THE ZOOPLANKTON OF LOCH LEVEN

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A. SUMMARY

1. The zooplankton of Loch Leven in 1969 is described.

2. The crustacean holoplankton was almost entirely *Cyclops strenuus abyssorum* Sars and only a few individuals of *Diaptomus gracilis* Sars and *Bythotrephes longimanus* Leydig were found. The most common rotifer was *Keratella cochlearis* Gosse.

3. Use was made of fluctuations in standing crops of the developmental stages and of a biometric analysis of the adult females of *C. s. abyssorum* to interpret the annual cycle.

4. *C. s. abyssorum* overwintered mainly as adults, giving rise to nauplii in March, and there was continuous reproduction thereafter until November.

5. The mean, maximum standing crop of individuals occurred in June when there were 1460/5 litres, comprising mainly copepodid stages and the peak of numbers of adults occurred in August (225/5L).

6. The egg stock was greatest in May and early June, when large females were producing large clutches of eggs, and in August, when small clutches were carried by a large number of small females.

7. Adult males were normally in excess of females and it is suggested that differential predation on the adults by fish may have been responsible.

8. Calculations of field developmental rate revealed that the females had a total developmental time of 85 days at 5°C, 46 days at 10°C and 25 days at 15°C and approximately six generations were possible in the year.

9. Differential vertical aggregations by age and sexual groups were noted, particularly in July and August, and a transitory thermocli in June resulted in no copepods being found deeper than 10 metres.

10. The older copepodids and adults are omnivorous, feeding upon large phytoplankters, their own younger stages, rotifers and chironomid larvae,

11. The seasonal changes in biomass of the copepod population were calculated by an approximate length/weight conversion formula, using known lengths of developmental instars and their numbers throughout the year.

12. Expressed in mean,,monthly units of energy per unit of surface area the standing crop rose in March from a winter level of 1 $kcal/m^2$ to a peak of 24 $kcal/m^2$ in July and declined thereafter until January. The seasonal, maximum standing crop occurred in early July (34.7 $kcal/m^2$) and the mean, annual level was 8.4 kcal/

13. A tentative estimate of annual production is 64 – 162 $kcal/m^2$.

14. The zooplankton of Loch Leven is compared with that in other lakes and the possible causes of the lack of filter feeding crustaceans are discussed.

B. INTRODUCTION

I. Aims and Reasons for the Study

In 1966 an International Biological Programme freshwater productivity study was initiated at Loch Leven, Kinross-shire, Scotland as a joint project between the Nature Conservancy, the Freshwater Fisheries Laboratory and the Wildfowl Trust. Rapidly supplemented by University workers, the project is now the combined part or full-time work of twenty one research scientists whose ultimate aim is to measure productivity at different trophic levels leading to fish and diving ducks.

A study in order to provide basic information about the zooplankton of the loch was undertaken in 1969-70 and is the basis of this thesis. The aims of the research were to assess the quality and quantity of the zooplankton, its temporal and spatial variation and its importance in the food web.

C. **REVIEW**

I. The Study Area

The study area has been described by Morgan (1970) and is summarised as follows: Loch Leven lies on the Plain of Kinross between Perth and Edinburgh (fig. 1, inset A), longitude 3°22'W and latitude 56°12'N, at an altitude of 107m. The bedrock is old red sandstone overlain with glacial drift and the lake fills a depression left by melting ice. The loch occupies 13.3km^2 and is relatively shallow, having a mean depth of 3.9m. However, there are two 'kettle holes' of 23 and 25.5m depth (fig. 1). About 70% of the catchment area is rich farmland and there are three main inflow streams, the North and South Queichs and the Gairney Water (fig. 1, inset B). The loch is drained to the east by the River Leven, the discharge into which is controlled by sluice gates. Lying within a wedge of hills, Loch Leven is frequently subjected to strong wind-induced circulation and severe wave action.

Loch Leven has long been known as an important trout fishery and as a wildfowl habitat. It was declared a National Nature Reserve in 1964.

II. Recent Changes at the Loch and Eutrophication

Although Loch Leven is naturally eutrophic, the rate of eutrophication is being increased by man. Large quantities of nitrogenous fertiliser are used by local farmers and much of this leaches into the loch.

In/.....

Figure 1 (opposite)

Loch Leven and Sampling Sites

(diagram by courtesy of The Nature Conservancy)

Depth contours in metres are shown by thin lines.

Sampling sites are designated (X1) etc. and all sites were sampled on 'major visits' while on 'minor visits' only the first two were visited.

The inflow streams in clockwise rotation from the map base are the Gairney Water, the South Queich, the North Queich and the Pow Burn. The outflow, by way of a sluice, is into the River Leven.

The islands are shown bounded by thick lines.

Inset A

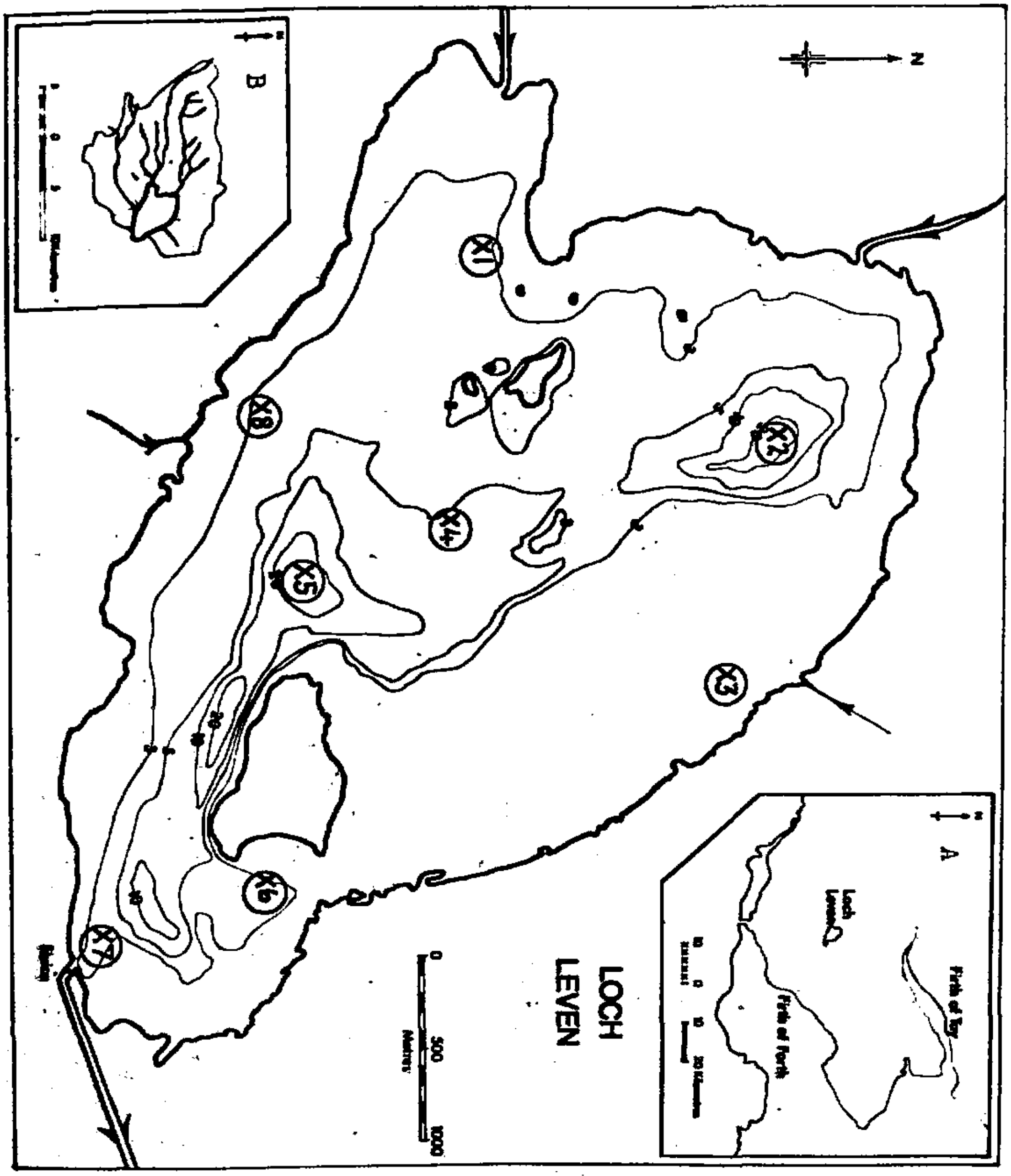
Loch Leven in relation to Fife and to the Firths of Tay and Forth

Inset B

The Drainage System leading to Loch Leven

(Loch Leven is shown bounded by the thick line)

Figure 1


LOCH
LEVEN
A
B
N
Loch Leven
Firth of Tay
Firth of Forth
0 500 1000
Metres
X1
X2
X3
X4
X5
X6
X7
X8

In addition the input of phosphate is excessive because of effluents affected by detergents from a local woollen mill and domestic sewage from Kinross and Milnathort.

The loch was contaminated by a discharge containing the chlorinated hydrocarbon pesticide Dieldrin from the woollen mill until the use of the chemical was discontinued in 1964. (Holden 1966).

Although several changes in the biota of a lake are to be expected in the normal course of eutrophication, there have been several marked fundamental changes in recent years in Loch Leven which are more difficult to explain: a large qualitative and quantitative decline in the occurrence of macrophytes, a succession of prolonged 'blooms' of blue green algae and diatoms, a decline in the number of species of green algae, a change from a zooplankton dominated by Daphnia hyalina var lacustris Sars to one dominated by Cyclops strenuus abyssorum Sars with an apparent disappearance of the former species, a decline in the number of species and biomass of benthic invertebrates, a decline in the number of wildfowl coming to the loch to moult, and a decline in the quality of the angling fishery for brown trout.

III. Changes in the Zooplankton

Scott (1898) in a survey of the invertebrate fauna of the inland waters of Scotland, reported that the Loch Leven zooplankton was dominated by Daphnia lacustris Sars (D. hyalina var. lacustris Sars) with Diaptomus gracilis Sars and Cyclops strenuus Fischer common.

He/.....

He also found Bythotrephes longimanus Leydig and Leptodora hyalina Lilljeborg present at times. Collecting near the shore and the weed beds he found thirty eight species of copepods and cladocerans (see Results, section II).

In 1954, Woodward (pers. comm.) recorded C. strenuus, D. gracilis, D. hyalina var lacustris, B. longimanus, Chydorus sphaericus (O.F. Müller) and Bosmina coregoni var obtusirostris (Sars) present in three pump samples taken from Kinross pier.

During phytoplankton sampling visits to Loch Leven in 1967 and 1968, Bailley-Watts collected seventeen zooplankton net haul samples, which were preserved and later examined by the author preparatory to the present study. Cyclops strenuus abyssorum was consistently and overwhelmingly dominant, with D. gracilis making up about 5% of the specimens caught. Leptodora kindti (Focke) and Bythotrephes longimanus were present in small numbers in the autumn, while Daphnia spp. and Bosmina spp. were not found at all. Effectively there was a zooplankton community dominated by the copepod C. s. abyssorum. It is extremely unusual for any zooplankton community to be dominated by a non-filter feeder.

IV. Review of Cyclops strenuus

1. Taxonomy

Cyclops are freeliving, cyclopoid, copepod crustaceans living mainly in freshwater, with a world-wide distribution.

Their/.....

Their developmental forms and structure have been described by Gurney (1931-33). The taxonomy of the group has been subjected to periodic reassessment and Harding and Smith (1960) report three genera, with ten subgenera and forty eight species in Britain, occupying niches in the benthic, littoral and limnetic zones of standing bodies of water.

Cyclops strenuus, in the genus Cyclops and subgenus Cyclops, has been described as a very variable species, or as a group of species. Gurney (1933) observed that "in a species so variable as this it is difficult to decide what form of it should be regarded as 'typical'." Kozminski (1927, 1932) stated that practically every author who had discussed the species found differences between their species and previous descriptions. Fryer (1954) considered Cyclops strenuus in the English Lake District from a systematic point of view and, while noting divergencies from the "typical" form of Sars (1913-18) and Kozminski, regarded these as being within the variability range of the species.

In Britain, two basic "types" of Cyclops strenuus are described by Harding and Smith; Cyclops strenuus (S. str.) (Fischer) and C. strenuus abyssorum Sars.

According to Harding and Smith, the S. str. form is the larger, the adult females ranging from 1.66mm to 2.35mm in length (minus furcal setae), whilst those of the abyssorum form range from 1.20mm to 1.47mm.

C./....

C. strenuus females from Loch Leven range from 1.47mm to 2.35mm, yet conform in all other respects to the description of the abyssorum form. It can be tentatively suggested that the Loch Leven form may be termed Cyclops strenuus abyssorum.

Clearly the taxonomy of the C. strenuus group is ambiguous. However it is important to make as precise a definition of the Loch Leven form as possible so that fair comparisons with the work of other researchers may be made. Therefore microphotographs of some of the more taxonomically salient features of the Loch Leven form are presented in Appendix 1.

2. Ecology

Cyclops strenuus is found in temperate and arctic regions (Smyly, 1968) and is rather rare in the U.S.A., although collected in Alaska (Wilson and Yeatman, 1959).

C. strenuus (S. str.) is rare in Scotland but very common in small ponds throughout England although not certainly described in the Lake District, while C. s. abyssorum is the commoner form in Scotland and the Lake District, living in the open water of lakes (Harding and Smith, 1960).

Smyly (1968) noted that C. s. abyssorum and Mesocyclops leuckarti (Claus) were the common limnetic species in the Lake District.

They/.....

They occurred together in three lakes, where their competition was restricted by differences in their depth distribution and seasonal cycles, and C. s. abyssorum was found alone in eleven of the lakes studied. Chapman (1965) found C. s. abyssorum together with M. leuckarti in Loch Lomond. However M. leuckarti is a temperate and tropical zone species (Smyly, 1968) occurring in the Lake District and Loch Lomond at the northerly limits of its range.

Gurney (1933) suggested that C. s. abyssorum has a monocyclic annual cycle, breeding in late summer and autumn. Chapman (1965) found that the species was monocyclic in Loch Lomond, breeding from June until early autumn. On the other hand, Smyly (pers. comm.) has found its annual cycle to be very variable, being monocyclic in some lakes and polcyclic, with continuous reproduction, in others.

It has been demonstrated that several species of Cyclopoida undergo resting stages during inclement periods such as in winter, or in mid-summer when temporary pools may dry up; Cyclops bicuspidatus thomasi Forbes (Cole, 1953), Mesocyclops leuckarti (Fryer and Smyly, 1954; Smyly, 1961 a, b), Mesocyclops oithonoides Sars (Elgmork, 1958), Cyclops strenuus strenuus (Elgmork, 1955, 1959) and Cyclops abyssorum Sars (Wierzbicka, 1962). Some species encyst during the period of quiescence; Microcyclops bicolor Sars (Fryer and Smyly, 1954).

Smyly (1961 a, b) found that Mesocyclops leuckarti overwintered as stage IV copepodids in the bottom deposits of Esthwaite Water, while Chapman (1965) deduced that Cyclops strenuus abyssorum in Loch Lomond overwintered as resting eggs, as the adult population died out in the autumn and the planktonic population consisted of young copepodids in the following early spring. Wierzbicka (1962), on the other hand, observed adults of Cyclops abyssorum (C. s. abyssorum) fall into mud and burrow down, remaining there for long periods.

Some Cyclops spp. are strongly carnivorous and although this was first recorded by Jurine (1820), Birge (1897), Naumann (1918) and Klugh (1927), there were only scattered references to the diet of Cyclops spp. until Fryer (1957 a, b) recorded the predatory behaviour of several cyclopoid species including C. s. abyssorum. He noted that the latter species was an active, planktonic predator, feeding chiefly on the calanoid copepod Diaptomus gracilis (Sars), and presumed that in waters where no calanoid copepod was available as a food item, Cladocera and rotifers would form the main food of the species. He found that a limited amount of algae was also ingested but considered that most of it might have been in the guts of prey animals. However Southern and Gardiner (1926) recorded diatoms in Cyclops strenuus (presumably C. s. abyssorum.

Fryer also reported that the predatory cyclopoids eat their own nauplii and copepodids, and McQueen (1969) has quantified cyclopoid cannibalism.

During/....

During the summer of 1967, C. b. thomasi copepodids IV and V and adults were estimated to have eaten 31% of their own nauplius standing stock in addition to 30% of a diaptomid nauplius standing stock.

V. Zooplankton Sampling

Zooplankton sampling has been effected by several means and the history of the subject has been reviewed by Fraser (1968). All of the methods have particular advantages for specific tasks and particular disadvantages to balance against them.

Simple towed nets have frequently been used and are excellent for qualitative investigations. However their quantitative use is restricted as their meshes tend to progressively clog with phytoplankton so that filtering efficiency alters throughout tows. Clogging can be partially overcome by using the maximum mesh size which is possible for the investigation in hand and by towing the net through as short a distance as possible. Filtering efficiency can be monitored by placing a flowmeter inside the mouth of the net and another outside it and calculating the volume filtered by the difference between the flowmeter readings. Filtering efficiency can also be improved by truncating the net mouth so that the area of filtration is great compared with the volume of the net mouth.

The Clarke-Bumpus sampler (Clarke and Bumpus, 1950) is a sophisticated towed net incorporating a flowmeter, a truncated entrance and an opening and closing device.

The latter enables the net hauls to be broken into stages and allows the operator to define the limits of the tow. Because of the often-reported uneven horizontal and vertical distribution of zooplankton sampling is necessary in both planes. This can be effected either by a series of vertical hauls at different sites, a series of horizontal hauls at different depths, by oblique hauls or by oscillations incorporating simultaneous vertical and horizontal towing, thus providing integrated samples of animals in both planes. The Clarke-Bumpus sampler has the advantage of filtering a large volume of water during a tow, thus helping to obviate the patchiness of the plankton. However it is rather inefficient when fine meshes are used (Langford, 1952). It is also more likely to be of use in a fairly deep body of water, since in a shallow one, such as Loch Leven, it may be in danger of touching the lake bed, which will render the sample useless and possibly damage the mechanism of the sampler.

Various pumps have been used for collecting zooplankton by drawing water upwards and then through a collecting mesh. The intake can be raised or lowered in the water column and the pump can be operated from a moving punt or boat so that horizontal, vertical, oblique or oscillating samples can be obtained (Colebrook, 1960). The volume of water containing the organisms can be accurately determined and thus the samples are likely to be highly replicable.

However/.....

However zooplankters are known to actively avoid an intake current (Fleminger and Clutter, 1965; Szlauer, 1968) and only motorised pumps are likely to be effective because of their fast intake rate. Such a pump requires a relatively large boat for transportation. Also the sampling depth is limited by the length of piping required.

Traps or bottle samplers can be effective, being lowered into the water to the required sampling depth with lids at top and bottom open. A messenger lead is sent down the line to a trigger mechanism and the lids spring shut. In this way a known volume of water is collected from a known depth. It can then be filtered for the desired organisms. The intrinsic efficiency of this method is unlikely to alter much between samples, although Smyly (1968) showed that unless the bottle or trap is closed at or immediately after it has reached its sampling depth, the organisms within it are likely to escape progressively. This can be overcome by timing the release of the messenger so that the lids close immediately the sampling apparatus reaches the required depth.

The trap or bottle is very simple and yet the quantitative results obtained by it can be directly compared with those obtained by similar apparatus used by other workers. This is certainly not the case in the use of towed nets. The main disadvantage is that each sample is from a very small volume of water compared with that sampled by nets or pumps.

Most/.....

Most traps or bottles used in freshwater zooplankton investigations are of five litres capacity, as this makes them convenient to lift and operate. It is therefore necessary to collect a large number of samples, the examination of which is time-consuming.

Essentially similar in effect to traps or bottles are tubes which are quickly lowered and closed (Pennak, 1962; Applegate, Fox and Starostka, 1968). This method is of course depth-limited, but should be excellent for shallow areas.

For the purpose of productional studies of freshwater zooplankton the water bottle sampler has been recommended by the I.B.P. Committee for the Measurement of Secondary Production (handbook in press) because of its ready comparability. The type of bottle used should have lids which do not impede the flow of water through the tube when tha apparatus is heing lowered. The Van Dorn Sampler, for example, has cup-shaped lids which may restrict water flow. However the Friedinger, Rodhe (1946), Bernatowicz (1953) ot Patalas (1954) types are thought to be suitable.

MATERIALS AND METHODS

D.

I. Sampling Procedure

A Friedinger water sampler, as modified by Mr. H.C. Gilson of the F.B.A. Windermere Laboratory (plates 1, 2, 3) was used to collect five litre samples throughout the period from January 1969 to January 1970. A small filtering cylinder (plate 4) with a 119 microns stainless-steel mesh was screwed to the base of the sampler after each sample was obtained. By opening a valve on the base of the Friedinger sampler the water was released and filtered, collecting most of the zooplankton in the perspex funnel base of the filter. The resultant water and zooplankton was then poured through a tap into a numbered polythene 3" x 1" tube, containing two mls of 40% formalin coloured by lignin pink or chlorazol black, to preserve and stain the animals. Three washes of the filter with tap water were then added to the tube, diluting the preservative to approximately 5% formalin.

Sampling was undertaken from a 12' rowing boat to which was attached a davit and winch for raising and lowering the sampler (plates 1, 2, 3). The boat was propelled by a 9½ H.P. outboard engine.

Sampling was divided into 'major' and 'minor' visits. On the major visits to the loch, which took place at least once a month, eight sites were sampled (fig. 1).

These/.....

Plate 1 (opposite)

5 litre Friedinger Sampler (as modified by H.C. Gilson - F.B.A., Windermere)
lids closed.

Plate 2 (opposite)

Sampler with lids open.
Winch, davit and messenger lead.

Plate 3 (opposite)

Sampler with lids open.

The sampler was raised and lowered on a braided nylon cord with metre markings. The lids were closed when the messenger released a spring-loaded catch on the top of the sampler frame.

Plate 1

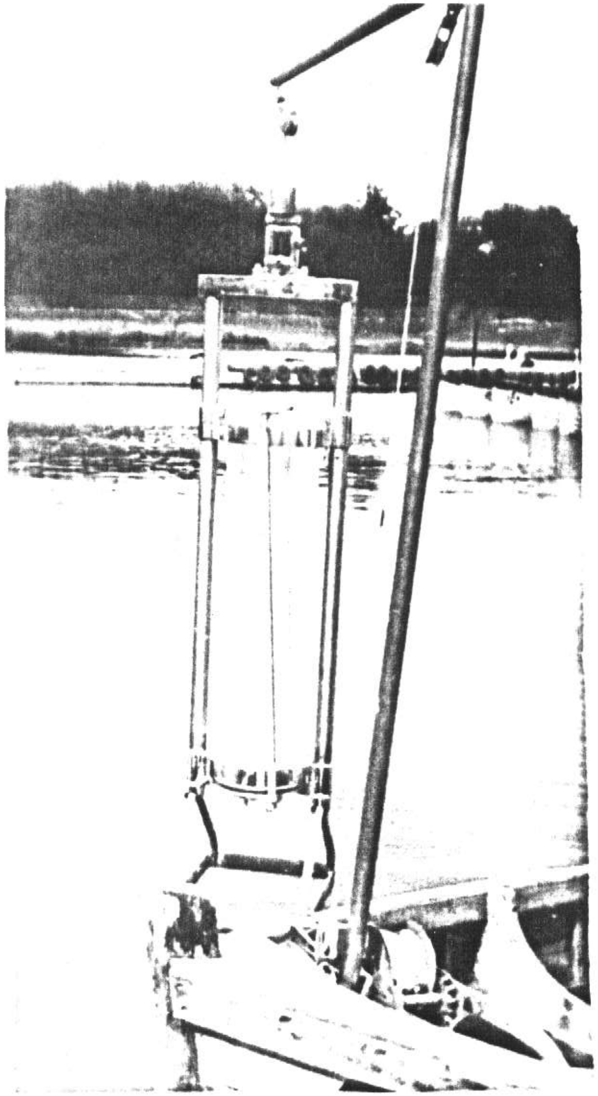


Plate 2

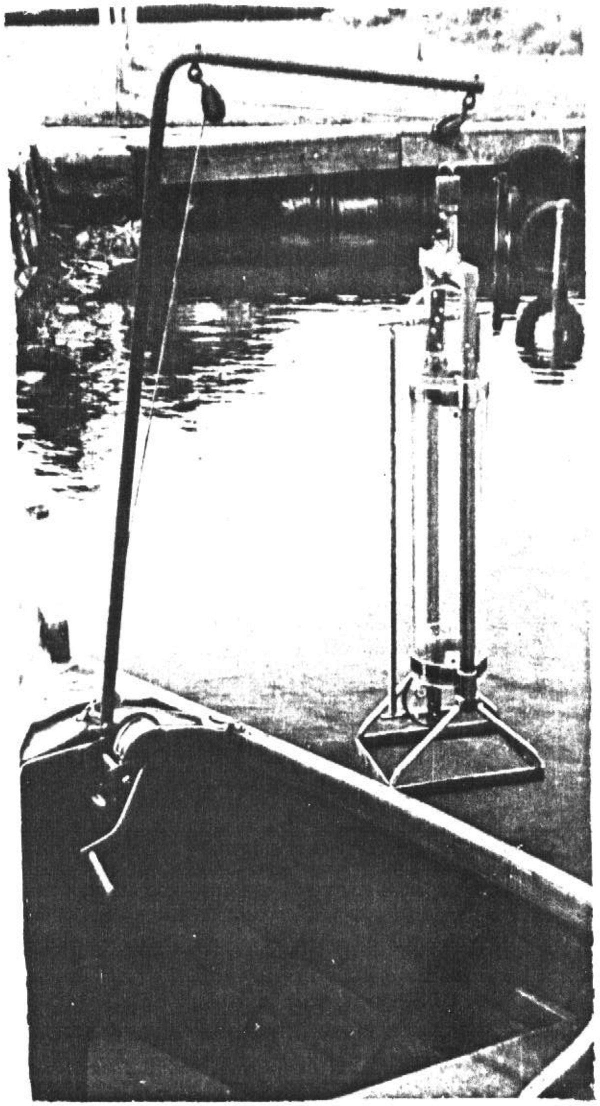
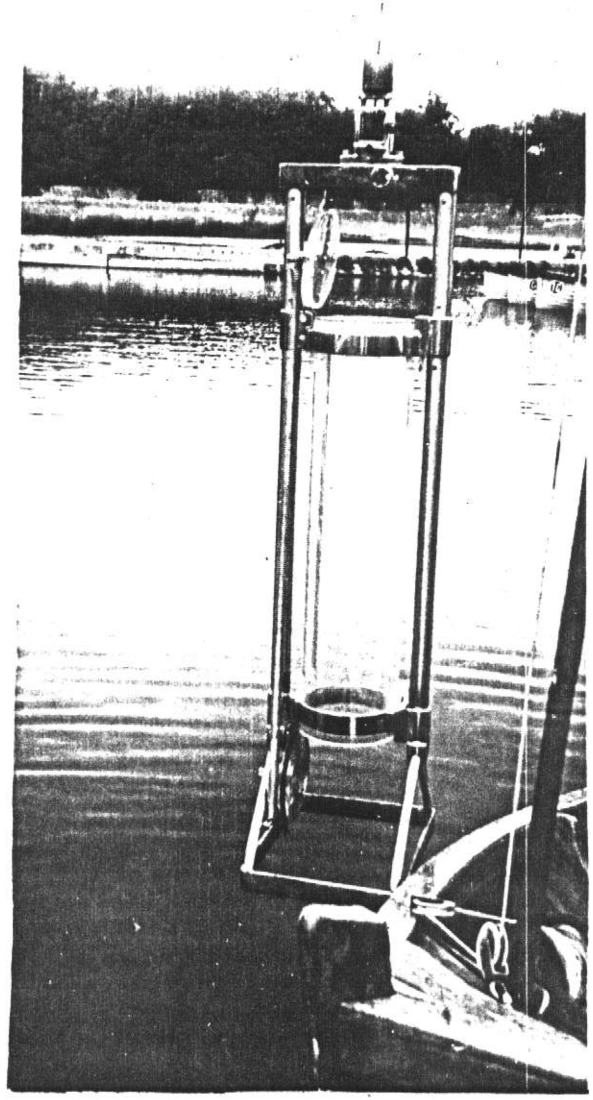


Plate 3



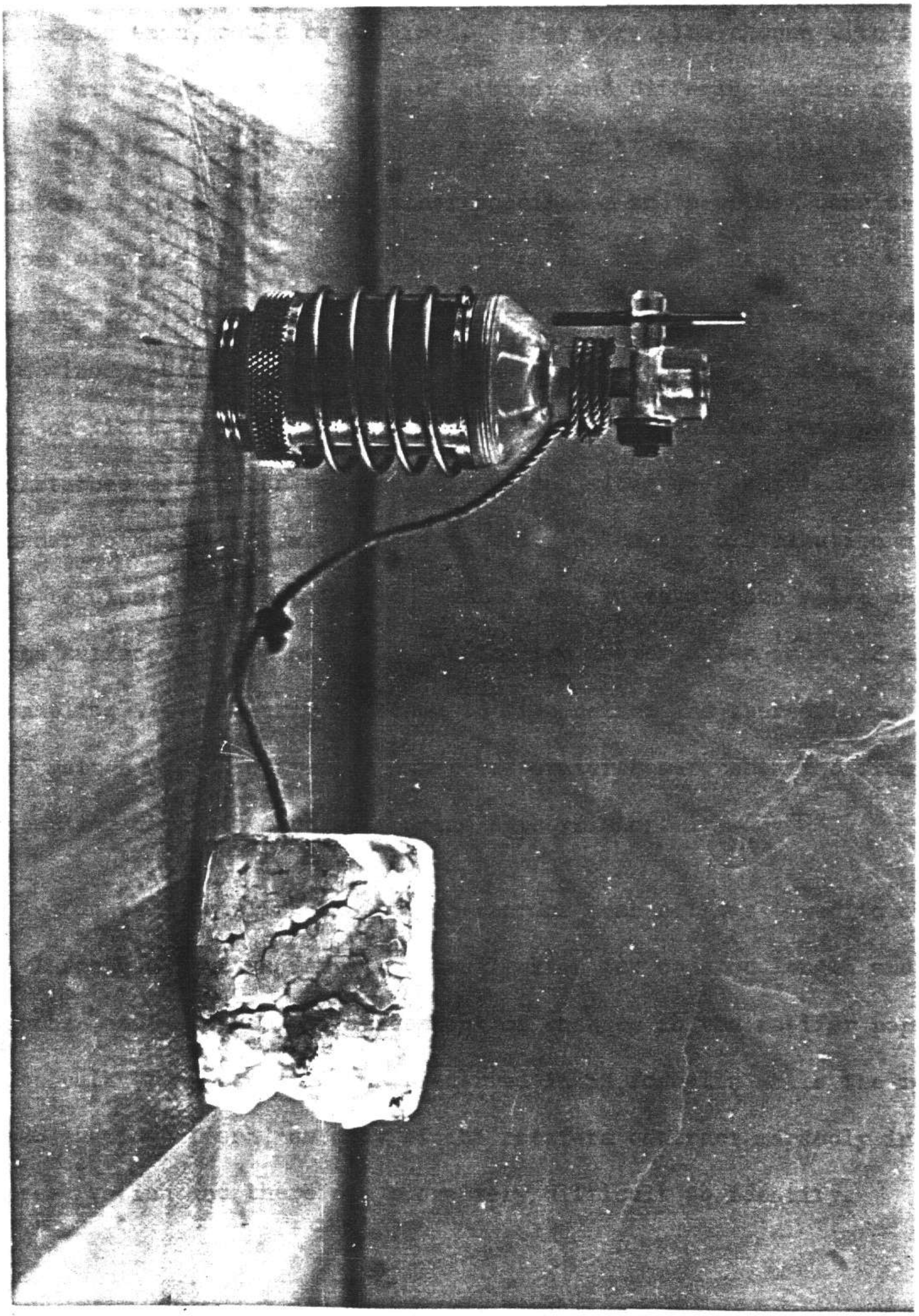
These were chosen with regard to their position in the loch so that transect lines in at least three directions, having at least three sites on each, could be obtained. They were also chosen with regard to their depth so that sites of similar and differing depths could be sampled. Minor visits were undertaken at more variable time intervals depending upon weather conditions and seasonal considerations. More sampling visits were necessary in the summer than in the winter because of the rapidity of population changes in the warmer conditions. On minor visits, one shallow and one deep site, the first two of the major visit, were sampled. However on five occasions this pattern was disturbed due to bad weather. Sampling sites were visited in a definite order so that temporal changes in the zooplankton distribution might be regularised. Replicated samples were taken at each metre depth from the surface to five metres. At the two deeper sites (nos. X2 and X5), sampling was similarly effected to five metres and thereafter at 10 metres, 15 metres and 20 metres. Water temperatures were obtained from each sampling depth at each site using a thermistor.

