIIs into this stage. Similarly, a part of the decline of the Vs is due to their maturation into adults, whose numbers did in fact increase slightly in this period. The Vs continued to decline during July and it was shown above that further new adults were maturing during this month. It is probable that by August most of the Vs left in the population after the June crash would have become adult, and this bears out the supposition made previously (p.45) that there was very little, if any, renewal of the adult population in the late summer.

From mid-July until the end of August the numbers of copepodites remained at a more or less constant level (except on 10.8.64, when they were rather low), with a mean of 4050. The numbers on 15.9.64 and on 2.10.64 were much lower, but there was not an even coverage of the basin on these dates and the samples were probably not adequate.

The curve of adult numbers in fig. 4 gives the impression that the numbers of adults continued to rise in November and December, although by that time there were few copepodites left to bring about such an increase. It is shown later that in November and December particularly large numbers of animals were found in the lower depths of the loch and it is suggested that they may have accumulated to some extent in the deeper basins. Under these circumstances figures from the deep stations could unduly weight the calculation of the mean figures for the whole basin and so give a higher figure than the true value.

During the summer the numbers of I-IIIs remained more or less constant, which suggests that a certain number of the eggs laid during this time were reaching the copepodite stage, as otherwise these stages would successively disappear as the young animals left in July gradually entered the later stages. The numbers of older stages do show some tendency to increase during the summer, which may be due to this further development of the original July population:

	III	IV	V	Total
16.7.64	1024	1659		2683
29.7.64		2734		2734
10.8.64		1842	448	2290
20.8.64		2290	916	3206
31.8.64		1845	1372	3217
15.9.64		791	1621	2412
2.10.64		594	2094	2688

(The low numbers on 10.8.64 have already been commented on, but it might be pointed out here that if this was a bad sample this would account for the unexpected drop in the IVs on this date, which removes the suggestion of a second peak seen in fig. 9. The uneven increase in the IVs before the 29.7.64 peak is the result of the June mortality coming simultaneously with the emergence of the IIIs into this stage).

Population Dynamics.

In the preceding sections the purely biological aspects of the annual cycle have been discussed. The relation between production and loss must now be examined more closely by considering the extent of the discrepancy between the numbers of eggs produced and the numbers of adults that actually result from them.

The usage of the terms 'production' and 'productivity' must first be explained. Davis (1964) has recently reviewed this and defines productivity as the potential rate of formation of organisms under ideal conditions, and production as the actual rate under existing conditions. Elster (1954a) has used the terms potential and actual production respectively for these two concepts. As Davis himself admits, the definition of productivity is ambiguous since it is so difficult to say what is meant by ideal conditions. He suggests that they should be regarded as the best combination of environmental factors that can be expected in a particular locality, but this seems a somewhat unrealistic approach, particularly if figures for a yearly period, when considerable variation is likely to occur, are being considered.

In this discussion the more usual definitions (e.g. Odum 1959, Steele 1959) of productivity as the rate of formation of organic matter, and of production as the amount of organic matter formed, will be followed, except that numbers of individuals rather than quantities of organic matter will be dealt with. We are concerned with the question of how the species survives rather than how much organic matter, or more fundamentally, how much energy, the population extracts from or donates to the ecosystem as a whole. The success with which a population maintains itself is the ultimate reflection of the balance between the production and the loss of individuals, and as a further refinement a distinction may be drawn between potential production (the absolute production of Elster 1954) which will be the number of eggs produced and the actual production, which will be the number of these actually reaching maturity, or more strictly, the number surviving to produce eggs themselves. Ideally, of course, a study of the population dynamics of a species should include an assessment of the loss occurring in each developmental stage. This poses a considerable problem if, as is the case with D. gracilis and many other planktonic species, there is a prolonged period of egg production so that new animals are constantly entering the population, and it is never possible to follow the fate of individual eggs from birth to maturity. Further complexity is introduced by the speed with which environmental factors can change, most notably the phytoplankton on which the animals are dependant. Changes in the food supply are reflected with equal rapidity by the animals, as events in June in Loch Lomond showed. To quote only one example, the marked change in the number of eggs per sac in the brief period between the 11th and the 25th of that month may be mentioned.

Elster (1954) has suggested an interesting approach to the problem. Use is made of experimentally determined rates of development at known temperatures to determine the renewal coefficient (Ek), a factor found by dividing the time between two sampling days by the time required for development at the mean temperature during that time. The product of the Ek and the stock found on the first day gives the expected increase in the numbers of the subsequent stage on the next day, and from the difference between this figure and the stock actually found the extent of mortality can be assessed. Elster studied the rate of development of the eggs only and used the data to find the 'absolute egg production' (i.e. potential productivity) from the product of the egg stock of D. gracilis in the Bodensee and the Ek. He examined the relationship between the seasonal fluctuations in the figures for egg production and stock, and for the stock of nauplii, copepodites and adults, finding that although there was a good agreement between these curves for the stock of eggs and nauplii there was little between these and the older stages, these latter also differing between each other. He concluded that the absolute egg production did not determine the numerical strength of the next generation and that both exogenous and endogenous factors were of importance.

His work suffers from the disadvantage, which he himself realised, that it is impossible to interpret the changes in the standing population merely from the fluctuations in the standing stock. This has been clearly demonstrated in the present study in the analyses of the copepodite and adult stock changes. The latter provide a particularly good example. As fig. 4 shows there was not a marked fluctuation in the total numbers of adults in the first seven months of the year, and yet within that time the winter population had died off and been replaced by successive waves of new adults. Again, the decrease in the numbers during the latter part of the summer does not indicate progressively fewer numbers of copepodites maturing, and the autumn rise does not result from suddenly favourable conditions. These are all interpretations which might be suggested from examination of the changes in standing stock only. Nevertheless, Elster's work is of great interest, and is notable for his clear understanding of the complexity of the factors controlling the fluctuations in population size.

The same approach has been made by a number of other investigators (Eichhorn 1957, Nauwerck 1963) working on a variety of copepod species. Eckstein's work (1964) is of particular relevance here since he also studied D. gracilis, in the Schluchsee. He extended Elster's work by finding the development rates of nauplii and copepodites as well as of the eggs, and use has already been made of his data in this study. Here again, however, the major criticism lies in the failure to determine whether the animals in the field were actually developing at temperature dependant rates, since the compositon of the population was not studied in detail, only the changes in the total numbers of each major developmental stage (nauplii, copepodites etc.) being considered. Eckstein's use of figures derived from the mean changes in the population over a period of two years is also greatly to be deplored.

The Loch Lomond population showed a relatively clear picture of the sequence of development of the animals and the rate of development could be inferred with some certainty from the field data on the copepodites. However, in habitats where there was a lesser degree of retardation a rather more confusing situation might be found. The extension of biometric analysis to the copepodites as well as to the adults could provide a useful means of determining the rate by following specific size groups through their development, although it is doubtful whether this would be less laborious and time consuming than the taking of samples at very frequent intervals of a few days.

Production and Loss in the Loch Lomond Population.

In this discussion no attempt will be made to trace the mortality occurring at each developmental stage and only the relation between the eggs produced and the number of adults which ultimately resulted will be considered.

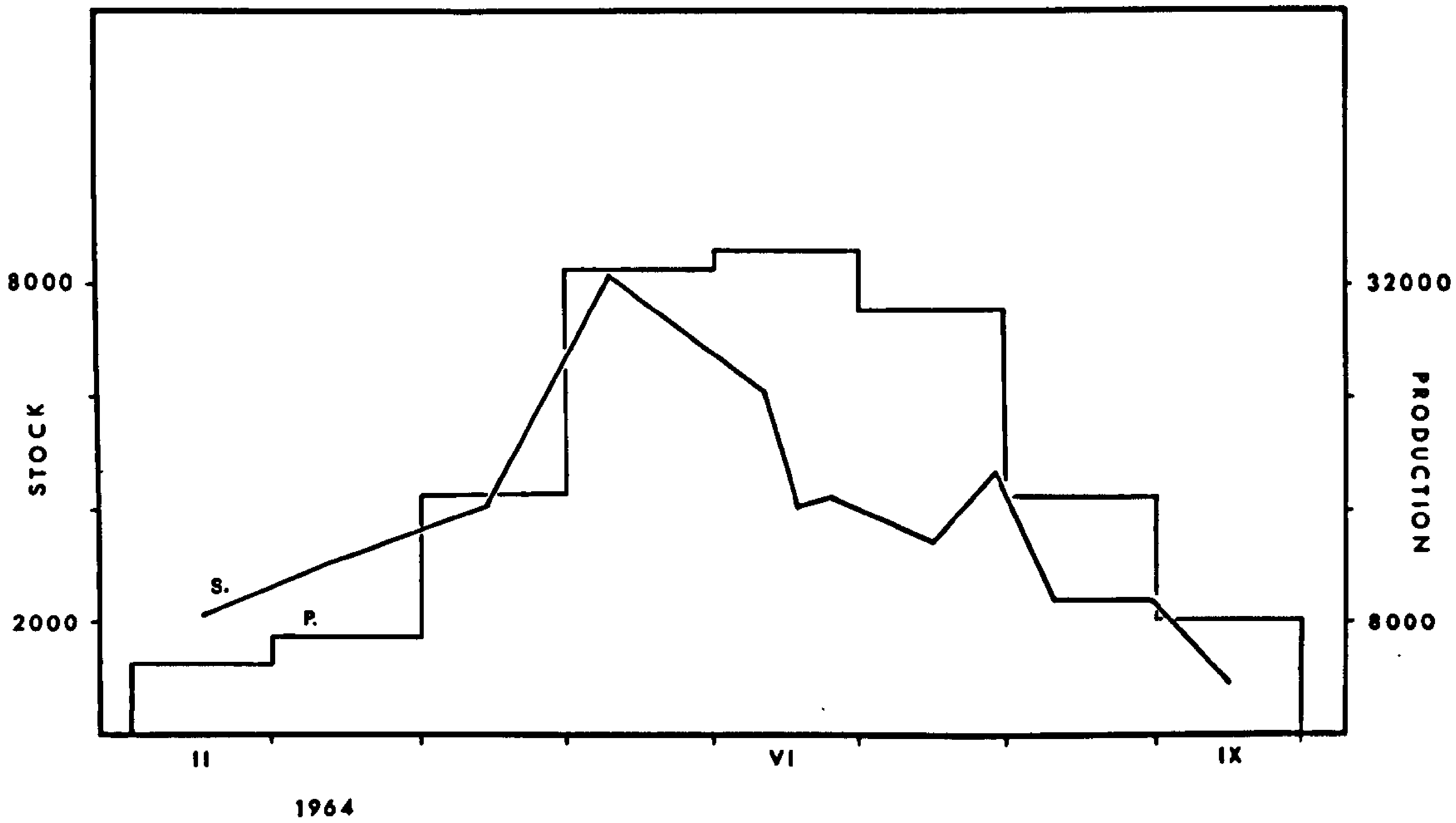
(a) Potential Productivity.

This has already been defined as the rate of formation of eggs, i.e. it is the rate at which new individuals could be expected to be entering the population.

The effect of the varying size of the breeding population and the changing numbers of eggs carried by each individual in determining the size of the egg stock have already been examined (p. 35). In considering the connection between this stock and the potential recruitment a third factor is of great importance, the temperature, which controls the rate of development of the eggs.

The potential productivity was calculated as follows: Since the eggs are retained by the females until the nauplii hatch the major part of the egg stock found on any specific date will have been laid prior to that day. Assuming that no great change in the factors controlling egg production have occurred in that period the daily rate can be found by dividing the stock by the time taken for development at the prevailing temperature. As before, the times are taken from Eckstein's (1964) data, and the temperature is the mean for the upper 10 metres (fig. 4). The times for development vary from 13 days in February to 4 from mid-June to August (Table 11b). Temperatures between March and June increased at the rate

Fig. 10: The egg stock (S) and potential productivity (P) of *D. gracilis*.


8000
2000
STOCK
32000
8000
PRODUCTION
S.
P.
II
VI
IX
1964

of 1° per month, and the development time dropped in the same period from 11 days to 5 days, i.e. 3 days per month. The change in temperature is thus not sufficiently great in relation to the duration of development to introduce an error. During June there was a rapid decline in the number of eggs per sac but the shorter development time of 4-5 days, together with a more rapid rise in temperature in this month should counteract possible overestimates in calculating the daily rates.

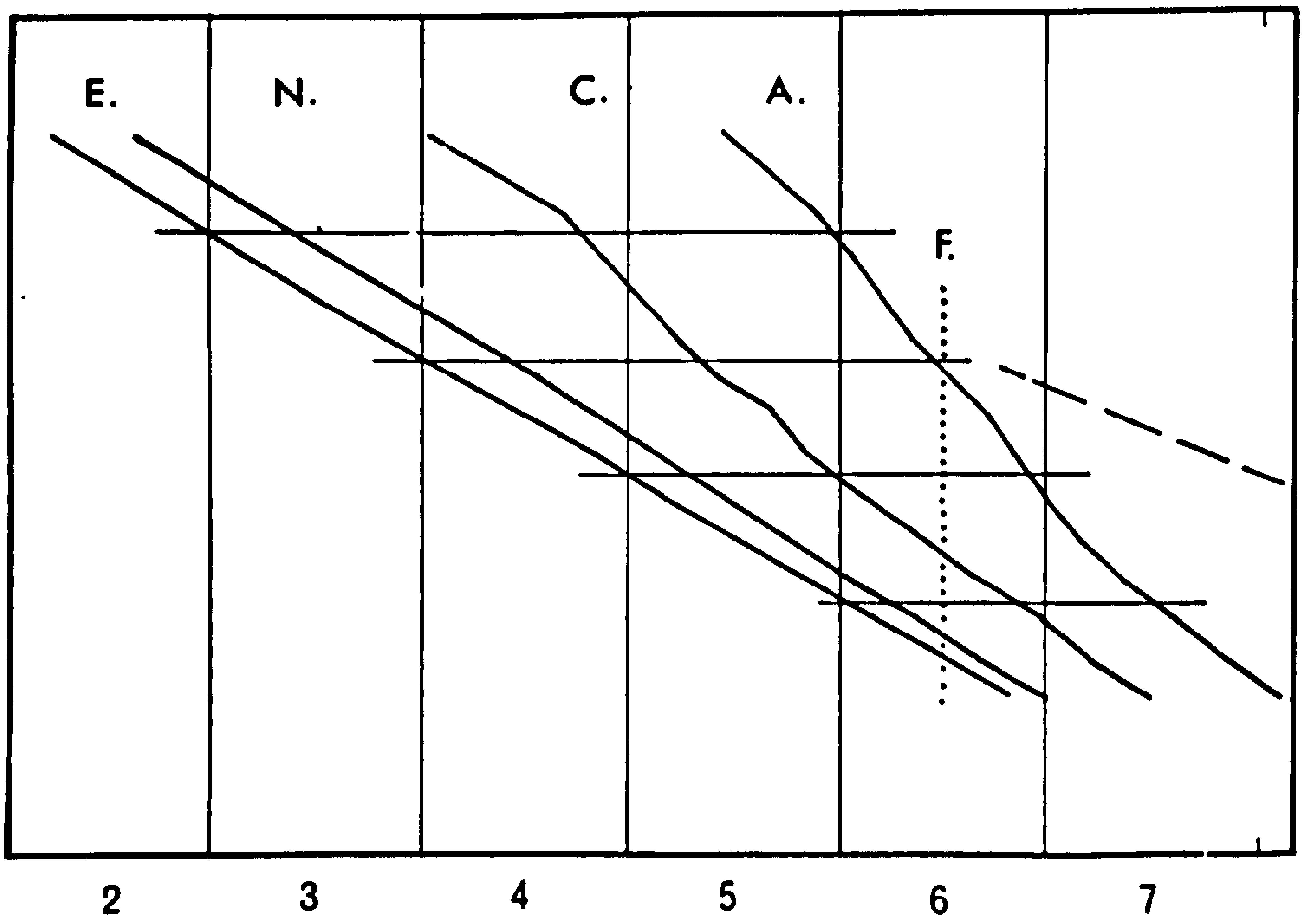
These daily rates can now be used to find the monthly production of eggs by taking the mean daily rate between two consecutive dates and multiplying by the number of days between them (App. Table 5). The figures are compared with those for the egg stock in fig. 10. It was shown earlier that the stock was high in May because of the large breeding population, and in early June because of the large number of eggs carried by each female. The stock then declined as both the female population and the number of eggs per sac were reduced. It can now be seen that productivity was high in May because of the large egg stock, in June because of shorter development times and a still relatively large stock, and again in July when yet shorter development times counteracted the smaller stock.

Figure 11 was prepared from Eckstein's data to show

Fig. 11: The time required for development of *D. gracilis* from egg to adult.

E = egg; N = nauplius; C = copepodite; A = adult.

The dotted line (F) indicates the approximate time when food became limiting, and the dashed line the altered times for maturation.


E.
N.
C.
A.
F.
2
3
4
5
6
7

the times when eggs laid at intervals of five days from February until June should come to maturity. The dates on which they would be in each major developmental stage have been joined by the oblique lines so that for eggs laid on any particular date it is possible to read off these dates from the horizontal time scale. The assumptions are made that firstly Eckstein's times from the Schluchsee animals can be applied to the Loch Lomond animals, i.e. that no genetic differences exist in the growth rates between the two populations and, secondly, of course, that the animals were developing at solely temperature dependant rates. Clearly, the diagram can be regarded as a gross approximation but some support to its general accuracy is given by the fact that the first copepodites did appear in April, as predicted.

Since the temperature and therefore the development times were changing during these months the timing of growth was found by assuming that an equal period is spent in each individual naupliar and copepodite stage (Eckstein did not discuss this, but Raymont and Gross (1942) found that in laboratory cultures that Calanus finmarchicus did spend slightly longer in the IVth and Vth copepodite stages than in the first three. No attempt was made to allow for this in fig. 11 however). Thus

Eckstein's times were divided by 5 to give the number of days spent in each stage. For example, if the eggs had hatched into nauplii at a temperature at which the total naupliar development time was say 50 days, then the temperature (from fig. 4) on the date 10 days later would be found, which perhaps had risen so that the development time in the next naupliar stage would be 9 days ...etc.

It will be seen that the eggs laid in February and March came to maturity between mid-May and mid-June, when these adults would join the breeding population, and indeed by June the latter would consist almost entirely of them, as the winter females had largely disappeared by then. It was in mid-June that the phytoplankton level dropped, and development became retarded. At this time the majority of the April eggs would have reached the late copepodite stages, whilst those of the May eggs which had completed their naupliar development would be in stages I-III. A few of the IIIs may have been from the April eggs but as a simplification this will not be taken into consideration. Of these copepodites, or rather, those which survived the population crash at the end of June, the older ones will give rise to the adults which matured in late June and July, whilst the younger ones will give rise to the overwintering generation in October.

About 75% of these consisted of the large number of IIIs which were so prominent on 25.6.64 (fig. 9) and whose further development was followed through the rest of the summer. If any animals matured between August and September their numbers were too few to be detected in the biometric analysis (p.45).

Since I-IIIs remained in the population at a relatively constant level, even in the later summer months, it was suggested that a few of the eggs being laid during this period were reaching the copepodite stage, but it is not possible to make a realistic estimate of their numbers.

The fate of the egg production of each month is summarised in Table 12. It must be emphasised that these figures are very approximate, as is the timing of the events postulated in fig. 11. Nevertheless, it seems clear that the overwintering generation, one of great importance since it ensures the survival of the species from year to year, originates within a relatively short space of time, in the first part of May. The egg production of the other months is apparently of little direct importance. Eggs laid in February and March would give rise to the new adult population in summer, but the eggs which they in turn produce would not reach the copepodite stage

TABLE 12

Approximate estimates of survival of eggs

Month	Total Nbr. of Eggs Produced	Nbr. of Copepodites	Nbr. of Adults	% of eggs surviving to maturity
February	4,901			
March	7,657	?		
Feb-March	12,558		2,074* (mid May-25.6.64)	16½%
April	17,125	3455 IV + V on 25.6.64 = 20% survival	2,270* (25.6.64-29.7.64)	13%
May	33,211	3200 IV + V in August = 9½% survival		
June	34,329			
July	30,323	90,246 (Approx. 1000 I+II in summer = approx. 1% survival.		
August	17,298			
September	8,296			
May-Sept.	123,457		4,000-5,000 (the overwintering population, exact size unknown).	3-4%

* Adult nbrs. found by doubling the peak female population of each influx shown to be present these dates (see p.44)

until late June at the earliest, after the phytoplankton has declined and so at a time when the chances of survival are slight. It will be those which do survive, together with those from the adults maturing in late June and July, which maintain the numbers of the youngest stages, which made up only about 25% of the summer copepodite population.

From the numbers of eggs produced per month and the numbers of resulting adults a very approximate estimate of the % survival of the eggs can be derived (Table 12). It will be seen that this percentage declines during the year and that it is 3-4 times less during the late summer than in early spring. The whole of the April egg production was regarded as a contribution to the late June-July adult production although it is possible that a part of it contributed to the late summer copepodite population. The June-September eggs were regarded as making up the small fraction of this population in stages I-III, and the May eggs were regarded as being largely as IIIs on 25.6.64. The eggs produced in the last part of May would be retarded in their naupliar development and would be included with the youngest fraction in the later summer population.

The adults produced in summer are therefore not of great significance in assuring the survival of the species since none, or very few, are able to give rise to copepodites by the crucial period in June. After this time the chances of survival of the eggs to maturity become almost negligible. However, the existence of these adults is of importance in that their eggs (or nauplii) would provide a reserve of new animals if for some reason the copepodite population became decimated during the summer. They would also be of some importance if an early autumn phytoplankton burst occurred if it lasted for a sufficient time to enable the eggs to attain maturity and so to swell the winter population.

Sufficient emphasis has already been placed on the impracticality of relating developmental events merely to changes in the standing stock of each major stage, and it is only necessary to note here that as in the Schluchsee and the Bodensee there is little agreement between their respective fluctuations, and above all between the potential productivity and the numbers of the later stages.

Elster (1954) questioned whether endogenous or exogenous factors were of importance in controlling the biological rhythm of a species. By endogenous he means (in so far as _D. gracilis_ was concerned) changes in the numbers of eggs produced by each female. In species such as _Heterocope borealis_ (also studied by Elster, loc. cit.) which produces winter eggs and _Mesocyclops leuckarti_, where dormant stages occur there can be said to be such factors, even though environmental stimuli may be ultimately responsible for this behaviour. However, as variations in egg numbers reflect very directly alterations in the food supply and are not the result of distinct physiological changes within the animals this term cannot be applied to them. It can be considered valid to state that the biological rhythm of D. gracilis is very largely controlled by exogenous factors, of which the two of fundamental importance are food and temperature. Food provides a direct linkage with the seasonal cycles of light and nutrients.

The reason for the lack of correlation between the potential productivity and the numbers of each of the other stages is apparent if the relative importance of food and temperature are considered. Temperature affects the rates of development of all the stages, but food, although it may control the numbers of eggs, does not affect their rate of development and hence does not play such a direct role in limiting potential productivity as it does in the later stages of the life cycle. Thus, in temperate lakes where there is a marked seasonal rhythm in the food available such a correlation cannot be expected since rising summer temperatures will to some extent counteract the limiting effects of food shortages on the potential productivity.

Lake	Author	Comments
Osbysjön	Pejler 1962	
All developmental stages:		
Schleinsee	von Klein 1938 & Kuntze 1938	
Bodensee-Obersee	Elster 1954	
Lunzer	Ruttner 1930	
Schluchsee	Eckstein 1964	
Ponds in S. Norway	Elgmorck 1964	

(Further references to early works are given in Tollinger 1911)

TABLE 13

Studies of *D. gracilis*

Lake	Author	Comments
Zugersee	Brutschy 1913	Does not separate the 3 Diaptomus spp. found.
Concerned with adult populations only:		
Lac de Zurich	Lozeron 1902	
Talsperren	Schneider 1913	
Concerned with total numbers:		
Shannon R. & Lough Derg	Southern & Gardner 1926	
Erlaufsee	Brehm & Zederbauer 1902	No figures
Lough Neagh	Dakin & Latarche 1913	
Hallstätter Sees	Hofman & Morton 1927	No figures
Bartschniederung	Ziegelmeier 1940	No figures
Bodensee	Auerbach et al. 1924	
Limited information on several developmental stages:		
Mjosa	Huitfeld-Kaas 1946	
Uberlinger See (Bodensee)	Kiefer & Muckle 1959	
Mindelsee	Einsle 1964	
Ohrid	Serafimova-Hadzisce 1957	
Schwarzwald ponds	Wolf 1905	
Llyn Tegid	Thomas 1959, 1961	

Discussion.

It is difficult to make any detailed comparisons of the annual cycle of D. gracilis in Loch Lomond with those occurring elsewhere since other workers have not analysed the changes in the adult and copepodite populations in detail, and in many cases their data concerns only the changes in the numbers of the total stock or even of the adults only (see Table 13 for a classified list of these studies). A few authors have described the seasonal changes in the stocks of all or most of the developmental stages, but without information on the rate of development and hence on the rate of turnover of the stock it is not possible to extrapolate from the fluctuations in the stock curves to determine the course of events with any accuracy.

Such curves are merely the resultants of varying degrees of production and loss, and the stock found on any particular day represents only a momentary balance between these two continually varying processes. Thus, a knowledge of the changes in the stock from day to day is of little significance unless the reason for the change, whether due to the losses (because of mortality or further development if the stock of specific developmental stages is being considered) exceeding the entry of new animals into the population, or vice versa, is known. This has already been emphasised in preceding sections and need not be further discussed here. It will be apparent, however, that the attempts of various authors, notably Ruttner (1930), Elster (1954) and Eckstein (1964) to determine production and loss in populations of D. gracilis from an examination of the relationship between the stocks of each major developmental stage throughout the year are to a large extent invalidated by their failure to determine precisely what changes were occurring in the field. The two latter authors have, however, made a most valuable contribution through their studies of the rates of development of the animals in optimal conditions which can be used as a yardstick against which to measure those actually found in the field. It is to be hoped that closer attention will be given to field studies of growth rates, particularly of the copepodites, in future studies.

From a comparison of the available information about D. gracilis in various habitats it is possible to make some comments about the annual cycles. These are:

1. The species is generally perennial, although the composition of the overwintering population may vary. In the Bodensee-Obersee (Elster loc. cit.), Bodensee-

Untersee (Kiefer & Muckle 1959), Lake Krasavitska (Ivanova 1960), Lunzer (Ruttner loc. cit.) and in Lake Ohrid (Serafimova-Hadzisce 1957) and of course in Loch Lomond, it consists largely of adults; in the Schleinsee (v. Klein 1938), Mindelsee (Einsle 1964) and in the Schluchsee (Eckstein loc. cit.) there are more copepodites than adults. In habitats with particularly severe winter conditions resting eggs may be produced, however, and in some Scandinavian ponds no planktonic stages were found between February and March or April (Elgmork 1964, Pejler 1962). Wolf (1904) suggested that winter eggs were produced by the Bodensee population since he did not find the animals in the winter plankton, but this was not confirmed by later workers (Auerbach et al. 1924, Elster loc. cit.). The possibility remains, however, that such eggs may be formed in lakes in exceptionally severe conditions.

2. Breeding is usually continuous throughout the year, although subject to considerable seasonal fluctuation. It may be noted here that the term 'breeding intensity' is often used as a blanket term in the literature, and that statements about the breeding cycles are often made without any clear explanation of whether the numbers of eggs carried by individuals, numbers of egg

carrying females or the total egg stock are being referred to, although the earlier discussion (p. 35) showed that these parameters could all vary independantly. The first of these is worthy of particular attention since the egg number per sac will reflect the abundance of food and thus provides a convenient indicator of changes in the amount of the phytoplankton.

Loch Lomond and Lake Krasavitska differ in that in the former breeding ceases from November until January, and in the latter for an even longer period between September and January.

3. In so far as the changes in the pattern of changes in the stocks of the developmental stages are concerned it is neither easy to distinguish any characteristic patterns nor even desirable to do so, since to make comparisons of the timing of changes in the numbers only is to neglect their essential meaning, since they reflect the variations produced by the differing environmental conditions which mediate them. However, it can be said that corresponding to the spring and autumn bursts of phytoplankton which usually occur in temperate lakes two pronounced peaks in breeding intensity (using the term in its widest sense) and in the numbers of most or all of the developmental stages also are found at these

times, although the timing and extent of these peaks may vary greatly both from place to place and from year to year. Here again, D. gracilis in Loch Lomond and in Lake Krasavitska differ in the absence of the autumn peak, although owing to the paucity of information on the developmental stages in most lakes it is not clear whether these lakes are notable exceptions or not. In the Scandinavian ponds a very different pattern is found with the maxima occurring in January.

Although in some habitats there may be slight rises in egg production in winter (e.g. in the Bodensee-Obersee in some years), the main increase does not occur until the spring, when the phytoplankton has its main increase. The further development of the eggs will at first be retarded by the low temperatures, however, and there will be a time lag before the appearance of the adults from these eggs. During this time the phytoplankton population will be multiplying rapidly, being at first not limited by either nutrient supplies or high grazing pressure. As the temperatures rise, thus speeding development, and as more and more eggs are produced owing to the abundant food available, more and more new animals will appear until the expansion of the population is brought to an end by the decline in phytoplankton numbers. The spring peak of the zooplankton is therefore due to a period of increasing egg production and rising temperatures, and is a peak, rather than a plateau, in a graph by virtue of the fact that food supplies are unable to remain at the high level which they too attain, and hence high mortality results amongst the animals. In the autumn rise temperature will not be of such importance since it will still be near the higher summer levels.

There are two aspects of particular interest which arise from the response of the zooplankton to these seasonal bursts of phytoplankton. The first concerns the very sharp rise in the numbers of the animals within a short period of time immediately preceding the attainment of the peak density. It seems possible that the last increase in the numbers of nauplii and copepodites in particular may result less from the hatching and rapid further development of increasing numbers of eggs than from a retardation of their growth rate, i.e. it is suggested that there is a brief time lag before the effect of the food shortage becomes sufficiently drastic to cause considerable mortality. A longer time is spent in the copepodite stages than in the naupliar stages, and again a longer time in the naupliar stages than in the egg, and so increased egg production is naturally followed by an increase in the total stocks of the later stages since more animals will be entering the populations of the latter than will be maturing (as long as egg production continues to rise; otherwise an equilibrium would eventually be established between the gains and losses). If the rate of maturation becomes slowed down by a retardation of development the stocks of nauplii and copepodites should therefore show an even greater increase. Since egg development is solely dependant on temperature and is not affected by food the increase in the naupliar stock would be expected to be more marked than that of the copepodites. A very detailed study of events during the time of the increase would be required to elucidate this, however, taking samples at very frequent intervals and checking the increases against those expected from known developmental rates of the eggs. (It is appropriate to add here the comment that the all too frequent presentation of results in terms of monthly means of the numbers found, or even worse, of the means of several years' results is greatly to be deplored since it obscures the precise pattern of events).

The second aspect is that of the mechanics of the decline and the extent to which it is due to nutrient limitation acting on the phytoplankton community and/or to grazing by the zooplankton (Cushing 1959, Steele 1959, Cushing et al 1963), although this activity may not be entirely harmful as nutrients may be regenerated as a result (Marshall & Orr 1961, Beklemishov 1957, Harris 1959). This is a question of great interest although it cannot be fully further discussed here (see reviews in Raymont 1963, Fogg 1965). Fogg comments that in freshwater habitats grazing is perhaps of less importance in bringing about the cessation of spring growth of the algae than is nutrient limitation, although Cushing and Steele believe that grazing is more so in temperate waters of the ocean. It is probable that this apparent divergence arises largely as a result of the paucity of information about precisely what algal species are eaten by the freshwater zooplankton, and hence the absence of detailed studies of the relationship between the herbivores and their food, apart from the preliminary study by Nauwerck (1963).

Although the occurrence of peaks of developmental activity in the spring and autumn are of importance, their presence or absence, and their extent, are of less significance in comparing D. gracilis in various habitats than is the amount of growth which follows, them. This can be expressed in more general terms by saying that the true basis for comparisons lies in the extent to which the prolonged or continuous egg production is realised in the turnover of the adult population. The times of the year which are of particular interest are, then, the summer and winter.

It was shown that in Loch Lomond few, if any, of the eggs produced during the summer reached maturity, and that after the maturation of the late copepodites left after the June decline, in July, there was little, if any, renewal of the adult population in August and September. This resulted from the enormously retarded rate of growth, which was caused by a shortage of food. Such a pattern of events can only be determined by analysing the changes in the relative proportions of the individual copepodite stages, and also by a biometric study of the adults, and information on these aspects is not available from other habitats. It would appear, however, that the situation in Loch Lomond is not unusual. In unpublished data on <u>D. gracilis</u> in Windermere Colebrooke (1956; I am indebted to Mr. W. J. P. Smyly for drawing my attention to this M.S.S.) gives the percentages of copepodite stages III-V which show that although there are increases in all the stages in spring and, in some years, in the autumn, it is possible to follow a consecutive pattern of development during the summer. The only other work of which I am aware which gives any details of the copepodite stages found is that of Ivanova (1960), who figures the percentages of the various stages at monthly intervals from L. Krasavitska. Unfortunately the total numbers are not given, and the time between samples is too great for any certainty about growth in this lake.

The changes in the numbers of adults during the summer provide some indication of events. In Loch Lomond they steadily declined and reached a minimum in September and early October when the last of the animals resulting from the productive phase in the early summer had almost all died off, before the overwintering generation matured. In Lunzer (Ruttner 1930) and in Llyn Tegid (Thomas 1961) a similar decline to a minimum has been described, and in some years Ruttner found no adults for periods of a month or more in the late summer. This strongly suggests that in these lakes a pronounced retardation of development of the copepodites also occurs, so that there is no renewal of the adult population. The supposition of Thomas that summer development was inhibited by the higher temperatures is not borne out by

Eckstein's (loc. cit.) experimental work, and his interpretation of the annual cycle, largely based on changes in the sex ratio of the adults, is very inadequate.

In other lakes it would appear that development is not so greatly retarded. Thus, in the Bodensee-Obersee (Elster 1954) the adult population remains at a relatively constant level between July and November, from which it would appear that sufficient animals are reaching maturity to maintain it. The surprisingly long length of life of the adults of up to two to three months in the summer in Loch Lomond should be borne in mind in interpreting adult curves, however, as their ability to survive for so long may obscure the effects of reduced rates of maturation on the stock curves. It is a curious feature of the Bodensee-Obersee population that there is a general tendency for the numbers of the copepodites to steadily increase during the summer to reach their peak in the autumn. This does not appear to occur in other lakes from which data is available (Lunzer, Ruttner 1930; Schluchsee, Eckstein 1964; Schleinsee, v. Klein 1938; Uberlingersee,Kiefer & Muckle 1959, etc.). It might be suggested that in this lake the food shortage is not sufficiently extreme to drastically reduce the numbers of nauplii and younger copepodite stages so that there is a continual and appreciable influx of new animals into the copepodite population, which therefore continues to increase in size because of the still delayed rate of maturation. This situation could be contrasted with that in Loch Lomond where the rate is more retarded, and where it is postulated that the food shortage is sufficient to cause very high mortality amongst the younger stages. The effects of such shortage are more likely to be extreme on the nauplii and the earlier copepodite stages, since for a given density of phytoplankton they would have to traverse a greater distance in relation to their size, with a correspondingly greater output of energy, than would the older, larger animals (neglecting the possibility of selective feeding on the smaller animals by predators). Hence there is no such striking accumulation of animals in the summer copepodite population in the loch.