On each sampling visit a 63 microns mesh net was towed to obtain a large qualitative sample of zooplankton for copepod length and egg-number analysis and for assessment of changes in the rotifer population. The bulk of this sample was preserved in 5% formalin while the remainder was examined fresh, as many of the rotifers contract markedly in preservation and therefore prove very difficult to identify.

Plate 4 (opposite)

Zooplankton Filter with stainless-steel mesh (119 microns).

The filter was screwed to the lower lid of the Friedinger and the water was released by the operation of a valve on the base. The polystyrene 'float' facilitates recovery of the filter if it is dropped overboard.



The fresh sample was also used for selecting copepods for gut analysis (see Results, section 3).

II. Laboratory Assessment of Samples

Individual tubed samples were pipetted into a revolving counting trough (plate 5) adapted from Ward (1955) and Warren (1958) and constructed in the workshop of the University of Stirling. The counting trough consists of a 0.5mm deep groove in a perspex disc which revolves on ball bearings on a base which has four legs of adjustable length. The groove is 0.7mm wide, being slightly less than the field of the Bausch & Lomb Zoom Binocular microscope used to study the trough contents. By slowly revolving the disc by hand, the zooplankton sample, whose limits were fixed by a block in the groove, could be fully enumerated. All organisms other than the rotifers were counted and identified. In practise, there were very few apart from *Cyclops strenuus abyssorum*. The copepods and cladocerans which could not be readily identified under the binocular microscope were removed and identified to species using Harding and Smith (1960) and Scourfield and Harding (1966). Chironomid larvae, oligochaetes, nematodes and water-mites were not identified further. All samples were retained in 5% formalin after examination.

C. s. abyssorum individuals were identified as nauplii (all five instars grouped) and separate copepodid instars I - VI.

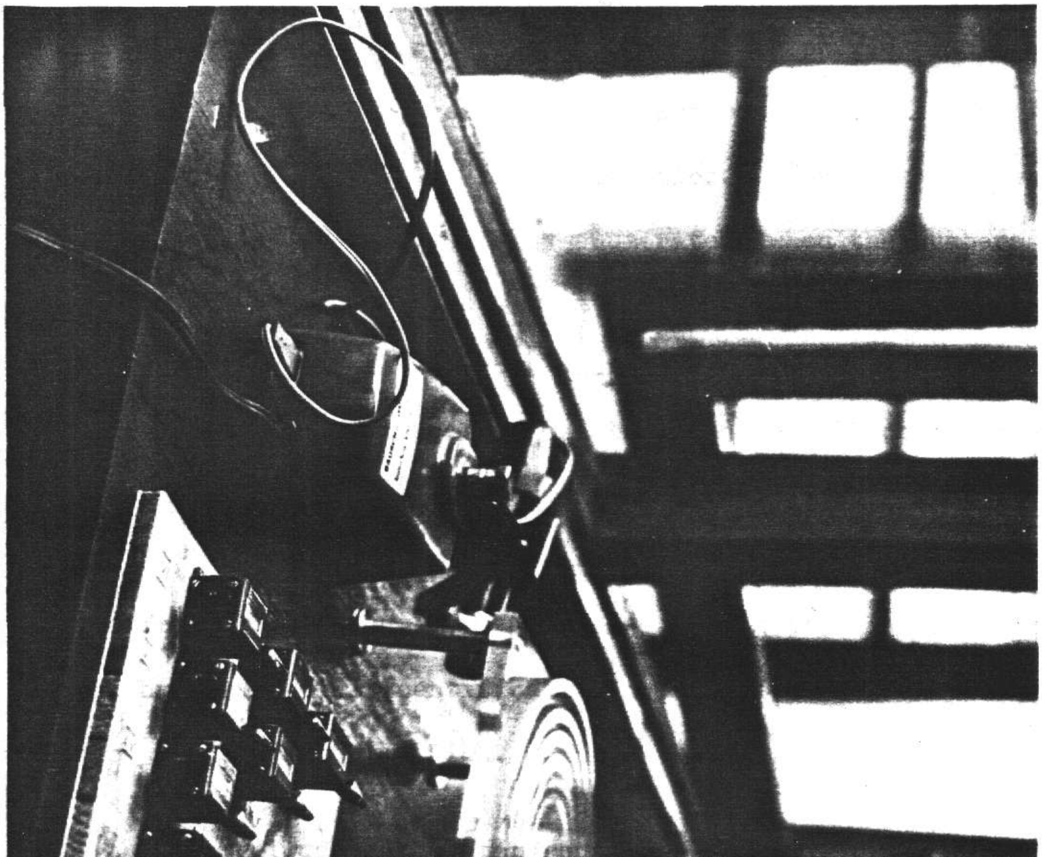
Sexes/.....

Plate 5 (opposite)

Zooplankton Counting Trough, Binocular Microscope and Tap Counters.

The counting apparatus consisted of a perspex disc with a groove into which the zooplankton sample was pipetted. The disc was then slowly rotated on ball bearings while the sample was examined using a Bausch and Lomb Binocular Microscope and enumerated using the tap counters.

Plate 5



Sexes were differentiated at instars V and VI (adult). Adult females were recorded as ovigerous or non-ovigerous and all egg sacs were counted, attached or otherwise. In practise it proved possible to identify the copepodid stages and sexes but copepodids III and IV presented some difficulty in differentiation. Consequently, whereas the other stages were always fully enumerated, when the numbers of the C.IIIs and C.IVs were in excess of about one hundred per sample, only a sub-sample, varying between one quarter and one half, of these were identified. The difference between the count of all copepodids in the sample and the sum of the fully enumerated ones gave the total of C.IIIs and C.IVs. This total was then divided in proportion to the figures derived from the sub-sample. The sub-sampling technique was occasionally checked by doing total identification counts after sub-sampling and the accuracy was consistently high.

A series of mechanical tap counters (plate 5) was used to record the different stages and sexes as they passed through the microscope field. Number 00. entomological pins set into sealing wax in glass tubes were used to manipulate the animals when necessary and the 'zoom' magnification of the microscope (28X - 120X) was used when greater detail was needed for instar identification. With practise this technique proved speedy and accurate. Length measurements of the copepods were made using a Reichert Visopan Projection Microscope and specially-calibrated ruler. The counts of number of eggs per egg sac were made by teasing egg sacs apart with dissecting pins and counting the eggs under the binocular microscope.

E. RESULTS

I. Cyclops strenuus abyssorum

1. Annual Cycle

By differentiating copepods into age groups or instars and examining standing crops throughout the year it may be possible to determine successional changes in a population. However, the standing crop is a measure of the numbers of animals present at an instantaneous moment in time and may give no direct information on the turnover or rate of change within the population. The number of animals found in a particular instar at any moment depends on the time which is spent in that instar and, therefore, the standing crop of an instar which takes a relatively long time to pass through will be consistently greater than that of an instar which may be undergone more rapidly. If the population has an extended breeding period or breeds continuously, it may be impossible to detect the progress of individual groups or cohorts of animals through the successive instars by using standing crop data. If a cohort of copepodid III moult to CIV, one might expect that the number of animals in the CIII instar will fall and the number of animals in the CIV instar will rise. However moulting to the CIII instar by some of the CII animals and to the CV instar by some of the CIVs will obscure the actual 'flow' of animals through the population.

Therefore standing crops alone are not always sufficient for determining copepod annual cycles.

However/.....

However, using supplementary information derived from body-length measurements and changes in breeding parameters, they can be used as a basis for such a study.

(a) Quantitative Standing Crops (Fig. 2)

The Cyclops strenuus abyssorum population at Loch Leven remained essentially planktonic throughout the year with continuous reproduction occurring, the rate varying with temperature.

The small, overwintering population comprised mainly adults (10/5 litres) and a few individuals of each of the developmental instars. The egg stock of this small population, calculated from the mean number of egg sacs carried by the adults per five litres multiplied by the mean number of eggs per egg sac (section c), was about one hundred. After continuous icecover throughout February and early March 1969, the water temperature rose steadily during the spring (fig. 3). Sampling after the ice had broken up revealed that the winter egg stock had fallen and the numbers of nauplii and copepodid I (CI) had risen by approximately the same amount, implying that the first increase in population after winter came from the eggs carried by the overwintering adults rather than from resting stages of development. The progeny of the overwintering adults then moulted through successive instars and some reached the adult stage (CVI) by the middle of April. The adult population then stabilised at about 30 - 40/5 litres, whilst the numbers of the developmental instars dropped.

During/.....

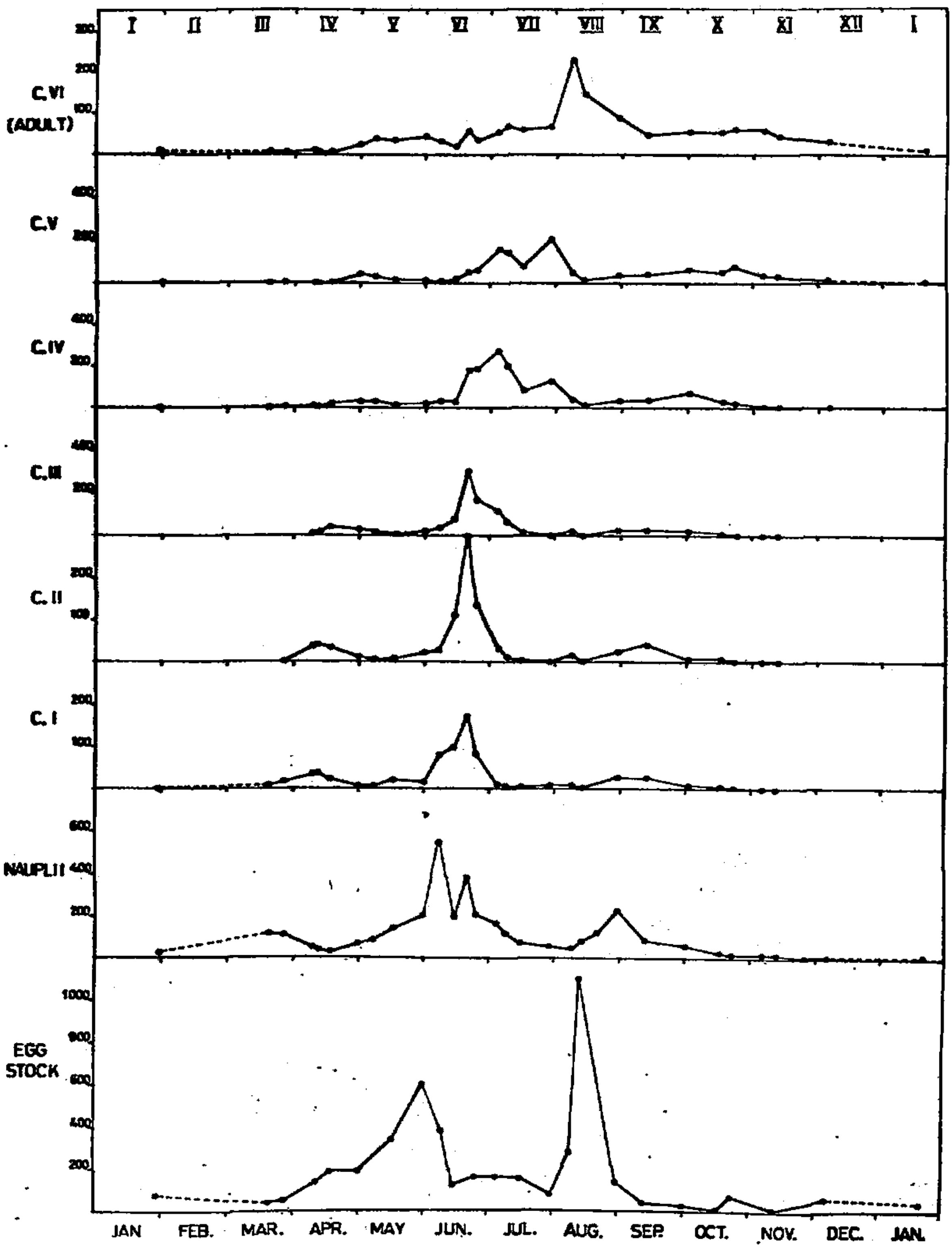
Figure 2 (opposite)

The Standing Crops of Cyclops strenuus abyssorum in Loch Leven in 1969/70

(mean numbers per 5 litres)

The Abcissae	-	the sampling period
The Ordinates	-	mean numbers per 5 litres of eggs, nauplii, copepodid instar I (CI), CII, CIII, CIV, CV and CVI (adult).
Egg Stock	=	mean number of egg sacs/5L x mean number of eggs/egg sac.
Nauplii	=	all naupliar instars grouped
-------	=	intermittent or continuous ice-cover

Figure 2



I
II
III
IV
V
VI
VII
VIII
IX
X
XI
XII
I
C.VI (ADULT)
C.V
C.IV
C.III
C.II
C.I
NAUPLII
EGG STOCK
JAN
FEB.
MAR.
APR.
MAY
JUN.
JUL.
AUG.
SEP.
OCT.
NOV.
DEC.
JAN.

Figure 3 (opposite)

The Water Temperature at the North Deeps (X2) of Loch Leven 1969/70

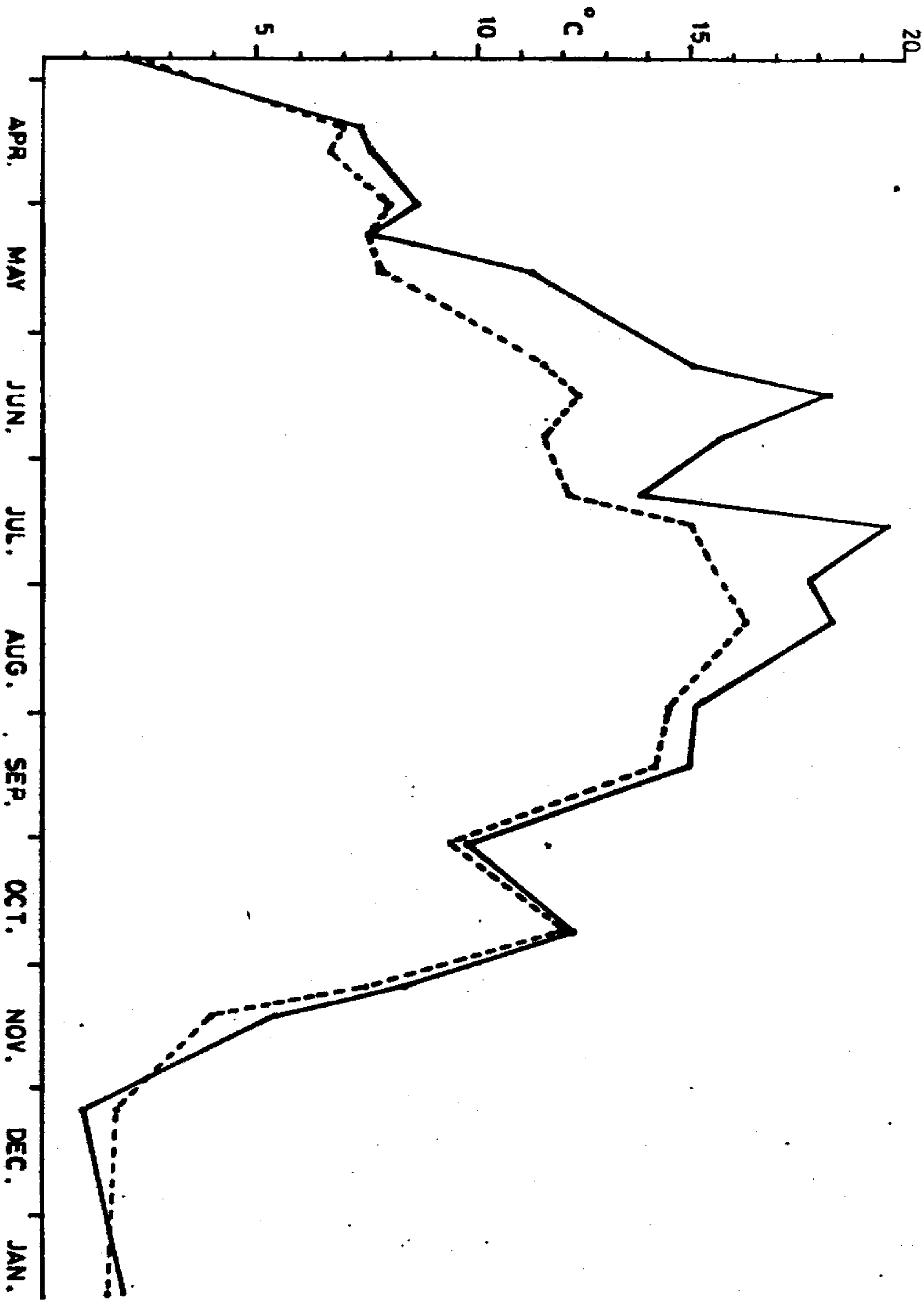
The Abcissa - the sampling period

The Ordinate - the water temperature in degrees Centigrade as measured by a thermistor

The solid line designates the surface temperature

The broken line designates the bottom temperature

Figure 3



During March, the egg stock carried by the overwintering adult females began to rise steadily and was soon supplemented by eggs carried by the newly-matured spring adults. The naupliar numbers steadily rose from mid-April, affecting the successive copepodid instars until the adult population was once more incremented in early June. Because of the rise in water temperature throughout spring and early summer, the developmental instars were undergone with increasing rapidity until the effects of the prolonged period of breeding made it impossible to follow the growth of specific animals. The population built up in June to a mean, maximum standing crop of 1460 individuals/ 5 litres comprising mainly copepodid stages and with about 50 - 60 adults/5 litres.

Owing to a reduction in the mean number of eggs carried by the adult females, the egg stock fell sharply in June and remained at less than 200/5 litres during July, when water temperatures were at the seasonal maximum.

In July, the animals passing through the developmental stages of the continuously-breeding population were only observed in large numbers in the older instars, where it appeared that there was a temporary delay in maturation. The build-up of CIVs and CVs matured into the adult stage in August and the mean, maximum standing crop of adults during the season (225/5 litres) was recorded in the second week of the month.

The dramatic adult increase in standing crop resulted in a very large egg stock (1100/5 litres), which arose and declined in August, providing autumnal increases in the older stages. The adult population fell from its early August peak to a steady level of about 50/5 litres, then gradually declined from November until January to the overwintering level (10/5 litres), after the younger instars had slowly declined in turn.

A slight rise in egg stock in October, concurrent with a rise in the previously cooling water temperatures, had no effect on the numbers of the nauplii or copepodids in the rapidly cooling conditions which prevailed in November and December.

(b) Body-Length Analysis

Many workers on copepods have noted that the lengths of the adults tend to follow a seasonal pattern, probably related to temperature modified by food availability during their development (Coker, 1933; Deevey, 1960; McLaren, 1963; Smyly, 1968), as successive adults mature into the existing population and this has been used as a means of elucidating the adult turnover (Tonolli, 1964; Chapman, 1969). In the present work, an attempt has been made to analyse the adult female population throughout the year by using body-length as a 'biological tag'.

For/.....

For comparison with the results of previous work on C. strenuus, measurements were made of the total body-length minus the furcal setae, the metasomal length and the cephalothoracic length (fig. 4). Fifty adult females were measured per sampling visit. Distribution histograms of their metasomal lengths are presented in figure 5 (cephalothorax ≙ 60% and total length minus setae ≙ 170%, of metasome).

The overwintering females were of body-length (metasome) 0.90 - 1.20mm with a modal length of 1.00 - 1.10mm. Slightly larger individuals began to appear in late March and became increasingly apparent in April. Within the first fortnight of May the overwintering females disappeared from the population and a group of larger females (1.20 - 1.50mm) became dominant. These in turn began to die off and were replaced by successive influxes of smaller females in June. By the middle of the month the modal length had fallen to 1.10 - 1.20mm and was continuing to decrease. The population in July had a modal length of 1.00 - 1.10mm with a broad range of 0.80 - 1.40mm, while only a few individuals occurred at these extremes. In August the mode dropped to 0.90 - 1.00mm and the length range contracted with the loss of the 1.10 - 1.30mm adults in September. In October the modal length was the smallest of the year at 0.80 - 0.90mm and this gradually rose until in January 1970 the length distribution was similar to that of January 1969.

In summary, there was an increase in mean body-length to a seasonal maximum in May, followed by a decline to a seasonal minimum in October and a rise to the winter mean body-length again during November and December.

Body/.....

Figure 4 (opposite)

An Ovigerous Adult Female of *Cyclops strenuus abyssorum*

A - cephalothorax

B - metasome

C - total length minus furcal setae

Figure 4

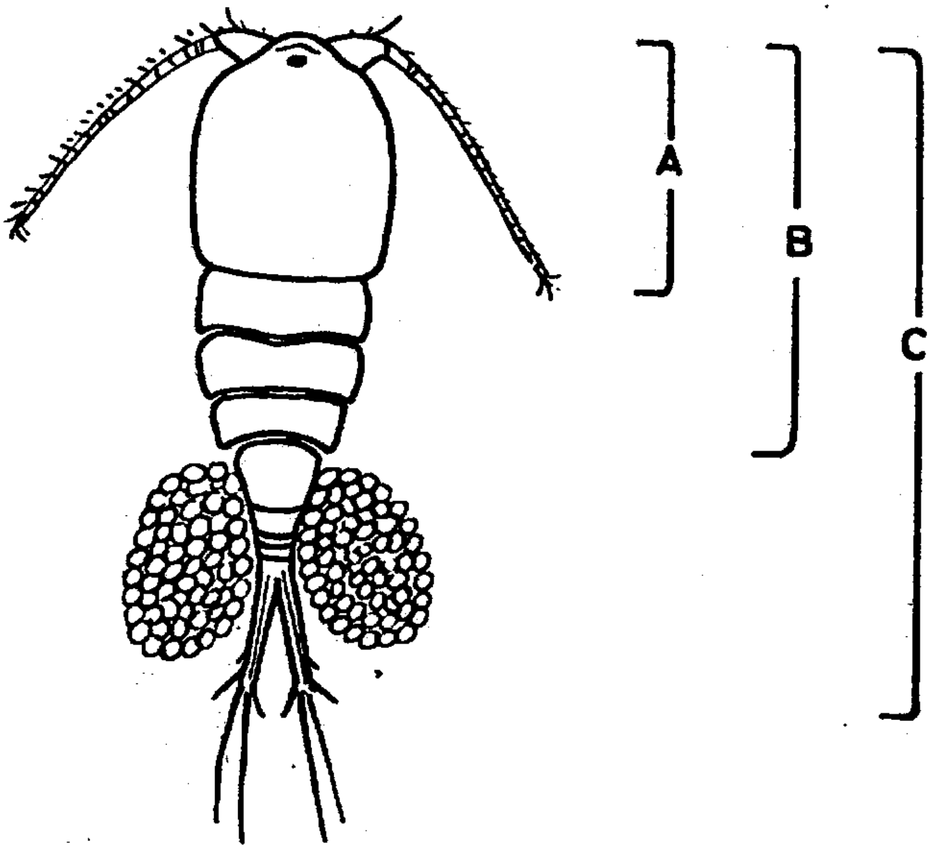
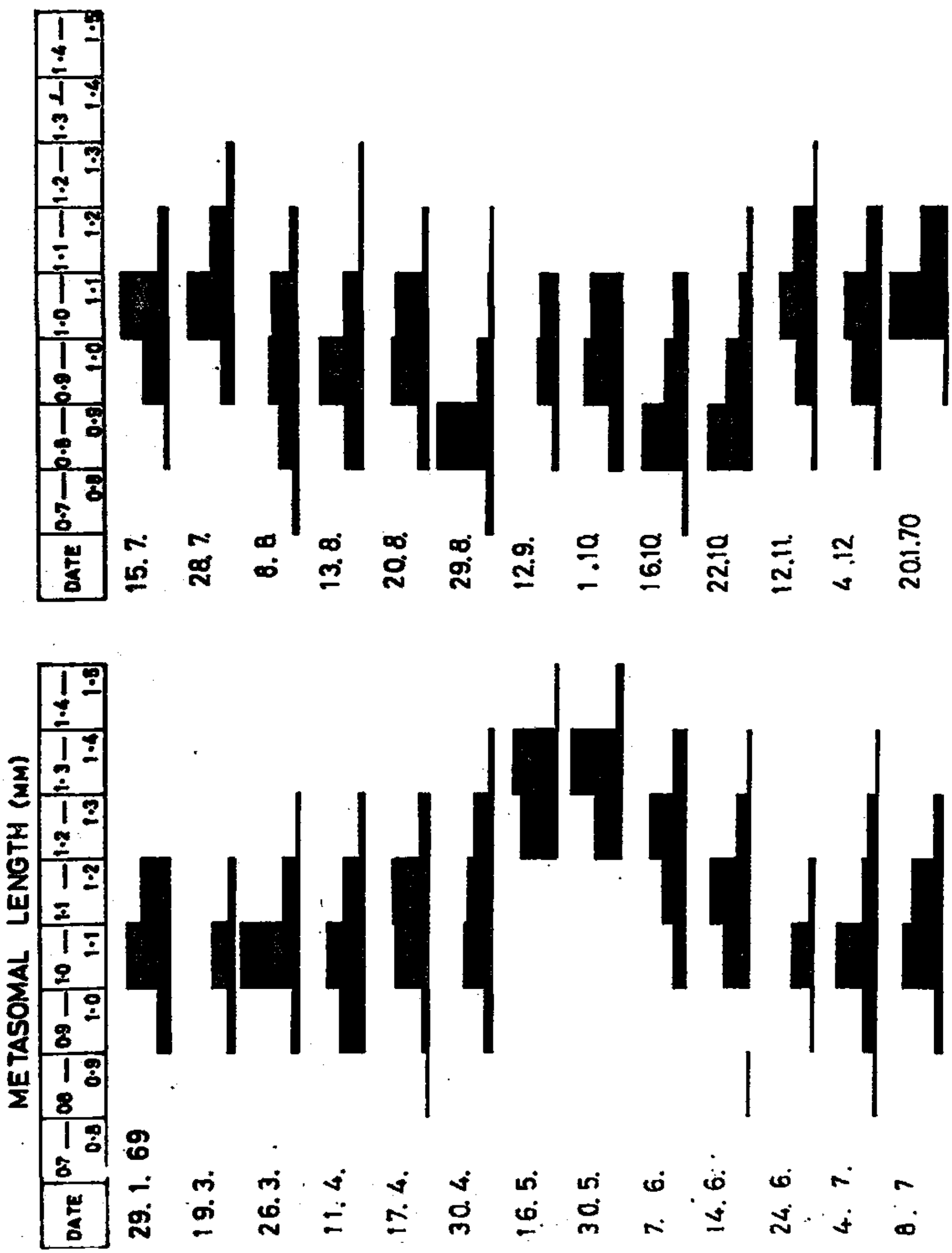


Figure 5 (opposite)

The Seasonal Metasomal Length Distribution of Adult Females of Cyclops strenuus abyssorum in Loch Leven 1969/70

Measurements of the metasomal length (mm) of fifty adult females were made using a Reichert Visopan microprojector except on 19.3.69, 24.6.69 and 12.9.69 when twenty individuals were measured.