In other lakes development may be more rapid (Schluchsee, Schleinsee) but it is profitless to further extend this discussion of events in the summer without adequate information. It is to be hoped that closer attention will be paid to them since they are of great significance in assessing the productivity of the species.

There are two features of the overwintering populations to be considered: their origin and their breeding activity. They may be derived from the delayed maturation of the eggs laid early in the summer. This was the case in Loch Lomond, and is also implied in the Krasavitska (Ivanova 1960) results, where a largely adult non-breeding winter population was found. It is almost certainly so in Lunzer as well. It was suggested above that the summer pattern of development was similar to that in the loch and there is the same marked rise in the adult population in November with the numbers remaining high over the winter period. Breeding ceased in most of the years investigated between October and January, and copepodites were often absent in February and March indicating a gap between the maturation of the last summer animals and the appearance of the first spring ones. In Lake Ohrid (Serafimova-Hadzisce 1957) the same high adult population originating in late autumn is found, which again implies a similar cycle.

In more productive lakes the origin of the overwintering population may lie in the autumn burst of reproduction, and within this category a further distinction may be drawn between those in which it is the autumn animals which form the major part of the breeding population in the following spring, and those in which the autumn 'generation' can give rise to a winter 'generation' which in turn produces the spring eggs. Here again the emphasis lies on the rate of turnover of the animals and again, unfortunately, detailed information is lacking. It may be tentatively suggested that the Bodensee-Obersee animals provide an example of the first category. Elster's results show that the high winter (January) adult population may have resulted from the autumn peak of copepodites after some delay (? due to low temperatures or ? due to the amount of food available). Few eggs were produced in November and December, and although the egg stock was at its maximum in January, largely because of the high adult population, the numbers of copepodites remained very low from December until March-April, when the spring rise began, which is probably when the eggs laid during the winter started to develop more rapidly. Elster does not discuss the composition of the overwintering copepodite population. In the Schluchsee it seems possible that there is an additional phase of reproductive activity. In the latter part of the year there were rises in the egg stock in September and in December or January, paralleled significantly by increases in the numbers of eggs carried by each female, which is a good indication of greater availability of food at these times. There were also increases in the adult populations, though of varying distinctness, and it is noticeable that the copepodite population, particularly from January onwards, was much greater than that of the adults. These all suggest that there is a greater degree of developmental activity than in other lakes. Similarly in both the Schleinsee and the Uberlinger See the winter population consisted largely of copepodites.

It will be apparent from the foregoing discussion that the key to an understanding of the annual cycle of D. gracilis lies in the use of an analysis of the changes in the copepodite population in order to indicate the rate of turnover of the stock. Without a knowledge of this there is little point in attempting to characterise the cycles merely by the fluctuations in breeding intensity, or by the varying size of the population. As a result of the generally bimodal appearance of the annual cycles of the stocks of each stage D. gracilis is often described as dicyclic (Wolf 1904, Tollinger 1911, Rylov 1935, Eckstein 1964). However, the peaks in egg production numbers and in those of the older stages are an inevitable consequence of the temperature and phytoplankton cycles in the temperate lakes in which the species is found and should not be given any great significance in comparing life cycles in different habitats.

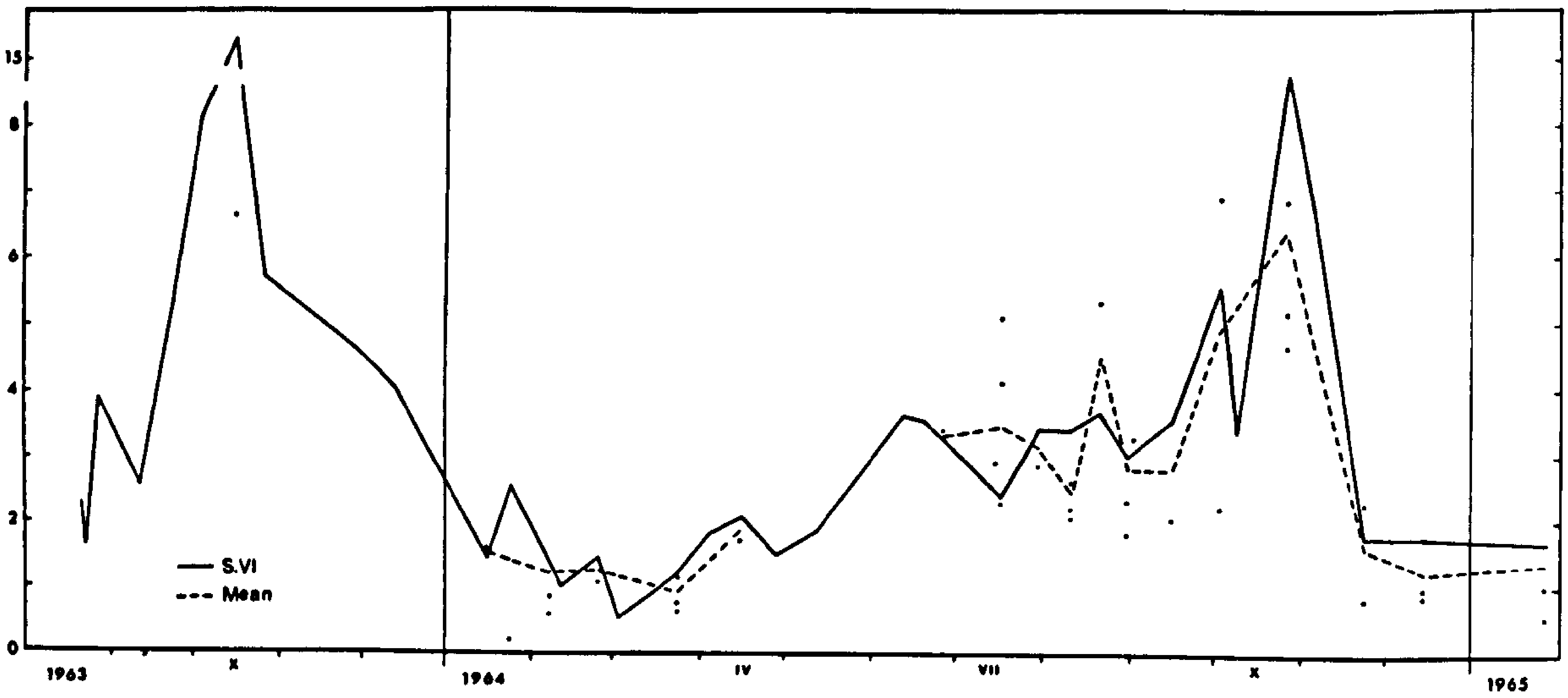
The usage of the term 'dicyclic' is not a very accurate one, since, strictly speaking, it implies that there are only two generations per year, or alternatively, that there are two breeding period, neither of which assumptions are correct. Eichhorn (1957) has proposed a rather different interpretation, defining dicyclic species as those in which breeding alternates between summer and winter eggs, and classifying D. gracilis as acyclic because reproduction is continuous in most habitats throughout the year. This is an acceptable usage, as would also be the case with 'polycyclic', which implies prolonged, though fluctuating in intensity, breeding.

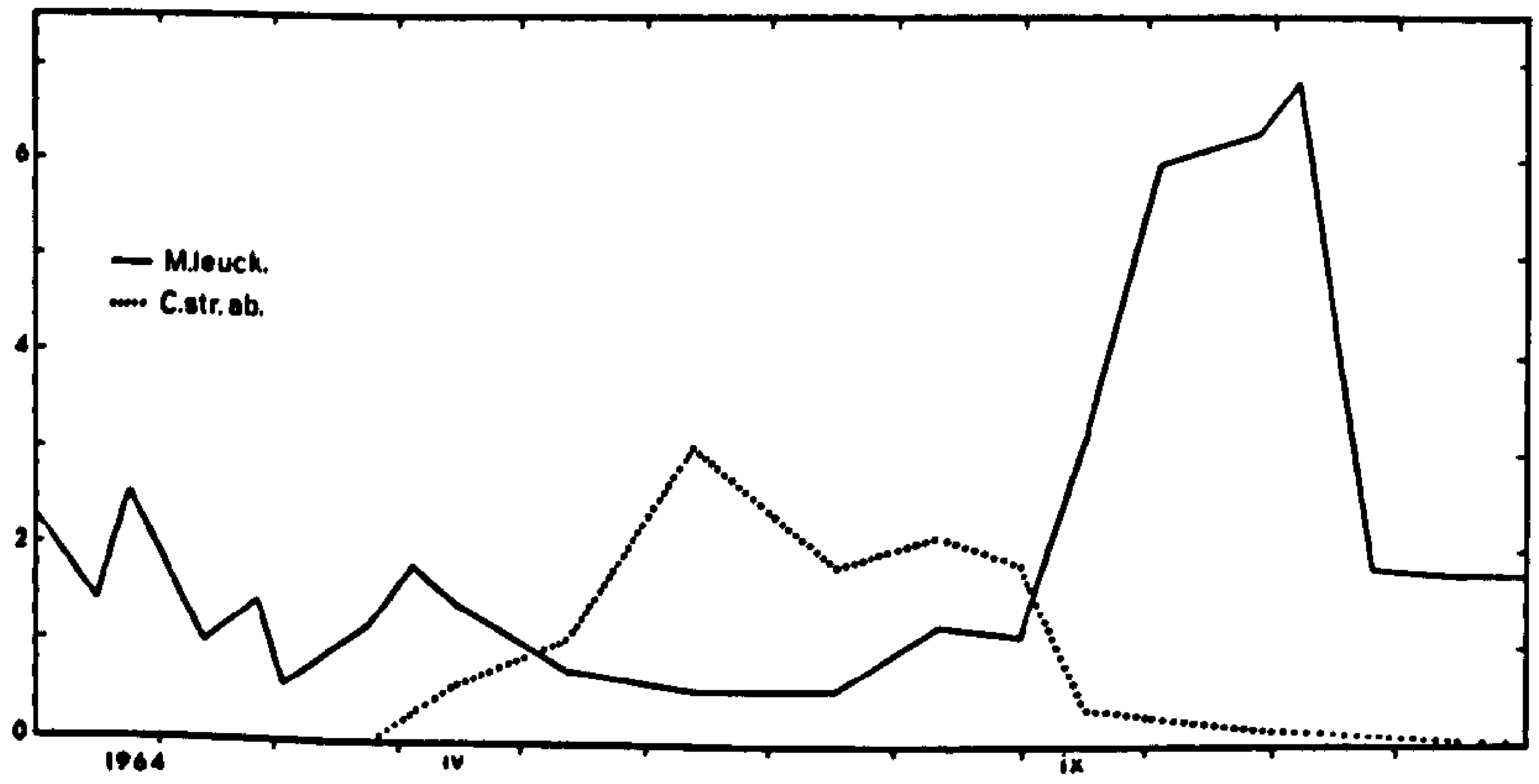
The introduction of the term 'generation' poses difficulties, although it follows logically from any consideration of such fluctuations because any description of the life cycle must include an assessment of the success of reproduction. Elster (1954) and Eckstein (1964) take the number of months in which animals reach maturity as the number of generations, which is misleading (in both cases their conclusions are, in fact, inaccurate, being based on theoretical assumptions about the rates of growth and turnover). The term should more properly be used to refer to animals the time of whose origin is specifically known. Thus, in Loch Lomond, there are only two generations of adults: those which mature in the late spring-early summer period from the eggs produced by the winter and those which mature in the late autumn, and it was shown in the last section that the animals that form the new overwintering population originate principally from eggs produced by the preceding winter population, so that there is therefore only one effective generation in so far as the maintenance of the species from year to year is concerned. If the usage of Elster and Eckstein is followed a total of 5 generations would be arrived at, as adults were maturing from May to July, and in October-November (ignoring the very few doing so in late summer, and in winter).

It should be noted that emphasis has been placed on the survival of the species from year to year by focussing attention on the success with which the adult population is maintained. The fate of the 'wasted' production, the individuals which did not reach maturity and so did not contribute to the maintenance of the population, is not considered here, although they may be of considerable importance to other members of the planktonic community. The role of D. gracilis in the ecosystem as a whole cannot be discussed here however.

Fig. 12a: (upper figure). The total numbers of cyclopoids. Dots show numbers at stations other than S.VI.

Fig. 12b: (lower figure). The numbers of *C. strenuus abyssorum* and *M. leuckarti* at S.VI.


15
8
6
4
2
0
S.VI
Mean
1963
X
1964
IV
VII
X
1965

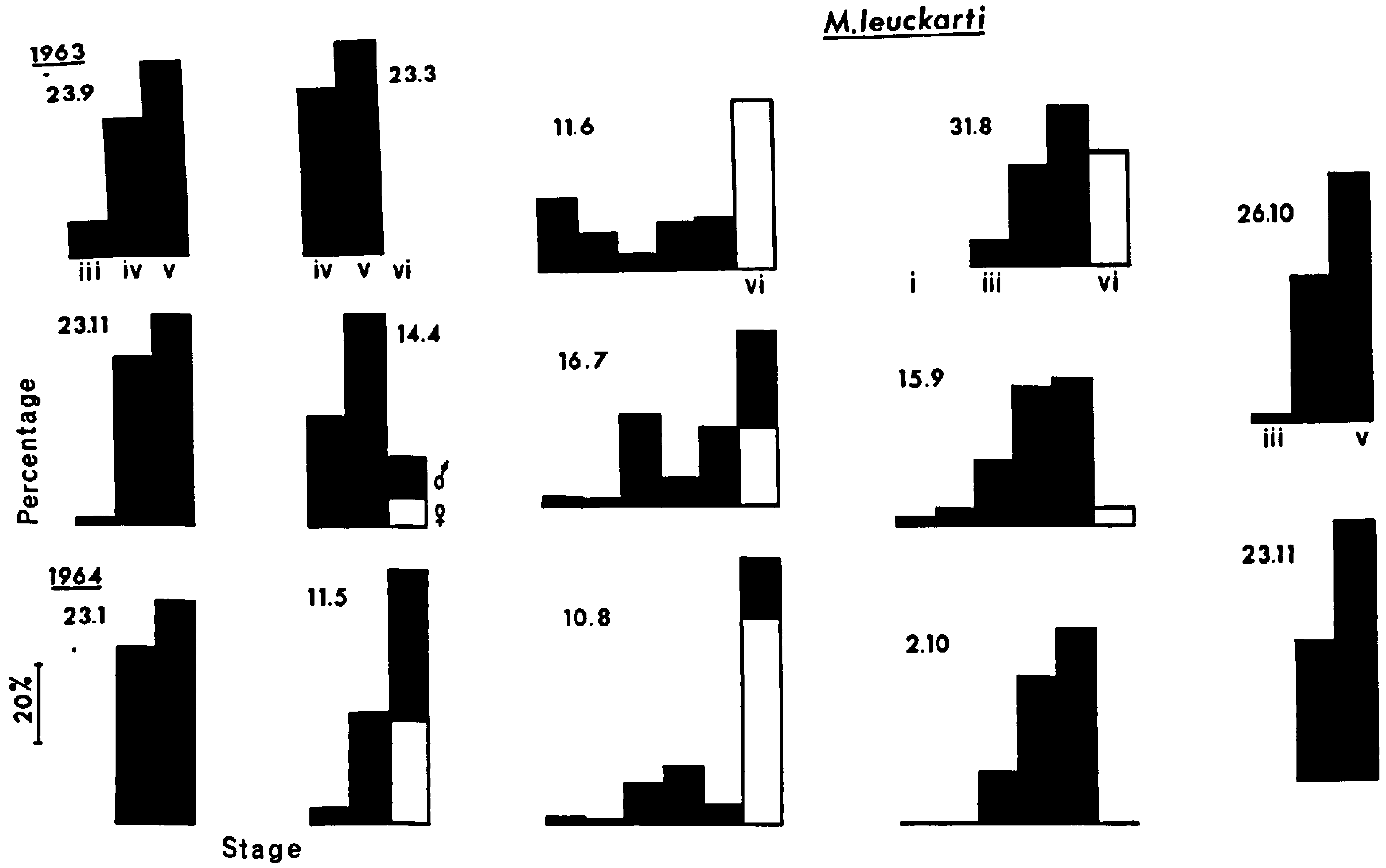

6
4
2
0
M.leuck.
C.str.ab.
1964
IV
IX

CYCLOPOID COPEPODA

Occasional specimens of Macrocyclops albidus (Jurine) and Eucyclops agilis s. str. (Koch, Sars) from the littoral zone were found in the plankton. The benthic species Acanthocyclops viridis (Jurine) occurred relatively frequently, although never more than two or three were taken per sample. It was, however, more abundant in surface tows taken at night.

The two principle limnetic species were Mesocyclops leuckarti (Claus) and Cyclops strenuus abyssorum Sars. They were not separated in the primary counts and hence both species are included in the figures for total cyclopoids between April and October (App. Table 6) After this time only occasional specimens of C. str. abyssorum were found, and the counts for total cyclopoids may be regarded as consisting of M. leuckarti only. These copepods were not studied in such detail as was D. gracilis and the samples have not yet been fully analysed. The two species were studied separately in selected samples from S.VI and the results are discussed largely in terms of the S.VI figures. The total numbers of cyclopoids at this station are compared in fig. 12a with the mean figures for the whole basin; it can be seen that there is not a great divergence between them

Fig. 13: The percentage composition of the *M. leuckarti* population.


M.leuckarti
1963
23.9
iii
iv
v
23.3
iv
v
vi
11.6
vi
31.8
i
iii
vi
26.10
iii
v
23.11
14.4
♂
♀
16.7
15.9
23.11
1964
23.1
11.5
10.8
2.10
Percentage
20%
Stage

and hence large errors in estimating the numbers of each species are not likely to have been introduced. These numbers are shown in fig. 12b.

(i) <u>MESOCYCLOPS</u> <u>LEUCKARTI</u>

The data on this species is given in full in App. Table 7. The summer population of 1964 is summarised in Table 14 and the percentage composition between autumn 1963 and autumn 1964 is shown in fig 13.

This species bred only in the summer months and development ceased in winter, when the rather small population consisted solely of stage IV and V copepodites, whose relative proportions remained unchanged from November 1963 until April 1964, when the first adults appeared.

During the winter ♂Vs were more common than were ♀Vs, and at first there were more adult males. They presumably died off earlier, however, since none were found in early June, although there were many females present at this time.

Copepodites I-III were first found in early June; probably the greater part of the eggs produced by the overwintering generation came to maturity at the end of July, as by early August the large adult population had many more females than males. No young copepodites

TABLE 14

Development of Summer Generations of *Mesocyclops leuckarti*
(Nbrs. at S.VI)

Date	I	II	III	IV	V	♀	♂	Total
14.4.64	-	-	-	402	775	103	149	1429
11.5.64	-	-	-	50	216	209	273	748
11.6.64	101	53	23	65	68	236	-	546
16.7.64	14	11	132	43	112	112	139	563
10.8.64	28	18	122	178	60	633	182	1221
31.8.64	-	-	76	280	449	314	6	1125
15.9.64	74	130	526	1130	1200	148	-	3208
2.10.64	4	24	681	1950	1559	1027	22	5267
26.10.64 (S.I)	-	-	135	2513	4226	-	-	6874

were seen at the end of August (although they could well have been present but in such low numbers that they were overlooked), but they were again found in mid-September, when the eggs produced by the first summer generation would be developing. These copepodites did not develop beyond stage V, however, and from August onwards adults made up less and less of the population, the last males being seen in mid-September and the last females in October. There were already few copepodites I-III in September and by November the animals were all in stages IV and V - the ratio of IV:♂V:♀V being almost exactly the same in November 1963 and November 1964.

The summer population was very small but the numbers rose in September to reach the maximum for the year in October, before falling rapidly in mid-November to the relatively constant overwintering level. The small size of the population in summer may be more apparent than real, however, as the animals at this time are developing rapidly, whereas in autumn the population is static. The differences in population size during this period may therefore be related to different rates of turnover rather than to differences between the breeding intensity and success of the two summer generations.

The cycle outlined above is similar to that described in detail in Esthwaite Water by Smyly (1961), in as much as (a) breeding is confined to the summer season, with the production of two generations per year, and (b) development beyond the last copepodite stage ceases in autumn. However, in Esthwaite, as in most other temperate lakes in which the species has been studied, it is entirely absent from the plankton during the winter. This was shown by Fryer and Smyly (1954) to be due to the ability of stage IV and V copepodites to go into a state of dormancy in the bottom deposits of the lake. Smyly (loc.cit.) found that at the time of the overturn the copepodites, which had previously been found in the upper layers only, became distributed throughout the whole water column, with a marked concentration first in the profundal water and then, in a state of dormancy, in the bottom mud. 'The last maximum in the plankton fell precisely on the first date of the overturn', and by November and December only very occasional animals were found in the open water. The animals reappeared in the plankton in March in Esthwaite and about a month later in Windermere. In more tropical latitudes (e.g. L. Maggiore, Ravera 1954; L. Nyasa, Fryer 1957b) M. leuckarti is found

Fig. 14: The vertical distribution of *M. leuckarti*.


10 8
15.9
2.10
26.10
23 11
0-5
5-10
10-15
15-20
20-30
30-42
(m.)
400

throughout the year.

A similar descent of the animals occurred in Loch Lomond (fig. 14 and App. Table 6). From May until August they were most abundant in the 0-10 metre samples, but by September, as the population numbers rose and as the thermocline dropped deeper they were extending into 10-20 metres. By the end of October the day distribution was the reverse of the summer one, with the maximum concentration at 20-42 metres. At the time when complete homothermy was established, i.e. in mid-November in 1964, and later in 1963, in December, there was a sudden and large fall in the numbers in the plankton, and although there were always rather more animals at 20-42 metres until the following spring, the very high numbers of late autumn were not found again.

The samples taken during the 24 hour series of 29-30.11.63 are of interest as the numbers of M. leuckarti in the 30-42 metres samples ranged from 782 to 4482 (Table 24), a variation which can only be explained by the assumption that the animals were accumulated just above the mud/water interface and hence would only be caught if by good luck the net was lowered right onto the bottom without disturbing the surface so much that mud entered the mouth to spoil the sample. The surprisingly low numbers found at 20-42 metres on 26.10.63 are probably due to the net not sampling the last metre or so. It is possible that the same explanation may hold for the difference between the numbers at 30-42 metres at S.VI on 26.10.64 and 5.11.64.

The descent of the population, the accumulation in the lower depths and the sudden fall in numbers at the time of complete mixing, all strongly suggest that at the time of the overturn a large part of the copepodite population are entering the bottom deposits, as in Esthwaite. Attempts to hatch out copepodites, if any, from mud samples did not prove very successful, largely, I believe, because of unsuitable sampling techniques. Samples taken with an Ekman grab proved too large, and on fractionation and stirring with filtered water the mud failed to sediment. The same difficulty was experienced with mixed core samples, although three copepodites were recovered from undisturbed core samples. They could however have been present already in the profundal water and more definite proof of the existence of copepodites in the mud is necessary. There was no clear indication in 1964 of the re-emergence of large numbers from the profundal. Much greater numbers in the 20-42 metres sample were found at S.VI on 23.1.64

Lake	Author	Planktonic phase of life cycle	Dormant Animals	Planktonic animals in winter	Composition of winter population
Erie (Canada)	Andrews 1953, Chandler 1940	May-Nov.	?	None.	?
Maggiore (Italy)	Ravera 1954	All year	None found.	Yes	
Dojran (Yugoslavia)	Popovska-Stankovic 1954	All year		Yes	
Tiberias (Israel)	Komarovsky 1959	All year		Yes	
Nyasa (Africa)	Fryer 1957b	All year		Yes	

TABLE 15

Periodicity of *Mesocyclops leuckarti*

Lake	Author	Planktonic phase of life cycle	Dormant Animals	Planktonic animals in winter	Composition of winter population
Shartash & Tavartny (N. Siberia).	Ulomskii 1953	May-Sept.		Descend to bottom but remain active.	All stages at time of descent but only IV & V overwinter.
Baltyn (U.S.S.R.)	"		None.	None.	Winter eggs.
Rybinsk (U.S.S.R.)	Monakov 1959	Some all year.	Some in plankton, some active in mud.		? V only.
Ponds in S. Norway	Elgmork 1964	April-Nov/Dec.	Yes	None.	IV + V
Erken (Sweden)	Nauwerck 1963	May-Dec.	Yes	None.	IV + V
Lomond (Scotland)		Some all year.	? some.	Some.	IV + V
Esthwaite & Windermere (England)	Smyly 1961	March/April-Nov/Dec.	Yes	None.	IV + V
Plöner See (W. Germany)	Herbst 1951, 1955	March-Nov/Dec.	?	None.	
Stary Davor (Poland)	Szlauer 1963	April-Oct.	Yes	None.	IV + V

though not at any other station or on any of the dates adjacent to this and this sample must be regarded as an anomaly.

The April figures, being slightly higher, may perhaps indicate an emergence of dormant stages.

It must be presumed, then, that in Loch Lomond M. leuckarti shows a duality of behaviour, some animals overwintering in the plankton, and some entering the bottom deposits. Such behaviour is very different from that in most European lakes (Table 15), where, as in Esthwaite, the animals disappear entirely from the plankton. Dormant copepodites have been found in Scandinavia (Nauwerck 1963, Elgmork 1964) and in Poland (Szlauer 1963) and if looked for would almost certainly occur elsewhere. In certain Russian lakes, however, although the copepodites overwinter in the bottom mud they remain active and do not become dormant (Ulomskii 1953), and Monakov (1959) has reported finding not only active copepodites in the mud at certain stations in Rybinsk Reservoir in January but also in the plankton in the water above these stations. (I am indebted to Mr. W. J. P. Smyly for allowing me to see a translation of Monakov's paper). It is not clear from his paper whether the planktonic animals were distributed right through the water column, or whether they were present in the lower levels only, nor if they were planktonic for the whole of the winter. Nevertheless, the behaviour of M. leuckarti in Rybinsk would seem to be comparable to that in Loch Lomond, with its inferred profundal population and the smaller planktonic population.

It is unfortunate that detailed information on events in the autumn populations in different lakes is not available to provide a broader basis for comparisons since, as Smyly (1961) pointed out, there are a number of aspects to be considered. These are:

1. The cessation of development beyond the last copepodite stage over the winter. No growth occurs in the dormant stages (Smyly loc. cit., Elgmork 1964) but even before dormancy ensues it was found both in Loch Lomond and in Esthwaite that the stage Vs (probably derived entirely from the second summer generation) were not maturing into adults. This was already apparent by August, if not earlier. A similar arrest is implied by Elgmork (1964) and probably occurs in most temperate habitats, although Ulomskii (1953) found adults still present at the time of the descent in Lake Shartash. It is interesting that even in the planktonic population in the loch development was suspended, and there was no significant change in the ratio of IV:Vs from October

until growth was suddenly resumed in the following April. It is evident that other factors besides those controlling growth are involved in dormancy.

This cessation of growth should not be confused with the retardation of development of the autumn stage IV-Vs due to food shortage and low temperatures found by Ravera (1954) in Lago Maggiore.

2. The extension into the profundal. In Esthwaite and Loch Lomond this is preceded during September, as the thermocline sinks and temperatures fall, by a downward movement from the surface layers where the animals were largely concentrated during the summer. Although Smyly (loc. cit.) found that the animals began to accumulate in the profundal water just above the mud surface at this time it was not until complete homothermy, or very shortly before it was established, that the greatest increase in numbers in the bottom deposits occurred. It was also at this time that the major fall in numbers in the plankton took place in the loch. Szlauer (1963) records a mass appearance of resting animals three weeks before full circulation was restored.

3. The assumption of dormancy. The discovery of active copepodites in the profundal deposits of Rybinsk Reservoir and L. Shartash is surprising, as is the

maintenance in the winter plankton of part of the Loch Lomond population, and since planktonic animals were also found in Rybinsk it would be of great interest to know whether or not the presumed profundal population in the loch is in a state of dormancy.

It is clear that there is no simple explanation of the causes of dormancy. Smyly (1961) showed that neither temperature as such nor its rate of fall were of primary importance, and found experimentally (1962) that low temperatures alone were not sufficient to induce dormancy. His findings are strengthened by the behaviour of the species in Loch Lomond. Similarly the presence of active animals during the winter in such a wide geographical range of habitats (Table 15) rules out the possibility that photoperiod may be the controlling factor. However, the close association of the descent into the profundal and the autumn overturn suggest that environmental stimuli are important, as does the variation in composition of the overwintering populations, which implies that dormancy is not associated with a specific stage in the growth cycle of the animals. In Esthwaite generally much less than 15% of the dormant population were in stage IV, and both Nauwerck (1963) and Szlauer (1963) found stage V to be dominant although

TABLE 16

Composition of the autumn populations of *M. leuckarti* in 1963

Date	Station	Percentage III	IV	♀V	♂V	V
23.9.63	VI	9½	37½	26½	26½	53
17.10.63	IV	2½	34	22	41½	63½
	VI	6	28	33	33	66
13.11.63	VI	4	42½	18	35½	53½
29.11.63	VI	2	43½	17½	37	54½
12.12.63	VI	½	44½	17	38	55

TABLE 17

Vertical distribution of *M. leuckarti* on 17.10.63

Station	Depth (m.)	Total Nbr.	Percentage III	IV	♀V	♂V
IV	0-10	2444	83	35½	30	32½
	10-20	2050	10½	28½	32½	28½
	20-32	2598	6½	36	37	39
	Total Nbr.	7092	192	2400	1572	2927
VI	0-10	4316	28½	30½	41	13½
	10-20	3939	37	26	32½	17
	20-42	6992	34½	43½	26½	69½
	Total Nbr.	15247	664	4654	5103	4823

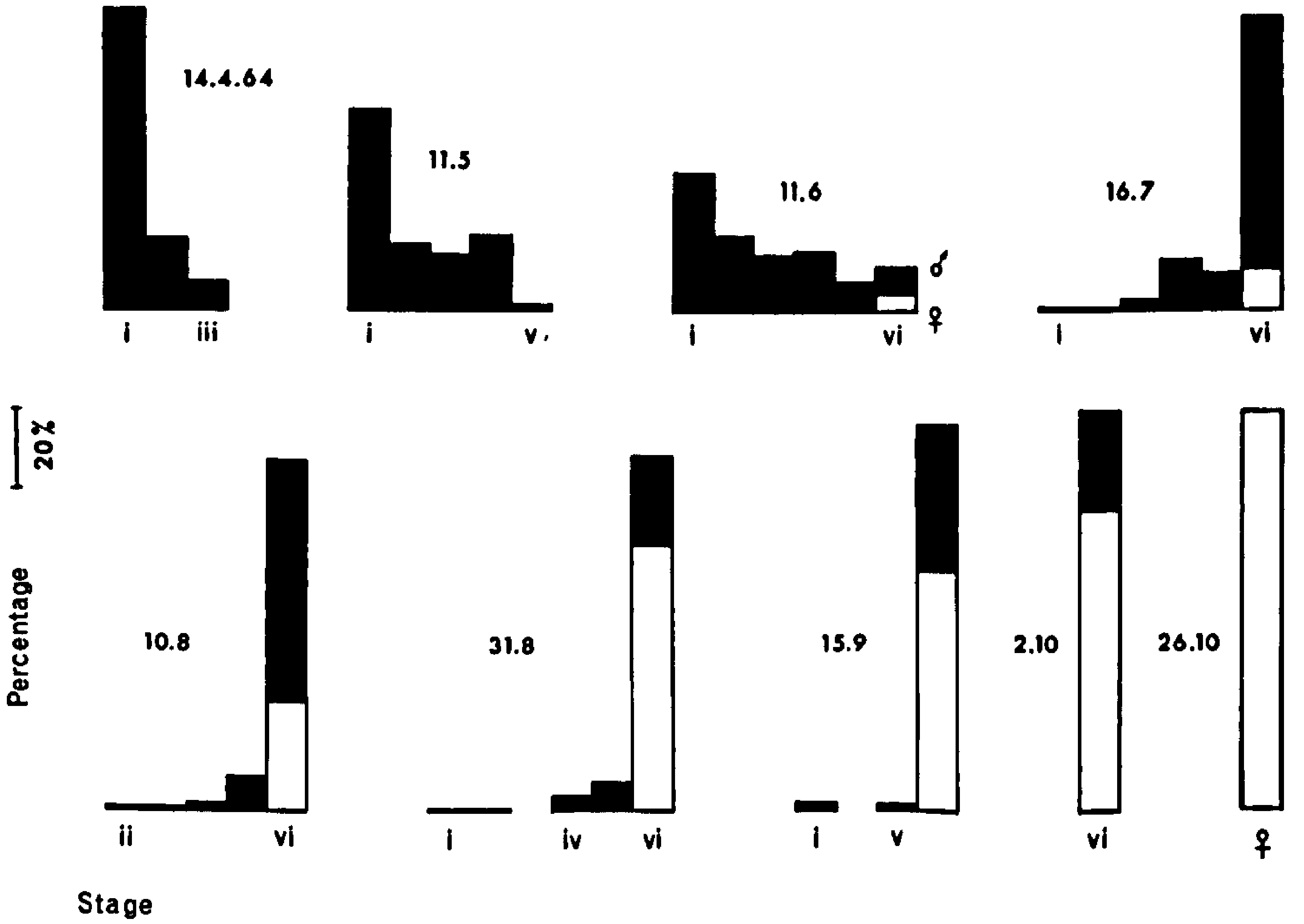
they do not state the exact percentage. On the other hand Elgmork (1964) found more than 50% to be in stage IV. In Loch Lomond they formed 35-45% of the planktonic population. Smyly (loc. cit.) found that a selective migration into the bottom deposits occurred, since within them stage Vs made up virtually the whole of the population, although they had formed only about 30% of the planktonic population. There is some evidence of a selective loss of animals from the planktonic population in Loch Lomond in the 1963 results (Table 16). It can be seen that between the end of September and early December a steady decrease in the percentage of IIIs and a corresponding increase in that of the IVs occurred, and that except for the October samples the proportion of Vs in the population remains unchanged. There was however, a striking change in the sex ratio of the Vs, the numbers of males and females being equal in the September series, and at S.VI in the October one, whereas at S.IV in October, and in the later series, males predominated. Since in these there was no increase in the total proportion of Vs this change cannot be due to the further maturation of large numbers of ♂IVs. There must therefore presumably have been a greater incidence of dormancy amongst the females than amongst the males, and the higher percentage of Vs in the mid-October samples may be taken as evidence for dormancy in stage V rather than in stage IV.