Figure 5


METASOMAL LENGTH (MM)
DATE
0·7 — 0·8
0·8 — 0·9
0·9 — 1·0
1·0 — 1·1
1·1 — 1·2
1·2 — 1·3
1·3 — 1·4
1·4 — 1·5
29.1.69
19.3.
26.3.
11.4.
17.4.
30.4.
16.5.
30.5.
7.6.
14.6.
24.6.
4.7.
8.7
15.7.
28.7
8.8
13.8.
20.8
29.8.
12.9.
1.10
16.10
22.10
12.11.
4.12
20.1.70

Body-length analysis of the adult females shows that there was an influx of adults in late March although the first increase in adult standing crop after the winter did not occur until mid-April. This emphasises the fact that standing crops do not necessarily record changes within the population as the gain of young individuals may be exactly balanced by the loss of older animals due to moulting or mortality. Similarly from late April until June the adult standing crop remained relatively stable whilst body-length measurements showed that the largest females of the year appeared and died out during that time.

The changes in body-length distribution were normally gradual as the length distribution of the newly-matured animals must have overlapped the existing adult population length distribution relatively slowly. Therefore it is impossible to define exactly when specific animals entered or left the population. However it is probable that the adult females which formed the overwintering population matured from late October onwards and would probably live until April, implying a maximum adult longevity of approximately six months.

(c) Breeding Parameters

Cyclopoid copepods carry their eggs in a pair of sacs attached to their abdomen until the eggs hatch into free-swimming nauplius larvae. Observations on the presence of these egg sacs and the number of eggs which they contain can be useful in giving a measure of the reproductive state of the population on any sampling date.

These/.....

These and associated breeding parameters were noted throughout the year.

i. Methods

The adult population was differentiated into males, females with attached egg sacs and females without sacs. All egg sacs were counted and recorded. Copepod egg sacs are only loosely attached to the female and some of them were dislodged in sampling and filtration. Occasionally egg sacs must have broken up and the individual eggs were lost as uneven numbers of egg sacs were sometimes recorded. These uneven numbers were rounded up to even numbers. It was assumed that the proportion of egg sacs retained would be constant throughout the year and as on some occasions nearly all of the females were seen to be ovigerous or were calculated from the total egg sac count to have been ovigerous, it is likely that the number of sacs lost was small.

At the same time as the length of the adult females was measured, the number of eggs in their egg sacs was counted and recorded, so that female body-length could be compared with the number of eggs carried. Egg sacs were removed from the females and teased apart in a drop of water on a slide. Fifty females were examined for each sampling date but on March 19 and June 24 only twenty were examined, owing to insufficient animals having been obtained.

ii. Eggs per Egg Sac

The mean number of eggs carried in each sac varied in a distinct seasonal pattern (fig. 6a) similar to the seasonal changes in body-length. From a winter level of about 15 eggs/sac (i.e. 30 eggs/female) the mean egg count rose steeply in March and April to 36 eggs/sac, fell to the seasonal minimum of about 10 eggs/sac in September and October, and then rose to the winter level of 15 eggs/sac.

It is well-established that the number of eggs carried by a copepod is mainly dependent upon its food supply (Marshall and Orr, 1952, 1955), whilst the actual number of egg sacs produced in unit time is primarily dependent upon temperature (Corkett and McLaren, 1969), although food supply may also affect this (McLaren, 1963, 1965; Edmondson, 1964). Smyly (1970) has shown that the type of food available to carnivorous copepods affects the number of eggs produced in each sac. A relationship between body-size and egg-number has also been postulated (Ravera and Tonolli, 1956). Therefore it is likely that the number of eggs carried by the female population at any time will be dependent upon the food quality and quantity at the time of laying down of the eggs, modified by the size of the ovigerous animals.

In the present study a good correlation was found between body-size and number of eggs carried on individual dates. Also, the seasonal changes in adult body-length were similar to those of egg-number per egg sac (fig. 7).

However/.....

Figure 6 (opposite)

Breeding Parameters of Cyclops strenuus abyssorum in Loch Leven 1969/70

The Abcissa - the sampling period

The Ordinates:

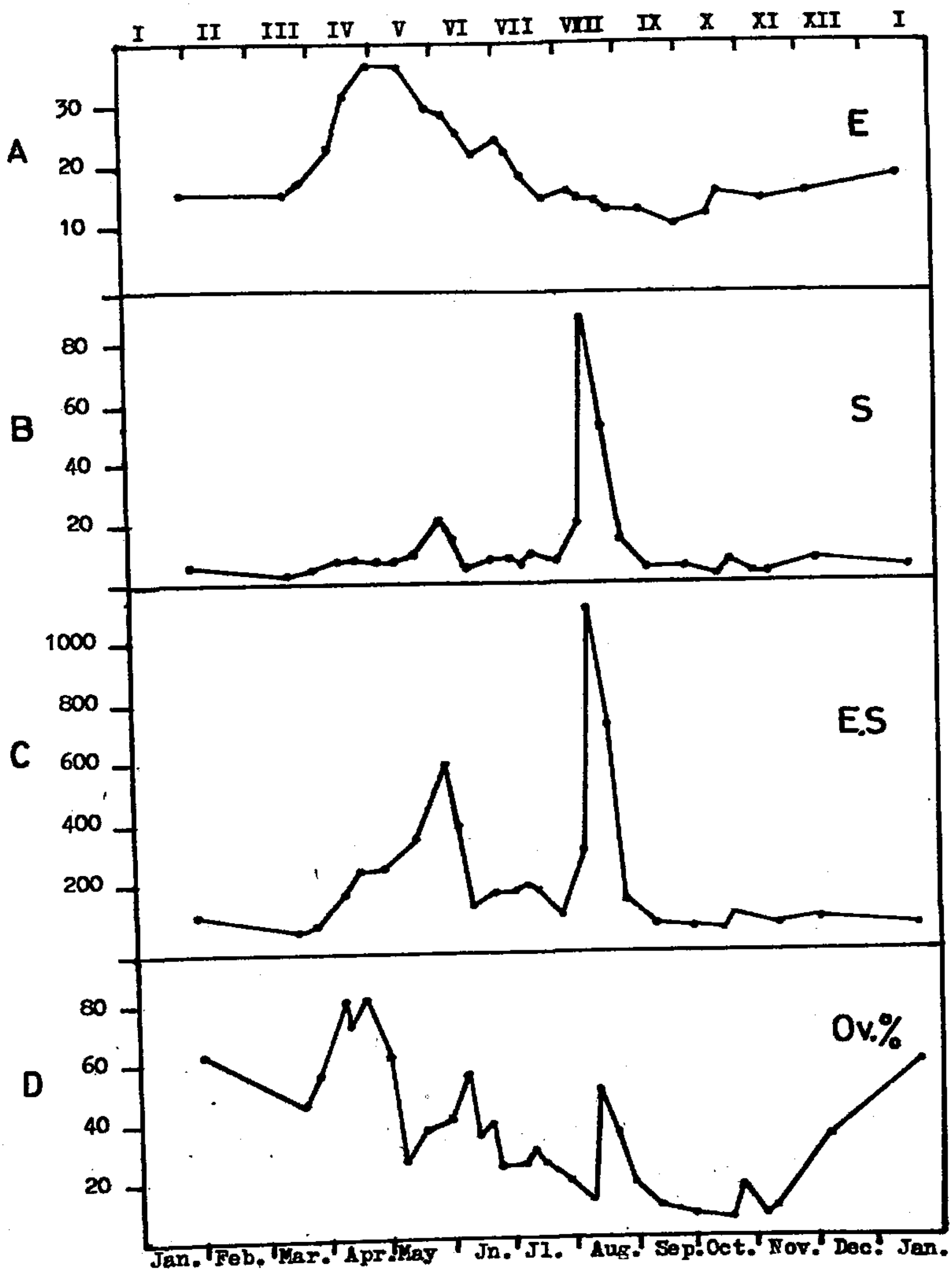
(A) - eggs per egg sac (E)

(B) - egg sacs per 5 litres (S)

(C) - egg stock per 5 litres (ES)

(D) - percentage of total adult females carrying eggs (OV.%)

Figure 6



I II III IV V VI VII VIII IX X XI XII I
A
30
20
10
E
B
80
60
40
20
S
C
1000
800
600
400
200
E.S
D
80
60
40
20
Ov.%
Jan. Feb. Mar. Apr. May Jn. Jl. Aug. Sep. Oct. Nov. Dec. Jan.

Figure 7 (opposite)

Seasonal Changes in Mean Body-Size and Number of Eggs per Egg Sac of Adult Female Cyclops strenuus abyssorum

The Abcissa - the study period

The Ordinate (A) - mean number of eggs per egg sac

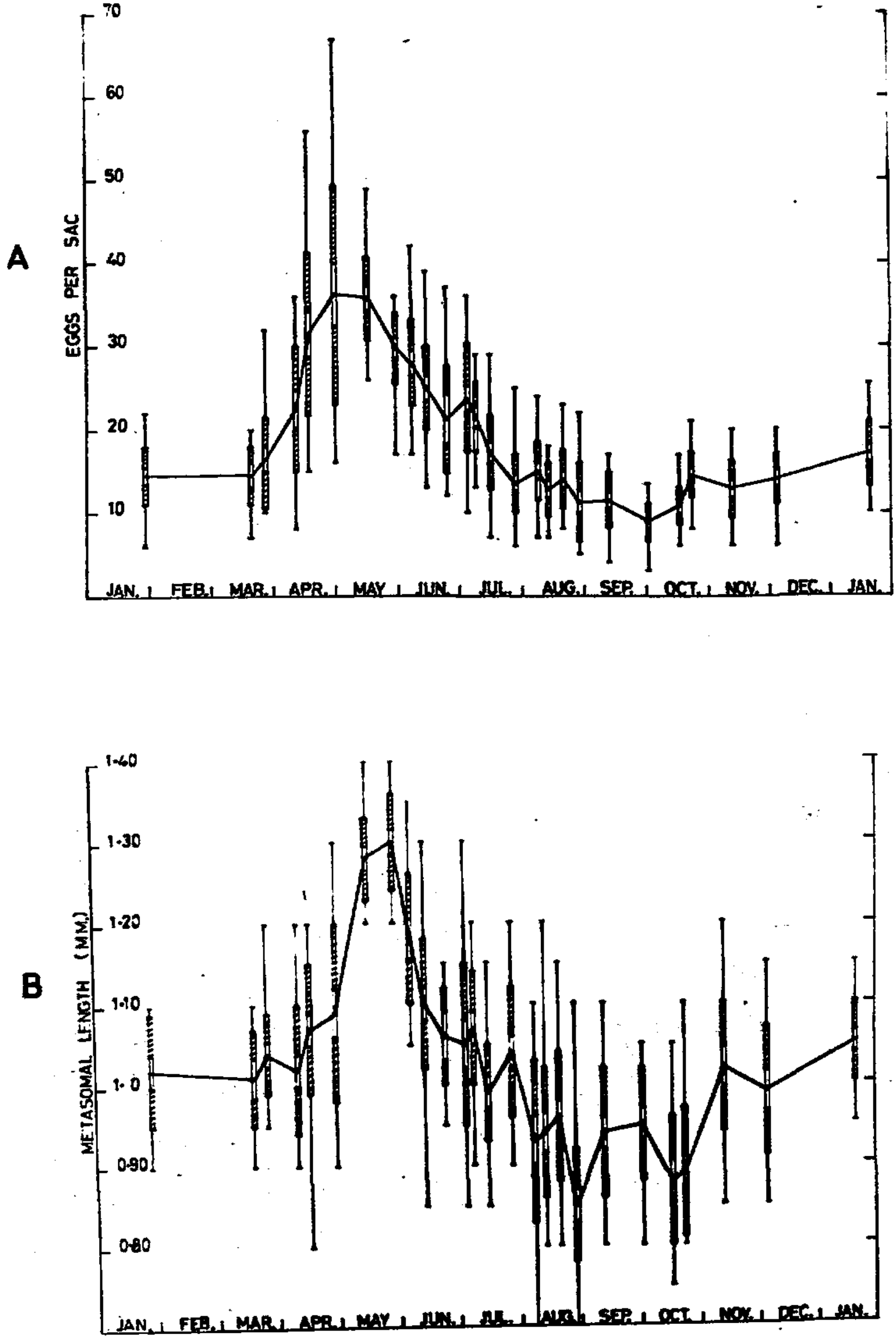
(B) - mean metasomal length (mm)

Measurements were made of fifty adult females per sampling visit except on 19.3, 24.6 and 12.9.69 when twenty individuals were measured.

Key:-

- the range
- the standard deviation of the mean
- twice the standard error of the mean
- mean

Figure 7


A
EGGS PER SAC
70
60
50
40
30
20
10
JAN. FEB. MAR. APR. MAY JUN. JUL. AUG. SEP. OCT. NOV. DEC. JAN.
B
METASOMAL LENGTH (MM.)
1·40
1·30
1·20
1·10
1·0
0·90
0·80
JAN. FEB. MAR. APR. MAY JUN. JUL. AUG. SEP. OCT. NOV. DEC. JAN.

However the peaks of body-size and egg-number were slightly offset as the largest females did not quite produce the largest clutches of eggs.

The food supply of the adult females and its effect on egg production is examined in Results, section 3 (d).

iii. Egg Sacs and Egg Stock per 5 Litres

The number of egg sacs and the egg stock per five litres are presented in figure 6b and c and follow similar trends. The egg stock is derived from the mean number of eggs per egg sac, multiplied by the mean number of egg sacs per five litres. Therefore the egg stock during the period March to July, responding to the peak of egg number per egg sac, is a more expanded version of the egg sac graph.

After a slight decline in egg stock during February and early March, a steady increase prevailed until the end of May, when there was a sudden decline in egg stock associated with a decline in both numbers of egg sacs per five litres and number of eggs per egg sac. During late June and July the egg stock underwent a slight increase followed by a decrease, whilst in August it rose and fell dramatically after attaining the greatest standing egg stock of the season. This peak was a direct result of a similar change in the number of egg sacs per five litres, while the actual number of eggs per egg sac remained constant.

After/.....

After August the egg stock remained relatively steady, mirroring a slight rise in eggs per egg sac and egg sacs per five litres in late October, whilst a rise in eggs/sac in December and January was cancelled out by a concurrent decline in the number of egg sacs.

iv. The Percentage of Ovigerous Females in the Total Adult Female Population

In comparison with the graphs of egg/egg sac, egg sacs/5L and egg stock the graph of the seasonal percentages of adult females carrying eggs shows more fluctuation and is seldom similar to them (fig. 6a, b, c, d).

From a winter level, when about 60% of the females carried eggs, there was an initial decline to less than 50%, followed by a sharp rise in late March and early April, to a period when about 80% of the females were ovigerous. Unitl this time similar, but less marked, changes were evident in the other three parameters. A steep fall in percentage took place in late April and early May, reaching a minimum of 25%. The ovigerous proportion of the adult females then rose to 55% in early June and fell again to almost 10% in early August. In August there was a sudden increase and then decrease, corresponding with similar changes in egg stock and egg sac number. However, in this case, the August peak did not exceed the spring peak as did the peaks in the egg and egg sac stocks.

Similarly/.....

Similarly in October and early November when only 5% of the females carried eggs there was a small rise and fall in ovigerous percentage and this peak also occurred in the graphs of the other three parameters. From this time a steady increase in the percentage of ovigerous females took place, reaching nearly 60%, the level of the previous year, by late January.

v. The Sex Ratio

The sexes were identified on a routine basis from the CV instar, although differentiation can be made from at least the CIV stage by using high power magnification.

The seasonal changes in percentage of males or females in the total numbers of CVs and CVIs (adults) are presented in figure 8. Each co-ordinate is derived from the mean numbers of males and females taken in the samples on that date. As the overwintering population was small, less significance can be attached to the percentage by sex of the sample counts from the winter population. It is evident, however, that the adult males were normally well in excess of the females and on only two dates in April and one in August were there more adult females than males. The copepodids V, on the other hand, had a preponderance of females almost as often as of males.

It is common for crustacean zooplankton communities to consist mainly of females, not just in cladoceran populations where the bulk of the reproduction is parthenogenetic, but also in copepod populations.

(Andrews/.....

Figure 8 (opposite)

The Percentage by Sex of Copepodid instar V and Adults of C. s. abyssorum in Loch Leven in 1969/70

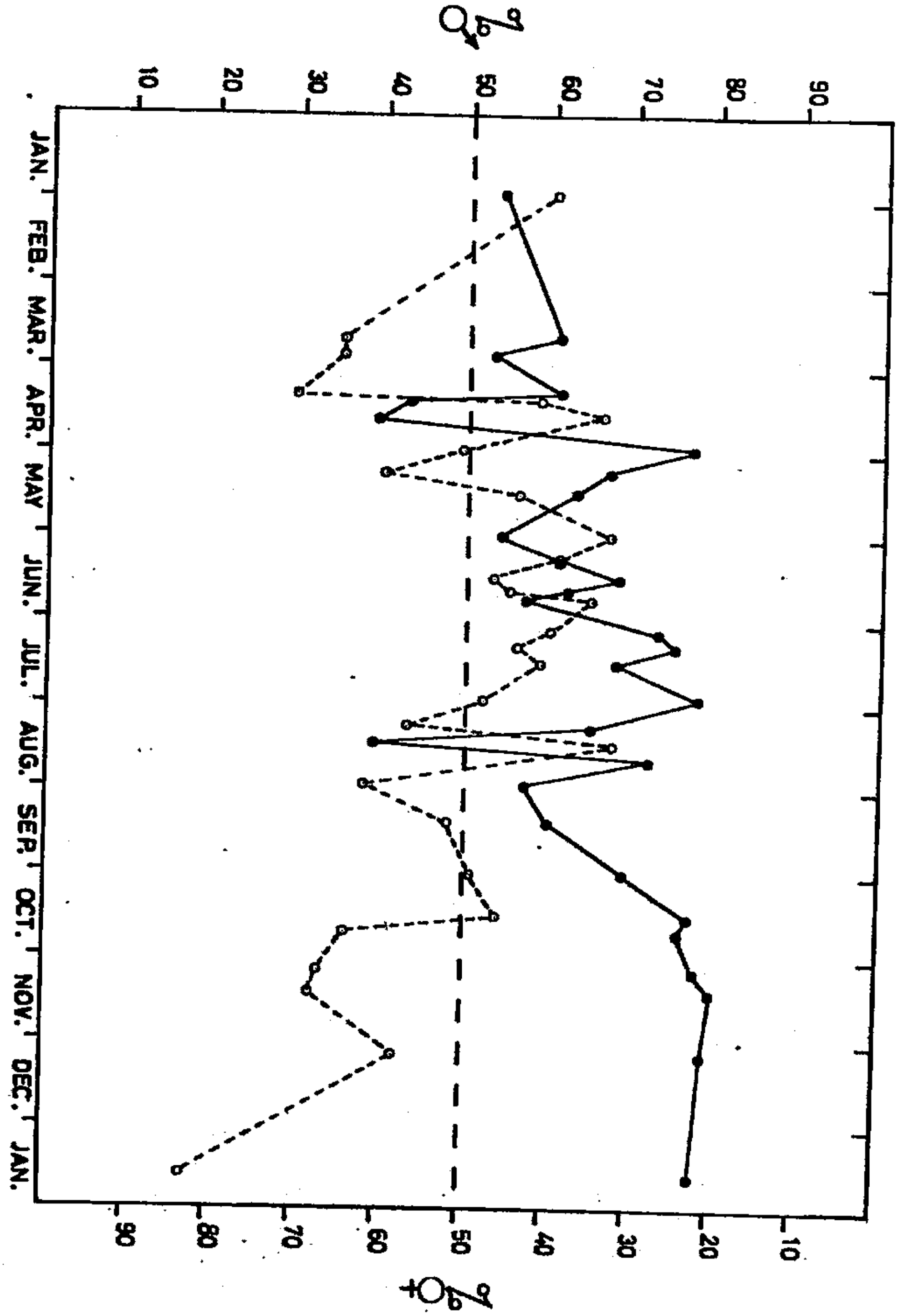
The Abcissa - the study period

Left Ordinate - the percentage of the total numbers of copepodid stage V and adults which were male

Right Ordinate - The percentage of the total numbers of copepodid stage V and adults which were female

Key - the adults are represented by the continuous line and solid circles and the Copepodids V by the broken line and open circles.

Figure 8



♂/♀
10
20
30
40
50
60
70
80
90
JAN.
FEB.
MAR.
APR.
APR.
MAY
JUN.
JUN.
JUL.
AUG.
SEP.
OCT.
NOV.
DEC.
JAN.
90
80
70
60
50
40
30
20
10
♂/♀

(Andrews, 1953; Ravera, 1955; Elgmork, 1959; Smyly, 1961; Chapman, 1969). The usual explanation for a preponderance of copepod females is that the males are shorter-lived. This would appear to be reasonable as the males present the females with spermatophores (sperm sacs) during copulation and the stored sperms then fertilise the successive egg broods (Corkett and McLaren, 1969). After copulation the males would be likely to impose an unnecessary strain on the food supply of the population, as Smyly (1970) noted. If they copulated with more than one female then fewer males would be required. However there were clearly more males than females in the Loch Leven Cyclops strenuus population.

Differential predation on the adults seems possible as the numerical superiority of the males is not evident in the CV instar. The females are significantly larger than the males and may be more easily filtered or selected by predators such as small fish. However it has not yet been possible to examine the stomach contents of perch fry which may be their main predators.

Another interesting feature is that the graph of percentage of CV sexes is often a mirror-image of that of the CVIs. An increase or decrease in one is mirrored by the opposite effect in the other. This seems reasonable as when, for example, a batch of males moult from CV to CVI, they will reduce the number of males in the CV instar and increase the number of males in the CVI instar. Therefore there will be a decrease in the proportion of males to females in the CVs with a concurrent increase in the proportion of CVI males to females.

Similarly/.....

Similarly an increase in the percentage of CV males at the same time as a drop in the percentage of CVI males implies that a number of females have moulted to the adult stage. If this hypothesis is correct, the entry into adulthood of the males and females is not usually concurrent. With more or less continuous reproduction this is perhaps surprising, however it seems that the bulk of the males may have matured at different times from the females during most of the year.

2. The Spatial Distribution

(a) Zooplankton Spatial Distribution in General

Zooplankton species are usually distributed non-randomly in an aggregated or "clumped" manner, although randomness has been described by Ricker (1937, 1938) and Langford (1938). Some of this variability may be ascribed to inadequate sampling since, for example, some zooplankters can evade capture more readily in some conditions than in others (Szlauer, 1964, 1968; Fleminger and Clutter, 1965; Smyly, 1968). However, most observations of non-random distribution are the result of real differences in spatial distribution perhaps yielding valuable information on the relationships between organisms and their environment.

Many zooplankton species are capable of some control over their depth-positioning, and vertical migrations are well described (see reviews by Kikuchi, 1930; Cushing, 1951). Tash and Armitage (1960) stated that "although temperature, food, sex, size and many other factors have been found to modify the vertical migration of individuals in populations of zooplankters, most workers agree that the twenty-four hour cycle of subsurface illumination is the essential stimulus." Similarly zooplankters may exercise some choice in their horizontal distribution by aggregating in areas of good food supply, suitable light intensity or temperature.

Alternatively they may be clumped by water movements such as eddies, or upwellings of water may affect their horizontal distribution by introducing to the surface animals which may have congregated at depth.

Whatever the cause, it is wrong to assume without further evidence that a sample of zooplankton from one position in a lake is representative of that lake as a whole. Therefore an investigation of the spatial distribution of the zooplankton is essential for a realistic assessment of sampling accuracy.

(b) The Horizontal Variation and Sampling Variability at Loch Leven

Preparatory to the programme of 5 litre Friedinger sampling, pilot sampling was undertaken in order to provide information on the horizontal distribution of the Loch Leven zooplankton. Unfortunately it was necessary to do this in winter when the *Cyclops strenuus* population was relatively sparse. On December 23, 1968 a series of five, five minute zooplankton net tows was taken along the longest axis of Loch Leven, from the north-east shore to the outflow sluice. The results are presented in Table 1.

Table 1

Volume of Zooplankton taken in 5 minute tows along the longest axis of Loch Leven on 23.12.68

1.	19.0 mls
2.	18.5 mls
3.	19.5 mls
4.	19.0 mls
5.	20.0 mls

On the basis of this isolated experiment, coupled with the knowledge that Loch Leven is normally well-mixed, being swept by the prevailing wind, it was assumed that uneven horizontal distribution in the zooplankton might not be as serious a problem as it is in more sheltered bodies of water. Nevertheless the Friedinger sampling programme was designed so that as many sites as possible could be visited and the overall standing crops were calaulated by combining the zooplankton counts from all of the samples taken on each sampling visit, in an attempt to 'smooth out' uneven horizontal distribution.

As explained in "Materials and Methods", section I, sampling visits were 'major', when sixty-eight samples were taken from eight sites, or 'minor', when twenty-two were taken from two sites. An analysis of the comparability existing between the standing crops derived from the major and minor sampling visits is presented in Table 2.

By/.....

TABLE 2

Horizontal Variation in Zooplankton Samples from 'Major' Visits to Loch Leven in 1969
(Zooplankton Samples as Mean No./5 litres)

Date	Sites X1 (6)	X2 (16)	X3 (2)	X4 (10)	X5 (16)	X6 (6)	X7 (6)	X8 (6)	Overall Mean (68)	Mean for X1 & X2 Samples (22)	Mean for X1 & X2 Samples As % of overall mean
26.3	105.5	137.4	204.5	102.8	*186.3	110.8	120.5	58.1	130.4	128.8	98.8
17.4	62.9	134.6	56.5	142.9	187.2	104.6	103.9	348.5	153.0	115.1	75.2
7.5	157.0	243.3	183.0	231.8	192.4	220.5	161.3	271.9	213.5	219.8	103.0
7.6	685.3	1121.8	518.0	372.2	890.0	450.4	453.6	982.4	770.1	1002.7	130.2
8.7	732.6	839.7	891.5	562.7	553.8	495.6	325.4	430.7	611.9	810.6	132.5
8.8	339.2	565.6	150.5	450.6	339.3	158.6	364.7	512.3	404.9	503.8	124.4
29.8	579.7	450.1	406.0	388.1	816.5	957.7	278.2	253.0	461.4	485.5	105.2
1.10	403.9	295.8	263.0	262.3	256.1	224.2	411.8	293.7	294.0	325.3	110.6
22.10	221.7	202.7	45.5	194.5	195.1	210.9	209.0	164.8	194.6	208.0	106.9

* fourteen samples

Table shows variability between mean counts of combined stages of *C. strenuus* taken from different sites on the same date and compares the mean derived from the first two sites (as in a minor visit) with the overall mean derived from the full eight sites (major visit). The numbers of samples per site on each visit are shown in parentheses. See figure 1 for explanation of sites.

By calculating standing crops from the first two sites, X1 and X2, as in a minor visit, and comparing them with the standing crops derived from the full eight sites, it can be seen that minor visit mean standing crops are likely to be similar to major visit ones, $\pm$ 32.5%. On five of the nine major visits analysed, a minor sampling programme would have given data within approximately $\pm$ 10% of that calculated from the full eight sites.

Normally when standing crops were calculated from sampling visits which were only a few days apart there was either a close similarity or a reasonable continuation in trend, providing a potent suggestion that the sampling means were not unreasonable. However table 2 shows several large discrepancies between mean counts at different sites on the same date and it is very difficult to assess whether this variability is real or is a function of the small, variable numbers of samples which were taken. In practise, errors due to insufficient numbers of samples are likely to have been reduced, as the overall standing crops which were used for annual cycle eludidation were derived from the combined sample counts, divided by the total number of samples taken.

The normal sampling programme was abandoned on five dates because of strong winds. On such days wind-induced circulation of the Loch can be very pronounced and Smith (Loch Leven Research Group) has found currents of up to 10cm/sec 25cm from the loch bed in a total water depth of 7 metres (Morgan, 1970).

Therefore/.....

Therefore it is very unlikely that the small number of samples taken on such days will have been as unrepresentative of the general water body as they might have been had they been collected during calmer conditions.

A comparison of the variance between sample counts within a site with the variance between sites ought to be of value in determining the nature of the variability shown in table 2. However this is not as simple as it may at first seem as the vertical zonation of the plankton may result in very large numerical differences between samples within a single site. Consequently, a sampling programme was designed to test the variability between a series of mean, sample counts taken from a single site during an extended period of time, while also providing information on the diurnal changes in vertical distribution of the zooplankton. Sampling was carried out at a site of 17.5 metres depth, near X2 in the North Deeps, at three-hourly intervals from 6pm on August 19, 1969 until 9am on the following day. Replicate 5 litre Friedinger samples were collected from alternate metres in the water column and the mean numbers of nauplii, copepodids I - V and adults per 5 litres, taken during each sampling period, are compared in table 3. Results indicating the diurnal distribution of Cyclops strenuus abyssorum are presented in section 2 (c) while information, gained simultaneously, on the presence of chironomid larvae and nematodes in the water column, is presented in Results, section IV.

Table 3/.....

Table 3

Within-site Variance in Sample Count Means on 19/20 August, 1969

Sampling means are mean numbers per 5 litres derived from 18 samples/sampling period and the times of sampling periods are recorded as the time when sampling was begun.

Sampling Period	Nauplii	Copepodids I - V	Adults
6pm	127.4	82.2	104.8
9pm	100.7	133.3	154.9
12pm	111.7	90.2	116.2
3am	77.1	72.3	117.7
6am	183.6	129.2	132.9
9am	118.4	79.8	113.9
Mean	119.8	97.8	123.4
Standard deviation	35.73	26.54	17.91
Standard error	15.98	11.87	8.01
Coefficient of Variation	29.8%	27.1%	14.5%

The coefficients of variation of the mean standing crop of nauplii, copepodids I - V and adults are 29.8%, 27.1% and 14.5%, indicating that even at a single site there may be found relatively large differences between mean sample counts. The water body is in motion, making it unlikely that the same zooplankton organisms will be exposed to sampling at intervals of three hours. Therefore there may be little difference in variability between means calculated from groups of samples taken during an extended period at a single site with that existing between the means of groups of samples taken from several sites at approximately the same time.

When/.....

When one considers the manifest problems inherent in zooplankton sampling, variation of the order of 30% does not appear to be unreasonable and, according to Cushing (1951), this is not excessive.

(c) <u>The Vertical Distribution</u>

(i) <u>The Seasonal Vertical Distribution</u>

Depth histograms of the seasonal, vertical distribution of <u>C. strenuus</u>, representing sampling in the North Deeps on 23 dates during 1969/70 in the course of the normal 'major' and 'minor' visits, are presented in figure 9. Complete sampling of the water column would have been desirable for an analysis of the vertical distribution, but the necessary sampling during routine visits would have resulted in more samples than it was feasible to examine. The programme of sampling selected, with replicate samples taken from each of the surface five metres and from ten, fifteen and twenty metres, was considered to be a reasonable compromise. In order to compare the vertical distribution patterns of variable sizes of standing crop, the combined counts of the samples taken at each depth are shown as a percentage of the combined sample counts from all depths. The <u>C. s. abyssorum</u> population is presented as nauplii and two groups of copepodid stages, CI - CIII and CIV - CVI (adults). The copepodids and adults were grouped in this way because feeding studies indicated that the CI - CIII might be trophically more similar to the nauplii than to the older instars (results, section 3) and it was considered that this might result in differential, vertical zonation between these groups.

Figure 9 (opposite)

The Seasonal Vertical Distribution of C. s. abyssorum in the North Deeps (X2) of Loch Leven during 1969/70

The animals are separated into groups of Nauplii, Copepodid instars I - III and C.IV - VI (CVI = adult).

The Abcissae - the study period represented by 23 sampling dates

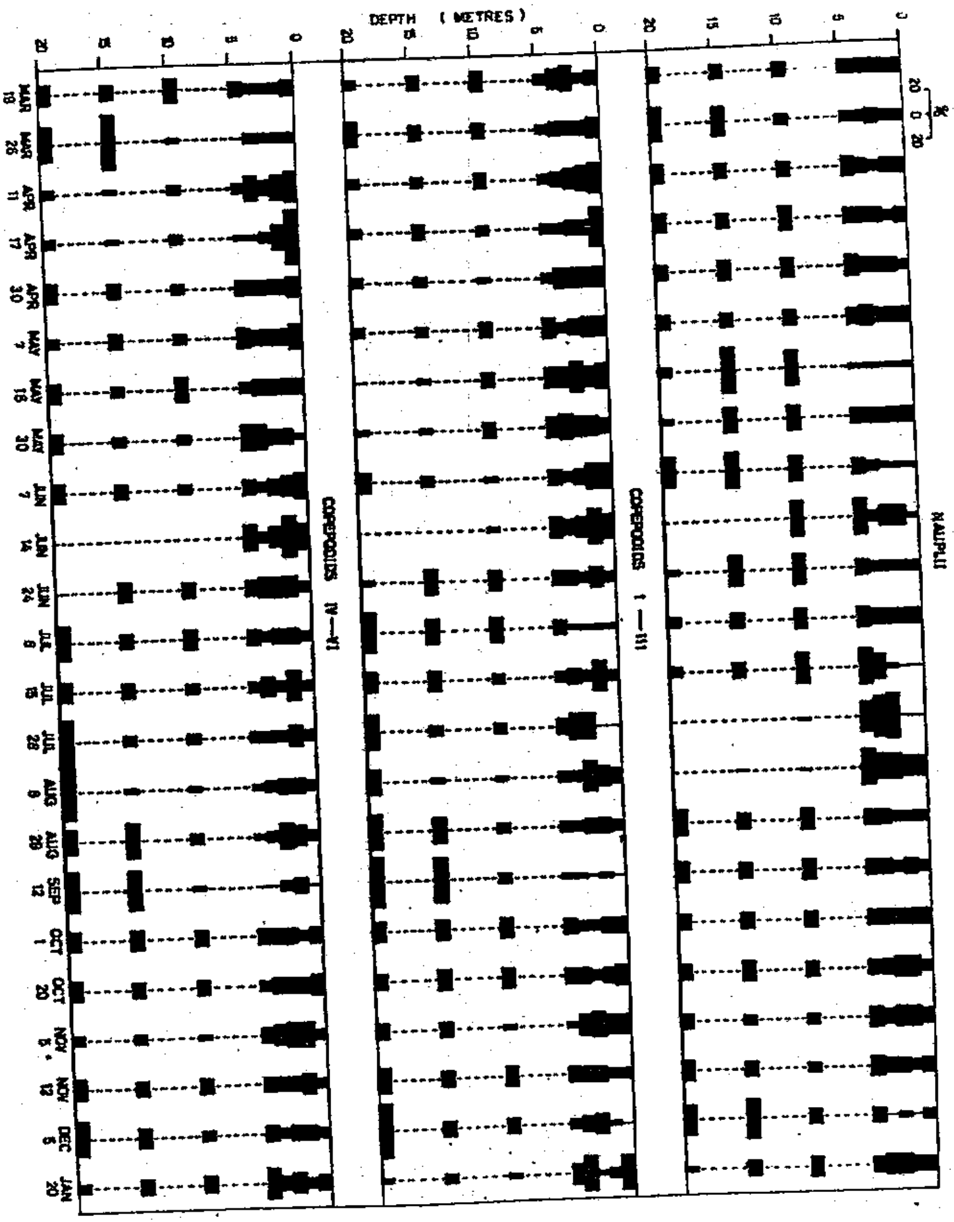
The Ordinates - the loch depth in metres (from the surface almost to the loch bed)

On each sampling date the mean numbers of individuals of each of the three age groups taken at each sampling depth are expressed as a percentage of the total numbers of individuals of these age groups taken in the water column. Replicate 5 litre Friedinger samples were taken at each metre depth from the surface to 5 metres, then at 10m, 15m and 20 metres.

The vertical broken lines indicate the depths which were not sampled except when they cross depths 0 - 5m, 10, 15 or 20m, where they indicate that no individuals were found.

Sampling was normally undertaken within two hours of noon and took 30 - 45 minutes.

Figure 9



The nauplii were well-dispersed throughout the water column during spring, after which there was a tendency for them to be collected in greatest numbers in the middle depths until early June. With rapidly-rising surface water temperature at this time a thermocline was established and persisted for a few days. Consequently on June 14 no nauplii were found deeper than 10 metres. By June 24 they had become scattered again, after the thermocline breakdown resulting from wind-induced water circulation, and they were found to be fairly evenly distributed throughout the water column in early July. On July 15 and 28 there were very few in the first two metres yet many were found immediately below this and this was especially marked when, on the latter date, there were hardly any below 5 metres. This distribution persisted into early August although the surface two metres were more densely occupied. After this the nauplii became scattered until there were apparent aggregations in December and January, when the population was very sparse.

The copepodids I - III were uniformly distributed in March but showed a tendency to collect in the surface layers in April and May. The thermocline in June resulted in none being found deeper than 10 metres, while by June 24 they were scattered again, although few were found at 20 metres. In early July there was an apparent 'preference' for the deepest water with progressively fewer being found towards the surface.

They/.....

They were scattered again during the rest of July but few were found in the first two metres from the surface on July 28. Their distribution in early August was again fairly well scattered although fewer were found in the middle layers of the water column than above and below. Deeper concentrations were found in late August and September, while scattered distributions were found after this, when the population size was too small for any reasonable conclusions to be made.

The copepodids IV - VI showed a mixed distribution on March 19 but aggregations were found at 15 and 20 metres later in the month. In early April the bulk of this group was concentrated in the upper metres, while a mixed distribution was found in late April and in May. The June thermocline coincided with a complete absence of the copepodids IV and VI in the water column below 5 metres, while on June 24, although only a few were found at 20 metres, the animals were well scattered above this depth. During most of July there was a mixed distribution, but a tendency for greater numbers in the deep water towards the end of the month became pronounced in August and September. This was followed by uniform distributions throughout the water column during the remaining months of the year.

There are several prominent features apparent in this analysis of the seasonal vertical distribution of C. s. abyssorum in Loch Leven:-

(1) Although well-mixed distributions were common, there were several instances of clear, vertical aggregations present on some sampling dates.

(2)/.....

(2) These aggregations were sometimes specific to the separate groups of nauplii, copepodids I - III and IV - VI. This was particularly evident on July 28 and August 8 when the nauplii and copepodids IV - VI had obvious, opposite distributions and the copepods I - III were distributed in such a way that similaritites with each of the other two groups existed.

(3) The concentrations of copepodids I - VI in the deeper water persisted into September while the naupliar distribution became scattered.

(4) The presence of a thermocline resulted in no individuals of *C. s. abyssorum* being found deeper than 10 metres on June 14.

ii. The Diurnal Vertical Distribution

As described in the previous section, there was a marked aggregation of adults and older copepodids close to the loch bed in the deep sites, during the latter half of July, in August and in early September. Consequently a sampling programme was designed to provide information on the distribution of the copepods during the diurnal cycle, while also giving information on the within - site sampling variance. Replicate five litre Friedinger samples were taken at a site near X2 in the North Deeps, at alternate metres from the surface to the loch bed at 17.5 metres, at three-hourly intervals from 6pm on August 19, 1969 until 9am on the following day.

Histograms/.....

Histograms showing the diurnal vertical distribution of the nauplii, copepodids I - V and adult males and females are presented in figure 10. The adult females maintained a deep aggregation throughout the sampling programme of 15 - 16 hours, although there was some indication of an upward and then downward movement between 9pm and 9am. The adult males, however, were more scattered, never having their greatest concentrations at the same depths as the females.

The distribution of the copepodids I - V was also scattered and inconclusive, although there was some evidence of a rise from the deeper water followed by a sinking again. However this was rendered uncertain by the scattered distribution of the copepodid stages at 9am.

The naupliar distribution is as interesting as that of the adults. At 6pm they were concentrated in the middle depths of the water column, fewer having been found in the deeper water than nearer to the surface. At 9pm their modal numbers were found at 13 metres while there were few deeper than this. At 12pm, even more of the nauplii (45%) were gathered at 13 metres while scattered numbers were found above and below this depth. At 3am the distribution pattern was markedly different as the nauplii were scattered, yet at 6am they had become aggregated in the 13 metres and shallower depths once more. By 9am most were found between the surface and eleven metres with nearly 30% at 9 metres and again few in the deepest water.

Clearly/.....

Figure 10

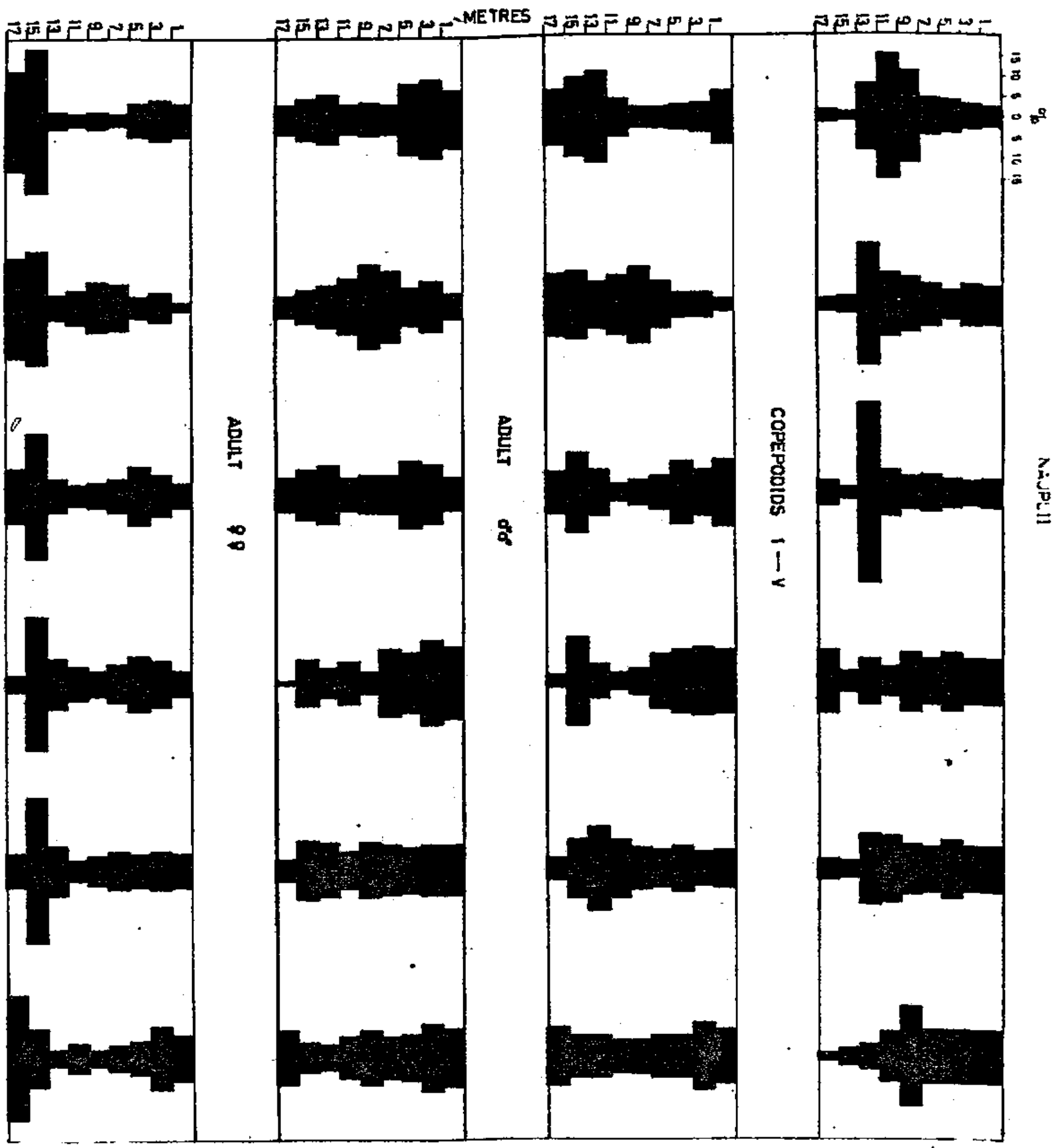

METRES
NAUPLII
COPEPODIDS I — V
ADULT ♂♂
ADULT ♀♀
6 PM
9 PM
12 PM
3 AM
6 AM
9 AM

Figure 10 (opposite)

The Diurnal Vertical Di[illegible] of C. s. abyssorum on 19/20 August, 19[illegible] [illegible] of 1[illegible].5 metres in depth near X2 in th[illegible] [illegible]s of Loch Leven

The animals are separated into [illegible] of Nauplii, Copepodid instars I - V and Adult males and [illegible]les.

The Abcissae - the sampling period, represented by 6 sampling periods at three-hourly intervals from 6pm on 19 August until after 9am on the following day

The Ordinates - the loch depth in metres (from the surface almost to the loch bed)

Replicate 5 litre Friedinger samples were taken at alternate metres depth from the surface until 1[illegible] metres and the catches at each sampling depth are expressed as a percentage of the total catch (as in figure 9).

Clearly the vertical distribution of C. s. abyssorum in Loch Leven varies between age and sexual groups. Although the adult females appeared to show a consistent 'preference' for the deepest water the greatest numbers of adult males and nauplii were never found there. However a clearly-defined, vertical migration pattern was not found.

3. Feeding

(a) Review

Jurine (1820) and Birge (1897) were first to recognise that the freshwater, cyclopoid copepods were at least partly carnivorous. Since then there have been occasional references to their diet which have been reviewed by Fryer (1957 a, b), who also contributed a great deal of information on the quality of the food they eat and how it is ingested. The quantity of food which they eat has been studied by Monakov (1958, 59), Monakov and Sorokin (1959 a, b), Shushkina (1964), McQueen (1969) and Smyly (1969, 70).

Fryer (1957 a, b) found that *Cyclops strenuus abyssorum* from Windermere and Coniston Water in the Lake District and from Loch Lomond had fed mainly upon the calanoid copepod *Diaptomus gracilis*. He considered that Cladocera and rotifers would probably form the main food of this species when calanoid species were not available. However he also found a limited amount of relatively large algae in their guts and suggested that, although some of this might have been in the guts of the prey animals, part of the algal remains was likely to have been ingested directly. Similarly Southern and Gardiner (1962) recorded that some *C. strenuus* (probably *C. s. abyssorum*) contained diatoms and Elbourn (1966) found that *C. s. strenuus* fed partly upon algae.

Phytoplankton/.....

Phytoplankton was also considered by Elgmork (1959) to be important in the diet of the younger stages of C. s. strenuus while the older stages were thought to be predatory. Smyly (1970), in a laboratory investigation of the feeding and development of Acanthocyclops viridis (Jurine), a relatively large species of benthic cyclopoid, found differences in their growth rate, longevity and fecundity when they were fed upon a variety of foods including algae (Scenedesmus sp.), Artemia salina nauplii and cladocerans. However McQueen (1969) found that copepodids IV, V and adults of Cyclops bicuspidatus thomasi, a planktonic copepod similar in size to C. s. abyssorum, did not feed upon cultures of seven species of algae which were offered to them in a laboratory study. As these algae were representative of the flora of Marion Lake, from which the copepods were taken, he concluded that it was unlikely that the later copepod stages were herbivorous. He further calculated that during the summer of 1967 C. b. thomasi copepodids IV, V and adults ate 31.0% of their own standing crop of nauplii, as well as 30.2% of the nauplius standing stock of the diaptomid species present in the lake. In addition to feeding upon animals of approximately the same size or smaller than themselves, Cyclops spp. are known to eat chironomid larvae and oligochaetes (Fryer, 1957 a, b) and will even attack small fish (Fryer, 1953; Davis, 1959; Hsu, 1963).

(b) Methods

Qualitative determinations of the food of the Loch Leven population of C. s. abyssorum were made throughout the year by several means:-

(1)/.....

(1) The contents of the guts were extruded carefully by compressing individual copepods in a drop of clean, tap water, between a slide and a cover slip. The extruded food was then teased apart using number OO. entomological pins set into sealing wax in glass tubes and examined under high magnification with a Watson Research Microscope.

The most serious drawback possessed by this method was that it was very difficult to differentiate between the extruded gut contents and epizoic organisms which commonly became detached from the copepods. Similarly, spines and setae were often dislodged from the animal being studied and lodged with the gut contents. However it was possible, with experience, to recognise these artefacts and discount them.

(2) Copepods were dissected using entomological pins, making it possible to be completely certain that the material under study came directly from the gut of a copepod.

(3) Faecal pellets were very common during parts of the year and they were selected from fresh zooplankton samples, squeezed between a slide and coverslip and examined under high magnification. Unfortunately the pellets tended to disintegrate during storage in formalin so that only fresh material could be used.

(4)/.....

(4) During counting and identification of the routine samples of zooplankton, relatively frequent observations were made of prey organisms in the process of being ingested by C. s. abyssorum. Each was recorded and where possible the stage of development of the prey and captor was noted.

(c) Results

Phytoplankton was observed in large quantities in the guts and faecal pellets of older copepodids and adults in May, when it consisted of diatoms, and in autumn, when it consisted of colonial green algae. Bailley-Watts (pers. comm.) has identified the diatoms as mainly Cyclotella sp. and the green algae as mainly Dictyosphaerium pulchellum. During May and June, when the rotifers were at maximum abundance, some loricas and trophi of Keratella cochlearis (Gosse) were observed in the gut contents, but after early July the rotifers were found to have very small standing crops, and despite their fast turnover rate, they could not have provided a large proportion of the food of the copepods present at that time. Occasionally Cyclops were found to have partially-ingested small chironomid larvae.

Cannibalism by the adults and older copepodids upon the nauplii and younger copepodids was regularly observed. In preserved samples, forty-five instances were noted of C. s. abyssorum holding partially-ingested younger instars in their mouth parts (table 4).

Table/.....

Table 4

Observations of Cannibalism in *Cyclops strenuus abyssorum*

Predator	Prey: Nauplii	CI	CII	CIII	CIV
CIV	5	-	1	-	-
CV	3	2	-	-	-
CVI	18	5	8	2	1

The numbers of prey refer to the observations of predation upon specific instars. However it must be emphasised that although cannibalism appeared to be a regular occurrence, the fact that the prey organisms were relatively large must have made it more likely that they would be held for a time before total ingestion could be accomplished. Therefore the likelihood of seeing such prey being eaten must have been greater than that of smaller prey. Consequently the frequency of observation of particular prey in the mouth parts cannot be considered as other than information of a qualitative nature.

From previous notes it can be deduced that the older copepodids and adult *C. s. abyssorum* in Loch Leven are omnivorous, feeding at least upon fairly large or colonial phytoplankton, nauplii and younger copepodid stages, rotifers and chironomid larvae.

The/.....

The feeding of the nauplii and copepodids I - III was not studied regularly, and the few gut extrusions which were attempted yielded unidentifiable material. It seems likely that these animals fed upon bacteria, small phytoplankters and Protozoa.

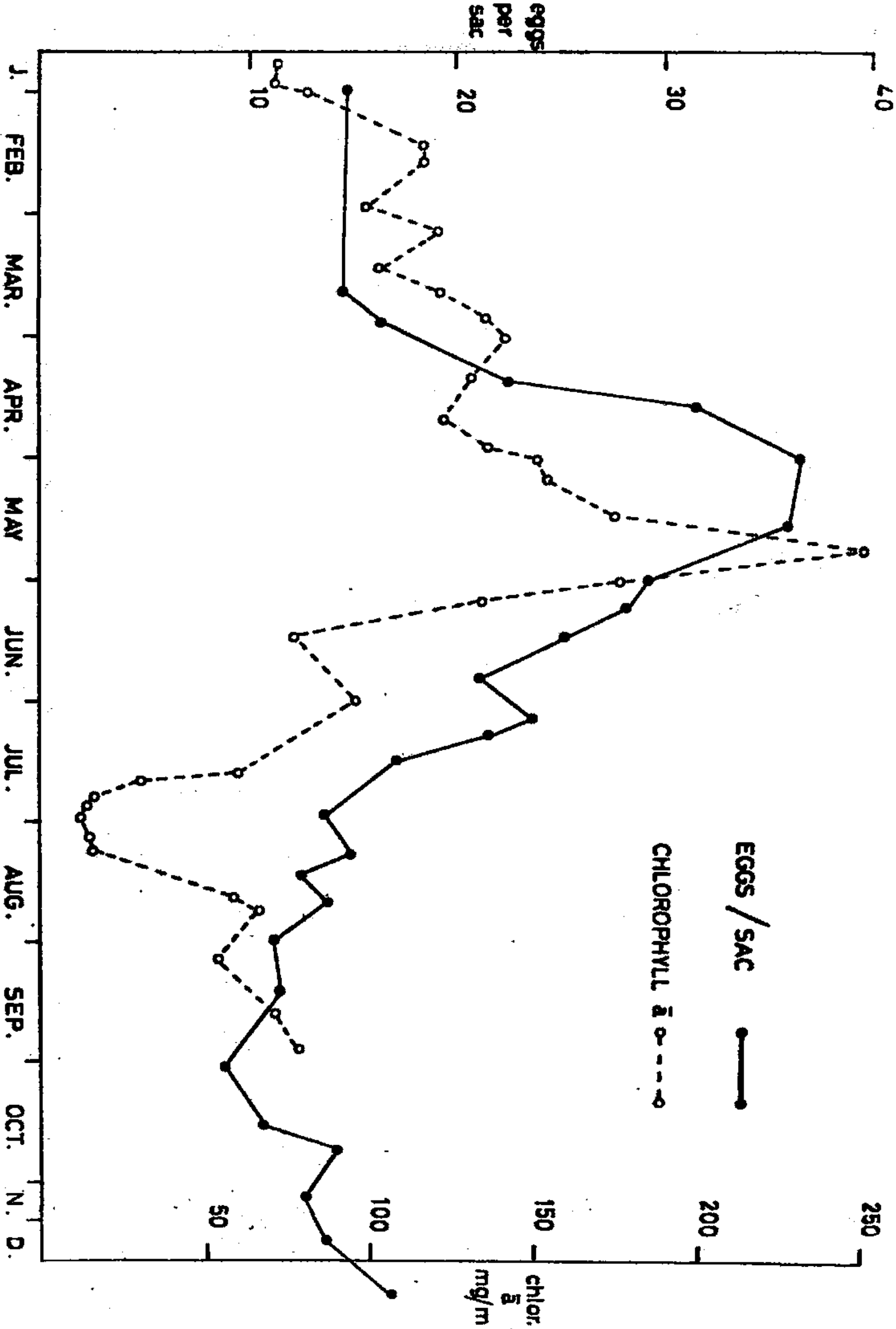
(d) The Relationship between the Food Supply and the Number of Eggs per Egg Sac of the Adult Females

Although it was impracticable to make a quantitative investigation of the food of *Cyclops strenuus abyssorum* in Loch Leven at the same time as the population study which was undertaken, it is interesting to compare parameters which may be associated with *C. s. abyssorum* feeding.

The number of eggs carried in each egg sac by the adult females is probably influenced by the food supply and the size of the ovigerous animals, as noted in the section on Breeding parameters. While figure 7 showed that clear similarities existed between the seasonal changes in adult female body-size and egg-number, a direct relationship between these changes is not entirely valid, as the largest clutches of the year were not carried by the largest females. A link between food supply and egg-number is even more difficult to substantiate as the diet of the adult females was omnivorous and not readily quantifiable. Presumably a decline in one food source will have resulted in a shift in feeding in order to exploit some other type of food. However, as the copepods must have been dependent, directly or indirectly, upon the phytoplankton, the seasonal changes in standing crop of phytoplankton (expressed as mg/m^3 chlorophyll $\bar{a}$) are compared with the variations in clutch-size in figure 11.