There was a striking difference between the two stations sampled on 17.10.63 not only in the total numbers caught and in the sex ratio of the Vs but also in the vertical distribution of the animals (Table 17). At S.IV the animals were relatively evenly distributed throughout the water column, and the vertical distribution of each stage (apart from the IIIs) was essentially similar. By contrast at S.VI there was a pronounced accumulation of animals in the lower depths, some 50% of which was made up of ♂Vs with only 19% of ♀Vs. There was in fact a reverse relationship between the percentage of ♂Vs and ♀Vs in the populations in the upper 10 metres and at the bottom since in the surface layers there were 48% of ♀Vs and 16% of ♂Vs. The vertical distributions of each stage were very different and the ♂Vs showed a distinct accumulation in the lower depths which was also indicated to a much lesser extent by the IVs, though not by the ♀Vs. This situation is the reverse of what would be expected if there was selective dormancy amongst the ♀Vs. It is perhaps possible that the ♀Vs develop, and become dormant, rather earlier than do the ♂Vs i.e. that they had already done so at S.VI when this sample was taken. Some support for this is found in the 1964 autumn results (App. Table 7) when ♀Vs were more abundant on 15.9.64 and 2.10.64, although after an intermediate period on 26.10.64 the same ratio of about 1♀V:2♂V was found as in the winter samples in 1963. It will be seen that the same temporary increase in the proportion of Vs in the population was found on 26.10.64 as in October 1963, although in this particular series there were no differences in the vertical distribution of any stage, all showing the same degree of aggregation into the bottom layers.

Smyly's valuable experimental work (1962) on M. leuckarti has emphasised the importance of the physiological state of the animals, both in controlling the entry into, and emergence from, a state of dormancy, and he has suggested that the controlling mechanism is likely to be hormonal. It is probable that the varying patterns of behaviour in different lakes result from the different effects on the animal's physiological condition of changing combinations of environmental factors such as food, temperature and other physico-chemical factors, photoperiods etc. It is tempting to postulate that falling temperatures and shorter day-lengths might lead in late summer to a cessation of development and to a switching over of metabolic pathways into the building up of a food reserve which must reach a critical level before dormancy ensues. Since it is in stages IV and V that the gonads are developing the animals could be expected to be particularly susceptible to such a metabolic switch, whilst the need to achieve a certain energy reserve before going into dormancy might explain the existence of active animals in some populations. Such a hypothesis must remain purely speculative until more is known about the physiology of the animals, however.

Fig. 15: The percentage composition of the *C.str.abyssorum* population.

C.s.a.


14.4.64
11.5
11.6
16.7
i
iii
i
v
i
vi
i
vi
♂
♀
20%
Percentage
10.8
31.8
15.9
2.10
26.10
ii
vi
i
iv
vi
i
v
vi
♀
Stage

(ii) CYCLOPS STRENUUS ABYSSORUM Sars

The results from 1963 and 1964 are similar but as the latter are more numerous they are used in the following description. The full data are given in App. Table 8.. The 1964 data is summarised in Table 18 and the percentage composition of the population is shown in fig. 15.

The means by which this species overwinters is not known definitely. Only very occasional unripe females but no males or copepodites are found in the plankton between late October and April, and the summer cycle begins with the appearance of stage I copepodites in spring. There is therefore no question of dormancy in any of the older stages and the mechanism for survival would appear to be either as planktonic nauplii and/or winter (i.e. resting) eggs. Before considering these possibilities the summer activity will be described.

The re-appearance of the species in the samples in 1964 was in mid-April, at which time the first three copepodite stages were present. Development was slow and a month later there were still few stage Vs. The first adults were found in early June, and after this time the numbers of copepodites fell rapidly until by August few were left.

TABLE 18

Summer development of C. str. abyssorum (at S.VI)

Date	Numbers of each stage							Total
	I	II	III	IV	V	♀	♂	
14.4.64	460	115	37					612
11.5.64	703	239	199	267	20			1428
11.6.64	1035	571	437	469	227	110	151	2755
16.7.64	14	17	60	235	172	214	1122	1834
10.8.64	-	21	18	42	183	596	1304	2164
31.8.64	6	4	-	63	128	1246	408	1855
15.9.64	6	-	-	-	4	207	129	346
2.10.64	-	-	-	-	-	244	81	325

It was noticeable that up to mid-August males were much more numerous than were females, but from the end of August onwards females predominated. The maximum numbers of the two sexes were reached respectively at these times (their remarkably close agreement may be noted : 1304 ♂♂ on 10.8.64, 1246 ♀♀ on 31.8.64), after which the population decreased rapidly in size until by the end of October almost none were left. No detailed analysis of the breeding population was made but throughout the summer and early autumn large numbers of females were carrying eggs (the few counts made showed about 14 eggs per sac). During the winter months only rare females occurred.

The peak numbers of all copepodite stages were found in June, i.e. about two months after the first appearance of these young animals. In this early period the Is were dominant. During the rest of the season the total numbers of copepodites were low and stages IV and V were successively the most abundant. There is therefore only one generation per year.

Overwintering is regarded as being almost certainly by means of winter eggs, and it is hoped that work in progress will afford definite proof of this. If the eggs produced during the summer were of the normal type a very much greater fraction of young copepodites would be expected in the later summer months than was found, even allowing for possible heavy predation. Further evidence is provided by the absence of any copepodite stages after early autumn. Survival as free-swimming nauplii without any further development over a period of at the very least 5 months (October-April) and possibly some for as long as 8 or 9 months (June/July-April) seems unlikely. It would imply an extreme retardation of development, if not a state of diapause which it would be surprising to find in such young animals. The possibility of dormant nauplii or copepodite Is in the bottom deposits is very remote. There are no records of such behaviour in other species and dormancy is confined to the later copepodite stages (IV & V) and the adults (Elgmork 1959, 1964), with the notable exception of <u>Cyclops</u> <u>scutifer</u> which has dormant stages II-VI (Elgmork 1962).

On the other hand, the steady rise in the numbers of stage Is found between April and June is consistent with development from nauplii hatching from winter eggs, and this two month period of hatching could well correspond to the two month period over which females are most abundant in the summer. By analogy with <u>D. gracilis</u> naupliar development would be likely to take about the same time as copepodite development, i.e. a period of about two months. Therefore nauplii would be hatching out in January or February (since the first 3 copepodite stages were present in mid-April the very first must have appeared in late March and hence the suggestion of hatching in January). This gives a period of about 8 months for the egg stage, calculating from the first adults in June to the presumed first hatchings in January, a figure which is also reached by working back from the peak of female numbers in August (and hence of egg laying) to the peak in copepodites in June (assuming that the 1964 results are typical in the timing of events). Some indirect support for the hypothesis of resting eggs is given by the close agreement of the summer cycle of development with that of Heterocope borealis in the Bodensee (Elster 1954), a species which produces winter eggs that begin to hatch out in January, and in which there is also a single summer generation.

If the above suggestion is correct it implies that hatching is due to endogenous stimuli. This follows from the gradual appearance of copepodite Is (and presumably therefore of nauplii), which would correspond with the rather lengthy period of egg laying in the summer. It may be noted here that the continued presence of the Is over the summer, even though very sporadic after June, may be correlated with the 6 month span for the presence of egg bearing females (June-October). If hatching is beginning in January and February it is difficult to suggest any external stimuli which could affect the eggs. Temperatures would still be minimal (fig. 3) and although light intensities and duration would be increasing by then it is doubtful if this could be perceived at depths of 30-40 metres. Similarly, there is no reason to suppose that water movements, which might provide mechanical stimuli, would be any different at this particular time of year. Hatching is therefore most likely to be due to internal factors.

There do not appear to be any reliable records of resting eggs in cyclopoids although they are well known amongst the calanoids (Elgmork 1959). However Lowndes (1930) suggested that Cyclops pictus (= C. str. abyssorum) from Skye produced such eggs because of differences in the egg membranes and rates of hatching between these and eggs of this species from other habitats. The observation of Wierzbicka (1962) that adults of C. str. abyssorum, particularly the egg bearing females, would sink to the bottom of cultures and cover themselves with mud is of particular relevance here. I have not found any records of a winter absence of this species from the plankton. Rylov (1948) regarded it as a 'bicyclic' species with winter and summer maxima, and Gurney (1933) as 'monocyclic'. The comments made earlier with reference to Diaptomus gracilis on the inaccurate usage of these terms and the importance of understanding the reasons underlying variations in the life cycle also apply to this cyclopoid, but it can be correctly described as monocyclic in Loch Lomond, since it has only one generation and a single breeding season. Gurney (loc. cit.) quotes the Scottish Loch Survey as finding a later generation of adults after the September one in Loch Ness, which suggests a different cycle from that in Loch Lomond. Smyly (pers. comm.) has found very variable cycles in the lakes of the English Lake District, ranging from a single generation per year and a limited breeding season to several generations and continuous breeding. Such variation in the life cycles is typical of all copepods.

The causal factors leading to the absence of C. str. abyssorum from the winter plankton are unknown and will not be speculated upon here, but the remarkable contrast which exists between this sub-species and the closely related C. str. strenuus should be mentioned.

In this latter the very different seasonal picture is found of diapause during the summer months, the animals becoming encysted in the bottom deposits in stages IV and V (Elgmork 1959). However, Einsle (1964a) suggests that in the variety which he refers to as *C. abyssorum prealpinus* there may be 'a certain stagnation in the fifth copepodid stage' in summer in the Bodensee, since at that time an accumulation of this stage was found in the deeper levels of the lake. There was some suggestion of similar behaviour in the Vs in Loch Lomond in August, and also amongst the adults in July and August (p.161). In the latter this may be related to egg laying which Wierzbicka's observation suggests might occur in the bottom deposits, but after late August the animals were again near the surface. Similar changes in the vertical distribution of the IVs and Vs of *D. gracilis* (p.161) were found in mid-summer, at a time when their development was retarded by a food shortage. Einsle's data, and in particular the fact that the Vs predominated for about two months during this season are not inconsistent with the supposition that a somewhat analogous situation may have occurred in the Bodensee; further information is necessary before any postulation of diapause. The Loch Lomond results do not indicate a particularly lengthy development in these stages, although more complete data would be desirable.

CLADOCERA

Although a considerable variety of species were recorded most of them occurred very sporadically in the samples, and were probably isolated individuals detached from their more usual littoral or profundal habitats. The species regarded as primarily littoral were:

Eurycercus lamellatus (O. F. Müller)
Sida crystallina (O. F. Müller)
Diaphanosoma brachyurum Liéven
Ceriodaphnia quadrangula (O. F. Müller)
Latona setifera (O. F. Müller)
Polyphemus pediculus (L.)

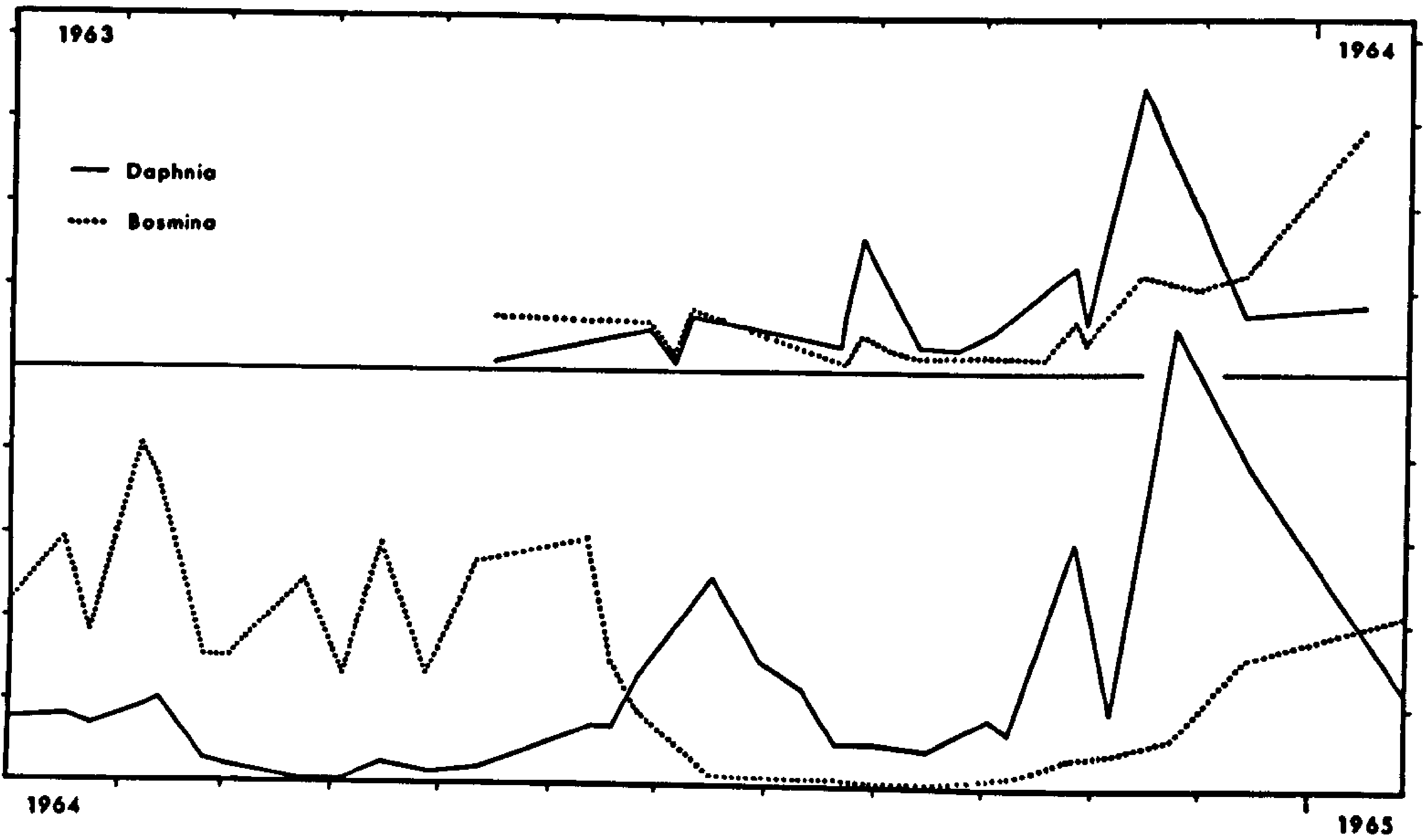
The profundal species included *Chydorus* and *Alonella* spp.

The four species which are regarded as belonging to the true limnetic plankton (although not necessarily confined to it) are discussed below. It was not possible in the time available for this study to attempt to deal adequately with the Cladocera, and only the fluctuations in the total numbers of the important species are considered.

(i) *DAPHNIA HYALINA* var. *LACUSTRIS* Sars (App. Table 9 , fig. 16)

This species was present throughout the year, although the numbers were at a very low level in spring.

Fig. 16: The mean total numbers per standard sample of *Daphnia* and *Bosmina*.


1963
1964
3000
1000
Daphnia
Bosmina
4000
1000
1964
1965

There were two periods of greater abundance : in the summer and again in the late autumn - early winter period when the numbers rose very rapidly to the maximum for the year at the time of the overturn and then remained high for about a month before falling again.

Parthenogenetic breeding occurred throughout the year. No males or ephippial females were found but ephippia of this species very occasionally occurred in plankton samples or in the bottom deposits.

A noticeable feature of the summer populations was the occurrence of the 'minnehaha' form (Herrick 1884), with its characteristic sharp angle at the back of the head. This variant is also known in other species of the genus, and Smyly (1955) found it in summer populations of _Daphnia longispina_ O.F.M. in tarns in the Lake District. It is regarded as a mutation (Johnson 1952) and a closer study of its occurrence in the loch would be of interest.

(ii) _BOSMINA COREGONI_ var. _OBTUSIROSTRIS_ (Sars)
(App. Table 10, fig.16)

The majority of the _Bosmina_ found in the samples belonged to this subspecies, but in the spring and autumn part of the population consisted of _Bosmina longirostris_ var. _similis_ (Lilljeborg) and it would be desirable for a more detailed examination to be made of this genus in Loch Lomond.

The numbers were high during the winter and spring but were at a minimal level in the summer and early autumn. Breeding animals could be found throughout the year.

Although the populations of both *Daphnia* and *Bosmina* were at a low level in the summer and early autumn, there is some suggestion of an inverse relationship between their numbers during the rest of the year. This may, however, be the result of differing availability of their preferred foods or of varying temperature preferences etc., rather than of competition between the species. The small summer populations could be related to the presence at that time of *Bythotrephes* and *Leptodora*, which are said to prey more on Cladocera than on Coppepoda since the former are more readily visible, although large *Daphnia* may not be attacked (Mordukhai-Boltovskaia 1958), but again a greater knowledge of the biology of the species is required to determine whether this is so.

(iii) *BYTHOTREPHES LONGIMANUS* Leydig & *LEPTODORA KINDTII* (Focke)

These two predatory Cladocera were present from late April until November. They were not abundant in the vertical hauls and usually only two or three of each was found in the standard samples, although considerable variation between samples could occur. The 1963 results, when records of the numbers caught were made, show that they were most abundant in September and early October. It may be noted here that their vertical distribution was similar to that of the copepods with the maximum numbers being found in the upper 10 metres.

GENERAL DISCUSSION

There are some general features of the annual cycles of the various species to which brief attention should be drawn. Firstly, the fact that it is the herbivores which are present throughout the year, whilst the carnivores are, broadly speaking, largely confined to the summer months. The predatory Cladocera are completely absent in the winter and the cyclopoids are essentially so- although the relative sizes of the overwintering population of *M. leuckarti* and the summer populations of *Daphnia* and *Bosmina* may be considered comparable, and this relationship should not be taken too far. All the predatory species confine their developmental activity to the summer months but its extent varies, at least in the cyclopoids. Thus *C. str. abyssorum* has only a single generation, whereas *M. leuckarti* is well advanced into the second generation before development ceases. It may be questioned whether these differences in the rates of development are related to the fact that algae form a higher proportion of the food of the latter (Fryer 1957a), thus enabling them to supplement their diet to a greater extent. It is a smaller species and would therefore require a smaller absolute amount of food which might cancel out the greater expenditure of energy, as compared with C. str. abyssorum, required for feeding in a given low density of food. The presence in summer of all the carnivores corresponds of course to the developmental season of D. gracilis, which in turn is related to the seasonal cycles of algae, nutrients and temperatures. The situation with regard to the herbivorous Cladocera remains obscure since it is not known whether their small summer populations represent a rapid turnover or a more static condition due to food or temperature limitations etc.

For the same reason it is difficult to know what validity to attach to the differences in the seasonal fluctuations of the herbivores. The variations are pronounced in the Cladocera but the population size of D. gracilis does not vary greatly. This of course is because for much of the year the species is held static, as it were, and the populations might be called 'maintenance' ones. Thus in winter they consist largely of the adults surviving until the gonads mature for the spring breeding period, and in summer and early autumn the population is held at a more or less constant level whilst the surviving copepodites slowly come to maturity. The expression of these results in the more appropriate unit of biomass would not greatly alter this picture, and the only pronounced peak in both measures would be the early summer one.

This leads to the question of the relative ecological importance of the various species, by which is meant the contribution in terms of the amount of organic matter made by each to the ecosystem as a whole. The numerical dominance of D. gracilis in the zooplankton as a whole may be of lesser importance than would appear at first sight if the rates of turnover of each species could be compared. However, this cannot as yet be done. The activity of animal populations may be likened to icebergs, only a small part being visible in the samples. The hidden part, those animals which do not survive, may not be of direct importance to the species to which they belong, but they will play an important role in the metabolism of the whole community and deserve closer attention than was possible in this work.

It would be appropriate to conclude this section by a more specific consideration of the inter-relationships between the zooplankton species (although it must be borne in mind that an important constituent of the community, the rotifers, have been ignored in this study), but I do not propose to do more than point out the possibilities since to do so would be extending further into the realm of speculation. The effects of competition and predation in limiting the numbers of animals and controlling the ecological balance of the community are difficult to assess without knowing more precisely the role played by other factors.

Thus, the small summer populations of *Daphnia* and *Bosmina* may be due to predation by *Leptodora* and *Bythotrephes* but may equally well be due to limitation by food. Possibly competition with *D. gracilis* for the available food may be of importance also. Similarly, the inverse relationship between the populations of *M. leuckarti* and *C. str. abyssorum* in summer and autumn (fig.12b) may reflect a competitive interaction between these animals or it may be related to differences in their rates of turnover. Fryer's data (1957a) on their food suggests that although there are distinct differences in the diets of these two species they share many food sources, and further complexity is introduced by the possibility of mutual predation. He showed that *D. gracilis* forms an important part of the diet of *C. str. abyssorum*, as do nauplii in that of *M. leuckarti*, and it is probable that these two species absorb much of the egg production of *D. gracilis* in the summer months by preying on the younger stages, although the relatively constant size of the population of the older stages during this time, when it is not being renewed, would seem to indicate that they have little effect on these latter animals.

It will be clear that until the relationship between the cycles of the herbivorous species and those of the phytoplankton on which they feed is known in greater detail, then that between the herbivores and their consumers cannot be fully analysed. The autecology of each species must be properly understood before any such synthesis can be made. There is therefore, as yet, no answer to the question of to what extent the ecological balance of the community is achieved through limitations imposed from lower trophic levels and to what extent from higher levels.

THE ZOOPLANKTON

PART II : THE SPATIAL DISTRIBUTION OF THE ENTOMOSTRACA

THE SPATIAL DISTRIBUTION OF THE ANIMALS

This is a topic which is not only of great intrinsic interest in itself, but also one with important implications for the designing of a sampling programme. Four aspects may be distinguished:

1. The variations in the distribution and in the numbers of the animals from place to place and from day to day.
2. The depth at which the maximum numbers are found during the day.
3. The extent and nature of the deviations of the population as a whole from this depth.
4. The diurnal changes in the depths in which the animals are found.

These questions can only be discussed in the most general way since their complete investigation would require a separate study which was beyond the scope of this work.

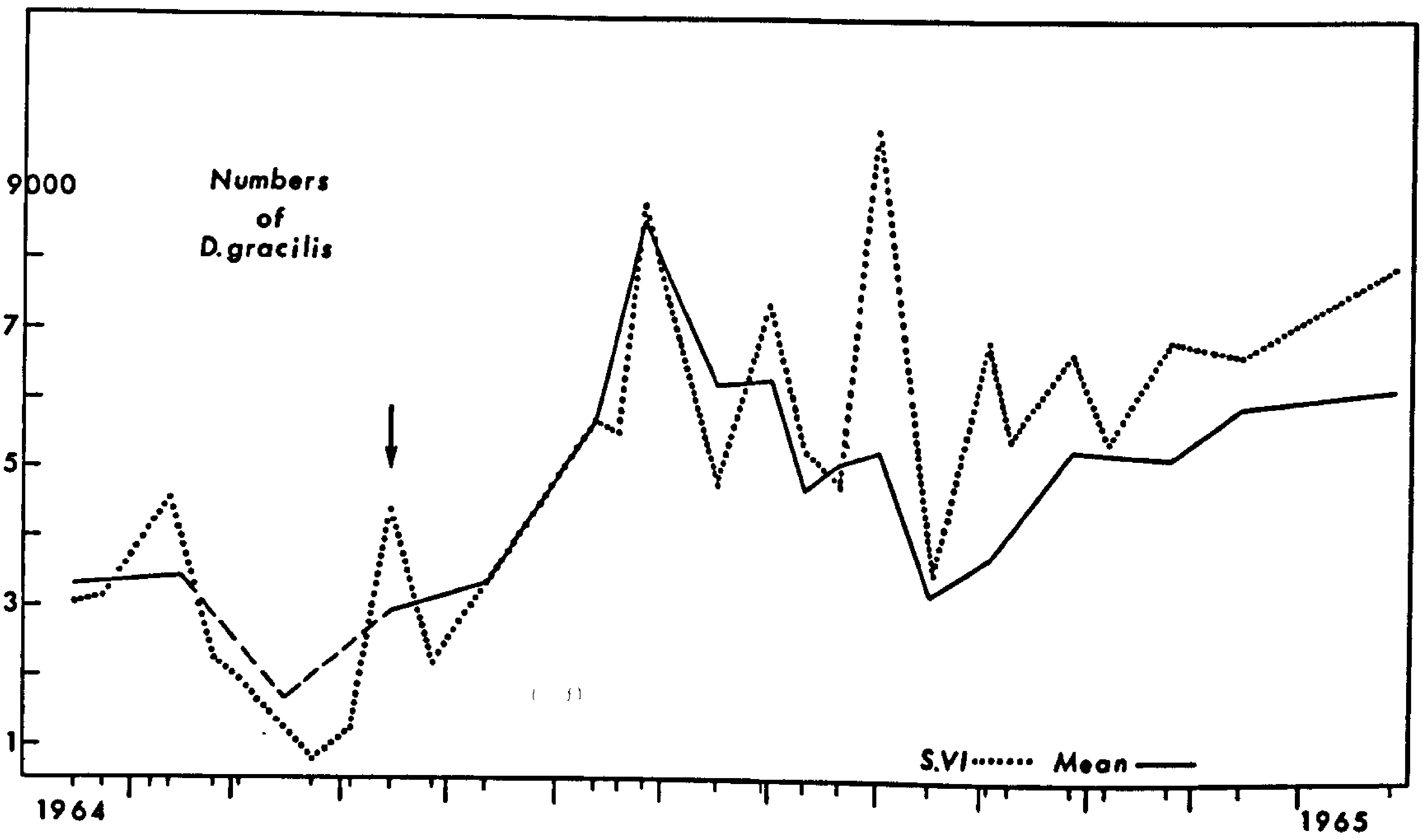
(a) HORIZONTAL DISTRIBUTION

Although it would be convenient if the plankton were randomly distributed over a horizontal plane, so that a sample taken in one particular place may be assumed to be typical of any from surrounding waters, in practice this desirable state is seldom, if ever, achieved. The organisms are always subject to passive transport by currents of diverse origin, and the resulting effects on their distribution may range in scale from the variation between areas some kilometres apart found by Tonolli (1961) to those ranging over a metre or so described by Schröder (1961, a work notable for the use of echosoundings and television to plot and identify differences in population density), or even to those between volumes as small as 10 $cm.^2$ Cassie (1959). Other factors such as swarming (Colebrook, 1960b, Crisp 1962) and aggregation at sharp physico-chemical boundaries (Schröder loc. cit.) may also contribute to patchiness in distribution. The importance of currents and of the effects of wind stress on the thermal structure of the lake in causing such inhomogeneities have been emphasised by Ragotskie & Bryson 1953, Colebrook 1960a, Schröder 1961 and Siebeck 1960.

The sampling programme was not designed to investigate the causes of the observed variations but some general comments may be made. It was originally intended to examine local patchiness (of the type recently reviewed by Cassie 1963) in more detail but the loss of the Van Doorn sampler prevented this. Accordingly, this section is concerned only with comparisons between different regions of the basin.

At all times of the year differences, which were often considerable, were found between the numbers of animals caught at different stations in Strathcashell. This is, of course, only to be expected, since a large proportion of the animals were usually present in the upper 5 or 10 metres, where they would be highly susceptible to passive transport by currents and wind-induced motion of the water. Although the differences between stations were not confined to the surface layers, they were almost always more pronounced in that depth range, and, particularly during stratification, were least below 20 metres. As a corollary to

Fig. 17: The numbers of *D. gracilis* caught at S.VI compared with the mean numbers in the Strathcashel basin.


9000
7
5
3
1
Numbers of D. gracilis
S.VI······· Mean ——
1964
1965

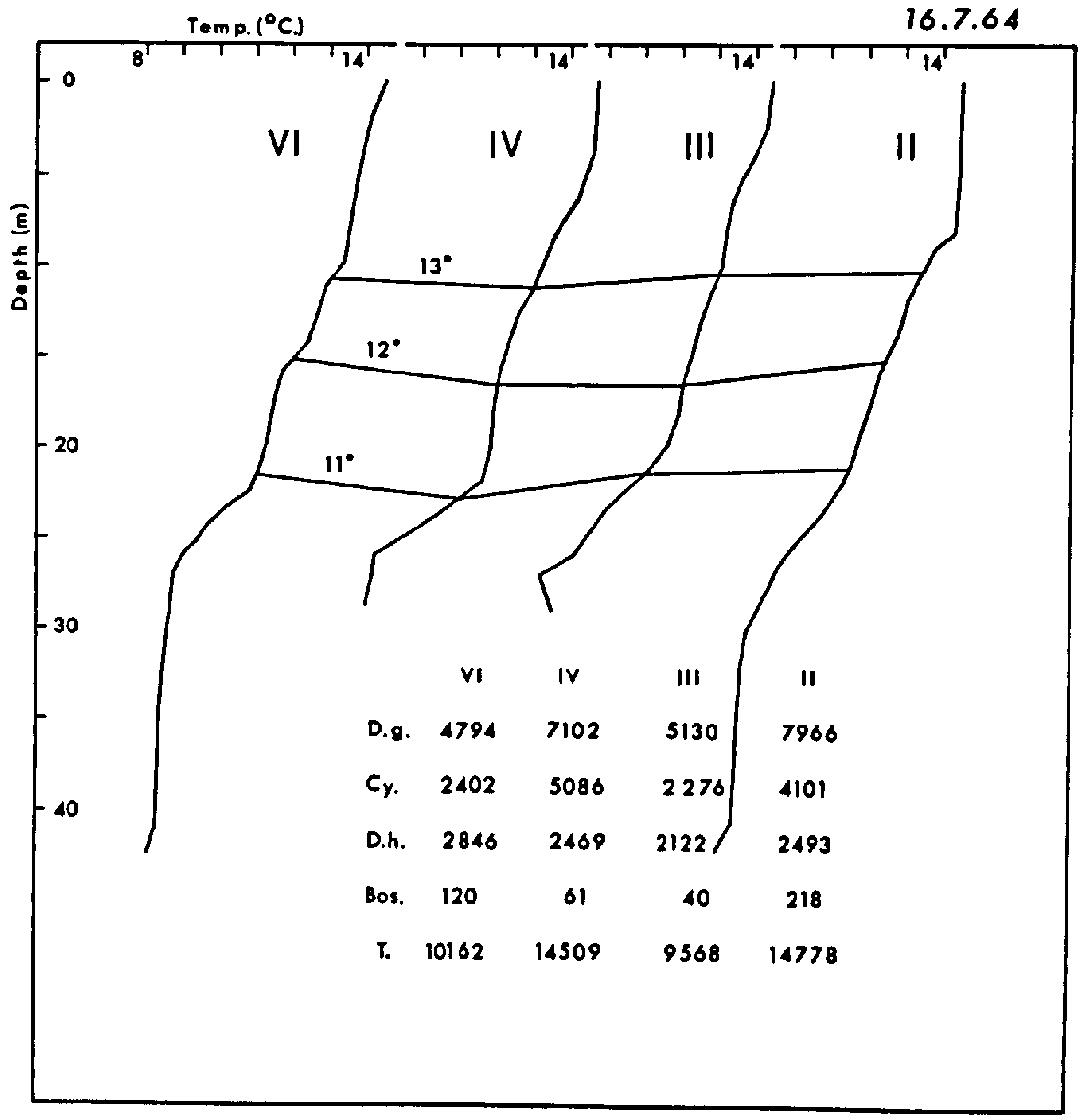
this it will be realised that there was no stability from day to day in the numbers found at any one station. This is shown very clearly in fig. 17 where the fluctuations of the numbers of D. gracilis at S.VI are compared with the mean number for the whole basin.

A comparison of the number of times the maximum total numbers of plankton in the basin were found at each station out of the total number of times each was sampled suggests that this happened more frequently at S.VI than elsewhere (S.VI 6/11, S.IV 1/7, S.III 2/6, S.II 2/4), although this cannot be regarded as more than a faint hint since it was sampled more often than the other stations. It is possible, however, that circular current patterns arising in the basin, ringed as it is by islands and the main shore, could lead to some accumulation of animals in the central area in which S.VI lies.

The effects of strong winds on the distribution patterns were very clearly seen on 16.7.64. Fig. 18 shows that at the two more westerly stations, S.III and S.VI, the isotherms were rather higher than at the easterly S.II and S.IV, suggesting a

Fig. 18: The differences in thermal structure and numbers of zooplankton at four stations, VI, IV, III and II.

D.g. = *D. gracilis*; Cy. = cyclopoid spp;
D.h. = *Daphnia hyalina*; Bos. = *Bosmina coregoni*; T. = total number.

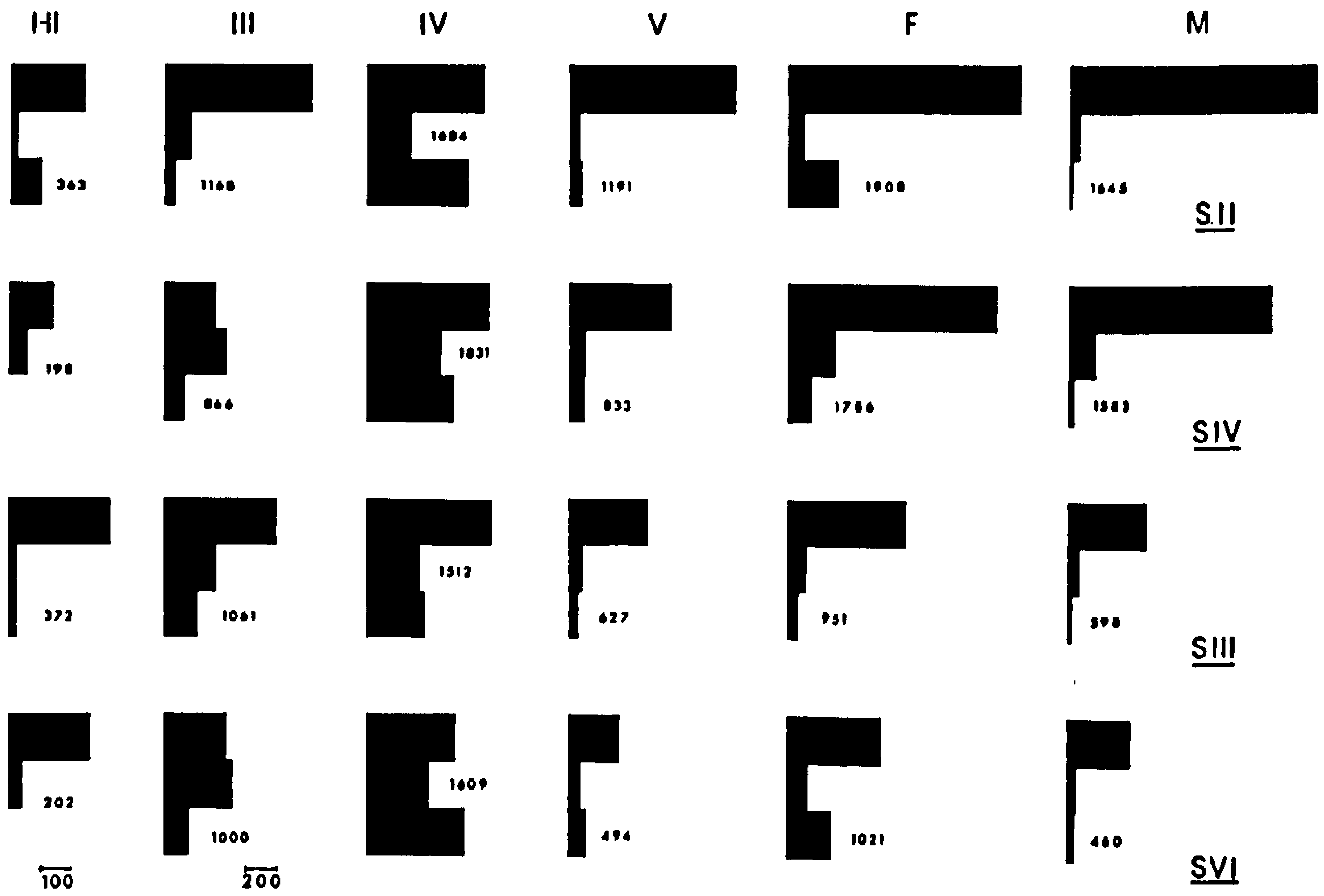


	VI	IV	III	II
D.g.	4794	7102	5130	7966
Cy.	2402	5086	2 276	4101
D.h.	2846	2469	2122	2493
Bos.	120	61	40	218
T.	10162	14509	9568	14778

Fig. 19: The numbers and vertical distribution of the stages of *D. gracilis* at 4 stations on 16.7.64.