Figure/.....

Figure 11



eggs per sac
10
20
30
40
chlor. ā mg/m³
50
100
150
200
250
J.
FEB.
MAR.
APR.
MAY
JUN.
JUL.
AUG.
SEP.
OCT.
N.
D.
EGGS / SAC
CHLOROPHYLL ā

Figure 11 (opposite)

The Seasonal Changes in Mean Number of Eggs per Egg Sac of C. s. abyssorum and in Phytoplankton Standing Crop in Loch Leven (1969)

(Phytoplankton data by kind permission of Bailley-Watts, Nature Conservancy, Edinburgh)

The Abcissa - the study period

Left Ordinate - the mean number of eggs per egg sac of *Cyclops strenuus abyssorum* (see figs. 6 & 7)

Right Ordinate - phytoplankton standing crop measured in mg/m^3 chlorophyll $\bar{a}$

Key - solid line and circles = eggs/egg sac

- broken line and open circles = phytoplankton

Figure 11 shows that there was a clear similarity between the seasonal changes in phytoplankton standing crop and number of eggs/egg sac, although the changes in phytoplankton standing crop fluctuated more sharply than did the changes in egg-number. This is understandable as the quantity of phytoplankton present at any moment will be dependent upon many inter-related factors such as its species composition, the degree of zooplankton predation and its specificity, the nutrient availability, the light and temperature conditions governing photosynthesis and the length of time that individual plant cells are exposed to light, as affected by wind-induced turbulence in the photic zone. The variations in egg-number are likely to be more stable as they are the result of gradual changes in the size-distribution of the population of adult females, whose ovaries are, in turn, producing eggs in relation to a dynamic balance between the food supply and the general demands of metabolism. Moreover, periods of intensive cannibalism by the older instars during times when other food sources were minimal may have maintained the size of clutches. In addition, the subsequent low survival of the resultant nauplii will have reduced the rate of incrementation to the older stages, leading to more food per individual and allowing larger egg broods than would otherwise have been possible.

4. The Development Rate

(a) Field Measurements of Growth Rate

An essential part of any investigation of the dynamics of a zooplankton population, such as that of C. s. abyssorum in Loch Leven, must be the determination of the growth rates and average longevity of the animals under study in the prevailing environmental conditions. Although such information may be estimated from work done on the same or different species of copepods in field or laboratory studies, it is very important to check that such data is consistent with the study in hand. While the length of development of copepod eggs has been found to be virtually solely temperature-dependent (McLaren, 1963, 1965), it has been shown that differences in the quantity and quality of food, as well as changes in temperature, affect the growth of the older instars and the later copepodid stages in particular (Smyly, 1970).

However field studies of growth rates are notoriously difficult owing to the number of uncontrolled variables which may be encountered. Water temperature, for example, can vary by several degrees overnight, while vertically-migrating animals may be subjected to marked changes in temperature while passing through thermally-stratified layers of water. Moreover, while it is relatively easy to observe the growth of copepods through their separate instars during a period of slow development, such as may occur in the cool water conditions of early spring, it may be virtually impossible to detect the same events when they are occurring more rapidly in the warmer conditions of summer.

Continuous/.....

Continuous reproduction during this period may ensure that the passage of cohorts of juveniles from instar to instar will be marked by continuous incrementation. Even during spells when development can be discerned easily, the peaks and troughs of numbers of successive instars will not necessarily occur on sampling dates, making direct observation of the length of time between stages at best only an approximation.

Laboratory studies of growth rate, on the other hand, are more easily controlled and should give accurate results for the conditions under study. However the problem remains that one cannot be certain that laboratory results are valid in field conditions where many inter-related variables combine to affect the actual growth.

An attempt was made to assess the field developmental times of C. s. abyssorum in Loch Leven during 1969/70, using graphs of seasonal standing crops of eggs, nauplii, copepodid stages and adults (figs. 12 and 2) in comparison with a graph of seasonal water temperatures approximating the average temperatures in the water mass (fig. 13). The time in days between peaks or troughs of successive age groups was calculated and compared with the prevailing water temperatures, taken as the mean of the water temperatures found at 5 day intervals during this period.

By/.....

Figure 12 (opposite)

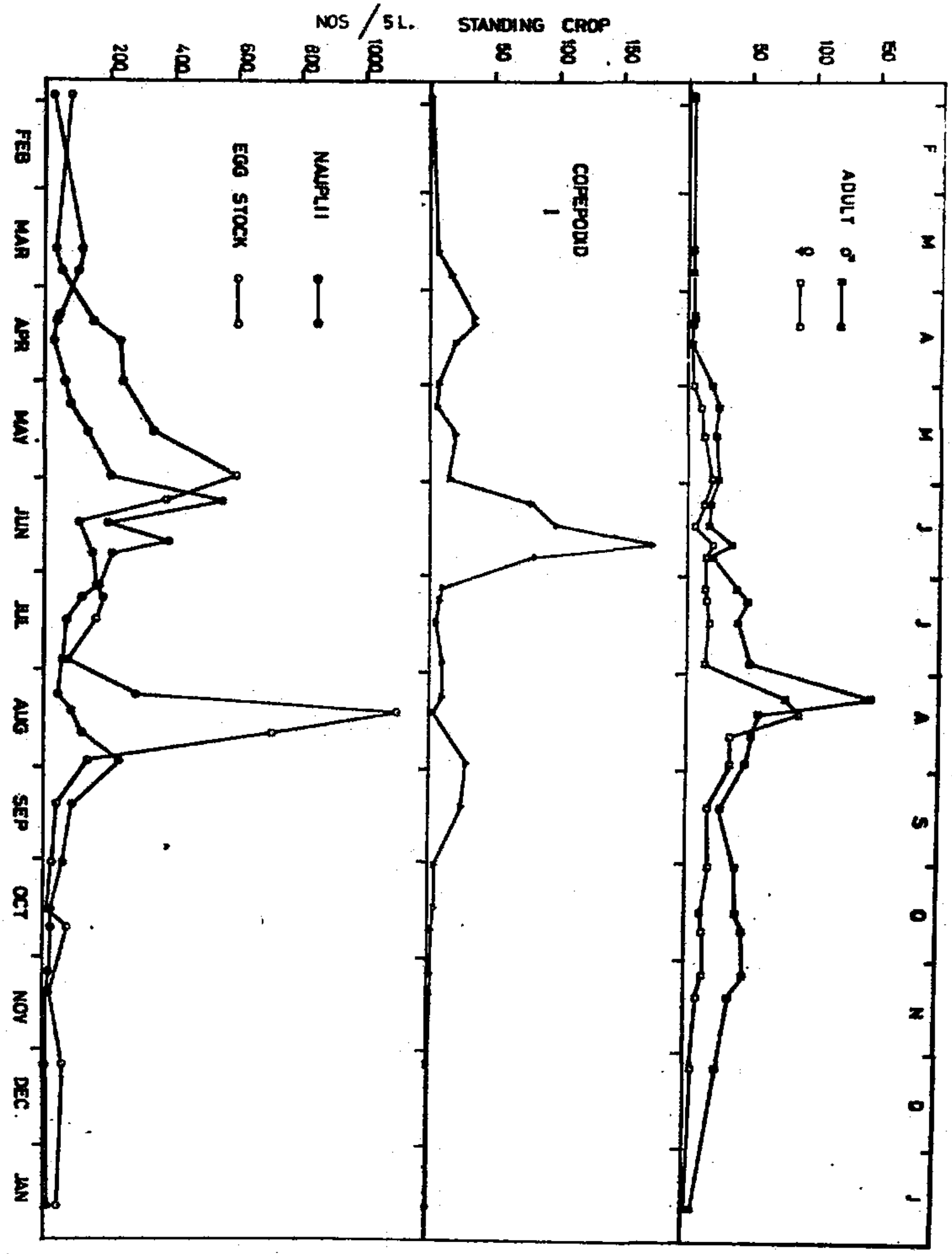
Seasonal Changes in Standing Crop of Eggs, Nauplii, Copepodids I and Adults of C. s. abyssorum in Loch Leven (1969/70) for use in Calculation of Generations

The Abcissae - the study period

The Ordinates - the standing crops in mean numbers per 5 litres

Key	-	open circles	=	egg stock
		closed circles	=	nauplii
		open triangles	=	copepodid I
		closed squares	=	adult males
		open squares	=	adult females

Figure 12



STANDING CROP
NOS / 5 L.
ADULT ♂
♀
COPEPOD I
NAUPLII
EGG STOCK
FEB
MAR
APR
MAY
JUN
JUL
AUG
SEP
OCT
NOV
DEC
JAN

Figure 13 (opposite)

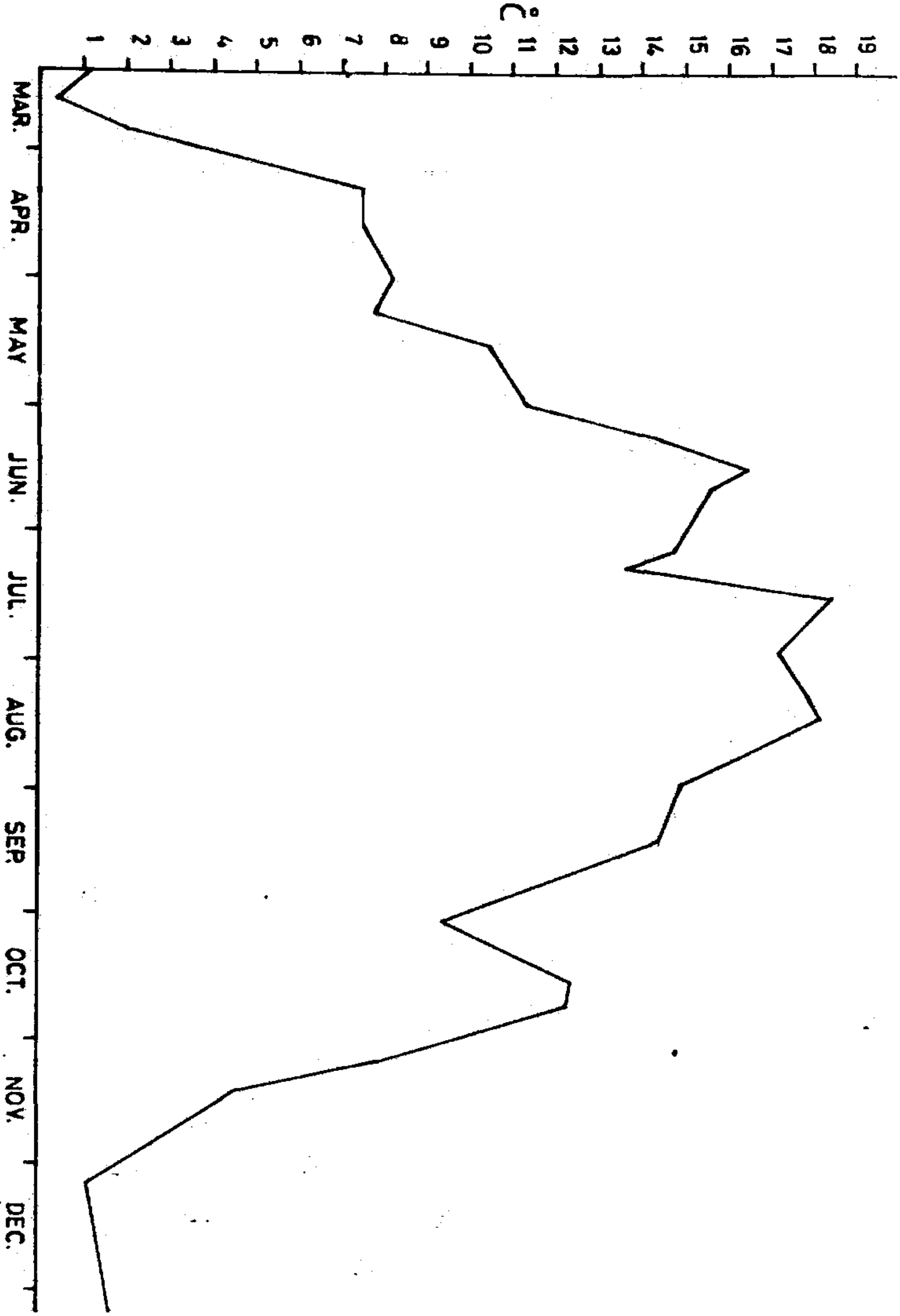
The Seasonal Changes in Mean Temperature of Loch Leven in 1969

The Abcissa - the study period

The Ordinate - water temperature in °C

Temperatures were obtained by thermistor from each depth sampled at each site on every visit. The overall mean temperature was calculated using the average of the arithmetic means of the temperatures at each site since there was normally little difference between the results from different sites.

Figure 13



°C
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
MAR.
APR.
MAY
JUN.
JUL.
AUG.
SEP.
OCT.
NOV.
DEC.

By necessity, owing to the effects of the continuous reproduction and fast development of the copepods during summer, the most confident observations were of events in the cooler conditions of spring and autumn. Table 5 lists the developmental data derived from the standing crops and temperature graphs and a multiple regression analysis of the observations of the length of development from egg initiation to adult female is presented in figure 14 as a curvilinear regression. The length of development appears to vary little when the mean temperature is greater than 13 or 14°C, remaining at approximately 25 days, suggesting that generation time may be constant from June until mid-September. However total development takes 46 days at 10°C and 85 days at 5°C. At still lower temperatures, development must be so greatly retarded that any juveniles which survive in mid-winter can undergo very few moults before the loch water begins to warm up again in spring.

Details of the data obtained by multiple regression are presented in table 6. As the naupliar stages were not completely sampled by the 120 microns filter used for concentrating the Friedinger samples, it is likely that the egg developmental time will be over-estimated and the naupliar development will be under-estimated by the same length of time. However this should have no effect on the calculation of generation time as these errors cancel each other out.

It is interesting at this point to compare the field growth of C. s. abyssorum with that determined for other species in laboratory conditions.

Smyly/.....

Dates of Observation of Corresponding Changes in Standing Crop of Age Groups

	Eggs	Nauplii	Copepodid I	Cop.II	Cop.III	Cop.IV	Cop.V	Cop.VI
1	-	Jan 29	Mar 19	Mar 26	Apr 9	Apr 11	Apr 17	Apr 30
2	Jan 29	Mar 19	Apr 11	Apr 11	Apr 17	Apr 30	Apr 30	May 7
3	Mar 19	Apr 17	May 7	May 7-16	May 16	May 16-30	May 16-30	May 30
4	May 16	May 30	May 30	June 7	June 7-14	June 14	June 14	June 14
5	May 30	June 7	June 14	-	-	-	-	June 20
6	July 28	Aug 8	Aug 13	-	-	-	-	Aug 20

	Egg - Nauplius		Naupl. - Cop.I		Cop.I - CVI		Egg - CVI		Naupl. - CVI	
	Days *	Temp °C **	Days	Temp °C	Days	Temp °C	Days	Temp °C	Days	Temp °C
1	-	-	49	1.5	42	5.0	-	-	91	3.5
2	49	1.5	23	4.0	26	7.5	98	3.5	49	5.5
3	29	4.0	20	8.0	23	11.0	72	7.0	43	9.5
4	14	11.0	-	-	15	15.0	29	13.0	15	15.0
5	8	13.0	7	16.0	6	16.0	21	15.0	13	16.0
6	11	17.5	5	18.0	7	17.5	23	18.0	12	17.5

* Time of development in days between age groups
** Mean of loch temperatures at 5 day intervals during developmental period

NB The series of observations are not necessarily from separate generations.

TABLE 6

Summary of Development Length of Stages of *C. s. abyssorum*

The percentages represent the proportion of total length of development spent in each stage.

Temperature °C	Egg - Nauplius		Naup. - CI		CI - Adult ♀		Egg - Adult ♀		Naup. - Ad. ♀	
	Days	%	Days	%	Days	%	Days	%	Days	%
1	27.5	21	47.0	36	55.5	43	130.0	100	102.5	79
5	18.0	21	27.5	33	39.5	46	85.0	100	67.2	79
10	12.0	26	10.5	23	23.5	51	46.0	100	34.0	74
15	8.5	34	5.0	20	11.5	46	25.0	100	16.5	66
Mean % of total development		25.5		28.0		46.5		100		74.5

Figure 14 (opposite)

The Developmental Rate of C. s. abyssorum
in Loch Leven during 1969

(development from egg initiation until the last moult)

The Abcissa - the water temperature in °C

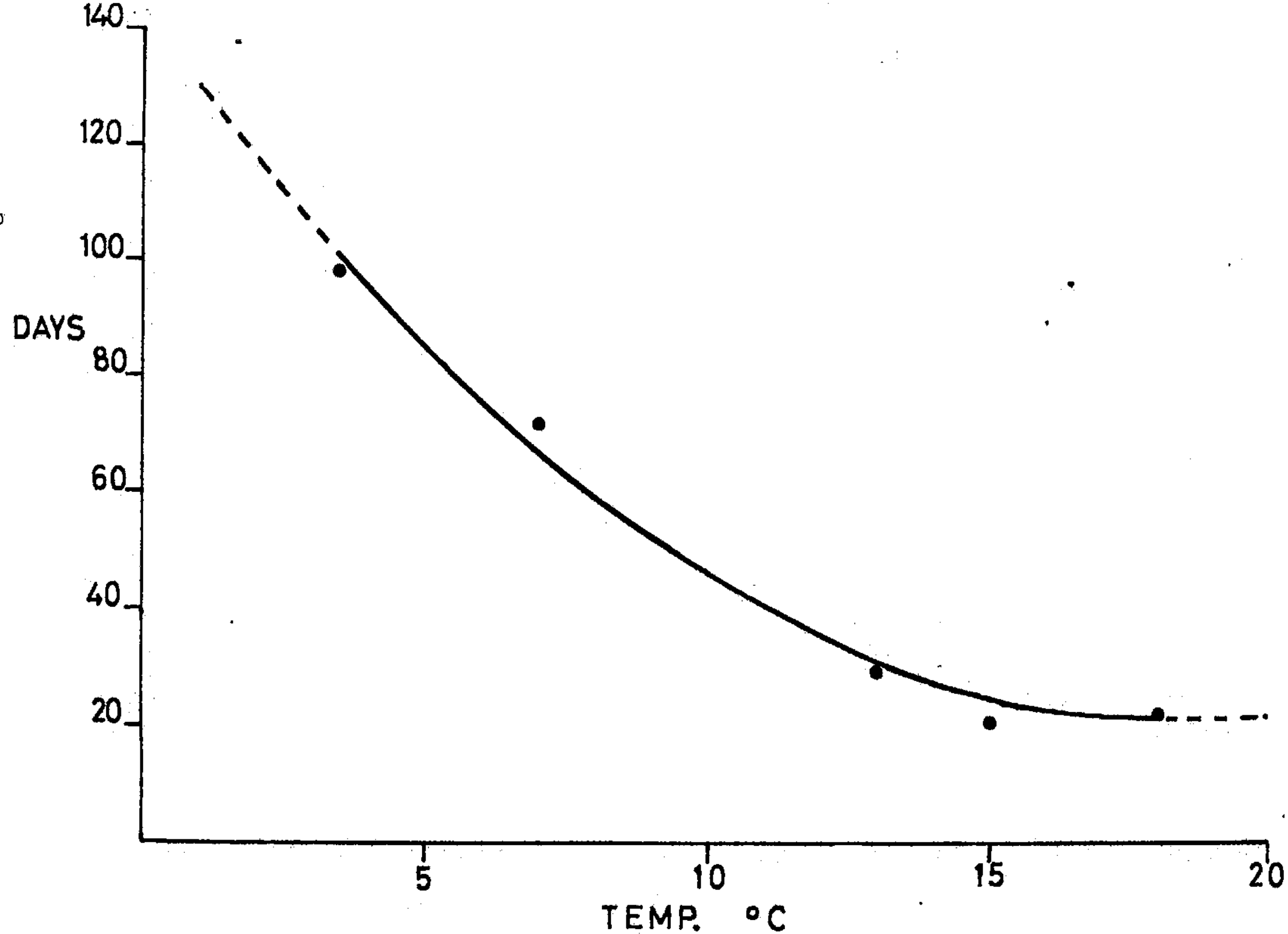
The Ordinate - the developmental length in days

The co-ordinates for developmental rate were plotted from observations of changes in standing crop of successive age groups (figs. 2 and 12) compared with the arithmetic mean of water temperatures at 5-day intervals during the period of development from egg to adult female (fig. 13).

The curve was fitted by multiple-regression analysis of this data using the formula $y = 143 + (-13.44X) + 0.37x^2$ which was significant at the 10% level.

The broken lines indicate the expected rate of development at temperatures outwith the data provided by standing crop analysis.

Figure 14



Smyly (1961) found that Mesocyclops leuckarti took 12 days to develop from hatching egg to copepodid I at 16 - 18°C. Development from CI to adult took a further 20 days, half of which was spent in copepodid stages IV and V. C. s. abyssorum appears to have developed faster, but if the naupliar life is an under-estimation there may not be a large difference. Corkett and McLaren (1970) recorded that in conditions of abundant food, Pseudocalanus minutus nauplii developed to copepodid I in 46.4 days at 0°C, 26.6 days at 3.44°C, 18.9 days at 7.52°C and 12.3 days at 11.92°C. Eckstein (1964) found that Diaptomus gracilis took 115 days to develop from egg to adult at 5°C, 60 days at 10°C and 38 days at 15°C. Smyly (1970), in a laboratory study of the developmental rate, longevity and fecundity of Acanthocyclops viridis in relation to type of food, found that the fastest rate of development from egg hatching to adult was achieved when the copepods were fed upon Artemia salina nauplii, although not initially, as development to CIII was fastest with algal feeding. In addition, males developed faster than females on all of the range of foods given. Thus at 16 - 18°C, development from hatching egg to adult male took 23.5 days on a diet of Artemia while females took 31.4 days. Fed upon algae, the males took 33.2 days while the females took 61.8 days. By comparison, C. s. abyssorum females in Loch Leven took 25 days to develop from egg to adult, including the egg stage, at 15°C.

Judging/.....

Judging by the range of developmental times achieved by feeding Acanthocyclops on different diets in the laboratory, it is possible that field developmental times may be shorter than laboratory ones, as there is likely to be a better choice of available food items in natural conditions, perhaps allowing the developmental stages to have access to the types of food which can give them optimal growth rates.

(b) The Number of Generations in a Year

On the basis of observation of the graphs of standing crops of the developmental instars of *C. s. abyssorum*, coupled with the regression analysis data of developmental length against water temperature, it is possible to estimate the number of generations which were undergone in 1969/70. However these generations were not clearly separated in time and tended to overlap. Therefore the following estimates are based on the times of first initiation of each generation.

The egg stock of the overwintering adults resulted in a generation of spring adults arising in April. Meanwhile another cohort of juveniles arose in March from a further synchronous egg batch maturation, coming to maturity in May. Both of the two spring 'generations' were the progeny of the overwintering adults and overlapped in the rapidly-rising water temperatures of April and May i.e. they were separate cohorts of the same generation. They may be designated generation 1a and 1b.

Breeding of the new adults then resulted in a further generation coming to maturity in the middle of June (generation 2). By then the water temperature was in excess of 13 - 14°C and complete development probably took place in about 25 days, so that generations 3, 4 and 5 arose in early and in late July and in the second half of August. The generations giving adults in August resulted in a large egg stock which maintained the flow of juveniles through the population during September, October and November. Thus the eggs arising from the adults which matured in late August resulted in adults entering the population in October and November (generation 6), having undergone an attentuated development due to the cooling conditions of autumn.

Therefore it is likely that approximately six generations were completed during the year as summarised in table 7.

Table 7

Approximate Generation Length			Generation Number
Jan.	-	April	1a
March	-	May	1b
April/May	-	mid June	2
mid June	-	early July	3
early July	-	end of July	4
end of July	-	late August	5
late Aug.	-	Oct./Nov.	6

5. Biomass and Production

(a) Biomass

The numbers of zooplankton present in a particular lake at any one time, or the standing crop, are not readily comparable with numbers of zooplankton from other lakes. Within one lake, these numbers may refer to different stages and sizes of a particular species, while between lakes, they may refer to entirely different species. It would not be meaningful to compare one hundred *Daphnia* sp. from one lake with one hundred of a much smaller species of *Bosmina* from another, and it is more useful to reduce the data to a common denominator such as weight, volume or potential energy units. The numerical standing crop data of *C. s. abyssorum* was therefore converted into biomass, to permit comparison with other studies.

i. Methods

Biomass is calculated less often by direct weighing of samples than by using length measurements and multiplying by an appropriate conversion factor into weights. In the present study, a length/weight conversion formula

$$W = 0.055L^{2.73} \quad \text{where } W = \text{wet weight (mg)}, \; L = \text{length (mm)}$$

was used to convert the numbers of the separate stages of *C. s. abyssorum* into weight units (pers. comm. K. Patalas - from Klekowski and Shushkina, 1966).

As/.....

As has already been shown in the section on Body Length Analysis (E, section I, 1 (b)), the successive adults maturing throughout the year were of dissimilar size, therefore it is likely that the instars leading to these adults will have undergone similar, seasonal changes in their mean length.

During winter, development was very slow and the sizes of the younger instars could reasonably be related to those of older instars. During summer, development and adult length changes were more rapid, thus the young stages could not be fairly compared with the older stages present at the same time, as they probably would not have matured to the same size. Therefore nauplii, copepodids and adults from a winter sample were measured and the percentage growth in length from stage to stage was calculated (table 8). Using the mean length of the adult females present on each sampling date as a base value, the mean lengths of the younger instars were calculated by proportion. As nauplii were not identified to instar, their mean length in the winter sample was taken as being representative of the group as a whole and this was calculated as a percentage of the adult mean length in the same way as were the copepodid lengths.

The calculated lengths of the stages of _C. s. abyssorum_ throughout the year were then converted into wet weight, using the conversion formula of Klekowski and Shushkina (1966) and the wet weights of the individual instars were multiplied by the numbers of these stages present on each sampling date to obtain the biomass of the nauplii, copepodids and adults.

The/.....

TABLE 8

Total Lengths (minus furcal setae) of Instars of Cyclops strenuus abyssorum from sample taken on 29.1.69

	Nauplii	CI	CII	CIII	CIV ♂	CIV ♀	CV ♂	CV ♀	CVI ♂	CVI ♀
	0.15 - 0.35	0.62	0.75	0.95	1.20	1.25	1.35	1.55	1.45	1.65
		0.64	0.85	0.97	1.15	1.10	1.30	1.59	1.41	1.60
		0.65	0.80	0.96	1.08	1.18	1.22	1.55	1.51	1.67
		0.65	1.83	0.97	1.17	1.25	1.20	1.60	1.42	1.75
		0.64	0.79	1.04	1.22	1.35	1.30	1.68	1.43	1.71
		0.65	0.80	1.05	1.19	1.38	1.33	1.57	1.47	1.66
		0.62	1.80	0.90	1.06	1.40	1.29	1.38	1.30	1.60
		0.60	0.72	1.05	1.20	1.30	1.33	1.45	1.45	1.71
		0.64	0.81	1.00	1.11	1.25	1.29	1.62	1.49	1.59
		0.63	0.80	1.07	1.14	1.26	1.30	1.50	1.42	1.60
Mean length mm	0.15 - 0.35	0.63	0.80	1.00	1.15	1.27	1.29	1.55	1.44	1.65
% of adult ♀ length	9 - 20	38	48	61	70	77	78	94	87	100

The density of a copepod egg was assumed to be little different from water. Therefore the mean diameter of a sample of eggs was used to calculate the volume, and thereby the weight, of an egg. The numerical standing stocks of eggs were then multiplied by this value and the combined egg weights were added to the biomass of the other stages.

ii. Results

The biomass of *C. s. abyssorum* in mg wet weight per 5 litres and g wet weight per m^3 is presented in figure 15. From a steady winter level of 2mg wet weight/5 litres the biomass rose in the last week of March, gained momentum in April and levelled off at 20 - 25mg/5 litres during May and the first half of June. A very large increase in biomass took place during the remainder of June and early July, reaching the seasonal maximum of 76mg/5 litres (15.2g/m^3), when there was a sudden drop to 30mg, followed by a rise to 56mg before the end of July. A steady decline then took place, slowing down in late August and levelling off at 15 - 20mg/5 litres in September and October. From late October there was a further decline until late January, reaching the biomass of the early part of the previous year (2mg/5 litres).

Assuming that dry weight is equal to 10% of wet weight and assuming a calorific equivalent of 6kcals/g dry weight of copepod, the mean monthly biomass of *C. s. abyssorum* in Loch Leven in 1969/70 was calculated planimetrically and converted into kcals/m^2 surface area (Loch Leven is 3.9 metres deep on average).

The/.....

Figure 15 (opposite)

The Biomass in wet weight of C. s. abyssorum in Loch Leven during 1969/70

The Abcissa - the study period

Left Ordinate - the biomass of C. s. abyssorum in mg/5L wet weight

Right Ordinate - the biomass of C. s. abyssorum in g/m^3 wet weight

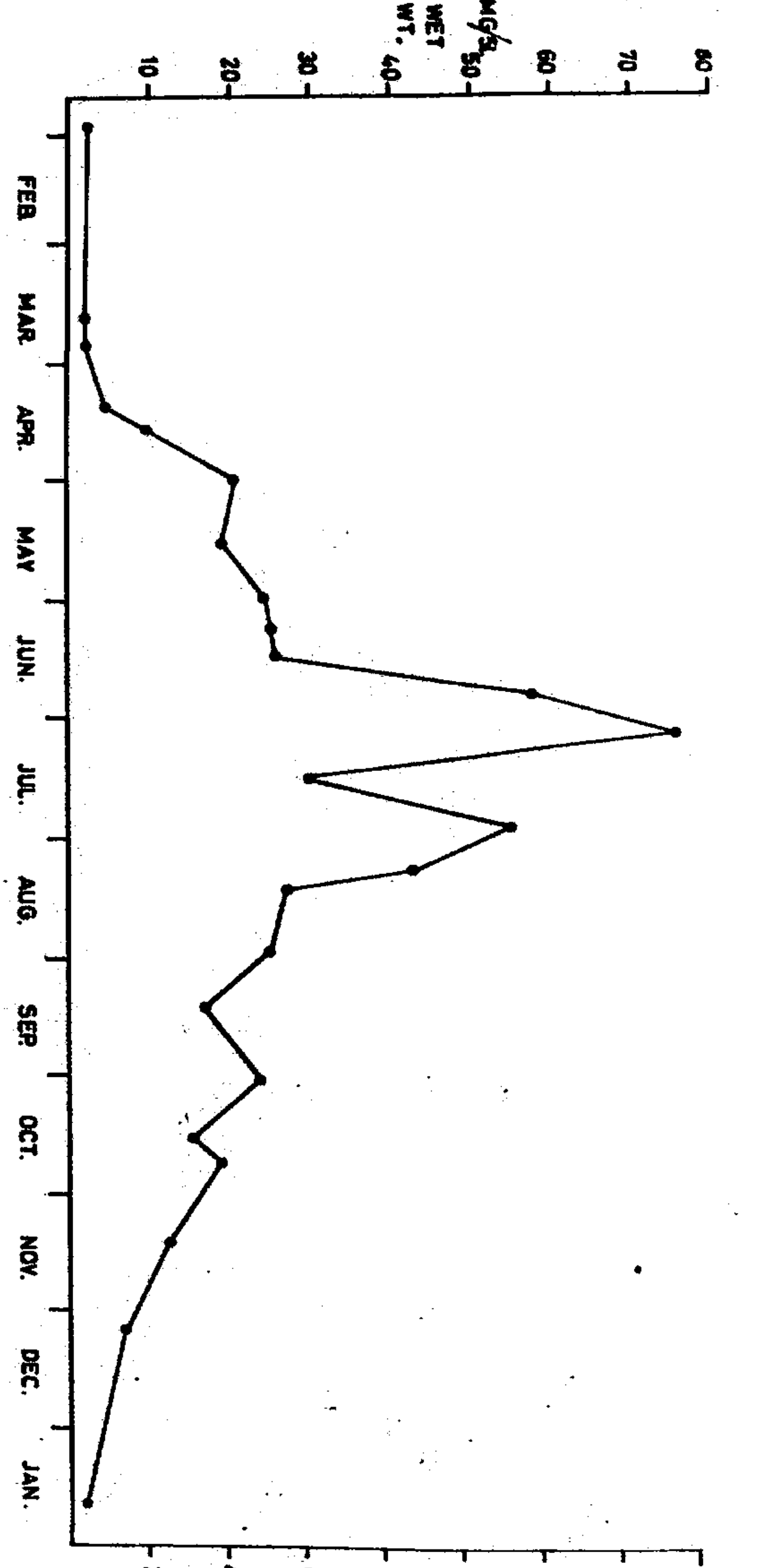
The biomass was obtained by converting the lengths of the different age and sexual groups of C. s. abyssorum throughout the year into wet weight, using the formula:-

$$W = 0.055L^{2.73}$$

W = wet weight in mg
L = length in mm

(pers. comm. K. Patalas - from Klekowski and Shushkina, 1966)

The wet weights of the separate groups were multiplied by their standing crops throughout the year and the totals were combined to gain the overall population biomass.


WET
WT.
10
20
30
40
50
60
70
80
FEB.
MAR.
APR.
MAY
JUN.
JUL.
AUG.
SEP
OCT.
NOV.
DEC.
JAN.
2
4
6
8
10
12
14
16
G/M³
WET
WT.

The results are presented in figure 16 and show that plotting mean, monthly data has had the effect of removing the twin, summer peaks of biomass which were evident in figure 15. A stable winter level was maintained until March, after which there was a steady rise to a mean, monthly peak of 24 kcals/m^2 in July, followed by a steep fall to about 8.5 kcals/m^2 in September and October and then a more gradual decline reaching nearly 1 kcal/m^2 in January. The mean annual standing crop was calculated to be 8.4 kcals/m^2, while the mean, maximum standing crop occurred in early July, when there were 34.7 kcals/m^2.

(b) Production

i. Review of Methods for Calculating the Production of Zooplankton

The biomass of a zooplankton community is not, however, sufficient for detailed comparison between lakes, being a measure of capacity rather than intensity, although it forms the basis of such a comparison. It is more appropriate to consider the production of biomass formed by the community in a given time, involving a calculation of the rate of turnover, or replacement, of standing crop.

The methods for assessment of zooplankton production have been reviewed by Hillbricht-Ilkowska and Patalas (in press) and Mann (1969). Hillbricht-Ilkowska and Patalas divided them into two basic groups:-

Figure 16 (opposite)

The Mean Monthly Standing Crop of C. s. abyssorum in Loch Leven in 1969/70 expressed as kcals/m^2

The Abcissa - the study period

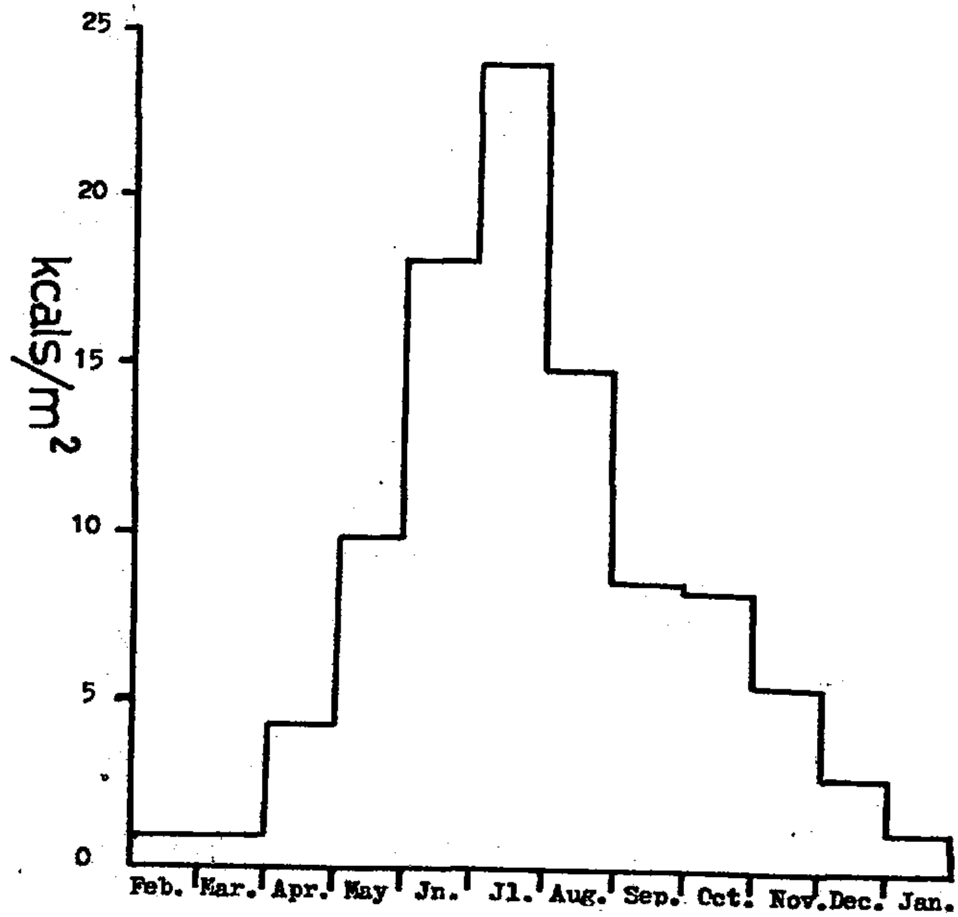
The Ordinate - the standing crop of C. s. abyssorum in kcals/m^2

Mean monthly values of biomass were calculated from figure 15 by planimetric integration and were converted into energy units using approximate conversion factors:-

dry weight ≡ 10% of wet weight

1g dry weight of copepod ≡ 6 kcals

Figure 16



kcals/m2
25
20
15
10
5
0
Feb.
Mar.
Apr.
May
Jn.
Jl.
Aug.
Sep.
Oct.
Nov.
Dec.
Jan.

(1) Based on calculations of the turnover of the number of organisms within a population.

(2) Based on the daily weight increase of individuals.

Among the first group are methods by Elster (1954), Straskraba (1963), Nauwerk (1963), Stros, Nees and Hasler (1961), Edmondson (1960, 1965), Edmondson, Comita and Anderson (1962), Eckstein (1964) and Galkowska (1965). Edmondson, for example, assessed the potential number of individuals which would arise from exponential growth using the ratio of eggs/female, the population number and the calculated length of egg development at different temperatures. On the basis of quantitative samples, knowing the ambient lakes temperatures, he calculated the potential increase in population during a given time and subtracted the actual population size found after this time from its theoretical size to assess elimination. This method has been used by several workers including Hall (1964) and Wright (1965), who calculated the population birth and death rates and estimated how long it would take for the population numbers to be replaced, i.e. the turnover time.

As Hillbricht-Ilkowska and Patalas noted, this method is very approximate, requiring unchanged population birth and death rates during the periods between sampling. These conditions are unlikely to prevail for long due to changes in such variable parameters as temperature, food supply or predation.

Moreover, in this form the method does not yield precise information on whether the popluation mortality is age-specific, merely noting changes in total numbers of all stages. It has been used mainly for correlation between the factors affecting elimination, such as predation pressure, and the ultimate population size.

Included in the second group of methods, based on the daily weight increase of individuals, are methods by Konstantinova (1961), and Greze (1965) and the reviewers considered that these methods were likely to be more accurate than those based on potential changes in population size. In this group of methods the curve of individual growth is gained from experimental evidence of the weight of individuals in the separate instars, plus their length of development at different temperatures and their longevity. In the method of Winberg et al (1965), the production of a given instar is obtained by multiplying the numbers of the stage by their daily weight increase during the period investigated. The main source of error appears to be in calculating the average length of life of the developmental instars in the given environmental conditions.

Mann (1969) reviewed techniques for measuring zooplankton production including details of methods by Edmondson (1960), Yablonskaya (1962) and Greze and Baldina (1964). The latter method was an attempt to overcome the difficulties involved in calculating the production of a polycyclic population of Acartia clausi in the Black Sea.

Having/.....

Having decided, on the basis of seasonal fluctuations in standing stocks, that there were seven generations per year, the authors used data on development time at different temperatures and published data on the weight of each developmental stage to construct growth curves appropriate to each developmental time. Daily growth rates were then calculated and multiplied by the number of animals present in each age class to give a series of daily production rates. The seasonal production was obtained by summing the daily rates for each generation. In this way they calculated that the annual production of A. clausi was about thirteen times the mean annual biomass ($^P/B = 13$).

While this method may be excellent for estimating the production of a population where there is clear evidence of the passage of cohorts of juveniles through the developmental instars, there is room for doubt as to its accuracy in estimating the production of overlapping generations or cohorts in a polycyclic population such as that in Loch Leven. However it appears to be the best method which has yet been devised.

ii. Tentative Estimate of Production

It was considered unjustifiable at this stage to attempt the complex calculations necessary for assessing the production of the postulated six generations of Cyclops in Loch Leven, because of the difficulties associated with growth rate uncertainties and generation overlaps. However it is intended that the basic information gained during the study of the C. s. abyssorum population may be used in calculations for future publication.

Meanwhile/.....

Meanwhile it is possible to make a tentative estimate based on the relationships between average biomass and production in a given period (the $^P/_B$ coefficient) as calculated by Greze and Baldina (1964) and Winberg, Pechen and Shushkina (1965).

Winberg et al calculated the $^P/_B$ coefficients for three Russian lakes of different trophic status and found that there was a tendency for the coefficient of all groups of zooplankton, including carnivorous copepods, to increase with progression from mesotrophic to eutrophic conditions. Table 9 illustrates the production, biomass and $^P/_B$ coefficients for the three lakes, listed in order of decreasing degree of trophication, for the five summer months constituting the growing season.

Table 9 (from Winberg, Pechen and Shushkina, 1965).

Production (P), Biomass (B) in g/m^2 wet weight and $^P/_B$ coefficients for Lakes Batorin, Myastro and Naroch

Groups	L. Batorin			L. Myastro			L. Naroch		
	P	B	$^P/_B$	P	B	$^P/_B$	P	B	$^P/_B$
Cyclopidae	18.3	1.8	10.2	24.6	2.4	10.2	20.7	2.7	7.7
Diaptomidae	14.4	1.5	9.6	49.2	6.0	8.2	34.2	4.5	7.6
Cladocera	307.5	10.5	29.3	86.4	6.0	11.4	18.9	1.4	13.5
Filter feeders	321.9	12.0	26.8	135.6	12.0	11.3	53.1	5.9	9.0

The/.....

The $^P/B$ coefficients for cyclopoids in the three lakes were 10.2, 10.2 and 7.7 and those for filter feeders were also approximately 10, except for the Cladocera of L. Batorin which had a coefficient of 29.3. The authors explained that in this case the abnormal $^P/B$ coefficient was as a result of the very short mean life cycle of *Chydorus sphaericus* in that lake.

Assuming that the high $^P/B$ coefficient can be discounted, the range of coefficients calculated for the different zooplankton groups by Greze and Baldina and Winberg et al is 7.6 - 13.5. The mean annual biomass of *Cyclops strenuus abyssorum* in Loch Leven in 1969 was estimated to be equivalent to 8.4 kcals/m^2. Therefore the annual production was likely to have exceeded this by 7.6 - 13.5 times.

i.e. $P = B \times {}^P/B$

$= 8.4 \times 7.6$ or 8.4×13.5 kcals/m^2

Production $=$ 63.8 - 113.4 kcals/m^2

However it is possible that these calculations underestimate the actual production as the $^P/B$ coefficients of Winberg et al were based on the growing season only and the use of the mean biomass for the growing season in Loch Leven would have the effect of raising the mean value of 8.4 kcals/m^2. As the standing crop of the overwintering population remained relatively steady during January - March at approximately 1.0 kcals/m^2, the growing season could be described as the period from April until the last adults matured in November.

The/.....

The mean standing crop during this period was equivalent to 12 kcals/m^2. Thus the production calculated from the $^P/B$ coefficients of 7.6 - 13.5 would then be:-

$$P = B \times {^P/B}$$

$$= 12 \times 7.6 \quad \text{or} \quad 12 \times 13.5 \text{ kcals/m}^2$$

i.e. Production in growing season

$$= \underline{91.2 - 162.0} \text{ kcals/m}^2$$

By using the extremes of the production figures gained by both calculations the net production of C. s. abyssorum in Loch Leven in 1969 was :-

63.8 - 162.0 kcals/m^2

The equivalent figures for the production of zooplankton in Lakes Batorin, Myastro and Naroch, calculated by combining the data for filter feeders and cyclopoids, were 204, 96 and 44 kcals/m^2 respectively and most of this production was contributed by the filter feeders. Therefore, despite the fact that the crustacean zooplankton of Loch Leven is dominated by a non-filter feeder, the production appears to be intermediate between that calculated for the three Russian Lakes.

Winberg et al extended their productional study by calculating the food consumption and assimilation rates of the zooplankton and found that 720 kcals/m^2 of the primary production would have required to have been consumed in Lakes Batorin and Myastro and 354 kcals/m^2 in Lake Naroch in order to permit the calculated production of filter feeders alone.

However/.....

However *Cyclops strenuus abyssorum* is an omnivore and cannot always exploit the primary production directly. It is possibly reasonable to apply filter feeding assimilation rates to calculations involving periods when the *Cyclops* were herbivorous but when their diet was carnivorous they were on a higher trophic level, exploiting food organisms, such as rotifers, chironomid larvae and their own nauplii, which had themselves utilised the primary production. Associated with each step between trophic levels is a potential energy loss due to conversion efficiency. Thus it is likely that the demands of the *C. s. abyssorum* population upon the primary production will have been greater than that had there been a filter feeding crustacean zooplankton of equivalent size. It is possible that if the cyclopoids were supplanted by filter feeders such as *Daphnia*, the production of zooplankton might become greater, as they would exploit the primary production directly and , thereby, more efficiently.

II. Other Crustacea

1. Species Lists for 1969/70 and 1898

As previously noted in Review, section III, Scott (1898) reported that the Loch Leven zooplankton was dominated by *Daphnia lacustris* Sars (*D. hyalina* var. *lacustris* Sars) with *Diaptomus gracilis* Sars and *Cyclops strenuus* Fischer common, while *Bythotrephes longimanus* Leydig and *Leptodora hyalina* Lilljeborg were present at times. Collecting with a hand net and a tow net near the shore and the weed beds he found 38 species of copepods and cladocerans and 28 species of ostracods.

During the current investigation in 1969/70 seven copepod and seven cladoceran species were recorded from the routine Friedinger samples, and an investigation of the very sparse weed beds which were found in mid-summer revealed no additional species. Table 10 lists the species of copepods and cladocerans found in 1898 and in 1969.

It is immediately apparent that many more species were found in 1898, despite the fact that Loch Leven has become more eutrophic since then and, although it is generally recognised that the process of eutrophication tends to increase species diversity in the ecosystem by increasing niche diversity, the zooplankton coenosis of Loch Leven has apparently become less diverse. Most of the crustaceans recorded in the 1898 list are characteristically benthic or live in close association with weeds.

As/.....

TABLE 10

The Cladocera and Copepoda of Loch Leven

(a) Copepoda

Scott, 1898	Present study, 1969
Diaptomus gracilis Sars	Diaptomus gracilis Sars
Cyclops strenuus Fischer	Macrocyclops albidus (Jurine)
" bicuspidatus Claus	Paracyclops fimbriatus (Fischer)
" vernalis Fischer	" affinis (Sars)
" bisetosus Rehberg	Cyclops s. abyssorum Sars
" viridis (Jurine)	Acanthocyclops viridis (Jurine)
" albidus (Jurine)	Canthocamptus minutus Claus
" serrulatus Fischer	
" macrurus Sars	
" fimbriatus Fischer	
Canthocamptus staphylinus (Jurine)	
" minutus Claus	
" schmeilii Mrazek	
Attheyella crassa (Sars)	
" pygmaea (Sars)	
" duthiei Scott	
" zschokkei (Schmeil)	
Moraria Anderson-Smith Scott	

(b) Cladocera

Sida crystallina (Müller)	Alona affinis Leydig
Simocephalus vetulus (Müller)	" quadrangularis (O.F. Müller)
Daphnia lacustris Sars	Chydorus sphaericus (O.F. Müller)
Bosmina longirostris (Müller)	Leydigia leydigi Schödler
" longispina Leydig	Monospilus dispar Sars
Ilyocryptus sordidus (Lievin)	Eurycercus lamellatus (Müller)
Eurycercus lamellatus (Müller)	Bythotrephes longimanus Leydig
Acroperus harpae Baird	
Alonopsis elongatus Sars	
Alona guttata Sars	
" affinis Sars	
" quadrangularis (Müller)	
Alonella exigua (Lilljeborg)	
" nana (Baird)	
Pleuroxus trigonellus (Müller)	
" uncinatus Baird	
Chydorus sphaericus (Müller)	
" barbatus (Brady)	
" ovalis Kurz	
Monospilus dispar Sars	
Leptodora hyalina Lilljeborg	
Bythotrephes longimanus Leydig	

As one of the most marked changes in Loch Leven is a reduction in the number of species and quantity of macrophytes it is probable that many species have lost their niches.

More relevant perhaps, from the point of view of the true limnetic plankton, is the apparent loss of Daphnia sp. and Bosmina sp. since 1898, as no new species of filter feeders have emerged to take their place.

2. Diaptomus gracilis

The only holoplanktonic filter feeder crustacean found in 1969/70 was Diaptomus gracilis and this species was found on such few occasions that its effect on the phytoplankton must have been insignificant. As so few individuals of this species were collected, little can be deduced concerning its annual cycle in Loch Leven. However the qualitative net hauls which were obtained by Bailley-Watts (The Nature Conservancy) from September 1967 - September 1968 suggested that the calanoids were present in the plankton throughout the year although their numbers appeared to be very low in July. From September 1967 until March 1968, they occupied 3 - 7% of the plankton, while during the remaining period they constituted less than 3%. Approximately equal numbers of all stages were present during winter, whereas Chapman (1969) found that the Diaptomus gracilis population in Loch Lomond overwintered mainly as adults.

A/.....

A further point of comparison between the *D. gracilis* of Loch Lomond and Loch Leven is that the clutch size of the latter population appeared to be much greater. The range of numbers of eggs per egg sac in Loch Lomond was 2 - 25 whereas egg sac counts from two ovigerous females taken at random from the Loch Leven samples gave 47 and 50 eggs per sac. This may indicate the greater trophic status of Loch Leven or it is possible that the small population of *D. gracilis* existing in Loch Leven has a greatly enhanced quantity of food per individual, allowing adult females to produce large clutches. This in turn might be expected to result in a population build-up, but the *C. s. abyssorum* population may supress this by predation pressure.

As the calanoid proportion of the copepods in Loch Leven fell to almost zero in 1969/70, it will be of obvious interest to continue to monitor the numbers of *D. gracilis* in order to see whether they disappear completely or perhaps stage a recovery.

3. *Bythotrephes longimanus*

The predatory cladocerans *Leptodora kindti* and *Bythotrephes longimanus* were both observed in the tow net samples taken in 1967/68, occurring in August, September and October, while only the latter species was found in 1969, when 38 were taken by Friedinger sampling in the months August to November. *Leptodora* and *Bythotrephes* are reputed to be relatively speedy swimmers perhaps making it unlikely that their capture could be quantitatively effected by Friedinger bottle sampling.

However/.....

However vertical and horizontal net tows also captured only relatively small numbers of Bythotrephes and no Leptodora. Consequently it does not appear likely that either species occurred in as large numbers as they apparently do in some other lakes. If in fact they do occur in larger numbers than suspected, perhaps having avoided sampling because of aggregated behaviour, it is dubious whether they could be significant predators upon cyclopoids. Mordukhai - Boltovskaia (1958) found that the sudden movements of the copepodid stages of copepods apparently saved them from being predated upon by Leptodora and Bythotrephes while adult cyclopoids actually captured and ate the carnivorous cladocerans themselves. They found, for example, that a fully-grown Macrocyclops albidus in one day could eat five Leptodora from 4 - 6cm in length. They inferred from their experiments that in Rybinsk Reservoir Leptodora and Bythotrephes fed mainly upon cladocerans, principally Bosmina and Ceriodaphnia. However they did not supply either rotifers or copepod nauplii as food and both of these may be important prey items in Loch Leven. On the other hand, as C. s. abyssorum adults and older copepodids also feed upon rotifers and nauplii and possibly feed upon Bythotrephes as well, the copepods themselves are likely to have exerted much the greater predatory control on their own population.

4. Benthic Copepoda and Cladocera

In/.....

4. Benthic Copepoda and Cladocera

In addition to the holoplanktonic species described above, a few individuals of three characteristically benthic cyclopoid species, five chydorid species and a harpacticoid species were observed as presumably unwilling excursionists into the plankton, swept up from the loch bed by current action. It would be interesting to know more of the ecology of such benthic populations, living at the mud/water interphase. The cyclopoid species Macrocyclops albidus and Acanthocyclops viridis, for example, may well be significant predators on the larval Chironomidae and on other groups living on the loch bed.

III. Rotifera

1. Species Composition and Seasonal Observations

The Rotifera of Loch Leven have apparently never been studied before and indeed little, if anything, has been written about them in Scotland. They are a difficult but interesting group to study being very active and also delicate, so that many of the soft-bodied forms contract so markedly in preservative that species recognition is troublesome, while the live animals move so quickly that observation of them under high-power magnification presents severe problems. The loricate rotifers, however, have a characteristic exoskeletal shape which is fairly easy to identify.

The small size of most rotifers would have made their quantitative capture in Loch Leven very time-consuming because of the large amount of phytoplankton which would have been sampled simultaneously. In addition many of the loricate species become trapped in the surface film or stick to the sides of tubes and sampling equipment rendering sampling and counting techniques difficult. Consequently the rotifers were sampled qualitatively with a towed net of 63 microns mesh size. A list of species in order of their approximate numerical importance in Loch Leven is presented in table 11. The list is not intended to be exhaustive but records the genera which were confidently identified using Voigt (1957), Edmondson (1959) and Donner (1966).

Table 11

The Limnetic Rotifera of Loch Leven in 1969/70

Keratella cochlearis var. tecta	(Gosse) (2 forms - tailed and non-tailed)
K. quadrata	(Müller) (? K. hiemalis Carlin)
Polyarthra dolichoptera	Idelson
Synchaeta (?) pectinata	Ehrenberg
Brachionus (?) rubens	(Ehrenberg)
Conochilus unicornis	Rousselet
Filinia longiseta	(Ehrenberg)
Asplanchna priodonta	Gosse
Pompholyx (?) sulcata	Hudson

In addition, two other rotifer species were observed alive in a fresh sample but their identification was impossible at the time and they were not observed again.

Although nine species of rotifers were noted, this diversity of species was only observed in early spring and to some extent in late autumn and only the first four were numerous (see Appendix 1).

While most of the species were present in spring, the colonial rotifer Conochilus unicornis was found only in autumn. The non-tailed variety of Keratella cochlearis was found only in summer, gradually having succeeded the tailed form of the same species, dying out eventually in July.

The/.....

The tendency was, in fact, for the rotifer population to increase in numbers and decrease in diversity from late winter to mid-summer, then to disappear until autumn when only small numbers were observed. A gradual fall in numbers of individuals and rise in numbers of species then followed until few individuals were found during winter.

The population peak of numbers of rotifers occurred in June when there was a very large bloom of *K. cochlearis* var. *tecta*. At the peak of the bloom, indirect estimates of the standing crop (calculated by comparing the number of rotifers per copepod in net samples with the known standing crop of copepods) were of the order of 10 individuals/ml or 10,000/litre. Bailley-Watts, studying the phytoplankton of the Loch, estimated that there were as many as five times that figure in places. Quite obviously they must have been a major factor in phytoplankton cropping at that time.

K. cochlearis is 50 - 100 microns in length and, according to Edmondson (1965), feeds upon organisms up to 10 microns in diameter, such as bacteria or species of *Chlorella*, *Stichococcus* or *Coccomyxa*. At the time of maximum abundance of rotifers, very large blooms of *Diatoma* spp. and *Oscillatoria* spp. were decaying (pers. comm. Bailley-Watts). These phytoplankters would be too large to be ingested by *Keratella* but the rotifers may have been utilising the bacterial build-up resulting from the senescent diatoms and filamentous algae.

The/.....

The bloom of rotifers died out in early July, possibly because of the combined effects of over-exploitation of their food supply and predation pressure from the Cyclops population, which reached its seasonal maximum biomass at that time.

2. Variation in Keratella cochlearis

The term 'cyclomorphosis' has been used to describe the seasonal morphological changes in zooplankters such as Daphnia spp. or loricate rotifers. The summer 'helmeted' form of Daphnia hyalina var lacustris, it has been argued, developed as a response to the decline in water viscocity with rising temperatures in spring in order to combat their resultant gradual loss of buoyancy. In rotifers, however, Pejler, (1962) pointed out that the morphological variation follows the pattern of a decrease in spinal length in summer and an increase in spinal length in cool seasons. Thus the spines are shortest at the time of minimum water viscocity. Pejler argued convincingly that the seasonal changes in spinal length of Keratella are associated with changes in body length (excluding spines) and therefore body weight. As the body length increases by one unit, its weight will increase by the third power of this unit. Therefore the compensatory increase in length of spine will be greater than might be expected. Systematic measurements of the rotifers in Loch Leven have not yet been made in order to check the veracity of Pejler's argument but it is a fact that the tailed form of K. cochlearis was apparently absent from the plankton from May until September.