(The depth zones are 0-10m., 10-20m., 20-bottom).

D. gracilis – Nbrs./Depth Zone 16.7.64



piling up of epilimnetic water and a tilting of the thermocline on the east side of the basin by strong westerly winds. There were corresponding differences in the numbers of animals and the zooplankton was more abundant at S.II and S.IV, with a very close agreement of the total numbers between each pair of stations (the higher numbers of Daphnia at S.VI than at S.III are due to the concentration of this species in the lower depths, S.VI being deeper). The distribution pattern of D. gracilis is compared in more detail in fig. 19 . At all four stations the maximum numbers of all stages (with the exception noted below) were found in the upper 10 metres, but at S.II and S.IV there were more animals in these layers than at S.III and at S.VI, as would be expected if some piling up of epilimnetic water had occurred. The apparently higher numbers, particularly of IVs and females, at 20-B. at S.VI and S.II merely reflect the greater depth of these two stations.

There are two surprising findings in the distribution, however. Firstly, the differences in the total numbers between the two pairs of stations are largely due to differences in the numbers of stages IV-VI only, although the numbers of I-IIIs would have been expected to differ also. Secondly, the distribution of these young stages. At S.IV and at S.VI, which are on opposite sides of the basin, there were more stage IIIs at 10-20 metres than at 0-10 metres as there were at the other two stations, and in addition there were no I-IIs below 20 metres at these two stations. These differences are relatively minor and it may be merely coincidence that they were found at two stations. The numbers of I-IIs were low and their presence could have been overlooked in the bottom samples. The vertical distribution of the IIIs could have been due to their physiological condition at that season (see next section). However, it is perhaps possible that very slight local currents, having more effect on the young stages, either because they are weaker swimmers or tend to be nearer the surface of the water, had partially re-established a more even horizontal distribution, although the causes of the vertical patterns remain obscure.

Although variations between stations were generally reflected more or less equally by all stages, at least of *D. gracilis*, on one occasion they were shown very largely by the young copepodites only, on 20.8.64:

Station	Numbers of *D. gracilis* stages.							
	I	II	III	IV	V	♀	♂	Total
VI	187	327	463	2167	847	406	397	4794
I	259	636	874	2150	706	453	288	5366

The difference in the total numbers found at stations VI and I is small enough to be regarded as random sampling variation. Detailed analysis shows that it was largely due to differences in the numbers of stages I-III which again suggests that they are more susceptible to passive transport.

These samples were also notable for striking differences in the numbers of cyclopoids:

Station	Depth						
	0-5m.	5-10m.	10-15m.	15-20m.	20-30m.	30-42m.	Total
VI	1890	308	513	481	294	180	3666
I	594	975	1456	1425	594	276	5320

TABLE 19

Numbers caught on 2.10.64.

Station	Depth (m.)						Total
	0-10		10-20				
	0-5	5-10	10-15	15-20	20-30	30-42	
D. gracilis							
VI	3024	2120	1452	192	99	22	6909
II	2464		287		136		2887
IV	828		418		234		1480
Cyclopoids							
VI	1272	1800	1760	576	144	44	5596
II	3869		2714		306		6889
IV	943		1159		130		2232

These are surprising as both the numbers and the vertical distribution of D. gracilis and of the Cladocera were very similar at both stations. On other occasions any differences were shown in more or less equal measure by all the planktonic species, i.e. if large numbers of one species were found, then large numbers of the others could also be expected.

Another possible relationship between thermal patterns and zooplankton distribution was found on 2.10.64. During the sampling moderate S.-S.E. winds were blowing, and there had been several days of S.W. gales in the previous week. The isotherms (App. Table 11) were lower at the more northerly S.II and a more rapid change in the temperatures with depth began at a much lower level, suggesting that an accumulation of water, and to some extent a mixing, had occurred at this station. There were correspondingly lower numbers of zooplankton at S.IV (Table 19). The most notable differences lie in the very small numbers in the upper 10 metres at S.IV. There is not a very great discrepancy between the numbers of cyclopoids at S.VI and at S.II, but there is between the numbers of D. gracilis, largely because of the much greater numbers in the intermediate depths (5-15 metres). This may perhaps be associated with different degrees in the vertical extent of wind induced turbulence, but the tendency for the copepod populations to lie at much deeper levels in late autumn may be operating by this time also, thus complicating the distribution patterns.

One further example may be discussed. On 31.8.64 notably high numbers of copepods and of Daphnia were found in the upper layers at S.VI:

Station	(Depth (m.)				Total
	0-10	10-20	20-30	30-42	
D. gracilis					
VI	7738	855	570	222	9882
III	2738	925	867		4233
II	1280	1258	770		3405
IV	2240	570	1067		3580
Cyclops spp.					
VI	2192	465	176	150	2983
III	1200	925	570		2695
II	600	748	153		1601
IV	927	405	154		1486
Daphnia hyalina					
VI	205	8	209	80	502
III	63	38	200		301
II	40	38	697		828
IV	105	60	84		249

The greater depth of the 14°C. isotherm at S.VI (App. Table 12) may be significant, although the thermal stratification at the 3 stations did not differ greatly. Temperatures were not taken at S.III, which was sampled the following day, but as both days were perfectly calm it is probably valid to compare the plankton catches. At this station there were again more animals than at the two more easterly stations, though not as many as at S.VI.

The remarkably close agreement of the numbers of copepods at both 0-20 metres and 20-30 metres at S.II and S.IV should be noted.

The reason for the rather large numbers of cyclopoids at 20-30 metres at S.III is not clear. The distribution of Daphnia is of interest, as here the greatest variations are found below 20 metres, where the greatest part of the population is found. Such differences which have been more fully analysed by Colebrook (1960a), could arise if the animals were migrating through the thermocline and whilst in the surface layers at night became passively transported to another part of the loch and there descended, or if their horizontal distribution was uneven at the time of the seasonal descent when inequalities would result in the hypolimnetic population. It is not clear whether the descent of Daphnia is diurnal or seasonal. Similar variations are found in the copepod populations in the lower levels of the loch at the time of their seasonal descent.

It should be noted that any statistical treatment of these results has been deliberately avoided as it was considered that neither the limited coverage of the basin on any specific day nor the absolute accuracy of the various processes involved in the sampling and analysis of the populations warranted such analysis, which cannot replace the obvious need for a much more detailed investigation to explain the causes of any particular distribution pattern. These examples have been discussed largely to show the variations in numbers and anomalies in distribution which could occur. They show very clearly the desirability of taking a large number of samples to cover the greatest possible area of the region studied, and they also indicate the caution which must be used in interpreting patterns of vertical distribution since they too may be greatly altered by the same factors which affect the horizontal distribution.

(b) VERTICAL MIGRATION.

A 24 hour series of samples was taken in each season in order to obtain some idea of the extent of diurnal vertical movement by the animals, and to amplify the information available from the routine daytime samples on their vertical distribution.

All the series, except for the September one at Inversnaid, were taken at S.VI. The usual sampling procedure was followed, with two hauls being taken through each depth range, the upper 20 metres being sampled at 5 metre intervals, and the lower depths at 10 or 20 metre intervals. Sampling was begun on the hour and the entire set from the bottom to the surface took about 40 minutes to complete. Weather conditions during the sampling are summarised in Appendix Table 13.

The series were taken in autumn, in early winter, at the beginning of spring and in early summer. An attempt to extend the investigation further with a mid-summer series, using the Van Doorn sampler by then available, which would have been of interest in view of the short period of darkness at that time, was hampered by the need to work from the dinghy and was brought to an ignominious and premature conclusion at 0100 hours by the loss of the sampler due to the parting of a weak cable.

It must be admitted that neither the net nor the bottle proved very suitable for this investigation. I do not consider that the net should be used for sampling through much less than a 5 metre range, but since so much of the zooplankton in the loch is found in the upper 10 metres a really accurate assessment of diurnal movement would require the taking of samples at intervals of one metre or less. The Van Doorn sampler permits this, but as was discussed earlier, the small numbers of plankters necessitate the filtration, with all its difficulties, of large volumes of water. Possibly the use of a pump for taking big samples might be advantageous.

The results discussed below must, then, be regarded as a very generalised picutre of the vertical movements of the animals and they have raised rather more problems than they have solved.

TABLE 20

Numbers of *D. gracilis* caught on 12-13.9.63

Depth (m.)	Time 1500	2100	2400	0400	0800	1200
0-5	1620	2281	1666	1482	1508	1702
5-10	1495	832	1616	636	58	96
10-15	644	616	76	1974	780	528
15-20	456	176	120	61	1729	1190
20-40	456	55	22	270	580	1168
Total Nbr.	4671	3960	3500	4423	4655	4684

(i) 12-13.9.63

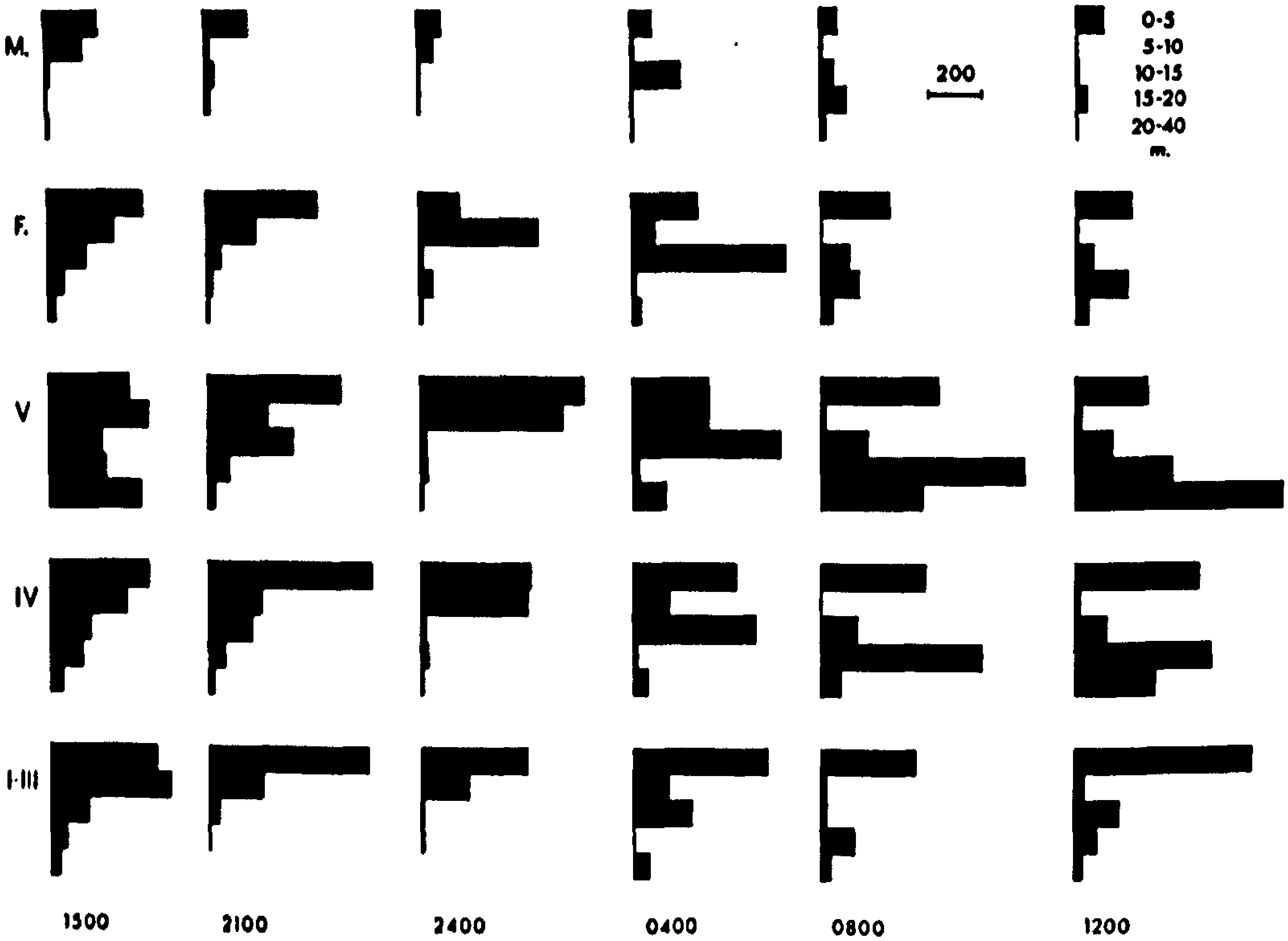
This particular series was taken near the Inversnaid Pier, in conjunction with an overnight fishing programme by Dr. P. Maitland. Although there were fewer animals here the daytime distribution was similar to that in Strathcashell and it is unlikely that the behaviour of the animals in the two areas differed. The station was in 200 metres depth of water, but sampling was confined to the upper 40 metres as virtually no animals were found below these depths.

<u>Diaptomus</u> <u>gracilis</u> (Table 20, Fig. 20)

Although the consistent pattern of changes in the numbers of animals in the lower depths (Table 20) indicated that a diurnal migration took place, there is surprisingly little corresponding variation in the numbers at 0-5 metres, and associated with this the total numbers caught fell to a minimum at midnight and then rose again to the original value by 0800 hours. The rhythmical nature of these changes suggest that they are not due to minor surface currents etc. altering the horizontal distribution of the animals but rather to some regular loss occurring in the sampling. It may be

Fig. 20: Vertical distribution of stages of D. gracilis on 12-13.9.64.

D.gracilis 12-13.9.63



merely coincidence that the midnight deficit is replaced so exactly by the following morning, and indeed the wind blowing throughout most of the time could have produced local inhomogeneities in the distribution of the animals. However, it does seem possible that the losses can be at least partially accounted for if it is accepted that some animals escaped capture because they were aggregated just at the 5 metre boundary between the upper sampling ranges. The copepod populations fell slightly after 2100 hours and then remained very constant, but although the numbers of Cladocera fluctuated to some extent there was no particular pattern to the variations, and in no case is there any strong indication that the wind was having a marked effect on the distribution.

A comparison of the distribution patterns of D. gracilis at 1200 hours and at 1500 hours (fig.20) suggests that the animals from the deeper layers began to move upwards soon after noon. By 2100 hours there had been a considerable increase in the numbers at 0-5 metres, and,of the deepest elements of the population, the large number of Vs was particularly obvious at 10-15 metres.

TABLE 21

Numbers of Cyclopoids caught on 12-13.9.63

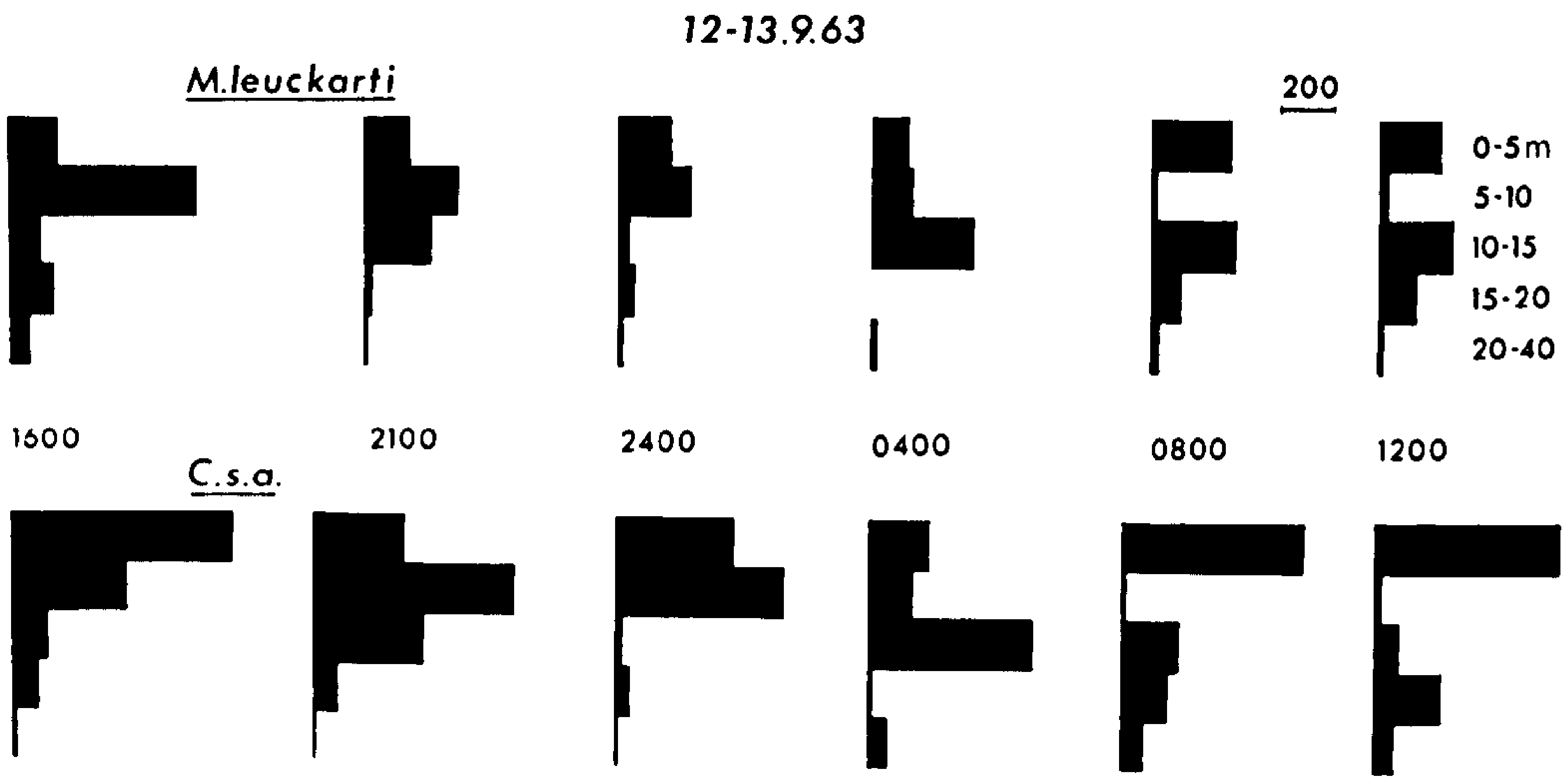
Depth (m.)	Time					
	1500	2100	2400	0400	0800	1200
C. str. abyssorum						
0-5	437	183	236	118	359	364
5-10	230	401	335	88	11	16
10-15	75	219	14	326	114	49
15-20	56	50	27	10	94	134
20-40	10	6	4	43	45	40
Total Nbr.	808	859	616	585	623	603
Mesocyclops leuckarti						
0-5	103	90	104	72	105	114
5-10	368	184	141	80	11	13
10-15	65	131	21	199	114	143
15-20	88	15	33	-	62	76
20-40	38	3	5	11	15	8
Total Nbr.	662	423	304	362	307	354

The numbers at 5-10 metres were lower than at 1500 hours and it appears that some animals were lost as they moved nearer the surface at this time. The numbers at 0-5 metres were lower at midnight but were again higher at 5-10 metres which suggests that the animals were sinking somewhat at that time. Those at 10-15 metres were surprisingly low and there is a strong possibility that this particular sample was a poor one. The maximum upwards extension of the population of the deeper levels was found at midnight, probably to about 5-10 metres and it may be largely these animals which were being 'lost' at the 5 metre boundary during the night. After midnight the descent, particularly of the numerous IVs and Vs, could be clearly followed; it was not complete until noon. It was notable, however, that from 0400 hours onwards large numbers of all stages remained in the upper 5 metres, and there is even a slight indication that the numbers in this surface zone may have increased towards noon.

Mesocyclops leuckarti and _C. str. abyssorum_ (Table 21, fig. 21).

In both species the majority of animals was in the upper 15-20 metres, and it is not easy to

Fig. 21: Vertical distribution of M. leuckarti and C. str. abyssorum on 12-13.9.64.


12-13.9.63
M.leuckarti
200
0-5m
5-10
10-15
15-20
20-40
1600
2100
2400
0400
0800
1200
C.s.a.

distinguish any clear pattern of movement, especially as the total numbers caught fell after 2100 hours. The behaviour was probably similar to that of D. gracilis, with migration into the upper layers beginning after noon and completed by midnight. In C. str. abyssorum there appears to have been a distinct movement to the surface after 0400 hours by many of the animals from above 15 metres, although at the same time some were also continuing to move down to 20-30 metres. Similar divergent movements from the 15-20 metres level during the morning hours are suggested in the results for D. gracilis and M. leuckarti.

The C. str. abyssorum population consisted largely of adults but there were no apparent differences in their depth distribution (App. Table 14), although the higher total numbers in the first two sets of samples were largely made up by females. The population of M. leuckarti was too small to justify analysing the whole series but no marked differences in the distribution of the various stages was found in a comparison of the midday and midnight samples (App. Table 15).

TABLE 22

Numbers of Cladocera caught on 12-13.9.63

Depth (m.)	Time					
	1500	2100	2400	0400	0800	1200
Daphnia hyalina var. *lacustris*						
0-5	72	84	340	190	28	69
5-10	91	156	170	60	1	3
10-15	28	168	11	84	12	-
15-20	36	104	24	10	130	70
20-40	240	61	4	30	270	464
Total Nbr.	467	573	549	374	433	606
Bosmina coregoni						
0-5	36	63	68	-	52	-
5-10	26	52	51	12	-	1
10-15	-	28	16	168	24	-
15-20	12	32	30	2	78	-
20-40	192	37	3	12	60	96
Total Nbr.	266	212	168	194	214	97

Daphnia hyalina var. *lacustris* (Table 22).

The greatest numbers during the daytime were found below 20 metres. Upwards movement probably began during the afternoon and by 2100 hours there was a large number of animals at 5-15 metres which had reached the surface layers by midnight. These were sinking again by 0400 hours and by 0800 hours had reached the lower levels, although the downward movement was not completed until midday. The surface concentration at midnight was more clearly marked than in the other species.

Bosmina coregoni (Table 22).

The population was rather small and variable, and the behaviour of the animals is not clear.

Fig. 22: Vertical distribution of D. gracilis (upper histograms) on 29-30.11.64.

(a) total numbers, (b) distribution of males, (M), females (F) and copepodites IV-V at midday and midnight.

Lower histograms - total numbers of M. leuckarti.

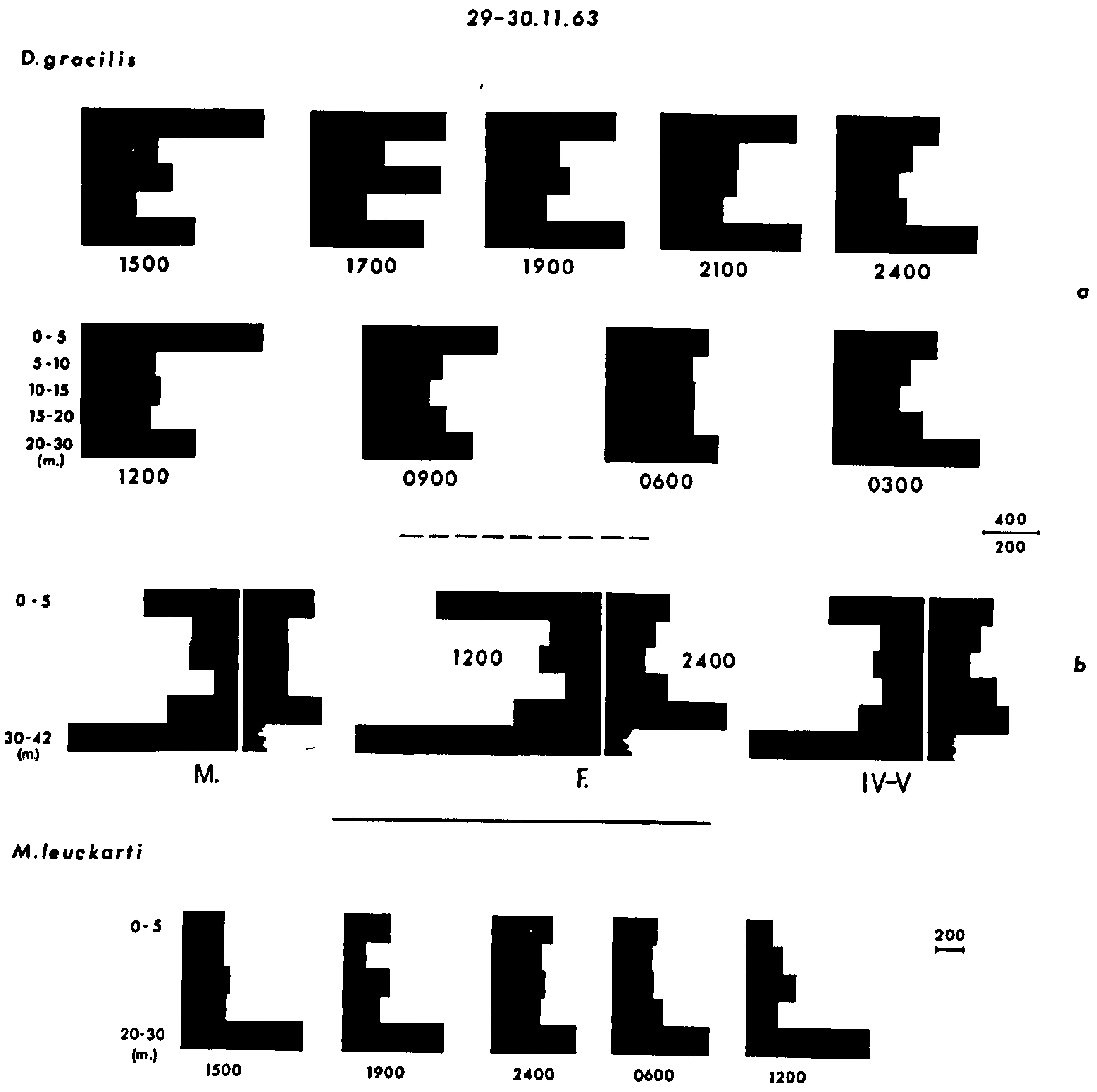

29-30.11.63
D.gracilis
1500
1700
1900
2100
2400
a
0-5
5-10
10-15
15-20
20-30
(m.)
1200
0900
0600
0300
400
200
0-5
30-42
(m)
1200
2400
b
M.
F.
IV-V
M.leuckarti
0-5
20-30
(m.)
1500
1900
2400
0600
1200
200

TABLE 23

Numbers of *D. gracilis* caught on 29-30.11.63

Depth (m.)	Time								
	1500	1700	1900	2100	2400	0300	0600	0900	1200
0-5	1415	999	961	1000	760	504	760	988	1352
5-10	555	550	544	576	414	570	640	576	693
10-15	672	966	616	560	465	486	666	486	585
15-20	400	408	783	460	525	660	658	612	513
20-30	684	840	1032	1166	1050	1083	814	810	962
30-42	2208	1428	1520	1320	2418	800	966	864	722
Total	5934	5191	5456	5082	5632	4103	4504	4336	4287

(ii) 29-30.11.63.

Diaptomus gracilis (Table 23 , fig. 22)

The population (the overwintering generation) consisted mainly of adults, which would breed in the spring, with some late maturing copepodites IV-V. All stages showed a striking bimodal distribution throughout the sampling period (fig. 22 b), with marked concentrations in the upper 5 metres, and at 20-42 metres. The lower concentration was at its most dense immediately above the bottom mud surface, and was difficult to sample without contaminating the net with mud; hence the considerable and irregular fluctuations of numbers in these depths, which for this reason are not fully shown in fig . 22.

The numbers caught in each depth range above 30 metres remained very much the same throughout the whole time, except in the upper 5 metres. These decreased during the evening to reach a minimal level from midnight until dawn, when they again rose to reach almost the same maximum figure as was found at 1500 hours on the previous day. It may be that two particularly dense local concentrations were sampled at noon and at 1500 hours, or it could be suggested that during darkness the

TABLE 24

Numbers of *M. leuckarti* caught on 29-30.11.63

Depth (m.)	Time 1500	1700	1900	2100	2400	0300	0600	0900	1200
0-5	304	222	341	475	440	312	323	260	182
5-10	300	350	256	360	365	375	288	256	266
10-15	350	350	336	380	390	234	306	288	360
15-20	325	264	270	322	360	374	376	324	216
20-30	900	1032	744	902	616	1178	726	720	910
30-42	2300	1848	2660	4422	2883	1700	782	738	760
Total in 0-30 m.	2179	2218	1947	2434	2171	2473	2019	1848	1934
Total in 0-42 m.	4479	4066	4607	6861	5054	4173	2801	2586	2694

TABLE 25

Numbers of Cladocera caught on 29-30.11.63

Depth (m.)	Time								
	1500	1700	1900	2100	2400	0300	0600	0900	1200
Daphnia hyalina var. lacustris									
0-5	760	592	527	550	560	504	361	520	533
5-10	285	1296	448	360	180	360	352	528	456
10-15	280	532	308	280	150	146	540	378	540
15-20	200	264	459	308	255	308	282	516	135
20-30	144	120	456	374	56	171	176	144	156
30-42	-	56	76	66	31	50	46	18	19
Total	1669	2860	2274	1938	1232	1539	1757	2104	1839
Bosmina coregoni									
0-5	323	259	248	200	240	96	190	266	208
5-10	165	288	320	204	162	165	128	208	171
10-15	98	280	196	180	105	108	126	162	225
15-20	25	72	135	196	165	176	141	204	243
20-30	72	144	288	176	84	95	88	54	130
30-42	138	56	-	44	62	50	23	36	19
Total	1821	1099	1187	1000	818	690	696	924	996

animals sink down a little from the surface and that boundary losses in the samples occurred. It is interesting that both in September and in November the same increase in the numbers at 0-5 metres was found around noon.

Mesocyclops leuckarti (Table 24), (Fig. 22).

The overwintering generation of stages IV and V of *M. leuckarti* made up about 99% of the cyclopoid population, the remaining *C. strenuus abyssorum* being too few in number to consider.

About 70% of the *M. leuckarti* population occurred below 20 metres depth, with a particularly high concentration immediately above the bottom, which, as in the case of *Diaptomus* was not adequately sampled at all times. The densities in the upper 30 metres showed some erratic fluctuation but there was no clear pattern of diurnal movement.

Cladocera (Tables 25).

Both species were relatively evenly distributed throughout the upper 20-30 metres, with very few individuals being found below 30 metres. The numbers, especially of *Daphnia*, fluctuated irregularly, but there was again no indication of any diurnal movement.

Fig. 23: Vertical distribution of *D. gracilis* and *M. leuckarti* on 2-3.3.64.

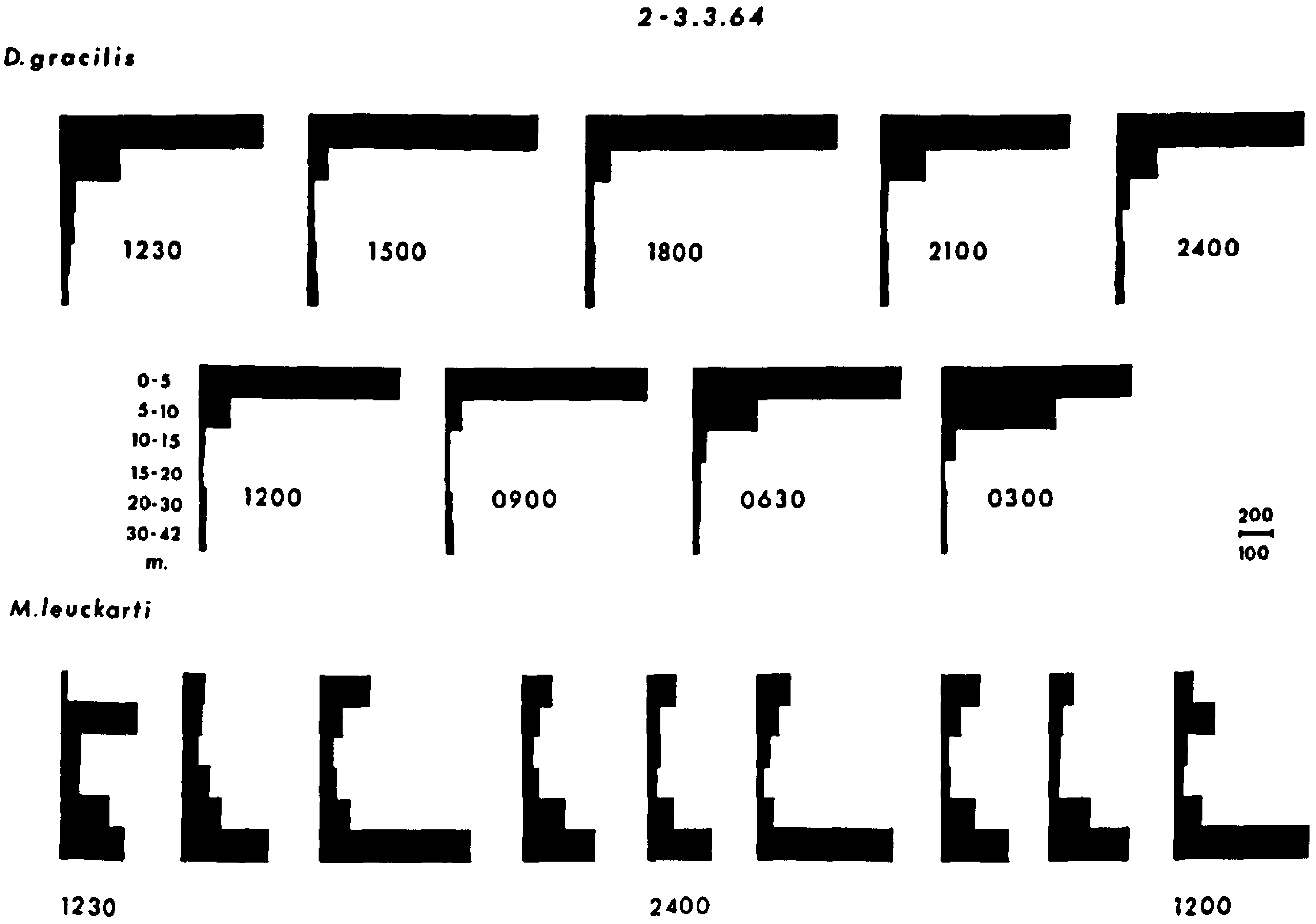

2-3.3.64
D. gracilis
1230
1500
1800
2100
2400
0-5
5-10
10-15
15-20
20-30
30-42
m.
1200
0900
0630
0300
200
100
M. leuckarti
1230
2400
1200

TABLE 26

Numbers of *Copepoda* caught on 2-3.3.64

Depth (m.)	Time								
	1230	1500	1800	2100	2400	0300	0630	0930	1200
Diaptomus gracilis									
0-5	1300	1680	1618	1188	1196	1196	1332	1300	1290
5-10	385	114	147	274	254	719	409	199	196
10-15	89	30	37	37	77	79	81	30	28
15-20	80	36	37	27	34	21	46	16	24
20-30	54	46	56	45	54	33	46	37	41
30-42	43	72	48	48	55	32	36	54	39
Total Nbrs.	1951	1978	1943	1619	1670	2080	1950	1637	1618
Mesocyclops leuckarti									
0-5	20	72	154	88	91	104	120	70	60
5-10	248	62	71	56	37	72	61	38	130
10-15	64	45	37	29	40	41	23	33	38
15-20	57	85	52	47	30	22	26	30	30
20-30	157	125	93	129	82	52	106	126	87
30-42	219	282	480	230	204	444	213	255	434
Total Nbrs.	765	671	887	579	484	735	549	552	779

(iii) 2-3.3.64

Copepoda (Fig. 23, Table 26).

Only M. leuckarti and D. gracilis were present, the animals belonging to the same over-wintering generations that were studied in November. A curious feature of the distribution patterns of the two species is that they were the reverse of each other - the bulk of the D. gracilis population, which consisted largely of sexually active adults, being found in the upper 5 metres, whereas the M. leuckarti population, of copepodites IV and V which had not yet resumed development, were more evenly distributed, with rather higher numbers at 20-42 metres. The numbers in the bottom samples varied somewhat, which suggests that there was still some accumulation of animals immediately above the mud, as in November. No differences were found in the vertical distribution of the various stages of the two species.

In general, the distribution of the two species remained unchanged throughout the 24 hours and no extensive migratory movement could be detected. However, it may be tentatively suggested that the D. gracilis in the surface layers may

TABLE 27

Numbers of *Cladocera* caught on 2-3.3.64

Depth (m.)	Time								
	1230	1500	1800	2100	2400	0300	0630	0900	1200
Daphnia hyalina var. *lacustris*									
0-5	60	216	110	110	78	143	192	52	90
5-10	118	34	32	30	14	47	47	28	58
10-15	17	10	13	6	10	6	10	3	8
15-20	12	7	8	12	1	3	7	9	6
20-30	9	11	10	10	7	3	1	6	6
30-42	2	11	3	9	9	3	5	5	10
Total Nbr.	218	289	176	177	119	205	262	103	178
Bosmina coregoni									
0-5	700	1464	748	1540	741	1235	1344	490	720
5-10	498	200	634	473	156	222	347	118	241
10-15	126	64	87	158	88	47	90	62	57
15-20	100	31	56	63	21	28	38	16	49
20-30	28	43	27	43	47	13	27	19	21
30-42	8	26	12	18	22	21	12	44	17
Total Nbr.	1460	1828	1564	2295	1075	1566	1858	749	1105

have moved upwards (for perhaps only a metre or so) in the late afternoon and early evening (1500 hours and 1800 hours) when slight increases in the numbers at 0-5 metres and slight decreases at 5-10 metres were found. This was reversed from 2100 hours to 0300 hours, and was followed by another slight rise during the morning. The changes were very slight and it is necessary to postulate that a boundary loss is occurring at times.

Rather surprisingly, in M. leuckarti the mid-day maximum lay at 5-10 metres, and there is some indication that there were rather more animals in the surface layers during the night hours.

Cladocera (Table 27).

The total numbers of D. h. lacustris and B. coregoni were rather variable. Both species were found at all depths, but had their maximum concentrations in the upper 10 metres, and no diurnal movement was detected.

TABLE 28

Numbers of Animals in 18 litres on 11-12.5.64.

Depth	Time				Depth	Time			
(m.)	1400	1800	2200	0100	(m.)	1400	1800	2200	0100
Diaptomus gracilis					Cyclopoids				
0	14	13	55	45	0	7	6	26	19
3	33	22	64	35	3	14	18	23	23
6	37	9	43	29	6	19	8	27	23
9	19	15	26		9	2	17	17	
12	14	18	10		12	2	11	2	
15	10	8	3		15	14	8	5	
Total	127	85	201		Total	58	68	100	
Daphnia hyalina					*Bosmina coregoni*				
0	-	-	4	3	0	5	9	14	9
3	-	2	5	1	3	4	10	22	3
6	2	-	-	-	6	11	6	19	8
9	1	3	1		9	42	9	19	
12	1	2	1		12	13	16	35	
15	2	-	-		15	10	38	25	
Total	6	7	11		Total	85	88	134	

(iv) 11-12.5.64

The Van Doorn sampler was used on this occasion to supplement the net hauls, samples being taken in triplicate at 3 metre intervals from the surface down to 15 metres. The engine powering the winch failed at midnight and as difficulty was also being experienced at that time with the release on the sampler the taking of the samples was greatly retarded and the series was cut short. The results of the bottle samples (Table 28) show that in all species an upward movement had occurred by 2200 hours, when increased numbers were found in the samples from the immediate surface layers, although by 0100 hours some sinking had occurred. About twice as many animals of each species were caught in the night samples as in the daytime ones, although it is not clear to what extent the increase is due to upwards movement from below 15 metres, if at all, or whether the animals were coming entirely from the intermediate depths above 15 metres which were not sampled.

The results of the net samples were more equivocable and for all species showed only slight indications of diurnal changes, which could well

TABLE 29

Numbers of *D. gracilis* caught on 11-12.5.64

Depth (m.)	Time					
	1230	1700	2100	2400	0500	0900
0-5	1800	900	1340	1178	775	692
5-10	432	768	931	1026	1054	740
10-15	456	555	336	616	660	635
15-20	285	225	228	216	244	337
20-30	480	403	351	260	334	419
30-42	528	460	176	120	352	499
Total Nbr.	3981	3311	3362	3416	3419	3322

be due to chance variations. It is probable that the length of the vertical hauls was too great to distinguish clearly diurnal movement of small amplitude.

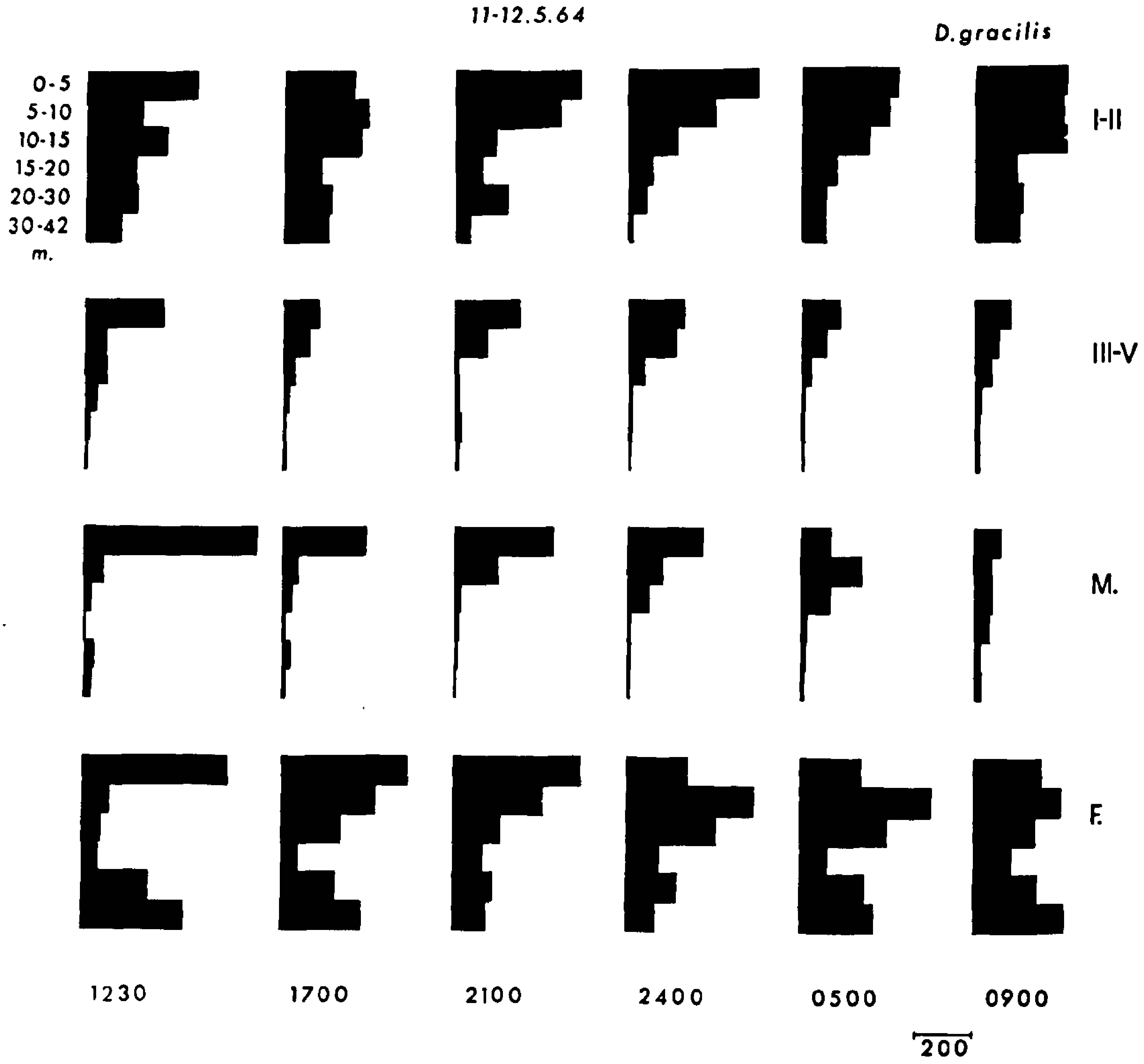
Diaptomus gracilis (Table 29, fig. 24).

The population consisted of the overwintering adults and the spring generation of copepodites, still largely in stages I-II. All stages were found throughout the water column although the lower population contained much greater numbers of I-IIs and of females.

The highest total catch was at 1230 hours, when notably high numbers were found at 0-5 metres. Apart from this series the total numbers remained very constant. The numbers at 20-42 metres fell to minimal values at 2100 hours and 2400 hours and then rose again. There were increased numbers at 0-5 metres at these times, and at 5-10 metres from 2100-0500 hours.

From fig.24 it might be tentatively suggested that a bimodal distribution developed at noon when many of the animals above 15 metres had moved into the surface layers, minimum numbers at 5-15 metres being found at that time. During the afternoon

Fig. 24: Vertical distribution of D. gracilis on 11-12.5.64.


11-12.5.64
D.gracilis
0-5
5-10
10-15
15-20
20-30
30-42
m.
I-II
III-V
M.
F.
1230
1700
2100
2400
0500
0900
200

it would appear that the animals sank away from the surface to some extent, but that the animals from the deeper layers were already moving up and that the upper animals did so again later, so that during the evening the population as a whole was rather nearer the surface than during the day. This upwards drift was probably at its climax at around 2100 hours, as is indicated by the surface maxima in both the net and in the bottle samples. After this the females and probably also the males and older copepodites began to sink again through 5-15 metres, and by 0500 hours the lower depths were becoming re-populated. By 0900 hours there was a very even distribution in the upper 15 metres. The I-IIs did not begin to sink until after 2400 hours but this apparently later descent may indicate that their maximum within the 0-5 metre layer was somewhat higher than those of the older stages.

The particularly high surface numbers at 1230 hours may have been due to the sampling of a localised concentration at that time. Higher numbers of C. strenuus abyssorum were also found then.

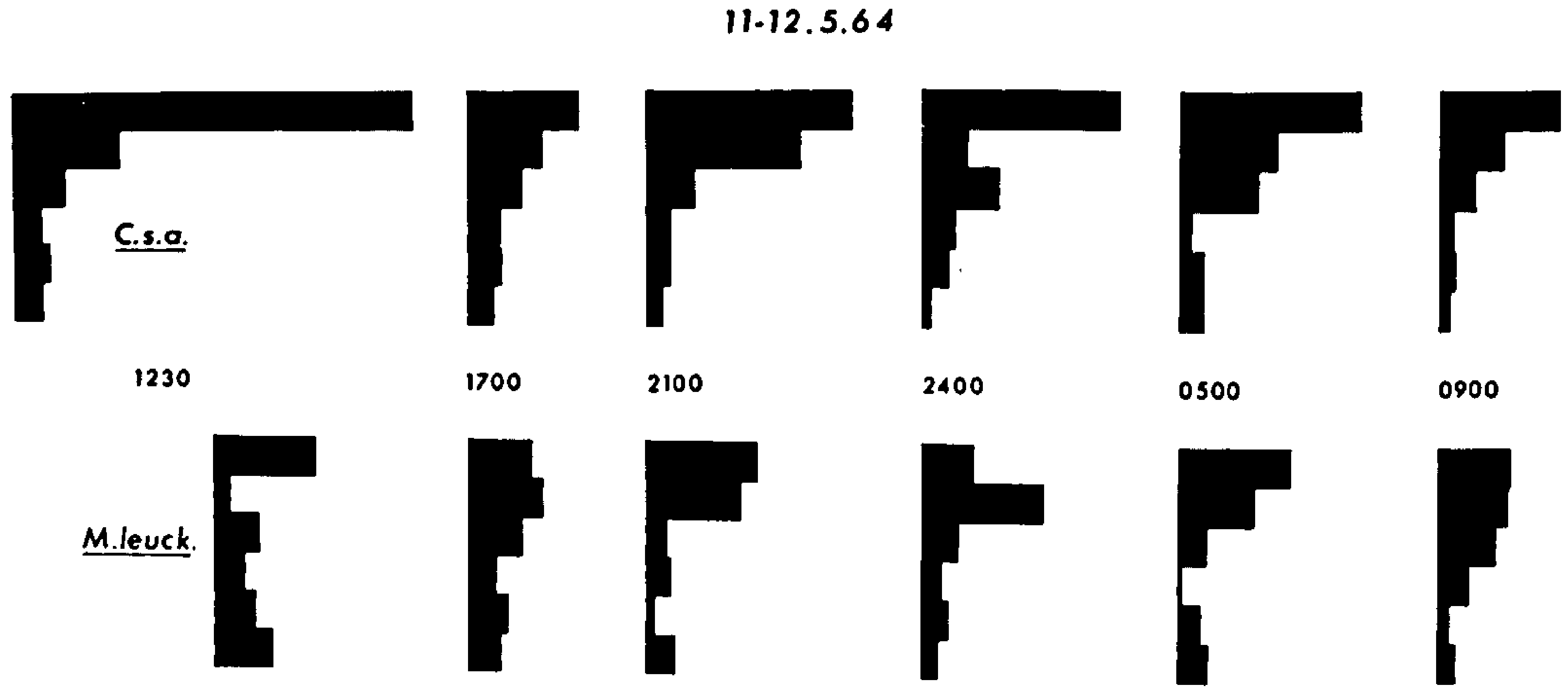
This outline is put forward very tentatively,

TABLE 30

Numbers of Cyclopoids caught on 11-12.5.64

Depth (m.)	Time					
	1230	1700	2100	2400	0500	0900
Cyclops strenuus abyssorum						
0-5	809	277	520	495	451	350
5-10	264	184	338	108	239	212
10-15	132	135	123	187	195	138
15-20	68	79	60	80	29	35
20-30	89	85	57	65	63	42
30-42	70	64	43	20	56	32
Total Nbr.	1432	824	1141	955	1033	809
Mesocyclops leuckarti						
0-5	260	163	280	132	278	177
5-10	39	184	239	306	193	174
10-15	115	135	51	93	71	145
15-20	82	71	60	40	7	81
20-30	106	97	21	105	54	28
30-42	149	86	69	40	76	46
Total Nbr.	751	736	720	716	679	651

Fig. 25: Vertical distribution of _C. str. abyssorum_ and _M. leuckarti_ on 11-12.5.64.


11-12.5.64
C.s.a.
1230
1700
2100
2400
0500
0900
M.leuck.

and if it is correct it represents a rather unusual course of events - notably in the rise towards the surface at noon and the subsequent slight downwards drift. The results imply that different behaviour is shown by the animals above and below a depth of about 15 metres. Such a divergence is not impossible, and Siebeck (1960) has suggested that not only the intensity of illumination and its rate of change are important in controlling the movements of the animals, but also the amount of light to which they have already been subjected. There is clearly a great need for a repetition of these series, sampling at closer intervals of depth and time, and correlating the changes with light measurements in situ.

Cyclopoids (Table 30, fig. 25).

The overwintering generation of Mesocyclops leuckarti, largely adult by this time, and the spring generation of copepodites I-V of C. str. abyssorum were present, both species being far more abundant above 15 metres than below this depth.

The total catches remained very constant, but, as mentioned above, there were exceptionally large numbers of C. str. abyssorum at 0-5 metres at 1230

TABLE 31

Numbers of Cladocera caught on 11-12.5.64

Depth (m.)	Time 1230	1700	2100	2400	0500	0900
Daphnia hyalina						
0-5	96	40	60	152	27	28
5-10	48	48	57	18	36	30
10-15	19	30	16	-	42	30
15-20	15	15	12	12	18	13
20-30	30	26	13	26	13	14
30-42	16	10	16	-	12	6
Total Nbr.	224	169	174	208	148	121
Bosmina coregoni						
0-5	456	240	300	1159	243	210
5-10	240	192	399	486	702	90
10-15	475	450	224	546	630	165
15-20	540	810	276	360	324	221
20-30	870	715	585	416	156	570
30-42	336	510	352	150	108	338
Total Nbr.	2917	2917	2136	3117	2163	1594

hours. The diurnal changes in the numbers in each depth range are very slight in both species, but they suggest a similar pattern to that postulated in D. gracilis although, even more than in this species, the details will have been blurred by the concentration of so much of the populations in the upper 15 metres.

Cladocera (Table 31).

Daphnia were not very abundant at this time. Most of them were found in the upper 10-15 metres. They also showed a surface concentration at noon, followed by a sinking and then by a rise again during the evening so that by midnight almost all of the animals found in the upper 15 metres during the day were at 0-5 metres. The daytime distribution had been re-established by 0500 hours.

The numbers of Bosmina were rather variable and were particularly low at 0900 hours. The results probably indicate a similar pattern of movement to that of D. gracilis.

Discussion

There are few general comments that can be made about these results, as they clearly require amplification. The seasonal differences in the general pattern of distribution throughout the water column will be more fully discussed in the next section. So far as the diurnal changes in the distribution are concerned it may be said that there appears to be some evidence that the behaviour of the animals differs according to their day depth. It was a characteristic feature of the results that there was a distinctive fluctuation in the numbers of animals in the upper 5 metres, rather more being caught there around noon than during the darkest hours of the night. These fluctuations were often related to changes in the total number of animals caught and it was suggested that if the same population was being sampled and if the sampling techniques could be accepted as having a high degree of accuracy then the 'disappearance' of some of the animals during the night and their reappearance during the day could be explained by assuming that they were not caught because they were at the position where the net was closed at the end of the 5-10 metres sample. The 'losses' were of the order of a few hundred animals only and were not beyond the possible sampling variation but it would be rather a coincidence for the same sequence of events to occur more than once. However, it is only very tentatively suggested that the animals in the surface layers, the upper 5 metres or so, may show a diurnal pattern of movement in which they rise somewhat nearer to the actual surface towards noon, possibly sink a little during the afternoon before again rising in the early evening, and that they are once more deeper later in the night. The amplitude of this movement may be of the order of a metre or less, and much more detailed sampling would be required to clearly demonstrate the presence of such a migration.

Diurnal movements of this kind have been described by Grainger (1957) from Gougenabarra Lake, a shallow lake lying, like Loch Lomond, in a peaty catchment area, and with water that was 'slightly brown in colour'. The samples were taken in 30 feet depth of water (5 metres). The water column could be divided into two regions:- 0-25' and 25-30'. Most species were found largely in the upper layer and usually in the upper 15' of it in the daytime, but during the night most of the population of *Diaptomus laticeps*, part of the *Daphnia longispina* and *Polyphemus pediculus* populations, and possibly some of the adult *Bosmina coregoni* sank into the deeper layer. Grainger suggested that the absence of a thermocline and the shallowness of the lake may have been of some significance. It would seem possible that the diminution of numbers in the upper 5 metres or so during the night found on two occasions in the humic L. Krasavitska (Secchi transparency 2 metres) by Ivanova (1963) and attributed by him to horizontal migration may have been due to a similar phenomenon. He implies that the migration was an active movement by the animals, on the first occasion to escape from a violent thunderstorm in the evening (when local inhomogeneities could well be caused by the associated turbulence without the active participation of the animals, a possibility which does not seem to have occurred to him), and on the second occasion because of the supposed nightly cooling of the epilimnion, although he previously stated that temperatures remained almost constant. Certain authors (e.g. Ruttner 1930, Rybak 1960) have suggested that a horizontal migration of pelagic animals to and from the shore does occur, basing this belief on the increases in the numbers of animals in the littoral region at night. A rather more rigorous proof of the existence of such a migration, whose mechanism remains obscure, is required, as the effects of currents (however small scale) and of local physiographic conditions do not appear to have been very carefully considered. It may be said than, that whilst in neither the Loch Lomond or the L. Krasavitska results can the possibilities of random temporary dispersal of the surface populations by wind or current action, or indeed even of horizontal migration be ruled out, yet in view of Grainger's description of reversed diurnal fluctuations in the surface layers the possibility of similar behaviour would appear to be rather stronger, although the details have been obscured by inadequate sampling techniques and particularly by the use of too long a vertical sampling range.

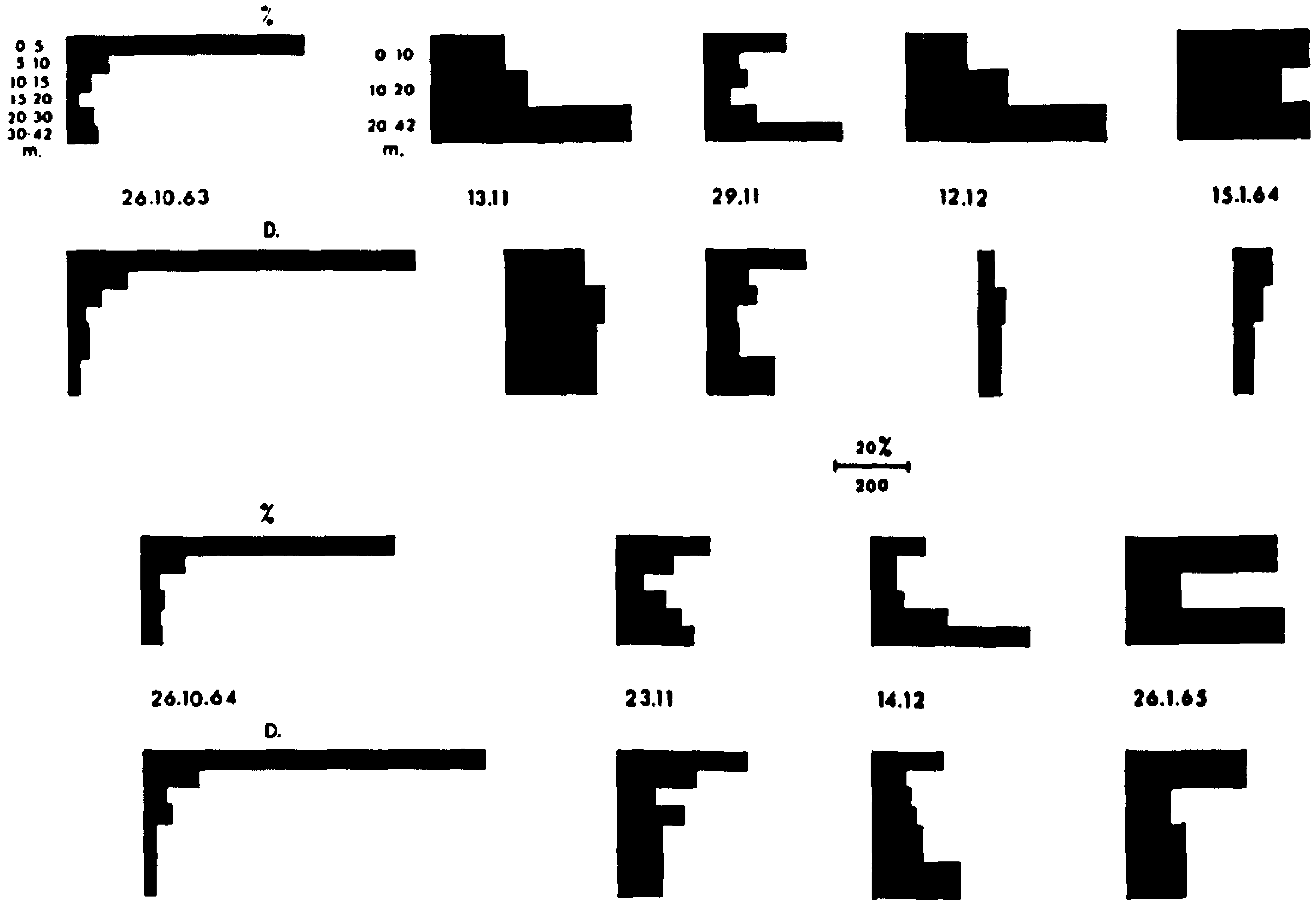
On the other hand, in September and in May a more typical pattern of movement upwards during the evening followed by a sinking during the morning was demonstrated in the animals found in the lower depths. No indication of such migration was found in November or in March. This may have been because the amplitude of any movement was too slight to be detected or because the penetration of light was too poor (either because of high turbidities on those particular dates, or due to seasonal differences (Hutchinson 1957) in the light intensities and their diurnal changes) to stimulate any movement. The only conclusion that can be drawn is that a great deal more needs to be known not only about the behaviour of the animals themselves but also about the precise light conditions in different depths of the loch. The work of Siebeck (1960) on the effects of rates of change of light of different intensities on the animals and of Schröder (1959, 1962a) on the effect of the spectral composition of the light, all factors which will vary both with depth and season, may be cited as evidence of the complexities to be taken into account.

(c) VERTICAL DISTRIBUTION

This section is concerned with the depths at which the maximum concentrations of the various species were found during the daytime, and the degree of aggregation into this depth which the population as a whole showed. It must be emphasised that it is the general picture which is considered here. There is no absolute constancy from day to day or from place to place and therefore a particular distribution pattern can only be regarded as typical if it is repeated over a reasonable period of time, and if the same trends are shown at more than one station. A further difficulty arises over the best method of presentation of the results. Strictly speaking they should be expressed in terms of the numbers per metres of vertical haul of the net to avoid confusion due to the use in sampling of depth ranges of unequal length. It is more convenient to use percentages to compare populations of different sizes, however, and this has been done. In assessing the results it must be remembered that the samples from the lower depths were taken through twice the distance and hence figures from them should be halved for comparison with the upper samples. This is emphasised in fig. 26 where both percentages and densities have been graphed. Finally, it should be pointed out that the choice of the depth ranges in sampling was arbitrary and if the numbers per metre were studied a rather different picture might emerge. Thus, it was frequently found that much greater numbers were at 0-5 metres than at 5-10 metres, but it may well be that the animals in the latter sample were mainly from say 5-7 metres and that the true maximum lay between perhaps 3-7 metres. This difficulty is unavoidable and statements about the depth preferences of the animals can only be made in a very generalised sense.

Fig. 26: Autumn distribution patterns of the _D. gracilis_ population.

D = density per metre of haul.


%
0 5
5 10
10 15
15 20
20 30
30-42
m.
0 10
10 20
20 42
m.
26.10.63
13.11
29.11
12.12
15.1.64
D.
20%
200
%
26.10.64
23.11
14.12
26.1.65
D.

DIAPTOMUS GRACILIS (App. Table 16 , fig. 27).

It is convenient to begin by considering the distribution of the overwintering generation in late autumn (Table 32 , fig. 26). The population at this time consisted largely of the overwintering generation of adults, with a small number of late copepodites.

In both 1963 and 1964 a distinct change in the vertical distribution occurred at the time of the overturn in November (Table 32, fig. 26). Prior to this the animals were largely in the surface layers and their density rapidly decreased with depth (e.g. 26.10.63 and 26.10.64). As the loch approached homothermy the animals became more evenly distributed throughout the water column, although a markedly higher aggregation in the upper 5 metres still remained (e.g. 23.11.64), and finally a bimodal distribution developed with concentrations in the surface and bottom layers (14.12.64, 29.11.63). The results of the 24 hour series of samples on 29.11.63, where there was a considerable and erratic variation in the numbers caught in the 30-42 metres hauls (Table 23), suggest that the animals were accumulated immediately above the bottom and hence

TABLE 32

Autumn and Winter Vertical Distribution of D. gracilis

(The figures in brackets are the densities per metre of vertical haul).

	Numbers in Each Depth Range						
	0-10		10-20		20-42		
	0-5 m.	5-10 m.	10-15 m.	15-20 m.	20-30 m.	30-42 m.	Total
S.VI							
26.10.64	4674 (935)	760 (152)	294 (59)	374 (75)	315 (31)	345 (29)	6762
23.11.64	1770 (354)	1080 (216)	486 (97)	901 (180)	1232 (123)	1460 (122)	6929
14.12.64	986 (197)	435 (87)	493 (99)	567 (113)	1330 (133)	2898 (241)	6709
26.1.65	3277 (327)		1210 (121)		3454 (157)		7941
S.C$_1$							
26.10.64	2257		812		840		3909
23.11.64	1428		980		1060		3468
S.IV							
26.10.64	4692		1260		1364		7316
23.11.64	2079		1485		1716		5280
14.12.64	2552		1760		2403		6715
S.III							
26.10.64	2880		264		157		3301
14.12.64	1564		897		2010		4471
VI							
26.10.63	4746	792	448	225	540	324	
13.11.63	2070		2655		5402		
29.11.63	1350	555	672	400	840	2208	6025
12.12.63	414		688		1344		2446
15.1.64	1034		816		1240		

were not sampled adequately on every occasion.

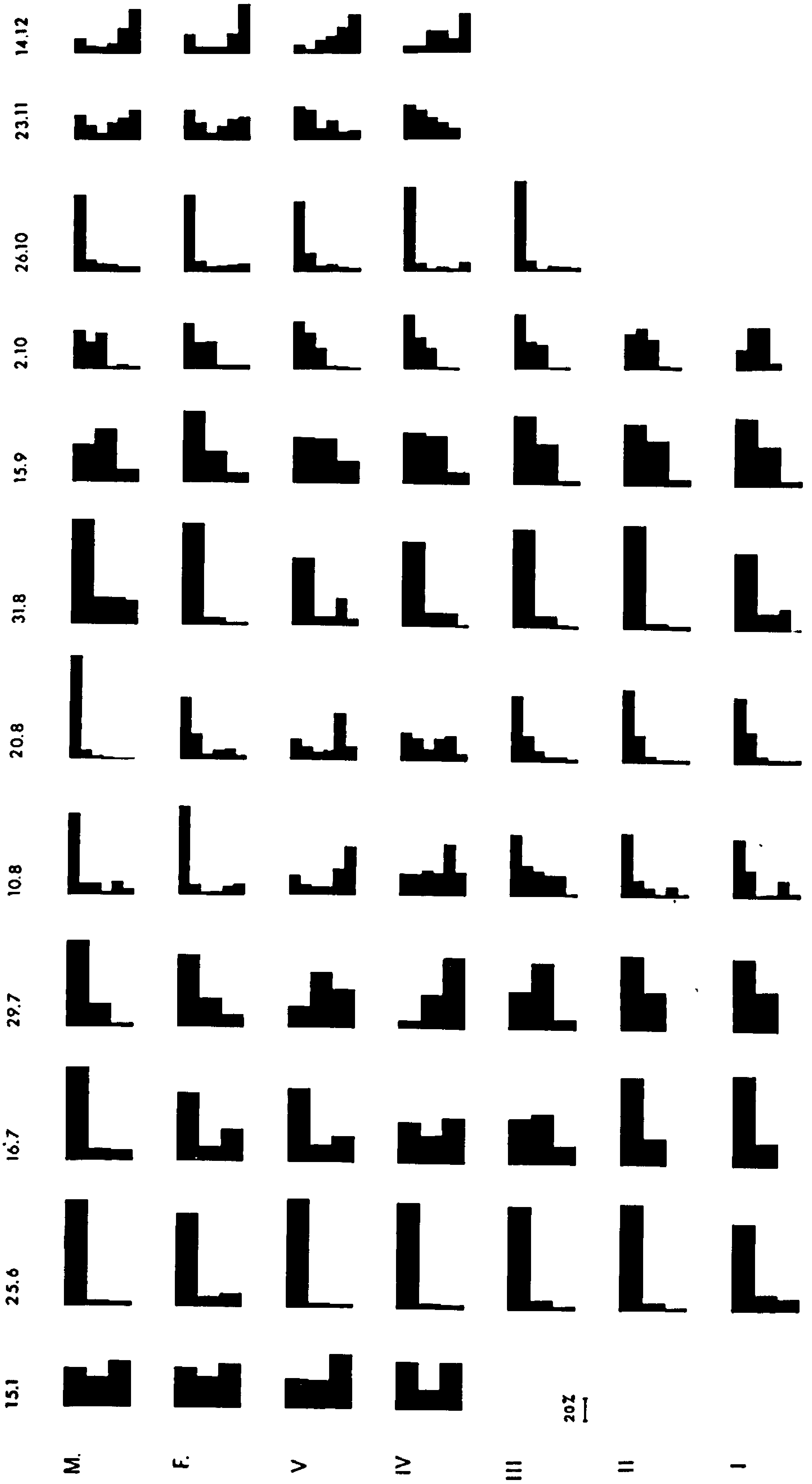
The same sequence of increasingly higher densities in the deeper levels is indicated in the less detailed samples taken from other stations in 1964, and C_1, S.III and S.IV all showed much greater densities below 20 metres in December than in October, although the pattern is not as clear as at S.VI because of the larger depth ranges sampled. The differences between the densities in the upper and lower depths are not as marked in these shallower stations as at S.VI and it is possible that some accumulation of the animals into the deeper hollows of the basin occurs.