However/.....

However no intermediate forms were observed between the tailed and non-tailed and both were found simultaneously in April, suggesting that, in Loch Leven, they may be genotypically distinct rather than, as Pejler suggests, environmentally determined. However further study is needed to substantiate this.

IV. Other Groups

1. Larval Chironomidae

One of the most striking features of Loch Leven is the size of the chironomid population. During summer evenings large clouds of adult Chironomidae are often to be seen hanging like smoke clouds over the surrounding fields. Staff of the Nature Conservancy are, in fact, studying the Loch Leven chironomids, assessing their species composition, annual cycles, biomass and production and work has recently been undertaken on their behaviour. Therefore observations of their larvae or pupae in the plankton may be of interest.

(a) Seasonal Observations

During the course of routine zooplankton sampling, during 1969/70, using the 5 litre Friedinger water bottle, twenty six observations were made of larval chironomids, three of which were actually being ingested by individuals of *C. s. abyssorum*. Details of the observations are presented in table 12.

The species or development instar of these chironomids has not yet been determined. No pupae were observed in the samples.

(b) Diurnal Observations

As/.....

TABLE 12

Observations of the Larval Chironomidae in Routine Seasonal Zooplankton Sampling by 5 Litre Friedinger

Shallow Water Sites (0 - 5 Metres)

Date	No. of Observations	Depth (metres)
19.3.69	1	1
26.3.69	1	3
11.4.69	1	3
16.5.69	1	2
20.6.69	1	1
24.6.69	1	2
8.7.69	1	5
29.8.69	1	2
5.12.69	2	1

Deep Water Sites (20 Metres)

Date	No. of Observations	Depth (metres)
11.4.69	1	5
17.4.69	1	3
30.4.69	1	10
7.5.69	1	20
16.5.69	1	3
16.5.69	1	4
24.6.69	1	2
8.7.69	1	4
8.7.69	1	15
15.7.69	1	15
28.7.69	4	15
22.10.69	1	20
12.11.69	1	20

As described in Spatial Distribution, section (c) ii on the diurnal distribution of C. s. abyssorum, a sampling programme was undertaken on 19/20 August, 1969 in order to provide information on the possible diurnal variations in numbers and depth zonation of the Cyclops population within a deep site (near X2 in North Deeps). As a result of the sampling, which involved obtaining replicate 5 litre Friedinger samples at consecutive metres from the loch surface to the loch bed at 17.5 metres, at three hour intervals from 6pm on 19 August until 9am on the following day, several observations were made of larval chironomids in the water column during the hours of darkness. The details are summarised in table 13.

Most of the 41 chironomid larvae were Pentaneura spp. with several individuals of species of Glyptotendipes and Procladius (pers. comm. A. McFarlane).

The twenty-nine larvae taken at 12pm were obtained from 90 litres of water.

$$\text{i.e.} \quad \frac{29}{90} \times 1000 \text{ indivs/m}^3$$

$$= \underline{322 \text{ indivs/m}^3}$$

If they had emerged from the loch bed below the point of sampling they can be represented in terms of numbers per area of loch bed by:-

$$322/\text{m}^3 \times 17.5\text{m} \quad \text{(depth of water column)}$$

$$= \underline{5635 \text{ indivs/m}^2 \text{ loch bed}}$$

However/.....

TABLE 13

Observations of Larval Chironomidae taken by 5 Litre Friedinger Sampling in an Overnight Investigation of the Zooplankton at the North Deeps of Loch Leven on 19/20 August, 1969

Time	No. of Observations	Depth (metres)
6pm	-	-
9pm	1	7
12pm	2	7
	4	9
	12	11
	3	13
	2	15
	6	17
3am	1	7
	2	9
	1	11
	5	15
6am	2	15
9am	-	-

However since they may have emerged at some distance from their point of capture it is possibly more accurate to use the mean depth of the loch in such a calculation:-

i.e. $322/m^3 \times 3.9$

$= \underline{1256 \text{ indivs}/m^2}$

Although the number of samples taken and their combined volume was small it is obvious that relatively large numbers of larvae were present in the water column between 9pm and 6am on 19/20 August, which suggests that nocturnal rising into the plankton may be an important part of chironomid larval behaviour, perhaps serving as a dispersal mechanism or serving to redress an oxygen debt incurred during the period which they spend in the low oxygen tension conditions of the loch bed. As chironomid larvae must eventually become pupae and then emerge from the water as aerial adults it is hardly surprising that some should be sampled in the plankton. However most of the larvae which were collected in the overnight sampling programme were in only their second or third larval instar (pers. comm. A. McFarlane).

Despite the numerous observations of chironomid larvae in plankton samples no pupae were found in either the seasonal or the diurnal series of samples.

2. Nematoda, Oligochaeta and Hydracarina

During/.....

During the diurnal sampling series described in section 1, in addition to the chironomid larvae which were taken during the night, twelve nematodes were sampled, although none was found in samples taken during daylight hours in the routine sampling programme in 1969/70. This suggests that nematodes as well as chironomid larvae may become active in the water column at night. However Nematoda have not been found in the mud of the deep sites in Loch Leven (pers. comm. P. Maitland) which makes it likely that they had been swept into the North Deeps area by currents. Therefore the chironomids may also have emerged from the loch bed at some distance from where they were eventually captured.

During the course of routine Friedinger sampling in 1969/70 eleven oligochaetes and eight water mites were captured which were not identified further.

3. Epizoites and Parasites of Cyclops strenuus abyssorum

Individuals of C. s. abyssorum of all stages were commonly very heavily infested with epizoitic organisms, at times causing them to appear green (see Appendix 1). Bailley-Watts (pers. comm.) identified the organisms concerned as Colacium sp. (Eugleninaea). Stalked ciliate protozoans were also commonly found attached to copepods.

In addition to observations of epizoic infestations upon C. s. abyssorum two instances were noted of similar large cestode cysts in the body cavity of adult males on 13 August and 12 November, 1969.

These/.....

These were photographed with a Vickers Microscope and camera so that identification could be made. However detailed identification has not yet proved possible and the photographs are presented in Appendix 1 in the hope that identification may be made in future.

As plates 18, 19 and 20 show, the cyst was very large in proportion to the body cavity of the copepod and contained prominent hooks. A stringy tape, several times longer than the host, led from the body of the cyst to the buccal region of the copepod.

Parasitic or possibly symbiotic ciliates were also regularly observed in the foregut of individuals of C.s. abyssorum which were dissected for gut analysis. These organisms were notable for their large size relative to the dimensions of the gut.

F. DISCUSSION

I. The Cyclops strenuus abyssorum Population

The most striking feature possessed by the crustacean zooplankton of Loch Leven is its complete, temporal and spatial, domination by an omnivorous cyclopoid species rather than by filter feeding herbivores. This situation is apparently almost unique and provides a useful opportunity to examine the dynamics of such a copepod population, living in a natural monoculture.

Much of previous zooplankton work has tended to be either confined to qualitative examination or has been quantitative only with respect to the dominant, normally filter feeding species. Relatively little attention has been paid to the more-usually, numerically recessive elements of the freshwater zooplankton, the cyclopoid copepods, although there are notable exceptions, such as the work of Smyly (1961) on Mesocyclops leuckarti in Esthwaite Water, Elgmork (1959) on Cyclops strenuus strenuus in southern Norway and McQueen (1969) on Cyclops bicuspidatus thomasi in British Columbia. Therefore work on the Loch Leven cyclopoid zooplankton is likely to add to the present 'pool' of knowledge concerned with this natural component of limnetic ecosystems.

1. Variations in the Annual Cycle

Despite the opinion of Gurney (1933) that British populations of *C. strenuus* undergo a monocyclic annual cycle, it is clear that the Loch Leven form is polycyclic, having virtually continuous reproduction and population replacement in all but the coldest periods of winter, when the temperature of the complete mass of water may fall to almost freezing point. At such times the water temperature is sustained at well below the 4^{o}C point of maximum density by strong winds and associated water mixing. Smyly (pers. comm.) found that populations of *C. s. abyssorum* in the English Lake District were very variable in their annual cycle, ranging from monocyclic in some lakes to polycyclic in others and it is very probable that this is also the case in Scotland as Chapman (1965) observed that the population in Loch Lomond was monocyclic.

It has often been recorded that the *C. strenuus* 'group' is very variable, with distinct although perhaps relatively inconspicuous differences existing in, for example, the length and/or breadth of the spines on the swimming legs. Probably geographic isolation of populations has resulted in such variations. It is not unlikely that variations in annual cycle have also arisen as a direct response to differences in environmental conditions. Water temperature, food supply and competition must each exert a prominent effect on the dynamics of a limnetic population and variations in these and other environmental factors may result in changes in the rates of growth and, therefore, the possible number of generations in a year.

Although/.....

Although such parameters are inter-related and cannot properly be viewed in isolation, it is probable, for example, that the altitude of a lake will affect its thermal history. Thus a high altitude tarn or lochan in an exposed position may take longer to reach sustained warm conditions in spring than a sheltered pond of similar size in a valley. The longer growing season in the latter may allow more generations to be undergone than are possible in the reduced growing season of the former. Similarly the food conditions, as perhaps related to the trophic status of the water body, may influence growth rates and generation length. Scarcity of food was considered by Ravera (1954) to be responsible for the arrested development and induction of diapause in late summer of *Mesocyclops leuckarti* copepodids in Lake Maggiore, and Smyly (1961) concluded that lack of food was one of the main reasons for similar events in Esthwaite Water. Moreover Chapman (1965) suggested that the development of *Diaptomus gracilis* in Loch Lomond was seriously food-limited in summer. In contrast the Loch Leven *C. s. abyssorum* population in 1969 appeared to be active throughout the year although there may have been a short-lived period in July when the development of the older copepodid stages was temporarily retarded. Since, in Loch Leven, even the standing crops of phytoplankton found in winter are greater than the highest summer levels reached in many other lakes (pers. comm. Bailley-Watts), the absence of winter dormancy in the population may be related to the comparative abundance of food which is present at that time.

The/.....

The same argument may be extended to cover events in summer when there appeared to be little developmental retardation. The absence of necessity for a quiescent period may have allowed the population to become polycyclic and this, in turn, may help to prevent the upsurge of a competitive species, if one were present. With no need for quiescence, development can be unrestricted into November and the presence of ovigerous females throughout the winter ensures that the population can quickly respond to the rise in temperature and food conditions in early spring, producing egg clutches of increasing size and ensuring a rapid population build-up. If the copepods had overwintered as resting eggs or dormant copepodid stages these would have required to mature to adulthood before a new generation could be initiated.

Therefore the effects that differences in environmental parameters have upon growth rates and upon the effective period of development in the year render it unsurprising that one species may undergo very variable annual cycles in different lakes. Moreover it is quite possible that such variations may occur from year to year within a single lake if suitable environmental changes occur. Elgmork (1959) was of the opinion that the upper limit of temperature tolerance of C. s. strenuus in southern Norway was approximately 20°C, although resting stages could survive temperatures within the range 0 - 30°C. The maximum water temperature reached in Loch Leven in 1969 was less than 20°C but perhaps a resting phase might have been invoked if conditions had been warmer.

2/.....

2. The Reproduction of the Population

The means by which the population can increase in size in rapid response to more clement conditions is interesting. Whereas cladocerans reproduce mainly by parthenogenesis copepods always reproduce sexually, and only the adult females, which may occupy a numerically minor part of the population, produce offspring. However the potential of overall fecundity is high as each female carries a large number of eggs and produces clutches of them at relatively short intervals of time after only one copulation with a male, since spermatophores passed from male to female ensure that the successive broods can be fertilised without further male assistance.

Active breeding periods are characterised by large numbers of nauplii entering the population, yet their standing crop is not itself sufficient to indicate the intensity of such events. A fast rate of growth may result in the nauplii moulting to successive copepodid instars before field observations can be made. Possibly the best gauge of breeding intensity is the number of nauplii being produced per day throughout the season, but in order to confidently assess this it would be necessary to know with some accuracy the length of development of the eggs, the period of time between clutches, the number of eggs per egg sac and their standing crop.

Although the calculation of egg development derived in the present field work is intended only as a rough guide to the actual length of development throughout the year, it may be used to give results which are comparative within this study. Thus during late May when the egg stock reached a peak of 600/5L, the water temperature was approximately 10°C and the developmental period of the eggs at that temperature was 12 days. Therefore 50 nauplii will have hatched per 5 litre/day. When the egg stock reached its August peak of 1100/5 litre the mean water temperature was over 15°C, egg development was estimated to take place in 8.5 days and the rate of naupliar production was nearly 130/5 litres/day. During the interval between the peaks the egg stock was about 175/5L, the mean temperature was over 15°C and the developmental period was about 8.5 days. Thus the production of nauplii was 20/5L/day; rather more than would be suspected from the standing crops of nauplii and early copepodid stages found at that time. Moreover this may well be a conservative estimate of the numbers of juveniles entering the population during late June and July since, while the growth rate of the species appeared to stabilise at temperatures in excess of 13 - 14°C, it is likely that this was partly caused by a delay in maturation of the older copepodids rather than by an unchanged rate of development in all of the instars. Thus there was an accumulation of numbers of copepodids IV and V, where development was retarded, while the numbers of younger instars remained low because of rapid development through these stages.

Despite/.....

Despite the added refinement of this method of assessing the population birth rate it is clear that understanding of the overall sequence of events remains little changed, with the graph of egg stock giving a reasonable indication of the more intensive periods of potential population growth. In spring and early summer a large egg stock was maintained by a relatively small number of large adult females, carrying large numbers of eggs. The later, shorter-lived, but larger, peak of egg stock which was found in August was the result of a large number of small individuals carrying less than half of the numbers of eggs per egg sac that were carried by their predecessors in April and May.

3. Inter-relations Between Body-Size, Egg-Number, Food and Temperature

The seasonal changes in mean body-size and number of eggs/egg sac of the adult females followed a similar trend to changes in phytoplankton standing crop and appeared to be inter-related. It has been suggested earlier that the numbers of eggs carried by the females is dependent upon the quality and quantity of food available at the time of initiation of the eggs, modified by the size of the ovigerous individuals, although their degree of senility must also be influential. Furthermore the size of the females is probably dependent upon the water temperature and food conditions during their larval development. Deevey (1960), for example, found that the relative effects of temperature and food on seasonal changes in body-size depended on the extent of the annual temperature range.

She/.....

She considered that when the annual mean temperature range was 14°C or less, food exerted the prime influence on development. When the mean range was greater than 14°C, she found significant negative correlations between body-length and temperature at the time of sampling. Moreover each species from every locality she investigated gave significant negative correlations between body-length and the mean temperature of the previous month. Thus in Loch Leven, which undergoes a temperature range in excess of 14°C, one might expect that temperature would be the most important factor in determining body-size changes. Negative correlations would be expected between the loch temperature during larval development of the adults and their size at sampling, while it might also be expected that similar correlations would be found between water temperatures at the time of sampling and adult body-size. From examination of the graphs of water temperature (fig. 13) and adult female body-length changes (fig. 5) it is clear that the latter conclusion is not tenable with regard to the results from the Loch Leven copepods, since, for example, the largest females were not found in the coolest temperatures. However a relationship between temperature during development and body-size at maturity may be noted as the largest females developed in the cold, spring months while the smallest females of the year developed during the warmest period.

The/.....

The graph of phytoplankton standing crop (fig. 11), intended as a tentative measure of food availability, shows a striking resemblance to that of body length changes (fig. 7), implying a possible direct relationship between food availability and body-size. Smyly (1968), studying the number of eggs and body-size of Diaptomus gracilis in the English Lake District, found that clutch-size and body-size of spring-caught, adult females could be significantly correlated with depth of water in forty-two lakes and tarns and suggested that a possible link between large body-size, large clutch-size and shallowness of water might be the greater accessibility of benthic and littoral algae in shallow water. In other words he concluded that a greater food supply allowed larger body-size as well as clutch-size. On the basis of comparison between populations of D. gracilis in Lake Windermere and Wise Een Tarn, Smyly argued that the seasonal changes in body-size undergone by the females in both the lake and the tarn could be explained by an inverse relationship between size at maturity and temperature during larval development, but pointed out that throughout the year the adult females of the tarn were larger than those of the lake. Moreover the minimal mean body-length in the tarn was greater than the maximal mean length in the lake. As the lake water was cooler than that of the tarn during the first eight months of the year it might have been anticipated that the lake adults would have grown larger than those in the tarn - the opposite of the true events.

Smyly/.....

Smyly, therefore, suggested that the observed difference in body-size between the copepods in the lake and those in the tarn could not solely be the result of temperature. He accepted that the enhanced rate of water renewal in a high-altitude, shallow tarn could have resulted in the evolution of a larger race of individuals capable of carrying larger numbers of eggs in order to compensate for greater population loss in the outflowing water (Ravera and Tonolli, 1956), but felt that the greater accessibility of benthic and littoral algae in the shallow tarn could have caused a short-term effect on body-size.

Therefore it is apparent that the mechanisms influencing seasonal changes in body-size and egg-number of the adults of C. s. abyssorum are very complex. However it is reasonable to conclude that the number of eggs which can be carried by a female is directly related to her body-size, while the number of eggs which she can produce must be related to her food supply and the energetic demands of her metabolic rate which, itself, is directly related to temperature. In addition, body-size is influenced by the food and temperature conditions experienced during larval development, while superimposed on this complexity of inter-related variables is the probability that longer-term genetic influences will have 'shaped' populations of copepods in different lakes in response to the requirements of body-size and egg-number governed by their own special conditions.

4/.....

4. Vertical Distribution

The apparent absence of a clearly-defined, vertical migration pattern in the *C. s. abyssorum* population of Loch Leven is not entirely surprising, as a full programme of diurnal sampling was of necessity restricted to one experiment in August. Consequently the results obtained from that single sampling programme cannot be taken as indicative of events throughout the rest of the year. It is generally agreed that light plays the most important part in determining the vertical migrations of a wide range of aquatic animals and, in fact, Ullyott (1939) found that the vertical distribution of *Cyclops strenuus* (*abyssorum*) in Windermere was best-correlated with blue light of 500 Å units. However Loch Leven has such prolonged and severe phytoplankton blooms that 99% of the visible light is extinguished within the first metre depth during a large part of the year and blue light is filtered out within this layer. When the diurnal sampling programme was undertaken in August the phytoplankton was no less dense than usual and it would be difficult to imagine that the adult females which were aggregated at 15 - 17 metres depth could be positioned with respect to light of this wavelength.

In addition to the very restricted light penetration during most of the year the vigorous current action within the loch would be expected to disturb any vertical migration and would tend to obscure its effect.

Nonetheless/.....

Nonetheless several instances of clear vertical aggregations were observed. Often there was age-specific or sex-specific demarcation between such aggregations, displayed most prominently by the nauplii and the older copepodid stages and adults. On July 28 and August 8, for example, the nauplii were almost entirely bunched in the first five metres depth below the surface in the North Deeps while the copepodids IV - VI (adults) were congregated mainly at the loch bed. Further examination of this phenomenon during the diurnal series of samples taken on August 19 and 20 revealed that at that time the adult females were most common near the loch bed while the males were scattered. Moreover the nauplii, although still having a strongly aggregated distribution, were never present in large numbers in the same depths as the bulk of the females.

During August the egg stock carried by the adult females was the greatest of the year, suggesting that many nauplii must have been hatching at that time. As nauplii hatch directly from eggs carried by the females it would be reasonable to assume that, if egg-hatching is a relatively continuous process within the population, the naupliar numbers would be greatest in the regions of greatest concentration of the females. This was never the case. However evidence has been presented that the nauplii were heavily predated upon by the older copepodids and adults and it is possible that such predation pressure could have resulted in the apparent difference between the vertical distributions of the adult females and their nauplii.

This/.....

This might also account for the relatively small numbers of autumn individuals arising from the very large August egg stock.

The deep-water aggregation of the adult females may have been associated with the high water temperatures which were maintained throughout July and August. The relatively bulky adult females, having a lower ratio of area of body surface to volume than the smaller instars and the adult males, may have found it very difficult to maintain the swimming speed necessary to prevent them sinking. Likewise the high energetic cost of respiration associated with constant swimming in the warm water may have made it necessary for them to congregate in the slightly cooler, deeper water. Apart from the benefit to be gained from a lowered metabolic rate in the reduced temperature conditions it is possible that the copepods may have rested on the loch bed, for it was noticeable, in this respect, that adult females and older copepodids of C. s. abyssorum spent fairly long periods on the mud surface of the bottom or clinging to the the glass walls of a tank in the laboratory. Therefore it is not so improbable that the adult females could temporarily forsake their normal planktonic existence by spending time on the loch bed.

The possibility of such a semi-benthic period of existence raises the question of the effect that this might have had on the flora and fauna of the mud surface.

If/....

If the copepods were active, rather than in dormancy, as is suggested by analysis of the slight nocturnal rise in the vertical distribution of the adult females in the diurnal sampling series, then it can be assumed that they must have been feeding. It has already been argued that they may have been exerting considerable predation pressure upon their own nauplii and it is not unlikely that chironomid larvae, oligochaetes, benthic protozoans and algae will also have been eaten. While this is entirely speculative, it is perhaps worth observing that the grazing effects of the normal crustacean inhabitants of this habitat, the benthic Copepoda and Cladocera, are equally poorly understood.

The distribution of the population with regard to the transitory thermocline which arose in June is interesting. No copepods were found deeper than 10 metres in the North Deeps sampling site (X2) on June 14 although on no other occasion in the year was a total absence of animals discovered in any depth stratum. At that time there was a thermal difference of approximately 6^{o}C between the surface and the loch bed with the most significant drop in temperature occurring between 7 and 10 metres. Only nauplii and copepodids I - III were found in the region of this thermocline while no stages were present in the hypolimnion.

In many lakes sustained summer thermal stratification causes deoxygenation of the hypolimnion leading to the disappearance and possibly the death of the non-anaerobically respiring animals in this zone.

As/.....

As a result there is usually a paucity of zooplankters in the hypolimnion. Smyly (1961) found that early in the year Mesocyclops leuckarti were scattered at all depths in Esthwaite Water, while from May until September, when the lake was thermally stratified, they were found almost entirely above 6 metres depth. Similarly Tash and Armitage (1960) found that Daphnia galeata mendotae Birge was limited for a time to the upper six metres of Leavenworth County Lake by an oxygen deficiency in the hypolimnion. A number of species of Cyclops can tolerate anaerobic conditions by migrating periodically into a oxygenated region or by undergoing a resting phase of development (Chaston, 1969), therefore the reason for the lack of C. s. abyssorum in the hypolimnion on 14 June is more likely to have been caused by an active migration out of this region than by a mass mortality within it. This hypothesis is substantiated by examination of the copepod standing crops of that period as only the egg stock and nauplii declined noticeably.

5. The Biomass of the Population

Contrary to the 'classical' zooplankton succession of spring and autumn periods of large numbers with a summer depression in population size, related to what is normally considered to be the cycle of phytoplankton standing crops in most temperate waters (Hardy, 1958), seasonal changes in biomass of the C. s. abyssorum population of Loch Leven revealed that there was a 'bloom' in summer rather than in spring and autumn.

The/.....

The overall pattern, presented in terms of mean monthly values of kcals/m^2 surface area, was that the population size exhibited an apparently normal distribution around a July mode (fig. 16). In fact there were two peaks in summer. The first pronounced increase in biomass in June (fig. 15) was as a result of the growth of juveniles which had hatched from the egg stock of May and early June, while the July decrease resulted from the eventual loss of these animals plus the loss of those which had developed in late June and early July. This biomass drop, occurring concurrently with a very sudden increase in water temperature to the seasonal maximum, may have been caused by mass mortality, or perhaps by a migration by the older copepodids to the vicinity of the loch bed where sampling may have been rendered only partially effective by their proximity to the mud surface. The almost immediate second increase in biomass recorded later in July may then have been caused partly by their re-emergence into more effective sampling range and partly by the rapid incrementation of the younger stages, supplementing the older instars without themselves being sampled in large numbers during their growth to those stages.

The gradual decline in biomass leading to winter followed a progressive reduction in the population birth rate in the cooling conditions of autumn. Thus the numbers of nauplii fell to a very low level during September and October, resulting in the decline in numbers of the successive copepodid stages to hardly-measurable levels so that few, if any, matured to adulthood after November.

Meanwhile/.....

Meanwhile the process of ageing, predation and possibly starvation caused the standing crops of adults to fall to the level of the previous winter.

6. Comparisons between the Mean Biomass in Loch Leven and in other Lakes

Since the Loch Leven crustacean zooplankton is a virtual monoculture of Cyclops strenuus abyssorum it is of interest to compare its biomass and production with that found in other lakes. However as the calculation of production is still at a tentative stage it is perhaps of more value to use the biomass data, which is known to be more accurate. The biomasses of the crustacean zooplankton in the three Russian Lakes studied by Winberg, Pechen and Shushkina (1965) are presented in table 14 and compared with that of Loch Leven in 1969.

Table 14

The Mean Biomass of Crustacean Zooplankton (g/m^2 wet weight) found in Three Russian Lakes and in Loch Leven

Groups	L. Batorin	L. Myastro	L. Naroch	L. Leven
Cyclopidae	1.8	2.4	2.7	14.0
Diaptomidae	1.5	6.0	4.5	-
Cladocera	10.5	6.0	1.4	-
Total	13.8	14.4	8.6	14.0

(table adapted from Winberg, Pechen and Shushkina, 1965)

The/.....

The zooplankton biomass in the two most-productive of the Russian Lakes (Lakes Batorin and Myastro) was, therefore, very similar to that of the C. s. abyssorum population in Loch Leven, whereas it might have been expected that the absence of filter feeding crustaceans in Loch Leven would have resulted in a reduced biomass. Furthermore the calculated biomass of the Loch Leven population represents the mean for the full year whereas the Russian figures were derived from only the five months growing season, when the mean biomass must have been greater than if it had been calculated for the full year. Thus the mean annual biomass of the purely cyclopoid population in Loch Leven may be assumed to be higher than that of the combined biomasses of the crustacean groups in each of the Russian Lakes. Patalas and Patalas (1968) studied the crustacean plankton of some Mazurian Lakes (Poland) and found that Lake Upinek was the most productive in terms of numbers of individuals and biomass per unit of surface area, having a mean summer biomass of about $9g/m^2$ wet weight. Ten pelagic species were noted, of which 4 - 6 were described as co-dominant. It seems, therefore, reasonable to assume that the Loch Leven crustacean zooplankton may be of the same order of size, despite its lack of diversity, as it would have been had the usual filter feeding species been present. On the other hand the annual production of the more diverse population might have been greater owing to enhanced rates of turnover of standing crop caused by heavier predation by fish upon the cladocerans than they appear to exert at present upon the cyclopoids.

II. The Zooplankton of Loch Leven in General

The basic 'role' of the marine or freshwater zooplankton in a food web is as an essential link between the production of the phytoplankton and the higher trophic levels. In freshwater ecosystems, part of the role of photosynthetic conversion is undertaken by the benthic and epiphytic algae and the higher plants, which are then grazed on by herbivorous invertebrates such as snails, mayfly larvae and caddis fly larvae. However, as the process of photosynthesis depends upon the penetration of light the relative importance of the benthic algae and higher plants is limited by water depth. Thus, while in a small, shallow pond the area of bottom on which such plants can grow may be quite large and they may contribute a great deal to the overall photosynthetic production of the pond, in a larger body of water such as Loch Leven, their effect is likely to be smaller because of the reduction in proportion of the littoral zone to the rest of the area of the water body. In such conditions, as in the sea, the phytoplankton normally provides the bulk of the trapped energy which can then be used by the herbivores and carnivores. Moreover Loch Leven has very prolonged and dense phytoplankton blooms which probably prevent the production of a large amount of benthic algae in the many shallow areas of the loch by shading out the available light. The macrophytes have indeed declined in quality and quantity so that the few weed beds which have persisted must have a minimal effect on the overall photosynthetic production of the loch.

Therefore/.....

Therefore most of the herbivores must feed upon the phytoplankton.

The most important phytoplankton grazers of Loch Leven are chironomid larvae, duck mussels (Anodonta anatina (L.)) and zooplankton, but the relative importance of their feeding is not yet fully known, although concentrated work on the production of the Chironomidae is well underway. If, at this stage, the tentative estimate of the population of Cyclops strenuus abyssorum in 1969 (63.8 - 162.0 kcals/m^2) seems a surprisingly large amount since they are non-filter feeders, it must be remembered that they feed upon diverse types of food including the phytoplankton and probably the bacteria involved in its decomposition, as well as upon rotifers and chironomid larvae which graze upon it. In addition allochthonous organic material brought to the loch by the inflow streams may have further contributed to the decomposer food chains leading to the younger instars of the species.