It will be noticed that considerable differences existed between the total numbers found at each station during this period in 1964, but that there was very little variation in the number at any specific station. Thus, at S.VI just under 7000 animals were recorded on 3 consecutive occasions, whilst the first two samples at C_1 had somewhat under 4000 animals, and though numbers were higher in the next sample they were not greatly so. This consistency is somewhat surprising as at the time of the overturn water movement are more extensive and would be expected to lead to considerable and frequent changes in the horizontal distribution of the animals. The higher and similar numbers at the centrally placed S.VI and at S.IV on the leeward side for the prevailing northerly and westerly winds, as compared with the lower, and also similar to each other, numbers at C_1 and S.III, may be significant in this context. However, this relationship may be more apparent than real, since, for example, on 14.12.64 the difference between the total numbers at S.VI and at S.III is largely due to the smaller numbers in the bottom zone at the shallower S.III, whilst the similar numbers found at S.VI and S.IV are not reflected by a similar distribution in each depth zone.

Such a stability of the total numbers at a station was not found at S.VI in 1963, where they varied greatly during this time.

The bottom concentration had disappeared by January in both years, although there was still a higher fraction of the population in the lower depths than at other times of the year. During the next four months, in 1964, the distribution varied between the dispersed pattern of, for example, 15.1.64

Fig. 27: Seasonal variations in the vertical distribution of the stages of D. gracilis. (Depth ranges as in fig. 26).


14.12
23.11
26.10
2.10
15.9
31.8
20.8
10.8
29.7
16.7
25.6
15.1
20%
M.
F.
V
IV
III
II
I

and the highly surface-oriented one of, for example, 25.6.64 (fig. 27). The 24 hour series of May and March (figs.23 &24) are also examples of the two contrasting patterns. The dispersed pattern, in which rather less than 50% of the animals were in the upper layers, was more frequent.

In further discussion it is best to consider each stage separately.

Adults.

The distribution of the overwintering adults is covered above. In the summer generations, i.e. the adults found from June until September, a high proportion are found in the upper 10 metres, generally 70-80%, with a very marked decline in numbers with depth (fig. 27). During September and October the adults became more dispersed throughout the water column as the late autumn reverse distribution described above developed.

It was noticeable that during the time of active breeding (Feb.-Sept.) there was a higher percentage of the male population in the upper layers (varying from 1½% to 36½%) than that of the females. As a typical example the figures from S.VI on 25.6.64 may be quoted:

Depth (m.)	♂♂		♀♀	
	Nbr.	%	Nbr.	%
0-10	976	94	846	81
10-20	31	3	74	7
20-42	26	2	117	11
Total Nbr.	1033	100	1037	100

From September until the end of the year the situation was reversed and a very slightly higher percentage of the females was found consistently in the upper layers.

The vertical distribution of the egg bearing females was similar to that of the female population as a whole (App. Table 17), although the percentage of egg bearing animals was often different in the separate depth ranges.

Copepodites.

Of the copepodite stages, the I-IIIs were present in significant numbers from May until October only. The highest percentages of I-IIs (generally over 70%) were found in the upper 10 metres, but some were always found in the lower depths, except at times when their total numbers were so low that their presence could be overlooked. There was a fairly consistent tendency for a slightly smaller percentage of the Is in the upper layers, as for example on 11.6.64 at S.VI:

Depth	Percentage	
	I	II
0-10m.	86	93
10-20m.	12	6
20-42m.	2	1
Total Nbr.	329	559

In May and early October there was a more even dispersion of these stages through the water column; as also on 29th July, which was exceptional for the summer period. The May figures are given for comparison with the June ones; they again show the small differences between the stages:

Depth	Percentage	
	I	II
0-5m.	26	33
5-10m.	11	19
10-15m.	19	22
15-20m.	13	12
20-30m.	18	7
30-42m.	11	6
Total Nbr.	753	603

The distribution of the IIIs was very similar to that of the youngest stages, with a high proportion in the upper 10 metres during the summer period, except in July when increased percentages were found at 10-20 metres. The finding of the maximum at this depth at two of the four stations sampled on 16.7.64 has already been referred to, and the percentage in the surface layers at the other two stations was very much lower than those of the Is and IIs. On 29.7.64 the maximum percentage was again at 10-20 metres at both the stations sampled. After this date, however, there was little difference in the distribution patterns of the three young stages.

In the early part of the year the distribution of stages IV and V was similar to that of the adults. In July, however, a marked difference began to develop, and from then until October a much smaller percentage of these stages was found in the upper 10 metres, as compared with that of the adults and younger copepodites. This shift away from the surface was first shown by the IVs. On 16.7.64 most of them were still in the upper 10 metres, but the greatest percentage there at any station was 53%, as against over 60% of the other stages (with the exception of the IIIs at two stations), and in contrast to over 90% of the IVs at 0-10 metres in the June samples. Below 10 metres the density of the IVs was the same or slightly greater at 20-bottom as at 10-20 metres, which again differs from the other stages, and also from the June pattern with a sharp decline in numbers with depth. By the end of July and in early August the maximum density is found below 20 metres (at 20-30 metres at S.VI on 10.8.64) and the numbers were least at 0-10 metres. There was again a surface maximum at 0-5 metres on 20.8.64, but there were still high densities at the lower depths (15-20 metres at S.VI and 20-30 metres at S.I). The lower concentration was lost after this time and from the end of August until the end of October there was the usual rapid decline in density with depth, with generally over 70% of the animals in the upper 10 metres.

The stage Vs showed a similar bottom accumulation during this time but it developed slightly later and persisted longer than that of the IVs. Thus on 16.7.64 the typical distribution pattern of a sharp decline in numbers below 10 metres was found, but on 29.7.64 the maximum was between 10 and 20 metres, and throughout August it was below 20 metres (30-42 metres at S.VI on 10.8.64, 20-30 metres at S.VI and S.I on 20.8.64). On 31.8.64 the maximum was at 20-30 metres at S.IV, 10-20 metres at S.II, and at 0-10 metres at S.VI, where, however, the total numbers of Vs were very much greater and there was a secondary maximum at 20-30 metres also. By September most of the animals were once more at 0-10 metres, although at S.IV there were still more below 20 metres than at 10-20 metres.

The numbers of IVs and Vs fell after September, as they matured into the overwintering adults, but those that remained showed the same early winter accumulation in the bottom levels as did the adults.

Discussion.

The interpretation of these results offers considerable scope for speculation, and the need becomes very apparent for a bridging of the gap between the studies of the diurnal changes in the position of the absolute maximum in population density, with which the extensive literature on vertical distribution is almost exclusively concerned, and the diurnal and seasonal changes in the spread of the population around this maximum.

Without attempting to go into any detail, particularly over the mechanisms controlling vertical distribution (see review by Bainbridge 1961), the results may be examined firstly with regard to the physical factors which may be involved in controlling the vertical distribution of the animals, and secondly, to the biological factors.

Considering the patterns of distribution as a whole, it will be noticed that a maximum was almost always found in the upper 10 metres, or more specifically, in the upper 5 metres. The only notable exceptions to this were the IVs and Vs during the summer. Even in November, when the greatest numbers were in the deeper layers, there was still a significant aggregation at 0-5 metres. As the vertical distribution is generally regarded as being primarily controlled by the intensity of light (Bainbridge loc. cit.), it can be accepted that for *D. gracilis* the optimum conditions of illumination lie close to the surface. Comparable situations have been reported from a number of other lakes, which also lie in peaty catchment areas and are of low transparency, e.g. Gougenabarra Lake in Ireland (Grainger 1957,) Lohjanjarvi in Finland (Jarnefelt 1958), and the

Lunzer lakes (Ruttner 1939, Siebeck 1960a) and the Schluchsee (Schröder 1959) in Austria. By contrast in the clear waters of the Vierwaldstattersee D. gracilis was almost absent from the upper 10 metres during the day in midsummer and the midday maximum lay at about 20 metres depth, (Worthington 1931).

We are not, however, concerned with the precise placing of the daytime maximum, but rather with the varying degrees of aggregation into these surface layers.

The vertical distribution arising as a result of specific light conditions could become altered as a result of a mixing of the waters, and hence of the plankton, through wind action, turbulence etc. (e.g. Lindstrom 1951). Such mixing will be more extensive and far-reaching in its consequences when the loch is not stratified, and the random alternations between a highly surface oriented distribution and one with a more dispersed distribution in the earlier months of the year, before stratification developed, may be regarded as examples. At no other time were there such striking alternations in the distribution patterns. During stratification wind induced mixing within the epilimnion could also be expected to disrupt the pattern, and it may be that the surprisingly large percentage of, for example, adults at 10-20 metres on 29.7.64 (20-36% as compared with 5-15% in mid-July and August) was due to this cause.

On the other hand, the more dispersed distribution found between October and May could perhaps be related to seasonal differences in light intensity and/or penetration. The possibility of such differences was suggested in the discussion on migration because of the apparent absence of diurnal migratory movement by the animals in the deep layers in the 'darker' months, November and March. If this is the case, then the less frequently occurring surface oriented distributions found during this period must be explained as the result of water movements.

It is not a safe assumption that the presence of the animals below the 'optimal' zone is fortuitous. It may well represent a definite difference in the behaviour of the animals and the distribution of the IVs and Vs in the summer provide a good example of this. The explanation probably lies in the development cycle of the animals. It will be remembered that from July until the end of September the rate of growth of the animals had been greatly slowed down, and further, that it was during this time that the bulk of the population matured from stage III in July to adults in October. It seems unlikely that the finding of greater numbers of IIIs below 10 metres in July, of IVs in late July and most of August, and of Vs in August and September, a sequence which follows that of the development of the copepodites (fig. 9) can be due to coincidence, particularly as the same changes are not shown by the other stages, as would be expected if they were the result of some seasonal change in the physical conditions of the environment. It may be that the light responses at any time vary according to the precise state of development within a stage, as they are known to do in other Crustacea (Waterman 1960). In a population developing at normal rates individual differences in behaviour would not be easily detected, but where development has become slowed down, as it was at this time in the loch, they could well become more obvious, since so many copepodites are simultaneously in the same stage for a relatively long time. In this context it is interesting that Nicholls (1933) suggested a similar mechanism to account for the existence of a small migratory population of stage V copepodites of *Calanus finmarchicus* in July in the Clyde, at a time when most of the Vs remained below a depth of 100 metres day and night. He postulated that the migratory animals might be those which had either just moulted from stage IV or were about to become adult, since both of those stages showed a well marked diurnal migration at that time.

The autumnal bottom concentration naturally invites comparison with the same phenomenon in *M. leuckarti*. In *D. gracilis* it is found just at the time when full circulation is completely restored, whereas in the cyclopoid it occurs prior to this, before the breakup of stratification is completed. Thus, in 1964, the aggregation was present at the end of October (fig. 14), when *D. gracilis* still showed a strongly surface-oriented distribution. In *M. leuckarti* the descent can be regarded as a distinct biological phenomenon; it is associated with definite physiological changes in the animals, notably the complete cessation of growth, and it occurs as a preliminary to entry into the bottom deposits in a state of dormancy (Smyly 1961). There is no indication that any of the *D. gracilis* overwinter in this way, and although dormancy, often with encystment, in mud is widespread in the cyclopoids, it is not known in any calanoid species (Elgmork 1964). The reversed distribution of D. gracilis is probably best regarded as a temporary phenomenon brought about by the extensive water mixing of the water at the time of the overturn. On the other hand, a closer parallel with M. leuckarti could be drawn. It will be remembered that the overwintering generation of adults with which we are dealing were just coming to maturity in October and November (fig. 4), and that they did not begin to breed until late January and February. The alteration in the vertical distribution and the return to the more typical pattern thus coincide respectively with the pause in, and the resumption of, full sexual activity. This delay in egg production is more likely to be the result of the effects of low temperatures and sparse phytoplankton rather than indicative of a definite physiological change in the animals. Nevertheless, this possibility cannot be ruled out at present. The changes in the vertical distribution could indicate physiological changes in the animals, equivalent to the true dormancy of M. leuckarti, which could be brought about by the falling temperatures, low food levels and decreasing intensity and duration of light, and terminated by the increased light and greater availability of food in the new year.

It is unfortunate that biological and physical events coincide so closely, as it is of course the same individuals which as late copepodites in summer and as young adults in late autumn show the same tendency to prefer the lower depths. However, I believe that this is a coincidence which may be accepted as such, since the most likely explanation of this behaviour is that it is due to external circumstances - in the case of the copepodites that a normally brief phase in the moult cycle has become emphasised by the prolonged development in unfavourable conditions, and in the case of the adults, that it is the result of the overturn.

Returning to more concrete aspects of the vertical distribution it will be apparent that, as a result of the interaction between the differences in the vertical spread, and the numbers present, of each stage, a considerable difference can exist between the composition of the total population in each depth range. For example, on 27.4.64 the vertical

TABLE 33

D. gracilis at S.VI on 27.4.64

	Depth (m.)	% distribution of each stage I	II-V	♀	♂
a.	0-10	90	99	80	93
	10-20	9	1	7	4
	20-42	1	-	13	3
	Total Nbr.	168	143	1102	771

	Depth (m.)	Total Nbr.	% composition of population at each depth. I	II-V	♀	♂
b.	0-10	1894	8	7½	46½	38
	10-20	126	12½	1	61½	25
	20-42	169	1½	-	86	12½
	% composition of the entire population.	2189	7½	6½	50½	35½

TABLE 34

D. gracilis at S.IV on 31.8.64

	Depth (m.)	% distribution of each stage I	II	III	IV	V	♀	♂
a.	0-10	90	87	85½	63	22½	88	100
	10-20	10	3	12	23	19½	11	-
	20-32	-	10	2½	14	58	1	-
	Total Nbr.	86	244	601	922	1037	587	101

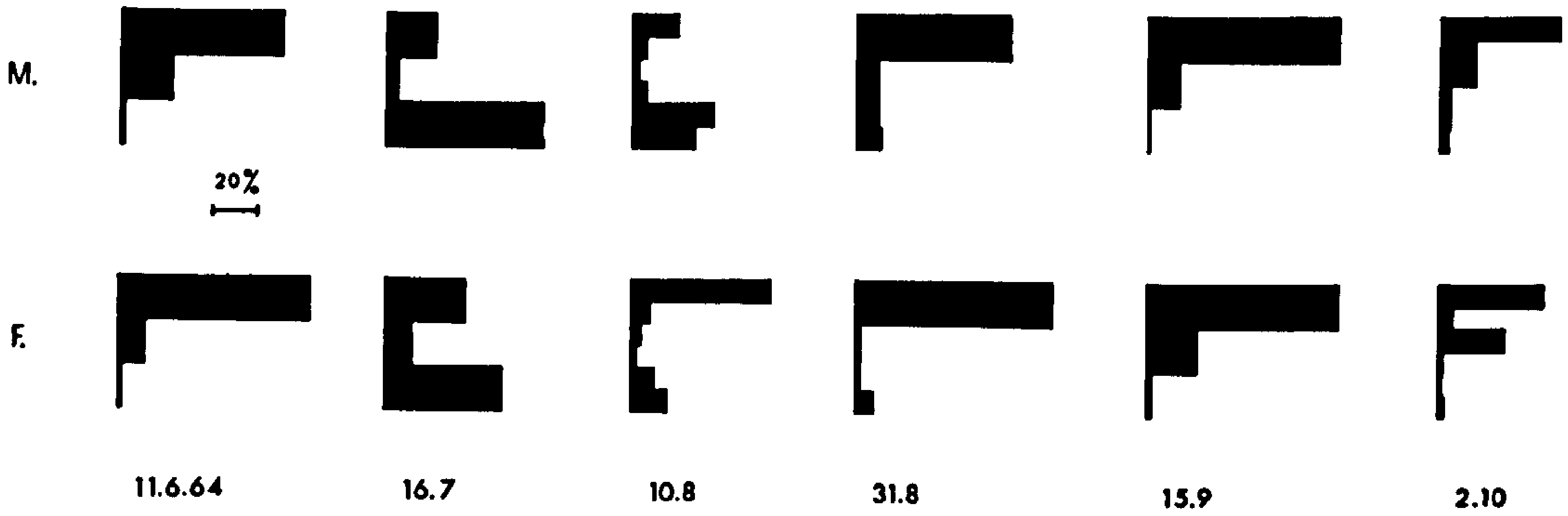
	Depth (m.)	Total Nbr.	% composition of population at each depth. I	II	III	IV	V	♀	♂
b.	0-10	2240	3½	9½	23	26	10½	23	4½
	10-20	570	1½	1½	12½	37½	35½	11½	-
	20-32	770	-	3	2	17	79	1	
	% composition of the entire population.	3578	2½	7	16½	25½	29	16½	3

distribution of the copepodites and of the adults at S. VI was very similar (Table 33a), but because the adults greatly outnumbered the juveniles the composition of the total population in each depth range was very different (Table 33b). When the vertical distribution of the various stages is different the variations become even more apparent, as for example on 31.8.64 (Table 34).

The necessity for ensuring an absolutely equal representation of the animals from each depth when sampling in order to follow accurately the course of the life cycle will be obvious. The value of a knowledge of the life cycle in order to interpret the vertical distribution should also be emphasised.

Fig. 28: Seasonal variations in the vertical distribution of males (M.) and females (F) of C. str. abyssorum. (Depth ranges as in fig. 26).

C.s.a.



CYCLOPS STRENUUS ABYSSORUM (App. Table 18).

The data on this and the next species are not extensive as relatively few samples were analysed in detail.

The young copepodites were always found largely in the surface layers, as were the adults at first, (e.g. 11.6.64, fig. 28). In July and early August, however, the latter were present in much greater numbers in the lower depths, and a bimodal distribution was found on 16.7.64 and 10.8.64, with the males on both dates being most abundant below 20 metres, whilst the bottom concentration was much less well developed amongst the females. In August the Vs also showed somewhat higher numbers at 30-42 metres than in the intermediate depths. By the end of August the distribution had reverted to the typical surface-oriented one, and remained so as the population declined in autumn.

These changes may be related, in the adults, to the deposition of resting eggs, prior to death; or there may be a connection with the changes shown by their possible prey, the late copepodites of D. gracilis, during this period.

MESOCYCLOPS LEUCKARTI (App. Table 19).

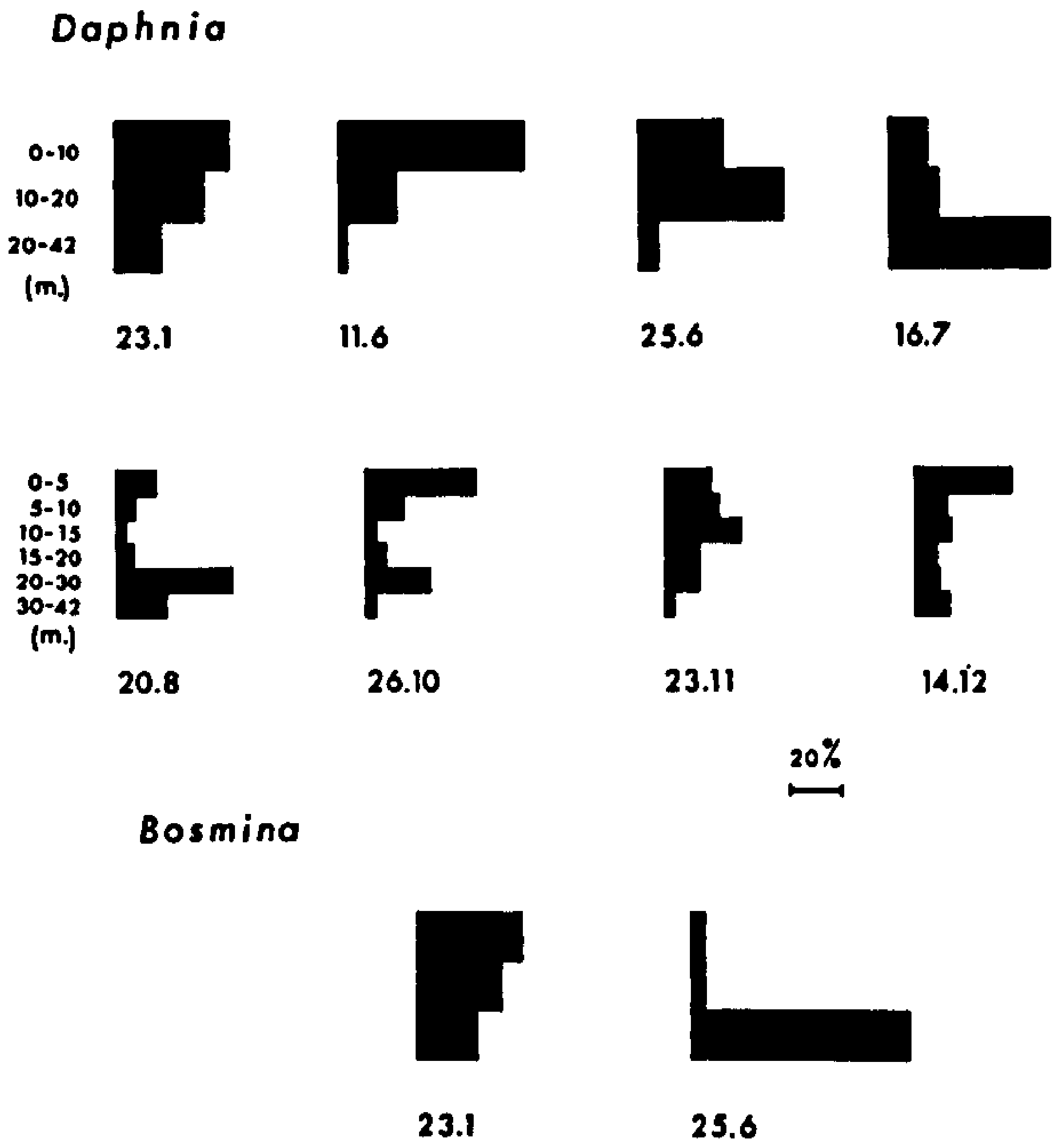
The very distinctive seasonal change shown by this species in autumn has already been discussed. There is some indication in the summer distribution patterns that throughout this period the copepodites may have been more dispersed through the water column than were the adults. More extensive data is required to assess the validity of this, however, particularly in early summer. Certainly in August when over 80% of the adults were in the upper layers, the maximum numbers of copepodites III-V lay between 10 and 20 metres, although these animals may have been beginning their descent by this time.

DAPHNIA HYALINA var. LACUSTRIS (App. Table 20, Fig. 29).

During the first part of the year the maximum numbers were in the upper 10 metres, where generally 40-50% of the population was found, and the minimum was in the bottom layers, although the disparity between the numbers in each depth range was of variable extent. Between the end of April and June the surface maximum was very pronounced with about 70% of the population in it but at the end of June increasing numbers were found at 10-20 metres, and from July until October the maximum was in the bottom

Fig. 29: Seasonal variations in the vertical distribution of *Daphnia* and *Bosmina*.

(Depth ranges as in fig. 26).


Daphnia
0-10
10-20
20-42
(m.)
23.1
11.6
25.6
16.7
0-5
5-10
10-15
15-20
20-30
30-42
(m.)
20.8
26.10
23.11
14.12
20%
Bosmina
23.1
25.6

layers, always at 20-30 metres in the more detailed samples. Unlike the copepods there was often not a great difference between the numbers at 0-5 metres and at the intermediate depths.

By the end of October the maximum was again at 0-10 metres, but even in November secondary deep maxima could be found at S.VI - at 20-30 metres on 26.10.64 and 5.11.64, and at 10-15 metres on 23.11.64. In general, however, the distribution patterns during this time were similar to those found in the first months of the year. In the last sample taken in January 1965 there was a strong surface maximum.

Essentially similar results were found in 1963, although the deep concentration was not found until the end of August and was not so distinctive.

<u>BOSMINA</u> <u>COREGONI</u> (App. Table 21, Fig. 29).

The vertical distribution of <u>Bosmina</u> followed a very similar seasonal course to that of <u>Daphnia</u>. During the winter and spring months there were generally more animals at 0-10 metres, with a more or less pronounced minimum in the bottom layers. From late spring until the beginning of winter the maximum density was found below 20 metres depth. This was shown particularly clearly in the 1963 results (May-December), when the population was greater than in 1964.

GENERAL DISCUSSION

Although the results of these studies in vertical distribution are inconclusive, certain postulates can be made. Concerning the effect of biological events on the vertical distribution, evidence was found in all the copepod species, in which the life cycle was known in some detail, of seasonal alterations in the patterns of vertical distribution which could be related to developmental events. This was very obvious in the copepodites of M. leuckarti in autumn, but similar relationships may be said to exist for the late copepodites of D. gracilis in summer, and also for the adults of C. s. abyssorum at that time. The small differences in distribution between each sex in the adults of these species can also be said to come under this heading.

There are scattered references throughout the literature to the possible effect on migratory behaviour (which is only one aspect of vertical distribution) of the physiological condition of the individual animals (e.g. Michael 1911, Clarke 1930, Siebeck 1960). There is also evidence that there are seasonal differences in respiration (Comita 1964, Raymont 1963), which may affect the activity of the animals and therefore their ability to react to stimuli, and Schröder (1962a) noted differences in the light responses of animals from spring and autumn generations.

Seasonal differences in the vertical distribution and in migratory behaviour are well known in marine organisms (reviewed in Raymont 1963) and have been lucidly summarised for Calanus finmarchicus by Marshall & Orr (1955). The changes vary according to both the developmental cycle and the latitude, suggesting that there is a complex relationship between biological and physical factors. Such 'ontogenetic' migrations do not appear to have been described by freshwater workers, who have in general paid little attention to comparative studies of vertical distribution.

Regarding the distribution patterns in more general terms differences are found between the species and in particular between the Cladocera and the Copepoda. These show seasonal changes which are the reverse of each other. During the summer months the Cladocera had a deep maximum in the region of the thermocline, whereas the Copepoda, with the specific exceptions mentioned above, had their maximum in the surface layers. It is not known to what extent these differences are related to the developmental cycle of the

Cladocera but the very pronounced diurnal migration of the Daphnia in September suggests that it is due to differences in the response to the gradients in illumination or other physico-chemical gradients, rather than to developmental events.

Herbst (1961) has suggested that the vertical distribution can be related to the food supply, having found in studies on a variety of lakes that patterns of distribution could be distinguished which were characteristic of the trophic status of the habitat. In the eutrophic lakes there was a small surface maximum during the summer, confined to the epilimnion, and a pronounced maximum at the bottom in late spring but rising to the metalimnion at the height of the stagnation period. In the oligotrophic lakes he found a uniform distribution at the overturn, and with the inverse stratification of winter there was a weak maximum at the bottom, followed by a big maximum at the surface during the spring. This gradually spread downwards as the summer advanced.

In the only one of his papers available to me (Herbst 1955) the results could be criticised as having been presented in too generalised a fashion, being expressed largely in terms of the broad taxonomic groupings of Cladocera, Copepoda etc., without any consideration of biological cycles of the various species. Nevertheless, it is an interesting view, although lacking in a consideration of the relationship of the patterns found to differences in transparency.

Herbst's approach was made in terms of the distribution of food but the work of Schröder (1962a & b) suggests that the more fundamental relationship may be with the physico-chemical conditions of the environment. His work on the distribution of the animals within the thermocline led him to postulate two orientation mechanisms, one related to the light gradient and the other to the gradients in gas tension. There are then, a multiplicity of stimuli which can affect the animals and their orientation behaviour will depend on the totality of factors operating at any particular depth'. He concluded that Cladocera seemed to determine their day depth preponderantly by optical factors, copepods by chemical and physical factors.

One can only conclude by repeating his exhortation to 'further, better, experiments', and add to this a plea for a greater consideration of the specific stages in the developmental cycle of the animals when studying behaviour both in the field and in the laboratory.

CONCLUSION

and

SUMMARY

CONCLUSION

This work was not designed primarily as a study of the trophic condition of the loch, and attention was principally directed on the population dynamics of the various species, but it may be noted that the analyses of the seasonal cycles of the zooplankton bear out the conclusions of other workers (Weerekoon 1953, Slack et al. 1957, Fedoruk 1964) regarding its oligotrophic status. Such factors as the limited Cladoceran fauna, the low rate of turnover of the Diaptomus gracilis population, its greatly retarded development in summer and the lack of any autumn breeding increase in this species, and the absence of Cyclops strenuus abyssorum in winter, are all indicative of the generally low level of productivity in the loch.

The complexity of the interaction of the various environmental factors which affect the animals, and the complexity of their resulting behaviour have been emphasised in the analyses of the temporal and spatial distribution of the plankton. No synthesis of the work will be attempted, but it may be noted in conclusion that they indicate a need for further attention to two aspects in particular.

Firstly there is a need for a more quantitative expression of the results in terms of the production of organic matter, and for a more precise defining of the channels through which this matter flows in the ecosystem. Such a study required an accurate knowledge of the life cycles and inter-relationships of the animals, and it is hoped that the foundations for this have been laid in the present work. It also depends ultimately on the physiological events affecting the growth and development of the animals and the accompanying changes in their behaviour. Thus, attention must be focussed not only on the populations in toto but also on the individual animal. The second aspect, then, lies in the physiological ecology of the animals. They live in a constantly varying environment and their behaviour will be the resultant of the effects of many single factors, but until these factors have been studied, singly and in combination, under precise experimental conditions no satisfactory understanding of the ecology of the animals can be gained.

It is hoped to make a closer study of these aspects in future work.

SUMMARY

1. The physiography and hydrography of Loch Lomond are briefly outlined. Studies of the zooplankton were made in Strathcashel basin.

2. The basin was thermally stratified between June and November, maximum temperatures being found in July and August, and the minima in February and March.

3. The results of some estimations of chlorophyll concentrations are presented.

4. The annual cycles of the Entomostracan zooplankton in the basin are discussed, those of the copepods being considered in greater detail.

5. The numerically dominant zooplankter was *Diaptomus gracilis* Sars. Use was made of a biometric analysis of the adult females, fluctuations in the clutch size, and changes in the composition of the copepodite population to interpret the annual cycle.

6. *D. gracilis* overwintered largely as adults which started to breed in February. Some of these animals survived until June and had an adult longevity of 5-8 months. They could produce up to 5 or 6 clutches each during the spring, the clutch size steadily increasing.

7. Young copepodites were found in April and development was initially fast, many new adults maturing in

late spring and early summer. These animals could survive for up to 2 months. The maximum lengths for females, and also maximum clutch size, were found in early June but these parameters rapidly decreased thereafter.

8. Growth was greatly retarded by a food shortage after mid-June, and it was possible to follow the development of the copepodites from stage III at this time until they matured in October to form the new overwintering generation.

9. The relationship between age and clutch size in the summer adults was discussed and the same changes were shown to occur simultaneously in animals which had matured at different times. Considerable differences between the clutches of the summer and overwintering females were found in June, however.

10. The relationship between the numbers of eggs produced and the number of resulting adults was discussed, the percentage surviving varying from 16% in the spring to 4% in the summer. Little of this production was of direct importance in the maintenance of the species from year to year.

11. The annual cycle in Loch Lomond was briefly compared with those found in other habitats. The need for more detailed analysis of field data was emphasised.

12. In Mesocyclops leuckarti (Claus) development was confined to the spring and summer months. Breeding started in late spring and the first generation came to maturity in early summer. The animals of the second generation did not develop beyond the last copepodite stage, many remaining in the fourth stage. At the time of the overturn there was a sudden decline in the size of the population, but a small number remained in the plankton over the winter. No further development occurred until the following April when they rapidly matured.

13. It is suggested that the major part of the population became dormant in the bottom deposits in autumn, as is known to occur in other temperate lakes.

14. Cyclops strenuus abyssorum Sars produced only a single generation per year, the first copepodites appearing in April. By mid-July the population consisted largely of adults, which died off in the autumn. Overwintering is believed to be by means of resting eggs.

15. Daphnia hyalina var. lacustris Sars was present throughout the year, the highest population densities being found in early summer and in autumn. During the summer the 'minnehaha' form was found.

16. Bosmina coregoni var. obtusirostris (Sars) was also perennial and was most abundant between autumn

and spring.

17. Leptodora kindtii (Focke) and Bythotrephes longimanus Leydig were present between April and November, but the sampling methods used were not adequate to define the size of the populations, which were small.

18. Possible competitive and predator-prey relationships are briefly discussed.

19. The oligotrophic condition of the loch found by workers on the bottom fauna is reflected in the annual cycles of the plankton also.

20. Diurnal vertical migration was examined in November, March, May and September. Movement into the surface layers at night by animals from the deeper layers was demonstrated only in the two latter series, but in all four there was some evidence of a separate diurnal cycle of movement, involving a sinking away from the surface during the night hours, and an upwards movement in daylight giving a surface maximum around noon, which was shown only by the animals in the upper 5-10 metres.

21. The seasonal changes in the vertical distribution of the animals are discussed and it is shown that they can be related to seasonal changes in environmental factors such as the thermal stratification and also to the developmental cycles of the animals.

22. A marked aggregation of D. gracilis was found in the upper 5 metres throughout the year and the maximum numbers of all stages were usually found in these surface layers, except briefly at the time of the overturn when the maxima were in the lower depths, as were those of the stage IV and V copepodites during the summer. The surface aggregation was usually less marked during the winter and spring.

23. The maximum concentration of C. str. abyssorum was found in the surface layers, although there was a deeper aggregation of adults in summer.

24. In M. leuckarti during the summer the copepodites tended to be more dispersed through the water column than were the adults. There was a pronounced accumulation of late copepodites immediately above the bottom just prior to the overturn. The overwintering population was dispersed through the water column.

25. The maxima of D. hyalina and B. coregoni were found below 20 metres depth during the summer, but in winter and spring they were most abundant in the surface layers.

26. Differences in the horizontal distribution of the zooplankton in the basin are discussed and the need for sampling over the widest possible area is emphasised. Differences in the vertical distribution

of the animals at different stations can arise because of their uneven horizontal distribution.

27. The need for closer attention to the physiological ecology of the animals in order to explain more adequately biological events in natural populations is emphasised.

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APPENDIX TABLES

TABLE 1

Conditions during Sampling

Date	Station	Time	Weather	Secchi Transparency (m.)
16.5.63	VI	11.45	Calm. Raining.	3
7.6.63	VI	14.15	Fine. Light variable wind.	5 1/3
8.6.63		10.45-15.15	Fine. Light variable wind.	-
24.6.63	VI	12.15	Calm. 7/10 cloud.	5½
28.6.63	VI	14.45	Fine. Light S. breeze.	-
5.7.63	SIII	14.00	Overcast. Slight S. wind.	5
	IV	15.00		
10.7.63	VI	12.15	Sunny. Light W. breeze.	4
	IV	15.30		
12-13.7.63	Off Inchmurrin	17.00-08.00	(Overnight series with J. D. Hamilton. Not discussed in text).	
16-17.7.63	Strathcashel Basin		(Overnight series with A. N. Fedoruk. Not discussed in text).	
21.8.63	VI	11.15	Cloudy, with sunny intervals. N.E. breeze.	-
22.8.63	III	15.00	Calm and misty.	5
27.8.63	VI	12.00	Strong N.W. wind. 7/10 cloud cover. Launch drifting at anchor.	5
5.9.63	VI	11.50	Strong N.W. wind. Overcast.	-
12.9.63	VI	12.45	Clear sunny day. Calm.	-
12-13.9.63	Inversnaid		(See App. Table	
23.9.63	VI	15.00	Calm. Overcast.	6
3.10.63	VI	11.15	Strong N.W. wind. 6/10 cloud.	4½
17.10.63	VI	11.00	Strong S.E. wind.	-
	IV	14.30		
26.10.63	VI	12.30	Fine. Calm.	4½
29.10.63	VI	11.50	Overcast. Occasional light S. breeze.	5½

Date	Station	Time	Weather	Secchi Transparency (m.)
7.11.63	Luss Basin	11.50	Slight occasional S. wind. 6/10 cloud. Sunny	5
13.11.63	VI	1300	Sunny intervals. Calm with occasional violent N.W. squalls.	3½
29-30.11.63	VI		(See App. Table	
12.12.63	VI	11.45	6/10 cloud cover. E-S.E. wind.	5½
15.1.64	VI	11.15	Overcast. Strong E-N.E. wind.	-
23.1.64	IV	11.45	Overcast with rain in afternoon.	6
	II	12.15	Strong S-S.E. wind.	
	VI	12.45		
6.2.64	IV	11.45	Overcast and drizzling. Slight S.	5½
	I	14.45	Breeze.	
11.2.64	VI	13.00	N.W. wind.	-
24.2.64	III	11.15	Overcast with rain in afternoon.	-
	VI	14.15	Strong E. wind.	
2-3.3.64	VI		(See App. Table	
23.3.64	IV	11.45	Overcast. N.E. breeze.	
	VI	13.15	(Preceded by several days of E. gales).	5½
	I	14.30		
	II	15.15		
3.4.64	VI	14.30	Fresh N.E. wind. 5/10 cloud cover.	-
10.4.64	Luss Basin		Slight S. breeze. Rain showers. Sunny. 5/10 cloud cover.	-
14.4.64	VI	14.30	Sunny. 4/10 cloud cover. Strong W-S.E. wind.	6
27.4.64	VI	14.00	Overcast but bright. Occasional rain showers. Calm.	4¾
11-12.5.64	VI		(See App. Table	
11.6.64	VI	13.45	S.W. wind. Clear and sunny.	4½

(Samples between 18.6.64 and 20.8.64 taken from dinghy whilst launch was being painted).

Date	Station	Time	Weather	Secchi Transparency (m.)
18.6.64	VI	14.00	Fine with flat calm.	5
25.6.64	VI	12.00	Variable light N-N.E. breeze.	$5\frac{3}{4}$
	IV	13.30	7/10 cloud cover.	
	III	14.15	S. breeze at S.III.	
16.7.64	VI	12.30	Light S. breeze. 4/10 cloud cover.	
	III	14.00	W. wind.	
	IV	14.30	W. wind.	
	II	15.15	S.W. breeze.	
29.7.64	III	15.15	Calm. Overcast and misty. Faint drizzle.	$5\frac{1}{2}$
	VI	16.00		
10.8.64	VI	12.45	Hot sun. Light variable S-S.E. breeze. 2/10 cloud cover.	$5\frac{1}{2}$
	Cl	13.45		
	BH	14.30		
	IV	15.15		
	III	16.00		
20.8.64	I	12.30	Rain at intervals. 7/10 cloud cover. S.W. wind.	
	VI	14.45	Brisk N. wind. Thunder.	$5\frac{1}{2}$
31.8.64	VI	12.00	Fine, calm, cloudless.	5
	II	13.45	Light S.E. breeze.	
	IV	14.30	Light S.E. breeze.	
1.9.64	III	15.10	Light S.E. breeze.	
15.9.64	VI	11.30	Calm, overcast.	
	IV	13.15		
2.10.64	VI	11.30	Moderate S.E. breeze.	$4\frac{1}{2}$
	II	14.30	Sunny. (Previous week had several days of strong S.W. wind).	
	IV	15.00	S. wind.	
8.10.64	VI	14.30	Gusty N-N.W. wind. 6/10 cloud cover.	-
26.10.64	Cl	11.30	Overcast. Light S-S.W. wind.	$6\frac{1}{2}$
	VI	12.30		7
	IV	13.45		$7\frac{1}{2}$
	III	13.15		7

Date	Station	Time	Weather	Secchi Transparency (m.)
5.11.64	Luss	13.30	Calm. Overcast, 10/10 cloud cover.	-
	VI	16.00		
23.11.64	C1	11.30	Overcast. 10/10 cloud cover. Moderate W. wind.	$5\frac{1}{2}$
	VI	12.00	Moderate-strong wind, veering to S.W.	
	IV	14.00	Light-moderate S.W. wind.	
	III	14.30	Light-moderate S.W. wind.	
	IV	15.00	Light-moderate S.W. wind.	
14.12.64	VI	12.00	Light S. breeze. 8/10 cloud cover.	$5\frac{1}{2}$
	IV	14.00		
	III	14.30		
	I	15.15		
26.1.65	I	13.00	Occasional rain flurries on sunny day. 5/10 cloud	-
	VI	14.30	cover. N. breeze.	
	III	15.00		
	C1	15.30	Strong N. wind. Impossible to stay at anchor.	
9.2.65	VI	14.00	Overcast. N. wind.	$5\frac{1}{4}$

TABLE 2

Numbers of *Diaptomus gracilis*

Date	Stn.	Numbers of each stage I	II	III	IV	V♀	V♂	♀	♂	Total
16.5.63	VI	64 4%	120 7½%	223 14%	89 5½%	63 4%	16 1%	512 32%	511 32%	1598
24.6.63	VI	68 3½%	72 4%	171 8½%	186 9½%	179 9%	189 9½%	618 31%	492 25%	1980
28.6.63	VI									2516
5.7.63	III									1406
10.7.63	VI	187 3½%	419 8½%	899 18½%	565 12%	327 6½%	326 6½%	1413 28½%	786 16%	4922
21.8.63	VI									3181
22.8.63	VI	18 ½%	516 9%	779 13%	1556 27%	301 5%	49 1%	1179 20½%	1397 24%	5795
27.8.63	VI									8243
12.9.63	VI	180 3%	383 6%	372 6%	1866 30%	1068 17%	920 14½%	745 12½%	687 11%	6227
23.9.63	VIa									5186
	b									5251
3.10.63	VI									8127
17.10.63	VI	6	205 1½%	1133 8%	2706 19½%	3665 26%	3682 26½%	1900 13½%	671 5%	13968
	IV									12477
26.10.63	VI									7075
29.10.63	III									6992
7.11.63	Luss									6268
13.11.63	VI	-	-	-	1108 11%	1389 13½%	1619 16%	4060 40%	1947 19½%	10127
29-30.11.63	VI	(See Table 23)								
12.12.63	VI	-	-	15 ½%	155 6½%	205 8½%	370 15%	845 34½%	850 35%	2440

Date	Stn.	Numbers of each stage								Total
		I	II	III	IV	V♀	V♂	♀	♂	
15.1.64	III									3669
	VIa									3030
	b	-	-	-	75	152	233	1338	1289	3087
23.1.64	IVa									2200
	b									3528
	VI									3160
January Mean		-	-	-	82	164	247	1432	1366	3293
					2½%	5%	7½%	43½%	41½%	
6.2.64	I	-	-	-	43	92	207	2589	2587	5520
	IV	-	-	-	44	86	182	1384	1080	2776
11.2.64	VI									3160
24.2.64	III	-	-	-	8	55	187	1437	1515	3202
	VI	-	-	-	22	60	95	1210	860	2247
February Mean		-	-	-	39	73	168	1655	1511	3446
					1%	2%	5%	48%	44%	
2.3.64	VI	-	-	-	4	85	123	893	844	1951
12.30 hrs.										
23.3.64	I	-	-	-	12	25	34	988	915	1974
	II									1355
	IV									300
	VI	-	-	-	9	24	47	494	218	792
March Mean					8	45	68	792	659	1595
					½%	2½%	5%	47½%	39½%	
3.4.64										1240
14.4.64	VI	75	17	6	6	6	23	2074	2191	4398
	III	43	16	-	-	18	30	1042	379	1530
Mean					3	12	26	1558	1285	2884
						½%	1%	55%	43½%	
27.4.64	VI	168	66	48	10	-	19	1102	771	2184
		7½%	3%	2%	½%		1%	50½%	35½%	

Date	Stn.	Numbers of each stage								Total
		I	II	III	IV	V♀	V♂	♀	♂	
11.5.64	VI	766	483	166	67	47	31	1313	484	3357
17.00 hrs.		23%	14½%	4½%	2%	1½%	1%	39%	14½%	
11.6.64	VI	329	559	1033	749	480	407	1234	919	5709
		6%	10%	18%	13%	8½%	7%	21½%	16%	
18.6.64	VI	228	938	1330	776	164	345	967	805	5553
		4%	17%	24%	14%	3%	6%	17½%	14½%	
25.6.64	III	104	809	2704	2329	861	785	1431	1026	10051
	VI	154	1162	2486	1797	585	554	1037	1037	8808
Mean		129	985	2595	2063	723	669	1234	1031	9429
		1½%	10½%	27½%	22%	7%	7%	13%	11%	
16.7.64*	IV	61	137	866	1831	396	437	1786	1583	7097
	VI	107	95	1000	1609	240	254	1021	460	4786
	III	177	195	1061	1512	343	284	951	598	5121
	II	70	293	1168	1684	756	435	1908	1645	7959
29.7.64	VI	136	400	790	3147	208	343	1598	789	7411
	III	141	357	465	2321	206	207	952	585	5234
Mean		137	378	627	2734	207	275	1275	687	6320
		2%	6½%	14½%	39%	4½%	4½%	18%	9%	
10.8.64	VIa	204	344	742	2047	226	273	958	453	5247
	b									4604
	C1									3978
	III									5116
	BH									3552
	IV									5824
Mean		189	307	685	1842	212	236	850	401	4725
		4%	6½%	14½%	39%	4½%	4½%	18%	9%	
20.8.64	VI	187	327	464	2167	350	502	406	397	4800
	I	259	636	874	2150	261	445	453	288	5366
Mean		223	481	669	2158	305	473	429	342	5080
		4½%	9½%	13%	42½%	6%	9½%	8½%	6½%	

Date	Stn.	Numbers of each stage								Total
		I	II	III	IV	V♀	V♂	♀	♂	
31.8.64	IV	86	244	601	922	458	579	587	101	3578
	II	37	102	319	1456	568	721	146	50	3399
	VI	56	793	1546	3178	1002	1369	1185	741	9880
Mean		54	357	792	1845	583	789	596	251	5267
		1%	7%	15%	35%	11%	15%	11½%	4½%	
15.9.64	IV	103	172	146	695	478	1036	223	59	2912
	VI	121	208	310	888	902	827	220	49	3525
Mean		112	190	228	791	690	931	222	54	3218
		3½%	6%	7%	24½%	21½%	29%	7%	1½%	
2.10.64	VI	165	515	754	1267	1753	1874	399	172	6899
	IV	8	54	24	170	363	618	149	90	1476
	II	61	116	258	346	647	1028	321	93	2887
Mean		78	228	345	594	921	1173	290	118	3759
		2%	6%	9%	16%	24½%	31½%	7½%	3½%	
26.10.64	C1	11	11	203	420	333	946	1131	845	3900
	IV	47	59	119	276	546	1424	3182	1658	7311
	VI	3	58	369	634	555	1344	2364	1424	6751
Mean		15	32	191	404	456	1104	1951	1159	5312
		½%	½%	3½%	7½%	8½%	20½%	36½%	22½%	
23.11.64	VI	-	12	43	252	227	449	3140	2799	6922
	IV	17	31	129	323	161	259	2442	1912	5274
	C1	-	-	14	86	50	169	1875	1270	3464
Mean		5	14	62	220	146	292	2486	1994	5219
		½%	½%	1%	4%	3%	5½%	47½%	38%	
14.12.64	VI	-	-	42	248	128	195	3623	2464	6700
	III	-	-	93	118	111	190	2115	1839	4466
	IV									6715
Mean		-	-	59	180	119	208	3072	2326	5964
				1%	3%	2%	3½%	51½%	39%	

Date	Stn.	Numbers of each stage								Total
		I	II	III	IV	V♀	V♂	♀	♂	
26.1.65	VIa									7941
	b									6763
	I									7114
	III									3040
Mean										6214
*16.7.64	Mean	104 2%	180 3%	1024 16½%	1659 26½%	434 7%	352 5½%	1416 22½%	1071 17%	6240

TABLE 3

Clutch Size in *Diaptomus gracilis*

Date	Stn.	Number of eggs per sac																								Total
		2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	Nbr.
24.2.64	VI		6	11	8	25	4	5	1																	60
2.3.64	VI		2	9	6	19	1	3																		40
23.3.64	VI			4	5	12	6	7	2	1	1	2														40
14.4.64	VI		1	4	6	25	5	4	4	2	2	3	1	-	1	2										60
27.4.64	VI	1	1	5	10	10	6	8	7	2	4	3	1				1									60
11.5.64	VI		1	6	12	18	13	25	19	11	10	7	6	3	5	3	1									140
11.6.64	VI	1		4	3	9	4	4	7	8	2	2	2	5	3	10	7	13	5	6	6	4	5	2	3	115
18.6.64	VI	1	2	8	4	9	4	2	8	5	7	13	7	17	8	5	6	3	3	3						115
25.6.64	VI & III	4	4	7	11	2	5	24	28	34	20	31	16	13	3	4	1									207
16.7.64	VI		1	1	5	30	23	38	14	10	1															123
29.7.64	VI			2	2	12	4	24	8	6	6	1		1												66
10.8.64	VI		1	1	2	8	10	18	4	1	4			1												50
20.8.64	VI		1	1	7	24	8	15	6	3	2	1														68
31.8.64	VI & III	2	2	3	10	46	13	8	10	6	4	4	1													109
15.9.64	VI		2	2	9	17	8	13	9	4	4	2	1													71

TABLE 4

The Size of Female *D. gracilis*.
(Lengths of the metasome, quoted in micrometer units. All samples from S.VI)

Depth	Number of each length																								Total
(m.)	3.5	.6	.7	.8	.9	4.0	.1	.2	.3	.4	.5	.6	.7	.8	.9	5.0	.1	.2	.3	.4	.5	.6	.7	.8	
12.12.63																									
0-10				3	4	8	8	5	4	3	3	2													40
10-20				1	4	12	9	8	3	3															40
20-42				1	4	6	8	8	8	2															37
Total				5	12	26	25	21	15	8	3	2													117
15.1.64																									
0-10		1	-	3	1	13	8	8	4	1	1														40
10-20			1	5	4	10	7	7	4	1	1														40
20-42			1	4	3	10	8	7	3	2	2														40
Total		1	2	12	8	33	23	22	11	4	4														120
2.3.64																									
0-5			1	1	2	5	3	3	3	2															20
5-10		2	2	1	2	4	2	2	3	1	1														20
10-15				3	1	3	4	4	1	1															17
15-20			1	1	2	4	3	3	5	1															20
20-30			1	-	2	7	2	2	1	1															16
30-42			2	2	1	4	4	2	4	1															20
Total		2	7	8	10	27	18	16	17	7	1														113
14.4.64																									
0-10				1	2	8	3	3	2	1															20
10-20	2	-	2	1	-	6	4	3	1	1															20
20-42			1	4	1	3	4	4	3																20
Total	2	-	3	6	3	17	11	10	6	2															120
11.5.64																									
0-10			2	3	4	8	4	8	6	3	1	1													40
10-15	1	1	-	2	-	8	-	4	2	-	2	-													20
15-20			1	2	3	-	4	4	1	2	2	1													20
20-40			2	3	4	8	4	8	6	3	1	1													40
Total	1	1	5	10	11	24	12	24	15	8	6	3													120

Depth	Number of each length																							
(m.)	3.5	.6	.7	.8	.9	4.0	.1	.2	.3	.4	.5	.6	.7	.8	.9	5.0	.1	.2	.3	.4	.5	.6	.7	.8	Total
11.6.64																									
0-10									1	1	1					1	1	4	8	3	5	4	8	3	40
10-20				3	-	2	7	5	3	-	1				1	1	2	-	2	2	7	2	1	1	40
20-42		1	-	3	1	1	4	3	4	2	2							1	1	3	4	5	3	2	40
Total		1	-	6	1	3	11	8	8	3	4				1	2	3	5	11	8	16	11	12	6	120
18.6.64																									
0-10		1	-	1	1	2	1	2	1						1	7	3	1	7	5	5	2			40
10-20					1	4	-	4	1	1	1	1			1	7	-	2	1	4	6				40
20-42			1	2	2	2	1	6	4	1	1					2	1	2	4	3	6	2			40
Total		1	1	3	4	8	2	12	6	2	2	1			2	16	4	5	12	12	17	4			120
25.6.64																									
0-10							2	-	1	1			1	4	1	15	7	6	6	9	11	7	7	2	80
10-20						3	2							1	-	7	4	6	4	6	6	-	1		40
20-42					1	4	1	3	3	2	1			1	-	4		4	5	2	5	5	1		42
Total					1	7	5	3	4	3	1		1	6	1	26	11	12	15	17	22	12	9	2	162
16.7.64																									
0-10										1	4	6	2	8	2	8	1	1	-	4	2	-	1		40
10-20											3	5	5	5	4	10	1	1	2	1	1	2	-		40
20-42										1	-	2	3	6	4	11	2	4	3	3	1	-	-		40
Total										2	7	13	10	19	10	29	4	6	5	8	4	2	1		120
29.7.64																									
0-10											3	4	7	11	6	5	1	2	-	-	1				40
10-20									2	1	4	8	7	8	2	8									40
20-42						2	-	-	-	-	5	10	3	5	3	6	3	2	1						40
Total						2	-	-	2	1	12	22	17	24	11	19	4	4	1	-	1				120
10.8.64																									
0-5										1	2	8	7	9	4	7	2								40
5-10								1	1	-	5	5	7	8	4	5	1	-	1	-	2				40
20-30											3	5	3	4	2	4		1	1						23
30-42											2	2	6	5	3	5	3	1	1	4			1		33
Total								1	1	1	12	20	23	26	13	21	6	2	3	4	2		1		136

Depth									Number of each length																
(m.)	3.5	.6	.7	.8	.9	4.0	.1	.2	.3	.4	.5	.6	.7	.8	.9	5.0	.1	.2	.3	.4	.5	.6	.7	.8	Total
20.8.64																									
0-5									1	2	6	3	8	10	2	8									40
5-10									1	1	4	9	9	5	5	6									40
20-30											1	4	2	9	2	4	1	1							24
30-42							1	-	2	2	6	5	4	7	2	7	2	-	2						40
Total							1	-	4	5	17	21	23	31	11	25	3	1	2						144
31.8.64																									
0-10											2	4	7	14	6	4	-	2	1						40
10-42							1	-	1	-	8	10	11	11	3	5	1								51
Total							1	-	1	-	10	14	18	25	9	9	1	2	1						91
15.9.64																									
0-10								1	2	5	10	20	18	16	4	2									78
10-20									1	2	7	8	11	12	7	12									61
20-42									2	4	5	7	1	-	1										20
Total								1	5	11	22	35	30	28	12	14									159
2.10;64																									
0-5							4	7	8	2	10	-	6	1	2										40
5-10					2	4	2	4	8	4	7	7	1	1											40
10-15					1	3	3	3	8	6	6	2	2	4	1	1									40
Total					3	7	9	14	24	12	23	9	9	6	3	1									120
26.10.64																									
0-5						1	3	6	13	13	18	4	1	1											60
30-42						6	4	6	11	6	5	1	1												40
Total						7	7	12	24	19	23	5	2	1											100
23.11.64																									
0-5						4	3	6	7	4	11	1	2	2											40
5-10						2	7	7	8	6	5	3	2												40
10-15			1		1	4	5	4	4	7	10	4													40
15-20					1	2	5	10	7	3	6	1	3	2											40
20-30						5	5	7	6	3	8	6													40
30-42						3	3	4	13	7	6	2	2												40
Total			1		2	20	28	38	45	30	46	17	9	4											240

Depth	Number of each length																								
(m.)	3.5	.6	.7	.8	.9	4.0	.1	.2	.3	.4	.5	.6	.7	.8	.9	5.0	.1	.2	.3	.4	.5	.6	.7	.8	Total
14.12.64																									
0-5					1	1	2	3	8	7	12	10	9	3	3	1									60
30-40						3	1	6	11	7	11	12	7	2											60
Total					1	4	3	9	19	14	23	22	16	5	3	1									120

(Note the lack of any obvious differences between the sizes of the animals in the various depth ranges on all these dates).

TABLE 5

Derivation of productivity of *D. gracilis*

Date	Egg stock	Days req. for dev.	Daily egg production	Mean	Days at this rate	Total egg production	Monthly egg production
February	2203	13	169		29	4901	4901
March	3212	13	247		31	7657	7657
14.4.64	4095	11	372		14	5208	
27.4.64-	8240	8	1030				
11.5.64				701	17	11917	
April							17125
May 1-11				701	11	7711	
11.6.64	7603	5	1521				
				1275	20	25500	
May							33211
June 1-11				1275	11	14025	
18.6.64	5165	5	939				
June 11-18				1230	7	8610	
25.6.64	4662	4½	1036				
June 18-25				987	7	6909	
16.7.64	3511	4	878				
June 25-30				957	5	4785	
June							34329
July 1-16				957	16	15312	
29.7.64	4688	4	1172				
July 16-29				1025	13	13325	
10.8.64	2455	4	614				
July 29-30				843	2	1686	
July							30323
Aug. 1-10				843	10	8430	
20.8.64	924	4	231				
Aug. 10-20				427	10	4270	

Date	Egg stock	Days req. for dev.	Daily egg production	Mean	Days at this rate	Total egg production	Monthly egg production
31.8.64	2422	4	605				
Aug. 20-31				418	11	4598	
August							17298
15.9.64	971	4	243				
Sept. 1-15				424	15	6360	
2.10.64	Negligible		0				
				121	16	1936	
September							8296

TABLE 6

The numbers and vertical distribution of the cyclopoids

Date	Stn.	0-5	0-10 (m.)	5-10	10-15	10-20 (m.)	15-20	20-30	20-42 (m.)	30-42	Total
			C. strenuus abyssorum + M. leuckarti								
16.5.63	VI		2068			220			144		2432
28.6.63	VI		810			500			416		1726
5.7.63	III		1140			170		255			1565
10.7.63	VI		2690			396			658		3744
21.8.63	VI	1020		168		1045			90		2323
22.8.63	III		961			616			58		1635
27.8.63	VI		2345			1240			550		4135
12.9.63	VI		1634			880			65		2579
23.9.63	VIa		3204			1494			30		4728
	b		4006			1948			39		5983
3.10.63	VI		3768			3746			584		8098
				Mesocyclops leuckarti							
17.10.63	VI		4316			3939			6992		15247
	IV		2444			2050		2596			7090
26.10.63	VI	1344		1650	1440		550	288		248	5704
29.10.63	III		1364			640		120			2124
	VI										1748
13.11.63	VI		1215			2700			4884		8799
29-30.11.63	(See Table 24).										
12.12.63	VI		253			1136			2632		4021
15.1.64	VI (See Table 1).										
	III		754			365		1562			2681
23.1.64	IV		80			54		72			206
	VI		282			280			1987		2549

Date	Stn.	0-5	0-10 (m.)	5-10	10-15	10-20 (m.)	15-20	20-30	20-42 (m.)	30-42	Total
6.2.64	IV		694 (0-20 m.)					280			974
	I		103			222			288		613
11.2.64	VI		255			219			549		1023
24.2.64	VI		350			384			733		1467
	III		121			344			611		1076
2.3.64	VI	(See Table 26).									
23.3.64	VI		299			352			560		1211
	I		162			190			300		652
	II		165			275		333			773
	IV		352			351		490			1193
3.4.64	VIa		289			455			1080		1824
	b										1610
			M. leuckarti + *C. str. abyssorum*								
14.4.64	VI		667			528			851		2046
	III		572			570		555			1697
27.4.64	VI		1193			126			156		1475
11.5.64	VI	(See Table 30).									
11.6.64	VI		3188			361			63		3612
18.6.64	VI		3258			228			30		3516
25.6.64	VI		2088			780			396		3264
	IV		2706			546		56			3252
	III		2592			704		76			3372
14.7.64	I										1452
16.7.64	III		1632			204		440			2276
	I		2699			252			1150		4101
	VI		1242			200			960		2402
	IV		3772			357		957			5086
29.7.64	VI		1638			506			1258		3402
	III		1462			777		630			2869

Date	Stn.	0-5	0-10 (m.)	5-10	10-15	10-20 (m.)	15-20	20-30	20-42 (m.)	30-42	Total
10.8.64	VIa	1536		306	210		240	555		528	3375
	b										2444
	C1										2031
	III										2044
	IV										2214
20.8.64	VI	1890		308	513		481	294		180	3666
	I	594		975	1456		1425	594		276	5320
31.8.64	VIa		2192			465		176		150	2983
	b										2662
	IVa		927			405		154			1486
	b										1812
	IIa		600			748		153			1601
	b										2014
	III	811		389	925		919	231			3275
15.9.64	VIa		1950			1460			156		3566
	b										2743
	IVa		1204			688			144		2036
	b										1150
2.10.64	VI	1272		1800	1760		576	144		44	5596
	II		3869			2714		306			6889
	IV		943			1159		130			2232
8.10.64	VI	1014		1344		297			722		3377
						M. leuckarti					
26.10.64	VI	533		900	1575		952	2184		2645	8789
	C1		999			2156			3720		6875
	III		1680			1584		1428			4692
	IV		1932			2370		902			5204
5.11.64	VI	520		646	1139		1155	2460		928	6848
	Luss		3002			2982			6320		12004

Date	Stn.	0-5	0-10 (m.)	5-10	10-15	10-20 (m.)	15-20	20-30	20-42 (m.)	30-42	Total
23.11.64	VIa	240		270	270		340	112		540	1772
	b										1199
	C1		588			860			840		2288
	IVa		297			231		234			762
	b										867
14.12.64	VI	153		120	238		162	836		231	1740
	IV		352			384		180			916
	III		357			364		315			1036
	II										1248
26.1.65	I										1653
	III										532
	VIa										1424
	b		116			77			1584		1777

TABLE 7

The Numbers and Vertical Distribution of *Mesocyclops leuckarti* at S.VI

Date	Depth	Stage									
	(m.)	I	II	III	IV	V♀	V	V♂	♀	♂	Total
16.5.63	0-10				88	88		46	157	159	538
	10-20				27	34		15	76	62	213
	20-42				8	9		4	25	12	58
	Total				123	131		65	258	233	810
					15½%	16%		8%	32%	28½%	
28.6.63	0-10				34	24		31	64	9	162
	10-20				-	7		9	4	4	24
	20-42				-	-		4	2	-	6
	Total				34	31		44	70	13	192
					17½%	16%		23%	36½%	7%	
27.8.63	0-10		52	261	392	157		130	261	52	1305
	10-20		-	266	341	160		224	74	-	1065
	20-42		-	-	10	16		23	16	-	65
	Total		52	527	743	333		377	351	52	2435
			2%	21½%	30½%	13½%		15½%	15%	2%	
23.9.63	0-10			411	1626	753		616			3406
	10-20			82	278	580		695			1635
	20-42			-	-	15		15			30
	Total			493	1904	1348		1326			5071
				9½%	37½%	26½%		26½%			
17.10.63 (S.VI)	0-10			259	1295	2071		690			4315
	10-20			335	1122	1634		847			3938
	20-42			314	1853	1328		3496			6991
	Total			908	4270	5033		5033			15244
				6%	28%	33%		33%			

Date	Depth					Stage					Total
	(m.)	I	II	III	IV	V♀	V	V♂	♀	♂	
17.10.63	0-10			159	855	476		953			2443
(S.IV)	10-20			20	687	512		841			2050
	20-32			13	858	584		1143			2598
	Total			192	2400	1572		2927			7091
				2½%	34%	22%		41½%			
29.11.63	0-5			9	106	79		109			303
(15.00	5-10			8	108	91		93			300
hrs.)	10-15			10	169	78		91			348
	15-20			3	146	70		105			324
	20-30			13	360	166		360			899
	30-42			47	1046	299		908			2300
	Total			90	1935	783		1666			4479
				2%	43½%	17½%		37%			
12.12.63	0-10			7	113	38		95			253
	10-20			23	522	170		421			1136
	20-42			-	1148	473		1012			2633
	Total			30	1783	681		1528			4022
				½%	44½%	17%		38%			
23.1.64	0-42				563	218		499			1280
					44%	17%		39%			
2-3.3.64					44%	15%		41%			
23.3.64	0-10				46½%	22½%		31%			
	20-42				42%	16%		42%			
											1211

Date	Depth (m.)	Stage									Total
		I	II	III	IV	V♀	V	V♂	♀	♂	
14.4.64	0-10				93	60		106	33	40	334
	10-20				38	58		64	29	76	264
	20-42				271	208		279	41	33	835
	Total				402	326		449	103	149	1429
					28%	23%		31½%	7%	10½%	
11.5.64 (12.30 hrs.)	0-5				31	48		32	70	79	260
	5-10				-	5		-	22	11	39
	10-15				-	5		16	37	57	115
	15-20				3	-		13	20	44	80
	20-30				8	31		10	26	31	106
	30-42				8	34		22	34	51	149
	Total				50	123		93	209	273	748
					6½%	16½%		12½%	28%	36½%	
11.6.64	0-10	81	43	13	43	12		16	221	-	430
	10-20	20	10	10	20	15		15	10	-	90
	20-42	-	-	-	2	5		5	5	-	17
	Total	101	53	23	65	32		36	236	-	546
		18½%	9½%	4%	12%	6½%		6½%	43%		
16.7.64	0-10	8	8	123	40		109		109	136	534
	10-20	6	3	9	3		3		3	3	30
	20-42	-	-	-	-		-		-	-	-
	Total	14	11	132	43		112		112	139	564
		2½%	2%	23½%	7½%		20%		20%	24½%	

Date	Depth (m.)	Stage I	II	III	IV	V♀	V	V♂	♀	♂	Total
10.8.64	0-5	19	-	19	19		19		537	153	768
	5-10	9	6	15	33		9		64	15	153
	10-15	-	7	44	47		10		14	3	126
	15-20	-	5	44	73		17		7	-	149
	20-30	-			6		5		-	-	11
	30-42	-			-		-		11	11	22
	Total	28	18	122	178		60		633	182	1221
		2%	1½%	10%	14½%		5%		52%	15%	
31.8.64	0-10			49	92		159		306	6	613
	10-20			16	168		208		8	-	400
	20-30			11	16		76		-	-	104
	30-42			-	4		6		-	-	10
	Total			76	280		449		314	6	1125
				6½%	25%		40%		28%	½%	
15.9.64	0-10	74	74	304	601	296		148	148	-	1647
	10-20	-	56	205	467	389		297	-	-	1416
	20-42	-	-	17	62	26		44	-	-	149
	Total	74	130	526	1130	711		489	148	-	3208
		2½%	4½%	16½%	35%	22%		15%	4½%		
2.10.64	0-5	-	16	61	328	467		222	16	-	1110
	5-10	-		305	733	427		279	-	-	1744
	10-15	-		229	660	560		225	-	-	1674
	15-20	-		62	178	87		238	-	-	565
	20-30	4	4	20	41	16		49	4	-	138
	30-42	-	4	4	10	2		14	2	-	36
	Total	4	24	681	1950	1559		1027	22	-	5267
			½%	13%	37%	29½%		19½%	½%		

Date	Depth (m.)	Stage									
		I	II	III	IV	V♀	V	V♂	♀	♂	Total
26.10.64 (S.I)	0-10			40	370	270		320			999
	10-20			21	841	539		754			2156
	20-30			74	1302	1004		1339			3720
	Total			135	2513	1813		2413			6874
				2%	36½%	26½%		35%			
23.11.64	0-5			5%	46½%	15½%		32½%			240
	30-42			4%	49%	16%		31%			540
	Total										1772

TABLE 8

Numbers and Vertical Distribution of Cyclops strenuus abyssorum at S.VI.

Date	Depth (m.)	I	II	III	Stage IV	V	♀	♂	Total
16.5.63	0-10	520	352	245	352	61	-	-	1530
	10-20	212	124	93	-	-	-	-	429
	20-42	26	34	26	-	-	-	-	86
	Total	758	510	364	352	61	-	-	2045
		37%	25½%	17½%	17%	3%			
28.6.63	0-10	52	107	52	129	191	52	58	641
	10-20	24	33	40	40	57	75	173	442
	20-42	-	-	16	22	55	16	299	408
	Total	76	140	108	191	303	143	530	1491
		5%	9½%	7%	13%	20½%	9½%	35½%	
27.8.63	0-10	48	25	87	24	136	321	160	801
	10-20	-	-	-	-	-	100	74	174
	20-42	-	-	-	-	-	300	184	484
	Total	48	25	87	24	136	721	418	1459
		3%	1½%	6%	1½%	9½%	49½%	29%	
23.9.63	0-10						120	61	181
	10-20						60	26	86
	20-42						2	3	5
	Total						182	90	272
							67%	33%	
14.4.64	0-10	293	40	-					333
	10-20	159	67	37					263
	20-42	8	8	-					16
	Total	460	115	37					612
		75%	18%	7%					

Date	Depth (m.)	Stage I	II	III	IV	V	♀	♂	Total
11.5.64 (12.30 hrs.)	0-5	283	151	151	204	20			809
	5-10	150	31	31	50	-			262
	10-15	81	25	16	9	-			131
	15-20	47	17	-	3	-			67
	20-30	74	14	-	1	-			89
	30-42	68	1	1	-	-			70
	Total	703 49½%	239 16½%	199 14%	267 18½%	20 1½%			1428
11.6.64	0-10	882	510	427	455	220	110	151	2755
	10-20	127	57	6	6	6	16	50	271
	20-42	26	4	4	8	1	2	3	48
	Total	1035 34%	571 18½%	437 14%	469 15%	227 7½%	128 4½%	204 6½%	3071
16.7.64	0-10	7	14	56	177	120	78	255	707
	10-20	7	3	4	29	23	26	75	167
	20-42	-	-	-	29	29	110	792	960
	Total	14 1%	17 1%	60 3%	235 13%	172 9½%	214 11½%	1122 61%	1834
10.8.64	0-5		15	15	15	100	368	253	766
	5-10		-	-	7	13	46	86	152
	10-15		6	3	4	7	21	42	83
	15-20		-	-	3	3	10	80	96
	20-30		-	-	5	5	54	478	542
	30-42		-	-	8	55	97	365	525
	Total		21 1%	18 1%	42 2%	183 8½%	596 27½%	1304 60%	2164

Date	Depth (m.)	Stage I	II	III	IV	V	♀	♂	Total
31.8.64	0-10	5	2		63	126	1100	282	1578
	10-20	-	-		-	-	26	39	65
	20-30	1	2		-	2	26	41	72
	30-42	-	-		-	-	94	46	140
	Total	6	4		63	128	1246	408	1855
		½%	½%		3½%	7%	67%	22%	
15.9.64	0-10	4				4	177	110	295
	10-20	2				-	24	18	44
	20-42	-				-	6	1	7
	Total	6				4	207	129	346
		2%				1½%	60%	36½%	
2.10.64	0-5						115	44	159
	5-10						41	13	54
	10-15						74	14	88
	15-20						5	4	9
	20-30						2	4	6
	30-42						7	2	9
	Total						244	81	325
							75%	25%	

TABLE 9

Numbers of *Daphnia hyalina* var. *lacustris*.

Date	Stn.	0-5	0-10 (m.)	5-10	10-15	10-20 (m.)	15-20	20-30	20-B. (m.)	30-B.	Total	Mean
16.5.63	VI		6			50			56		112	
28.6.63	VI		162			300			16		478	
5.7.63	III		62			60			58		180	
10.7.63	VI		428			108			112		648	
21.8.63	VI	187		14		55			36		292	
22.8.63	III		279			224			179		682	
27.8.63	VI		266			220			775		1261	
12.9.63	VI		114			100			78		292	
23.9.63	VI		60			54			162		276	
3.10.63	VI		122			77			286		485	
17.10.63	VI		260			351			368		979	
	IV		517			328			660		1505	
26.10.63	VI	504		176	256		225	72		44	1277	
29.10.63	III		880			1088			240		2208	
	VI										608	
7.11.63	Luss		648			196			243		1087	
13.11.63	VI		1080			1125			1184		3389	
29.11.63	VI	(See Table 25)										
12.12.63	VI		138			176			392		706	
15.1.64	VIa		254			396			458		1108	
	b		378			215			307		900	
	IIIa		425			260			408		1093	
	b		154			130			132		416	879
23.1.64	IV		390			364			158		912	
	VI		304			230			121		655	783
6.2.64	IV			636 (0-20m.)					120		866	
	I		604			220			414		1238	1052
11.2.64	VI		522			357			127		1006	
24.2.64	VIa		155			80			82		317	
	b										448	

Date	Stn.	0-5	0-10 (m.)	5-10	10-15	10-20 (m.)	15-20	20-30	20-B. (m.)	30-B.	Total	Mean
24.2.64	IIIa		198			32			13		243	
	b										375	346
2.3.64	VI	(See Table 27)										
23.3.64	VI		26			11			20		57	
	I		54			30			15		99	
	II		33			22			9		64	
	IV		16			9			14		39	65
3.4.64	VIa		17			13			36		66	
	b										46	56
14.4.64	VI		215			96			92		403	
	III		22			38			15		75	239
27.4.64	VIa		124			18			26		168	
	b		92			-			-		92	130
11.5.64	VI	(See Table 31)										
11.6.64	VI		488			150			18		656	
18.6.64	VI		474			209			15		698	
25.6.64	VI		504			840			108		1452	
	IV		615			210			56		881	
	III		384			638			456		1478	1270
14.7.64	I										607	
16.7.64	III		666			136			1320		2122	
	I		752			216			1525		2493	
	VI		447			575			1824		2846	
	IV		728			289			1452		2469	2482
29.7.64	VI		288			207			850		1345	
	III		301			273			1092		1666	1505
10.8.64	VI	48		54	21		32	375		608	1138	
	C1										819	
	III										1452	
	BH										832	
	IV										1464	1141

Date	Stn.	0-5	0-10 (m.)	5-10	10-15	10-20 (m.)	15-20	20-30	20-B. (m.)	30-B.	Total	Mean
20.8.64	VI	90		44	19		39	252		108	552	
	I	90		13	32		45	270		60	510	531
31.8.64	VIa		205			8		209		80	502	
	b										566	
	IVa		105			60			84		249	
	b										227	
	IIa		40			38			697		775	
	b										625	444
1.9.64	IIIa	30		28	4		36		260		358	
	b	56		12	4		40		140		252	
15.9.64	VIa		204			40			204		448	
	b										586	
	IVa		112			32			272		416	
	b										180	407
2.10.64	VIa	96		80	32		32	378		11	629	
	b										598	
	IIa		159			345			595		1099	
	b										610	
	IVa		161			247			273		681	
	b										744	727
8.10.64	VI	182		168		88			228		666	
26.10.64	VI	1435		480	147		289	840		115	3306	
	C1		1591			644			51		2286	
	III		1440			352			525		2317	
	IV		2530			810			518		3858	2942
5.11.64	VI	208		153	85		90	300		64	900	
	Luss		456			378			325		1159	
23.11.64	VIa	540		621	864		391	392		80	2888	
	b										3313	
	C1		700			280			140		1120	
	IVa		3432			2871			3081		9384	
	b										10923	5525

Date	Stn.	0-5	0-10 (m.)	5-10	10-15	10-20 (m.)	15-20	20-30	20-B. (m.)	30-B.	Total	Mean
14.12.64	VIa	357		120	136		81	95		126	915	
	b										2040	
	IV		6644			4064			1956		12664	
	III		663			364			195		1222	
	II										2418	3852
26.1.65	I										1393	
	III										988	
	VIa		1276			132			132		1540	
	b										801	1180

(Where only the total numbers are given the sample was from the surface to the bottom).

TABLE 10

Numbers of <u>Bosmina coregoni</u>

Date	Stn.	0-5	0-10 (m.)	5-10	10-15	10-20 (m.)	15-20	20-30	20-B. (m.)	30-B.	Total	Mean
16.5.63	VI		96			142			428		666	
28.6.63	VI		36			360			208		604	
5.7.63	III		19			20			100		139	
10.7.63	VI		64			108			588		760	
21.8.63	VI		52			-			48		100	
22.8.63	III		31			14			35		80	
27.8.63	VI		38			80			330		448	
5.9.63	VI		23			4			234		261	
12.9.63	VI		2			20			156		178	
23.9.63	VIa		30			18			201		249	
	b		-			24			138		162	205
3.10.63	VI		30			25			155		210	
17.10.63	VI		104			39			92		235	
	IV		94			41			44		179	207
26.10.63	VI	-		22	64		75	252		212	625	
29.10.63	III		44			64			240		348	
7.11.63	Luss		96			140			1197		1433	
13.11.63	VI		90			315			777		1182	
29.11.63	VI	(See Table										
12.12.63	VI		115			336			756		1207	
15.1.64	VIa		362			592			1034		1988	
	b		601			487			576		1664	
	IIIa		501			420			894		1815	
	b		210			338			420		968	1609
23.1.64	IV		790			628			444		1862	
	VIa		544			640			580		1764	
	b										2040	1888

Date	Stn.	0-5	0-10 (m.)	5-10	10-15	10-20 (m.)	15-20	20-30	20-B. (m.)	30-B.	Total	Mean
6.2.64	IV			1984						720	2704	
	I		2971			1236			2130		6337	4520
11.2.64	VIa		2067			1203			406		3676	
	b			3974 (0-20 m.)								
24.2.64	VIa		621			360			275		1256	
	b										2100	
	IIIa		1507			184			78		1769	
	B										2700	1956
2.3.64	VI	(See Table										
23.3.64	VI		507			286			270		1063	
	I		918			320			300		1538	
	II		1188			330			90		1608	
	IV		264			198			168		630	1210
3.4.64	VIa		374			442			492		1308	
	b										1702	1505
10.4.64	Luss		722			765			291		1778	
14.4.64	VI		1959			1536			1242		4737	
	III		308			532			240		1080	2908
27.4.64	VI		1150			72			91		1313	
11.5.64	VI	(See Table										
11.6.64	VI	75		240		1620			1152		3087	
18.6.64	VI		545			532			375		1452	
25.6.64	VI		72			80			1135		1287	
	IV		61			189			98		348	
	III		80			286			456		822	819
14.7.64	I										185	
16.7.64	III		2			2			40		44	
	I		2			18			200		220	
	VI		-			-			120		120	
	IV		-			17			44		61	111

Date	Stn.	0-5	0-10 (m.)	5-10	10-15	10-20 (m.)	15-20	20-30	20-B. (m.)	30-B.	Total	Mean
29.7.64	VI		-			-			68		68	
	III		20			21			63		104	86
10.8.64	VI	-		9	-		-	22		80	111	
	C1										72	
	III										36	
	BH										104	
	IV										17	68
20.8.64	VI	18		3	5		13	42		36	117	
	I	18		-	4		-	27		3	52	84
31.8.64	VIa		8			-		11		10	29	
	b										22	
	IVa		-			-			14		14	
	b										14	
	IIa		5			4			17		26	
	b										22	
1.9.64	IIIa	30		-	-		-		26		56	
	b	7		3	-		3		5		18	25
15.9.64	VIa		-			-			3		3	
	b										20	
	IVa		-			4			4		8	
	b										60	23
2.10.64	VIa	24		10	5		16	18		11	84	
	b										51	
	IIa		-			23			17		40	
	b										92	
	IVa		11			-			19		30	
	b										38	56
8.10.64	VI	26		4		44			38		112	

Date	Stn.	0-5	0-10 (m.)	5-10	10-15	10-20 (m.)	15-20	20-30	20-B. (m.)	30-B.	Total	Mean
26.10.64	VI	82		20	42		136	42		69	391	
	C1		148			224			180		552	
	III		96			44			42		182	
	IV		46			150			66		262	347
5.11.64	VI	26		8	8		45	100		208	395	
	Luss		76			147			305		528	
23.11.64	VIa	60		27	54		34	112		80	367	
	b										383	
	C1		280			280			180		740	
	IVa		165			297			273		735	
	b										873	619
14.12.64	VIa	204		150	102		72	76		10	614	
	b										476	
	IV		2288			1056			219		3563	
	III		272			208			60		540	
	II										1248	1288
26.1.65	I										878	
	II										456	
	VIa		319			44			44		407	
	b										324	514

TABLE 11 & 12

Depth (m.)	Temps. on 31.8.64 (°C) S.II	S.IV	S.VI	Temps. on 2.10.64 (°C) S.VI	S.II	S.IV
Surface	15.2	15.90	15.4	12.70	13.20	13.30
1	15.2	15.70	14.75	13.12	"	"
2	15.0	15.65	14.75	13.12	"	"
3	14.65	15.00	14.60	13.20	"	"
4	"	14.88	14.60	"	"	"
5	14.55	14.80	14.58	"	"	"
6	"	"	14.50	"	"	"
7	"	"	"	13.1	"	13.10
8	"	14.74	"	"	"	"
9	"	14.70	"	"	"	"
10	14.4	14.52	"	"	13.05	"
11	14.33	"	"	"	"	"
12	14.20	14.36	14.40	13.2	"	"
13	"	14.28	14.34	"	12.98	"
14	14.10	14.28	14.26	"	"	"
15	14.02	14.2	14.20	13.0	"	13.0
16	14.00	14.05	14.13	"	"	"
17	13.80	13.94	14.00	"	"	12.85
18	13.67	13.85	13.75	"	12.90	12.75
19	13.58	13.62	13.46	"	"	"
20	13.47	13.55	13.28	12.94	"	"
21	13.26	13.28	12.60	12.75	12.85	12.60
22	13.0	12.75	12.20	12.68	"	"
23	12.42	12.35	11.51	12.50	"	12.32
24	11.40	11.40	10.94	12.20	12.70	"
25	10.90	11.00	10.80	11.80	12.50	11.95
26	10.90	10.58	10.32	11.60	12.28	11.80
27	10.60	10.35	9.92	11.32	12.00	11.65
28	10.10	10.10	9.84	11.0	11.70	11.50
29	9.98	10.00	9.74	10.85	11.40	11.20
30	9.85	"	9.67	10.60	10.85	10.75
31	"	"	9.60	10.32	10.40	10.50
32	"	9.78	9.50	10.00	10.30	10.45
33	9.62	9.82 (B)	9.44	9.85	9.84(B)	10.20(B)
34	9.37(B)		9.35	"		
35			9.35	9.75		
36			9.24	"		
37			9.24	9.6		
38			9.2	"		
39			"	"		
40			"	"		
41			"	"		
42			9.1	"		
43			9.1	9.4		
44			8.95(B)	9.38(B)		

TABLE 13

Weather conditions during the 24 hour series of samples

12-13.9.63

15.00 hrs. (B.S.T.) - Sunny with light southerly breeze.

17.46 hrs. - Sunset.

21.00 hrs. - Dark. Calm with clear sky.

24.00 hrs. - Overcast with southerly breeze.

04.00 hrs. - Slight lightening of sky. Drizzling. Southerly breeze.

05.42 hrs. - Sunrise.

08.00 hrs. - Overcast and southerly breeze.

12.00 hrs. - Southerly breeze and overcast.

Air temperature at 14.30 hrs. - 12.55°C.

Water temperatures -

Depth (m.)	Temp. (°C.)
Surface	12.5
5.7	12.2
17.6	11.82
20.1	10.42
20.8	9.6
22.2	8.45
25.3	7.8
27.1	7.15
29.8	6.68
33.6	6.32
39.4	5.9
45.2	5.43
52.1	5.1
63.5	4.8
91.1	4.5
115.2	4.6
176.7	4.6

No further cable

<u>29-30.11.63</u>

15.00 hrs. (G.M.T.) - Calm after bright sunny day.

15.30 hrs. - Sun sank behind the hills.

15.52 hrs. - Sunset.

17.00 hrs. - Slight N.W. breeze.

17.30 hrs. - Fully dark.

19.00-24.00 hrs. - Calm, but occasional light zephyrs. Bright moon and clear sky.

03.00-06.00 hrs. - Moon gone and sky overcast. Slight mist over water. Light N.W. breeze. Still dark at 06.00 hrs.

08.19 hrs. - Sunrise.

09.00 hrs. - Overcast and slightly misty. Calm.

12.00 hrs. - Overcast and calm. Air temperature 5.5°C.

The water was essentially homothermal, with 0.55°C difference between the surface (7.15°C) and the bottom (6.95°C). The Secchi transparency was 4½m.

There was a 20° frost overnight leading to surprisingly pleasant dry working conditions in spite of the film of ice over the launch.

<u>2-3.3.64</u>

12.30 hrs. (G.M.T.) - Calm. Sun shining through low mist.

15.00 hrs. - Slight southerly breeze and launch swinging slightly at anchor.

17.00 hrs. - Sun sank behind hills.

17.53 hrs. - Sunset.

18.00 hrs. - Faint zephyrs. Twilight.

19.00 hrs. - Fully dark.

21.00 hrs. - Flat calm. Bright stars hidden by slight mist.

24.00 hrs. - $\frac{3}{4}$ moon, partly hidden by clouds. Some mist.

03.00 hrs. - Mist rising. Some light cloud.

06.30 hrs. - Almost fully light. Overcast and calm.

07.05 hrs. - Sunrise.

09.30 hrs. - Calm.

12.00 hrs. - Calm. Sky overcast but bright.

There was a temperature difference of only 0.75° between the surface (5.4°C) and the bottom (4.98°C at 43m.). Secchi transparency was 6.5m., and the water was distinctly green in colour. Air temperatures ranged from 6.9°C. at midday to 4.4°C. at 03.00 hrs.

11-12.5.64

12.30 hrs. (B.S.T.) - Overcast with light showers, and occasional gleams of sun. Southerly breeze.

14.15 hrs. - As at 12.30 hrs.

17.00 hrs. - As at 12.30 hrs.

20.14 hrs. - Sunset.

21.00 hrs. - Raining. Calm.

22.00 hrs. - Completely dark.

24.00 hrs. - Calm and raining. Samples hauled by hand due to winch breakdown.

05.00 hrs. - Slight southerly breeze. Almost fully light but overcast.

05.11 hrs. - Sunrise.

09.00 hrs. - Overcast and slight southwesterly breeze.

Further sampling impossible owing to a gale force wind, which also prevented the taking of temperatures.

Secchi transparency - 5 metres.

TABLE 14

Numbers of *C. str. abyssorum* on 12-13.9.63

		Time					
Stage	Depth (m.)	1500	2100	2400	0400	0800	1200
Males	0-5	146	55	45	42	100	153
	5-10	70	104	133	24	4	6
	10-15	26	44	5	124	51	21
	15-20	15	11	17	4	22	59
	20-40	4	2	2	16	16	15
Total Nbr.		261	216	202	210	193	254
Females	0-5	290	128	191	75	259	211
	5-10	160	296	202	63	7	10
	10-15	49	175	9	202	63	28
	15-20	41	39	10	6	73	75
	20-40	6	4	2	27	28	25
Total Nbr.		546	642	414	373	430	349

TABLE 15

Vertical distribution of stages of M. leuckarti on 12-13.9.63

Depth (m.)				Stage				
	♀	♂V	♀V	IV	III	II	I	
1200 hrs.								
0-5	10	4	10	31	19	36	4	114
5-10	-	1	1	4	7	-	-	13
10-15	28	12	16	48	24	12	-	140
15-20	2	22	8	24	22	-	-	78
20-40	1	2	1	2	1	1	-	8
Total Nbr.	41	41	36	109	73	49	4	353
%	11½	11½	10	31	20½	14	1	
2400 hrs.								
0-5	19	10	2	52	19	-	-	102
5-10	5	5	12	65	26	25	-	138
10-15	-	2	1	9	5	3	2	22
15-20		10	3	5	6	4	3	31
20-40				too few				
Total Nbr.	24	27	18	131	56	32	5	293
%	8	9	6	44½	19½	11½	1½	

TABLE 16

Vertical distribution of D. gracilis stages

Date	Station	Depth (m.)	% of the total nbr. of each stage I	II	III	IV	V	♀	♂
15.1.64	VI	0-10				41½	26½	35	33½
		10-20				7	25	27½	26
		20-42				41½	48½	37½	40½
6.2.64	IV	0-10				25½	28	38	39½
		10-20				46½	23½	18	16½
		20-30				28	48½	44	44
	I	0-20				77	76	81	84
		20-30				23	24	19	16
24.2.64	III	0-10					77½	92	92
		10-20					15	5	5
		20-28					7½	3	3
	VI	0-10				33	37½	39	42½
		10-20				33	16½	28	24½
		20-42				33	46	33	33
23.3.64	I	0-10						46½	67
		10-20						19½	12
		20-30						34	20
	VI	0-10						42	53½
		10-20						20	17½
		20-42						38	29
14.4.64	VI	0-10						42	51½
		10-20						26½	28½
		20-42						31½	20
	III	0-10						50	51
		10-20						35	43
		20-28						15	6
27.4.64	VI	0-10	90					80	93
		10-20	9					7	4
		20-42	1					13	3
11.5.64 (12.30 hrs.)	IV	0-5	26½	33	54	48½		39	78½
		5-10	11	19	13½	14		7	9
		10-15	19½	22½	15½	16		5	3½
		15-20	13½	12	10½	14		4½	1
		20-30	18½	7½	5	4		17½	5
		30-42	11	6	1½	3½		27	3½
11.6.64	VI	0-10	86½	93	95½	97	96½	80	90½
		10-20	12	6	4	2½	2	11	8½
		20-42	2½	1	½	½	1½	9	1
25.6.64	VI	0-10	78	93½	91	94	95½	81½	94
		10-20	13½	5½	7½	3½	3	7½	3½
		20-42	9½	1	1½	2½	1½	11	2½

Date	Station	Depth	% of the total nbr. of each stage						
		(m.)	I	II	III	IV	V	♀	♂
25.6.64	III	0-10	83½	91½	87	84½	87½	85½	89½
		10-20	16½	4½	6	4	3½	6	2½
		20-28	-	4	7	11½	9	8½	8
16.7.64	IV	0-10	75½	67	37½	43	78	75	87½
		10-20	24½	33	47	26½	11½	16½	10½
		20-31	-	-	15½	30½	10½	8½	2
	VI	0-10	79½	77	40	35½	64	60	82
		10-20	20½	23	44	24½	13½	12½	9½
		20-42	-	-	16	40	22½	27½	8½
	III	0-10	81½	93	68	52½	81	80	84½
		10-20	8	4½	31	22½	12	12½	12
		20-28	10½	2½	1	25	7	7½	3½
	II	0-10	85	61½	80	45	88½	77½	95½
		10-20	15	4½	14	16½	5	5½	3½
		20-42	-	34	6	38½	6½	17	1
29.7.64	VI	0-10	64½	66½	33½	5½	18	64	77
		10-20	35½	33½	58½	30	48½	25	20
		20-42	-	-	8	64½	33½	11	3
	III	0-10	50½	35½	27	9	34	61½	54½
		10-20	49½	59	60½	23	36	32½	36
		20-28	-	5½	12½	68	30	6	9½
10.8.64	VI	0-5	51½	55½	54	8	16	77	70½
		5-10	24½	25	16½	7½	7½	7	8
		10-15	2½	7½	12	11	8½	1	8
		15-20	3	1½	8	9	6	1½	1
		20-30	15	9	7½	45	22½	6	9½
		30-42	3½	1½	2	19½	42½	7½	3
20.8.64	VI	0-5	59	65	58	24	18½	54½	91
		5-10	28	24	23	19	11½	22½	6½
		10-15	5½	6½	9½	9½	7	4	1½
		15-20	2½	1½	4	19	9	7½	1
		20-30	2½	1½	4	22	41½	9	-
		30-42	2½	1½	1½	6½	12½	2½	-
	I	0-5	57	45½	43	22½	19½	43	77½
		5-10	24	23½	27	13½	12½	5½	9½
		10-15	12½	19½	14½	10½	3½	20½	4½
		15-20	2½	10	12½	11½	14½	26	8
		20-30	4	-	2	39½	39	2½	-
		30-42	-	1½	1	2½	11	2½	½
31.8.64	IV	0-10	90	87	85½	63	22½	88	100
		10-20	10	3	12	23	19½	11	-
		20-30	-	10	2½	14	58	1	-
	II	0-10	67½	81	80	42½	14	53	96
		10-20	-	19	20	36	44	4	4
		20-42	-	-	-	21½	42	43	-

Date	Station	Depth (m.)	% of the total nbr. of each stage I	II	III	IV	V	♀	♂
31.8.64	VI	0-10	68	92	87½	75½	60½	91	93½
		10-20	14	5	9½	11½	8½	5½	3
		20-30	18	1½	2½	12	24½	2	3
		30-42	-	1½	½	1	6½	1½	½
15.9.64	IV	0-10	93½	85½	83	73½	44	70	57½
		10-20	6½	8	9½	23	10½	14½	23½
		20-30	-	6½	7½	4½	45½	15½	19
	VI	0-10	61	55	61	46½	40½	63½	33
		10-20	35	40	36	43½	39½	28½	57
		20-42	4	5	3	10	20	8	10
2.10.64	VI	0-5	18	32	50	49	44	41½	35
		5-10	38	37	25	28½	32½	24	24½
		10-15	38	26½	22	19½	18½	25	33½
		15-20	6	3	1	2	3	3½	2
		20-30	-	1½	1	1	1½	3½	3½
		30-42	-	-	-	-	½	2½	1½
	IV	0-10	100	100	84	75	58½	16½	18
		10-20	-	-	16	25	26	49	46½
		20-30	-	-	-	-	15½	34½	35½
26.10.64	C1	0-10	100	100	100	91	54½	49	46½
		10-20	-	-	-	5	24½	22½	25½
		20-42	-	-	-	4	20½	28½	28
	IV	0-10	100	80	80	76½	63	65½	58
		10-20	-	20	10	13½	22	14	18½
		20-30	-	-	10	10	15	20	23½
	VI	0-5			82	77	64	69	69
		5-10			9	7	17	9	10
		10-15			1	2	5	3½	6½
		15-20			3½	4	6	5	6
		20-30			2½	2	4½	6	4½
		30-42			2	8	3½	7	4
23.11.64	VI	0-5			40	31	30½	27	22
		5-10			40	25½	27	15	12
		10-15			10	19½	9½	6	6½
		15-20			10	14½	17	12	13
		20-30			-	9½	7½	19	20
		30-42			-	-	8½	21	26½
	IV	0-10			-	16	49	42	41½
		10-20			40	39	26	27½	26½
		20-30			60	45	25	30½	32
	C1	0-10			100	82½	42	41½	37
		10-20				11½	27	27	31½
		20-30				6	31	31½	31½

Date	Station	Depth (m.)	% of the total nbr. of each stage						
			I	II	III	IV	V	♀	♂
14.12.64	VI	0-5				5½	7½	17	13
		5-10				5½	4½	6	7
		10-15				20½	12½	6½	6
		15-20				20	15½	6½	9
		20-30				13	24½	17½	23½
		30-42				35	35½	46	41
	III	0-10				58	33	34½	32½
		10-20				1½	41½	20	18½
		20-28				40½	25½	45½	49

TABLE 17

Comparisons of the vertical distribution of egg bearing females with that of the entire female population (bracketed figures) of D. gracilis

	Percentage in Each Depth Range								
Station	0-5	0-10 (m.)	5-10	10-15	10-20 (m.)	15-20	20-30	20-42 (m.)	30-42
6.2.64									
I		12 (38)			5½(18)			82½(44)	
24.2.64									
IV		90			6		4		
VI		37 (39)			36 (28)			26½(33)	
2.3.64									
VI	70 (71½)		19 (15½)	2 (4)		2 (4)	5 (2½)		2 (2½)
23.3.64									
I		53½(46½)			17 (19½)			29½(34)	
VI		51½(42)			24 (20)			24 (38)	
27.4.64									
VI		86½(80)			1 (7)			12½(13)	
11.5.64									
VI	46 (43)		3 (5)	2½(3½)		2½(3½)	12½(15)		33½(30)
11.6.64									
VI		80 (80)			10 (11)			10 (9)	
18.6.64									
VI		75 (82½)			16½(13)			8½(4½)	
25.6.64									
VI		77 (81½)			8 (7½)			14½(11)	
III		77 (85½)			9½(6)			13½(8½)	

Station	Percentage in Each Depth Range								
	0-5	0-10 (m.)	5-10	10-15	10-20 (m.)	15-20	20-30	20-42 (m.)	30-42
16.7.64									
IV		66 (75)			25½(16½)		8 (8½)		
VI		54½(60)			21 (12½)			24½(27½)	
III		74½(80)			20½(12½)		5 (7½)		
I		59 (77½)			10 (5½)			31 (17)	
29.7.64									
VI		70 (64)			27½(25)			2½(11)	
III		53 (61½)			44½(32½)		2½(6)		
20.8.64									
VI	42½(54½)		40½(22½)	2½(4)		5½(7½)	7 (9)		2 (2½)
31.8.64									
IV		93 (88)			6 (11)		1 (1)		
II		59½ (53)			36 (4)		4½(43)		
VI		91½(91)			6 (5½)			2 (2)	
1.9.64									
III	66		13	10½		10½	-		-
15.9.64									
IV		35½(70)			11 (14½)		53(15)		
VI		66½(63½)			25½(28½)			8½(8)	

TABLE 18

Date	Depth (m.)	Percentage Distribution of Stages of C. s. abyssorum at S.VI						
		I	II	III	IV	V	♀	♂
14.4.64	0-10	63½	35					
	10-20	34½	58					
	20-42	2	7					
11.5.64	0-5	40	63	76	76½	100		
	5-10	21½	13	15½	18½			
	10-15	11½	10½	8	3½			
	15-20	6½	7	-	1			
	20-30	10½	6	-	½			
	30-42	10	½	½	-			
11.6.64	0-10	85	89	98	97	97	86	74
	10-20	12	10	1½	1	2½	12½	24½
	20-42	3	1	½	2	½	1½	1½
16.7.64	0-10	50	83	93	76	69½	36½	22½
	10-20	50	17	7	12	13½	12	6½
	20-42	-	-	-	12	17	51½	70½
10.8.64	0-5					54½	61½	19½
	5-10					7½	7½	6½
	10-15					4	3½	3
	15-20					1½	1½	6½
	20-30					2½	9½	36½
	30-42					30	16½	28
31.8.64	0-10						88	69
	10-20						2	10
	20-30						2	10
	30-42						8	11
15.9.64	0-10						85½	85
	10-20						12	14
	20-42						2½	1
2.10.64	0-5						47	54
	5-10						17	16
	10-15						30	16
	15-20						2	5
	20-30						1	5
	30-42						3	4

TABLE 19

Vertical Distribution of Mesocyclops leuckarti

Date	Station	Percentage at each depth I	II	III	IV	V♀	V	V♂	♀	♂
14.4.64	0-10				23	18½		23½	32	27
	10-20				9½	18½		14	28	51
	20-42				67½	63		62½	40	52
11.5.64	0-5				62	39		34½	33½	29
	5-10				-	4		-	10½	4
	10-15				-	4		17	17½	21
	15-20				6	-		14	9½	16
	20-30				16	25		10½	16	11
	30-42				16	28		24	13	19
11.6.64	0-10	80	73	56½	66	37½		44½	93	
	10-20	20	27	43½	31	47		44	5	
	20-42	-	-	-	3	15½		11½	2	
16.7.64	Numbers very low but all stages with over 90% in the surface layers									
10.8.64	0-5	68	-	15½	10½		31½		85½	84
	5-10	32	33	12½	18½		15		10	8½
	10-15		34	36	26½		16½		2	1½
	15-20		33	36	41		28½		1	-
	20-30		-	-	3½		8½		-	-
	30-42		-	-	-		-		1½	6

Date	Station	Percentage at each depth								
		I	II	III	IV	V♀	V	V♂	♀	♂
31.8.64	0-10			64½	33½		35½		97½	
	10-20			21	60		46½		2½	
	20-30			14½	5½		17		-	
	30-42			-	1		1		-	
15.9.64	0-10	100	57	57½	53	41½		30	100	
	10-20	-	43	39	41	54½		61	-	
	20-42	-	-	3½	6	4		9		

TABLE 20

Vertical Distribution of <u>Daphnia</u> <u>hyalina</u> var. <u>lacustris</u>

Date	Stn.	Percentage in each depth range 0-5	0-10 (m.)	5-10	10-15	10-20 (m.)	15-20	20-30	20-42 (m.)	30-42	Total Nbr.
15.1.64	VI		23			35½			41½		1108
			42			24			34		900
	III		39			23½		37½			1093
			37			31		32			416
23.1.64	IV		42½			40			19½		912
	VI		46½			35			18½		655
6.2.64	IV			73½ (0-20m.)				26½			866
	I		48½			17½			34		1238
11.2.64	VI		52			35½			12½		1006
24.2.64	VI		49			25			26		317
	III		81½			13		5½			243
2.3.64 (12.30)	VI	27½		54	7½		5½	4½		1	218
23.3.64	VI		45½			19			35½		57
	I		54			30½		15½			99
	II		51½			34½			14		64
	IV		41			23			36		39
3.4.64	VI		25½			19½			55		66
14.4.64	VI		53			24			23		403
	III		29½			50½		20			75
27.4.64	VIa		74			10½			15½		168
	b		100								
11.5.64 (12.30)	VI	43		21½	8½		6½	13½		7	224
11.6.64	VI		74½			23			2½		656
18.6.64	VI		68			30			2		698
25.6.64	VI		34½			58			7½		1452
	IV		70			24		6			881
	III		26			43		31			1478

Date	Stn.	Percentage in each depth range									Total Nbr.
		0-5	0-10 (m.)	5-10	10-15	10-20 (m.)	15-20	20-30	20-42 (m.)	30-42	
16.7.64	III		31½			6½			62		2122
	I		30			8½			61		2493
	VI		15½			20			64½		2846
	IV		29½			11½		59			2469
29.7.64	VI		21½			15½			63		1345
	III		18			16½		65½			1666
10.8.64	VI	4		4½	2		3	33		53½	1138
20.8.64	VI	16½		8	3½		7	45½		19½	552
	I	17½		2½	6		9	53		12	510
31.8.64	II		5			5			90		775
	VI		41			1½		41½		16	502
	IV		42			24		34			249
1.9.64	IIIa	8½		8	1		10	72½			358
	b	22		5	1½		16	55½			252
15.9.64	VI		45½			9			45½		448
	IV		27			7½		65½			416
2.10.64	VI	15		13	5		5	60		2	629
	II		14½			31½			54		1099
	IV		23½			36		40½			681
8.10.64	VI	27½		25		13½			34		666
26.10.64	VI	43½		14½	4½		8½	25½		3½	3306
	I		69½			28		2½			2286
	III		62			15		23			2317
	IV		52			16½		31½			3858
5.11.64	VI	23		17	10		10	33		7	900
23.11.64	VI	19		21½	30		13½	13½		2½	2888
	I		62½			25		12½			1120
	IV		36½			30½		33			9384
14.12.64	VI	39		13	15		9	10½		13½	915
	IV		52½			32		15½			12664
	III		54			30		16			1222
26.1.65	VI		83			8½			8½		1540

TABLE 21

Vertical Distribution of *Bosmina coregoni*

Date	Stn.	Percentage in each depth range 0-5	0-10 (m.)	5-10	10-15	10-20 (m.)	15-20	20-30	20-42 (m.)	30-42	Total Nbr.
13.11.63	VI		8			26½			65½		1182
12.12.63	VI		9½			28			62½		
15.1.64	VI		18			29½			52½		1943
			36			29			35		1664
	III		27½			23		49½			1554
			21½			35		43½			705
23.1.64	IV		42½			33½		24			1862
	VI		31			36			33		1764
6.2.64	IV			73½	(0-20m.)			26½			2334
	I		47			19½			33½		5774
11.2.64	VI		56			32½			11½		3676
24.2.64	VI		49½			28½			22		1256
	III		85			10½		4½			1769
2.3.64 (1230)	VI	48		34	8½		7	2	½		1460
23.3.64	VI		47½			27			25½		1063
	I		59½			21		19½			1538
	II		74			20½			5½		1608
	IV		42			31½		26½			630
14.4.64	VI		41½			32½			26		4737
	III		28½			49		22½			1080
27.4.64	VI		87½			5½			7		1313
11.5.64	VI	15½		8	16½		18½	30		11½	2679
11.6.64	VI	2½		7½	52½			37½			2941
18.6.64	VI		37½			36½			26		1452
25.6.64	VI		5½			6½			88		980
	IV		17½			54½		28			
	III		9½			34½		66			822
8.10.64	VI	23½		3½		39			34		112
26.10.64	VI	21		5	11		34½	11		17½	391

Date	Stn.	Percentage in each depth range									Total
		0-5	0-10 (m.)	5-10	10-15	10-20 (m.)	15-20	20-30	20-42 (m.)	30-42	Nbr.
26.10.64	I		27			40½		32½			552
(Contd.)	III		52½			24		23½			182
	IV		17½			57		25½			262
5.11.64	VI	6½		2	2		11½	25½		52½	395
23.11.64	VI	16½		7½	14½		9½	30½		21½	367
	I		38			38		24			740
	IV		22½			40½		37			735
14.12.64	VI	33		24½	16½		12	12½		1½	614
	IV		64			29½			6½		3563
	III		50			38½		11½			540
26.1.65	VI		78			11			11		516