A search through the extensive literature of zooplankton work has revealed only one other lake ecosystem totally dominated in this way by a cyclopoid species. Pejler (1965) found that the zooplankton of Lake Hemfjärden in central Sweden was "remarkably poor in species, dominated by cyclopoids and Keratella cochlearis." The lake was heavily polluted by the city of Orebro and, when visited, was "green and thick as spinach soup with water-blooming algae (transparency only 18 cms!)."

The/.....

The similarity between the description of Lake Hemfjärden and the prevailing conditions in Loch Leven is obviously very close.

There was no scarcity of filter feeders when Scott visited Loch Leven in 1898 and indeed both Daphnia sp. and Bosmina sp. were present until at least 1954, when Woodward (pers. comm.) took three pump samples from the jetty at Kinross. Therefore their disappearance has taken place during the last sixteen years.

Although the gradual process of eutrophication is normally expected to increase species diversity several workers have stressed the basic stability of the species composition of lake zooplankton. Baldi (1951) noted that the species composition of Lake Maggiore in Italy had remained constant over a 40-year period and Tappa (1965) observed the same zooplankton species in Aziscoos Lake in Maine (U.S.A.) as had been found twenty-five years previously. Smyly (1968) also observed that stability was the general rule as he found in a survey of the planktonic and profundal Crustacea of the English Lake District that nearly all of the observations of crustacean species made by Gurney in 1923 had been repeated. Therefore it is particularly important that the cause of the recent disappearance of Daphnia and Bosmina from Loch Leven may be ascertained.

In/.....

In order to determine whether there was a link between persistent phytoplankton blooms and limited numbers of individuals and species of crustacean filter feeders in the zooplankton communities, sampling visits were made during 1969/70 to several lochs, lying within 25 miles of Loch Leven, where eutrophication was enhanced and where blooms were troublesome. Qualitative samples were taken by towed net from suitable points on the shore, from landing stages or from boats. The zooplankton species found during the sampling visits are listed in table 15. Obviously the species lists in table 15 are not exhaustive since each loch was visited only once and sampling was not extensive. However it is evident that there was no scarcity of crustacean filter feeding species in each of the lochs except Kilconquhar Loch, which appeared to contain only one - Daphnia magna Straus. A 'spot-check' on Loch Leven in 1969, carried out in similar fashion, would very likely have revealed the presence of only Cyclops strenuus abyssorum, although occasional individuals of Diaptomus gracilis and Bythotrephes longimanus might have been found.

Staff of the Nature Conservancy, currently examining wetland ecosystems throughout Britain, have made towed net examinations of the occurrence of zooplankton Crustacea in twenty-one eutrophic lakes where algal blooms have been reported and have found no other zooplankton community as lacking in crustacean filter feeders as that found in Loch Leven (pers. comm. Britton).

The/.....

TABLE 15

The Occurrence of Crustacean Zooplankton Species in Eutrophic Lochs Lying within 25 miles of Loch Leven

Sampling Date	Site	County	Diaptomus gracilis	Daphnia hyalina var.lacustris	D.magna	Cyclops strenuus abyssorum	C.viridis	C.albidus	C.agilis
11.11.69	Loch Fitty	Fife	+++	++++	-	++	-	-	-
14.11.69	Loch Gelly	Fife	++++	++++	+++	++	-	-	-
1.7.70	Kilconquhar L.	Fife	-	-	+++	+++	+	-	-
1.7.70	Lindores Loch	Fife	++++	++++	-	++	+	+	+
5.5.69	Airthrey Loch	Stirlingshire	++++	++++	-	++	-	-	-

+ = present

++ = common

+++ = very common

++++ = abundant

The lakes studied contained, on average, three species of filter feeding crustaceans (Cladocera and Calanoida) and one non-filter feeding species (Cyclopoida), approximating Pennak's (1957) observation, that at any one time, most limnetic habitats include 2 - 4 species of Cladocera and 1 - 3 species of Copepoda. Therefore there is no firm evidence to suggest that the Loch Leven algal blooms have resulted in the virtual monoculture of Cyclops strenuus abyssorum which is found there.

Brooks (1968) found that freshwater planktivorous fish could exert a potent influence upon the composition of the zooplankton due to their high degree of food selectivity and that the facultative planktivores trout and yellow perch appeared to prefer large Cladocera, especially Daphnia, and switched to non-planktonic food when they were not available. If the decline in macrophytes and the possibly-associated decline in littoral and benthic invertebrate diversity took place at Loch Leven relatively recently it is possible that the fish may have overcropped the cladoceran zooplankton due to a lack of availability of other food items at certain times of the year. Brooks also noted that when planktivory was intensive the larger zooplankters were cropped sufficiently to allow small, hitherto-suppressed species to become numerous. In the case of Loch Leven the Daphnia may have been cropped more heavily than the Bosmina, which are smaller, or the Cyclops, which have a more vigorous escape-reaction (Smyly, 1968). However the Daphnia would surely not have disappeared but would have been held at a low density of population, while the Bosmina, which appear to have died out also, might have been expected to multiply to take their place.

Selective/.....

Selective predation by fish is therefore unlikely to have resulted in the apparent total loss of the Daphnia and Bosmina populations.

A further possibility for the change in zooplankton species composition is the undetermined effect on the loch biota of the organochlorine pesticide Dieldrin which was discharged into Loch Leven from the woollen mill in Kinross during the period 1958 - 64. However the presence of the chemical has been regularly monitored in fish tissue by staff of the Freshwater Fisheries Laboratory at Pitlochry, and Holden (pers. comm.) is of the opinion that the pesticide levels in the loch were never high enough to kill the filter feeders. He pointed out that the literature on toxicity showed that when exposed to the pesticide in various tests trout were susceptible to lower concentrations than were Daphnia spp. As the maximum possible concentration in the South Queich (which discharged the pesticide in to the loch) was never toxic to fish and dilution by the loch would have reduced this considerably, Holden feels that it is unlikely that the pesticide can be blamed.

Sanders and Cope (1966), experimenting upon the toxicity of several pesticides, including Dieldrin, to two species of cladocerans, found that susceptibility to a very wide range of toxicity levels varied with the species used, the age of the test animals and the ambient test temperatures.

For/.....

For example, Malathion was 8.8 times more toxic at 50°F than at 70°F to Simocephalus serrulatus (Koch) and DDT was 2.6 times more toxic at 60°F to first-instar organisms up to 18 hours old than to 7 day-old organisms. Moreover toxicity experiments upon zooplankton species are usually restricted to the rapid screening of insecticides and herbicides, deriving toxicity levels for producing a required response (immobilisation or death) of 50% of the animals under test in a given number of hours (Anderson, 1960; Wollerman and Putnam, 1955; Sanders and Cope, 1966; Macek and Sanders, 1970). It is very unsatisfactory for such toxicity values to be quoted when the long-term effects of much lower concentrations of a toxin, persistently released into a natural ecosystem, are unknown. Furthermore it is obvious from the work of Sanders and Cope; firstly, that values for one species of zooplankter cannot be applied to another; secondly, that the effects of the toxin may be more drastic on the very young individuals of a species; thirdly, that the values derived from one specific test temperature may be very different from those derived from another. The possible effects of the pollution of Loch Leven by Dieldrin cannot, therefore, be discounted.

In Chew Valley Lake near Bristol, Dieldrin poisoning was suspected to be the cause of the drastic reduction in numbers of Daphnia sp. and Bosmina sp. in 1968 (Bays, 1969) and although the filter feeders declined in abundance the cyclopoids persisted. In 1969 the zooplankton returned to its pre-1968 condition with the numerical recovery of the Daphnia and Bosmina, while the numbers of Cyclops remained constant.

Although/.....

Although Dieldrin was suspected to be the cause of the zooplankton disturbance, there was a sharp rise in phosphate in the lake in 1966/67, a prelude to the bloom of green algae which occurred concurrently with the temporary decline in the numbers of filter feeders. Therefore it is possible that natural changes in the phytoplankton probably due to increased phosphate concentrations, may have resulted in the quantitative changes in zooplankton.

Further evidence of the ability of *Cyclops* spp. to cope with drastic changes in their environment is provided by an account by Woodward (pers. comm.) who was concerned with the removal of unwanted pike by 'Rotenone' (derris root extract) poisoning from Loch Kinardochy in Perthshire. He recalled that after a virtual elimination of the crustacean plankton following the poisoning, there was a bloom of rotifers together with *Cyclops strenuus*. *Daphnia* later re-appeared and at the end of about 4 years the zooplankton was back to the original regime, with *Diaptomus* and *Bosmina* occurring in large numbers and with *Cyclops* and *Daphnia* in smaller numbers. Woodward was certain that *C. strenuus* dominated the zooplankton in the years immediately following the application of 'Rotenone'.

In both the cases of Chew Valley Lake and Loch Kinardochy the eventual return to zooplankton normality gives hope for the return of the filter feeders to Loch Leven. However Loch Leven is so large that it is hard to imagine that wind-blown ephippia or those introduced by initerant ducks should constitute a sufficiently large-scale recolonisation to effect this, unless the *Cyclops* population was at a seasonal low-density

point/.....

point and predation on the juvenile cladocerans could be reduced. Such conditions might arise during a sustained spell of very warm weather or during winter but, unfortunately, both might be associated with lower phytoplankton density and the immigrants might not find sufficient food for both survival and reproduction.

Laboratory populations of Daphnia, fed upon yeast, have survived for long periods in Loch Leven water and it does not seem unreasonable that they might once more exist in the loch itself. Daphnia might reduce the standing crops of micro-algae which dominate the phytoplankton in Loch Leven (pers. comm. Bailley-Watts), thereby increasing light penetration into the water, and an extension of the photic zone would be likely to have a widespread effect on the loch flora and fauna, allowing recolonisation by weeds and providing favourable conditions for the invertebrates associated with them.

The possible advantages of Daphnia supplanting the Cyclops strenuus abyssorum would seem to be sufficient reason to attempt to establish small populations in cages from which Cyclops could be excluded. Basic information might then be obtained on the feasibility of artificially re-introducing them to the loch. If they survived in the cages, very large numbers could be transported from other lochs and introduced into relatively enclosed areas such as the boat harbour. Yet it seems unlikely that such an operation could be successful since, although the Diaptomus gracilis population is very small relative to the numbers of Cyclops, their numbers throughout the loch must be many times greater than those of the Daphnia which could be introduced.

Despite this, there appear to have been fewer D. gracilis in Loch Leven in 1969 than in the previous year.

The probable future of Loch Leven does not give grounds for optimism. The nitrate input due mainly to the use of nitrogenous fertilisers in the arable drainage area is continuing to increase annually and is expected to do so further. The input of phosphate likewise is expected to increase, since plans have been put forward for the woollen mill at Kinross to increase the size of its effluent by several times. Little, if anything, can be done to alleviate the nitrate problems but pressure is being brought to bear upon the mill proprietors to treat their effluent in an attempt to reduce the proposed increase in phosphate. In addition Loch Leven has been proposed as a possible source of public water supply and a pilot experiment has been conducted to see whether the phytoplankton of the loch would create too great a nuisance. Apparently the scheme is now regarded as economically viable and it is proposed to abstract somewhere in the region of 6 million gallons of water per day, which would lower the minimum level of the loch by 16". As partial compensation, water would be diverted from the headwaters of the River Devon and would enter Loch Leven via the Gairney Water. The scheme is still believed to be under consideration at present.

Thus/.....

Thus the condition of the Loch Leven zooplankton in 1969 must not be considered the 'status quo', if indeed such a term could ever be used in connection with a biological system, and it is very important that continued study be made of the loch ecosystem in general in further years. Shorter-term studies of the zooplankton could be useful in providing further information on the importance of the rotifer production as little time has been devoted to their study in the present work. More intensive study of the growth rate of C. s. abyssorum ought to be undertaken in order to complete calculations of the production of the population. Their trophic position in the ecosystem ought also to be subjected to continued examination as little is yet known on the quantities of food which they eat, since their diet is omnivorous, while the degree to which they are predated upon by fish is unclear. Long-term zooplankton sampling ought to be undertaken in order to provide information on any further qualitative and quantitative changes which may take place in the hope that fact may take the place of speculation with regard to such changes. Now that Loch Leven has been declared a Nature Reserve there is abundant opportumity for further valuable study of this highly eutrophic lake.

Finally, it is my hope that the study presented herein of the annual cycle, standing crops, feeding, dynamics and spatial distribution of the virtual monoculture of Cyclops strenuus abyssorum which at present dominates the Loch Leven zooplankton, may contribute to our understanding of limnetic cyclopoids in general and, in particular, may form a framework

of/.....

of basic information upon which further detailed field and laboratory investigations may be based.

G. ADDENDUM - August, 1970

In an attempt to ensure continuity of zooplankton sampling between the present study and possible future work, monthly samples were taken at site X4 (5 metres deep) in the middle of Loch Leven, between St. Serf's Island and Castle Island (fig. 1). Replicate Friedinger samples were taken from each metre depth from the surface to the loch bed while a towed net of 63 microns mesh size was also used to obtain a 5m vertical haul sample from the site. The samples were stored in 5% formalin for later examination.

Until June the samples revealed a parallel situation in the zooplankton to that found in 1969 with Cyclops strenuus abyssorum continuing to dominate. On July 20 however Diaptomus gracilis were evident, although they made up less than 1% of the total numbers of zooplankters. Bythotrephes longimanus, which were found in June, were more common in late July, whereas they were not found until August in 1969.

However it was in late August that the most dramatic difference was found. Both Friedinger and towed net samples revealed the presence of small numbers of Daphnia hyalina var. lacustris (in its summer, 'helmeted' form), while Diaptomus gracilis were very common and Leptodora kindti were also prominent. The numbers of C. s. abyssorum, on the other hand, were much less than at the same time in 1969.

As/.....

As a result of the discovery of the prominence of the filter feeders at sampling site X4 a towed net sample was obtained from the shallow bay near the Boathouse at Kinross in order to see how widespread the phenonenon actually was. The percentage composition of the catches at X4 and in the Boathouse Bay are presented in table 16.

Table 16

The Percentage Occurrence of Zooplanktonic Crustacea in Samples taken at Loch Leven on 27.8.70

Method	Site	C.s.abyssorum	Diapt.	Daphnia	Leptodora
Friedinger 5L.bottle	X4	37	48	2	13
Towed net	X4	59	35	3	3
Towed net	Boathouse Bay	64	22	1	13
	mean %	53	35	2	10

This information serves to underline the necessity for continued zooplankton sampling at Loch Leven so that such changes may be related to the various physical, chemical and biological parameters which are at present being measured. As a result of this year's monthly samples it has been possible to ascertain that the species composition changeover must have taken place between late July and late August. Whether or not it is a temporary situation is of obvious interest.

It/.....

It is worth recording that the Loch Leven ecosystem has looked 'healthier' this year than it has done for several years. The algal blooms have not been as prominent and at least one large weedbed has become noticeable where none was seen last year; the anglers have been catching larger trout in better physical condition than previously and Thorpe (pers. comm.) has confirmed that growth rates are enhanced; the filter feeding crustaceans seem to be recovering. There lies in this situation the exciting possibility that we may be able to discover the causes of such changes so that we may ultimately learn to manage rather than merely to observe.

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Plate 6 (opposite)

C. s. abyssorum ♀ - furcal rami

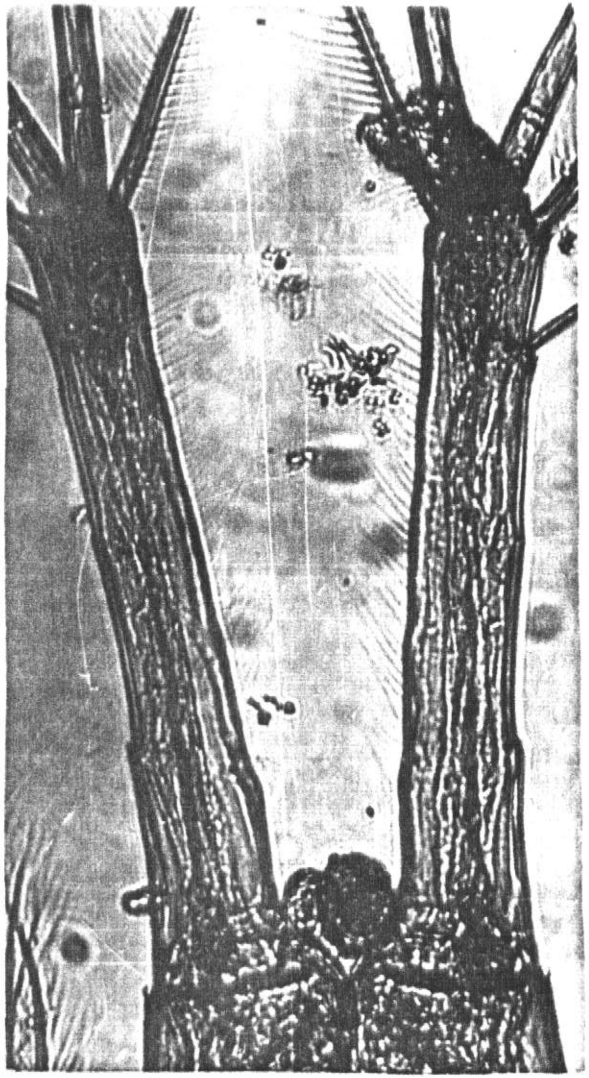
Plate 7 (opposite)

C. s. abyssorum ♀ - fifth leg

Plate 8 (opposite)

C. s. abyssorum ♀ - distal end of antennule

Plate 6



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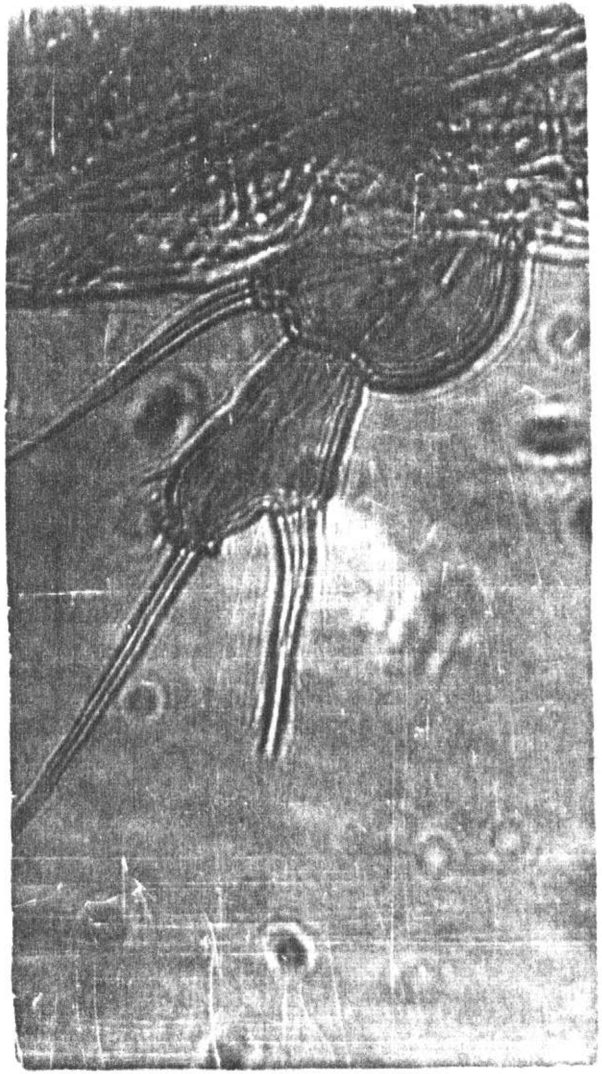

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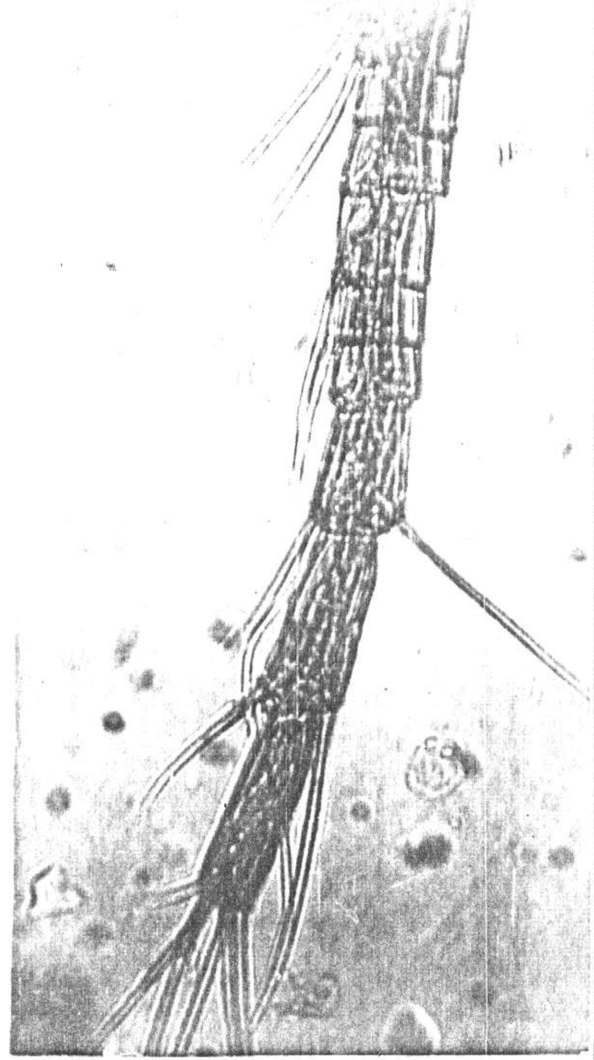


Plate 9 (opposite)

C. s. abyssorum ♀ - leg IV

Plate 10 (opposite)

C. s. abyssorum ♀ - leg III

Plate 11 (opposite)

C. s. abyssorum ♀ - leg II

Plate 12 (opposite)

C. s. abyssorum ♀ - leg I

Plate 9

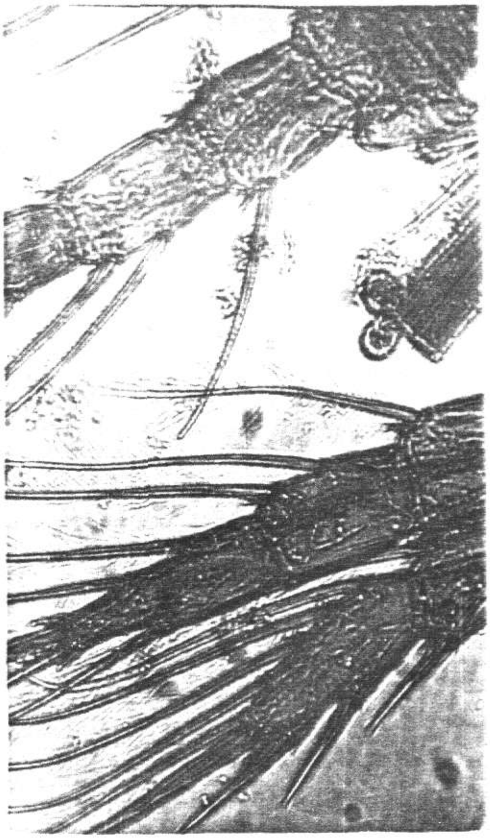


Plate 10

Plate 11

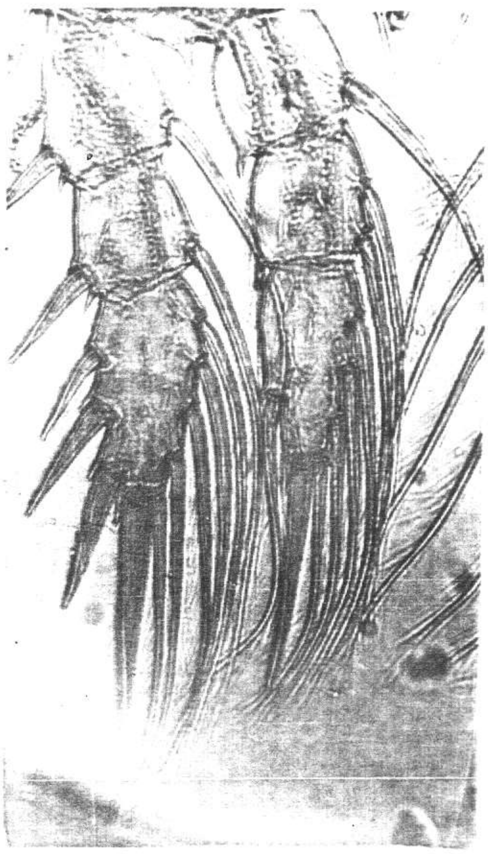


Plate 12

Plate 13 (opposite)

Polyarthra dolichoptera (with attached egg)

Plate 14 (opposite)

Synchaeta (?) pectinata (foot contracted)

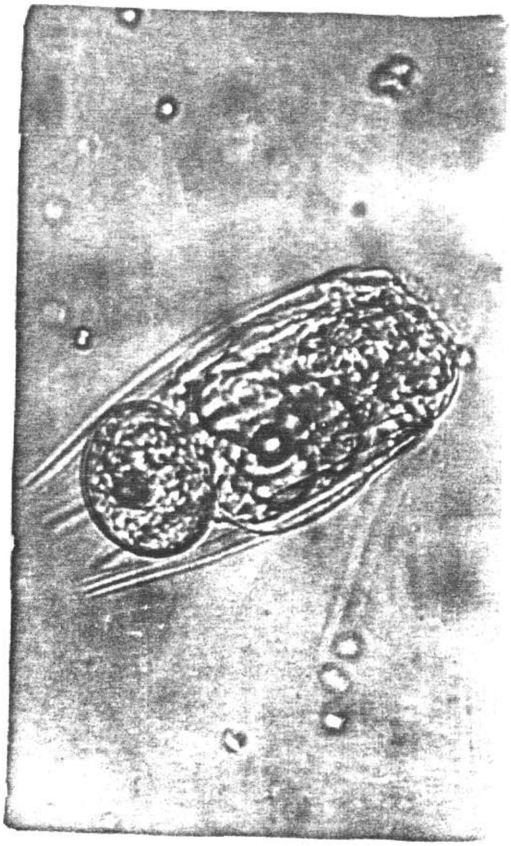
Plate 15 (opposite)

Keratella quadrata (? hiemalis)

Plate 16 (opposite)

Keratella cochlearis var. tecta (non-tailed form)

Plate 13



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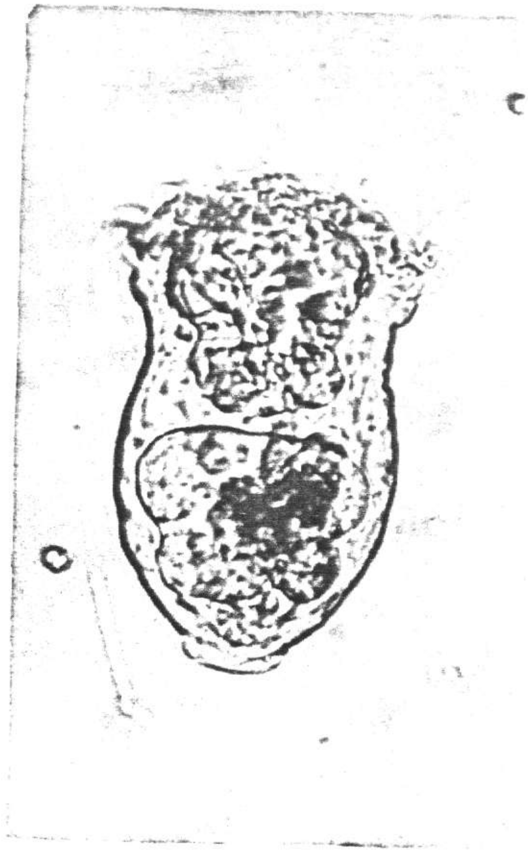

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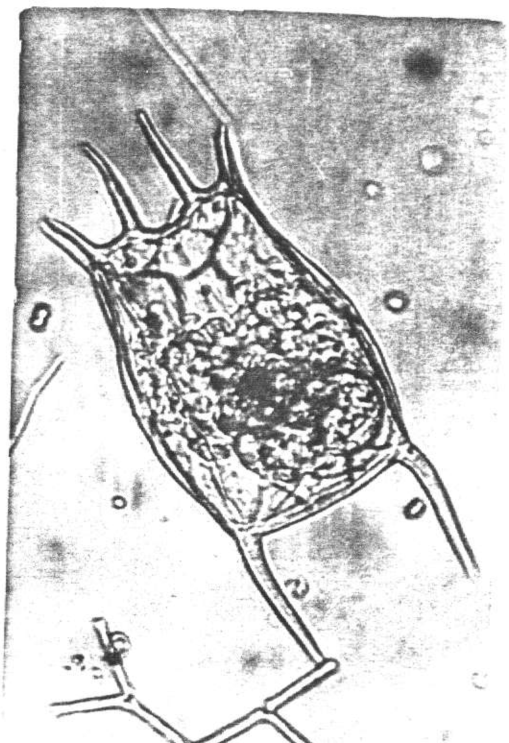

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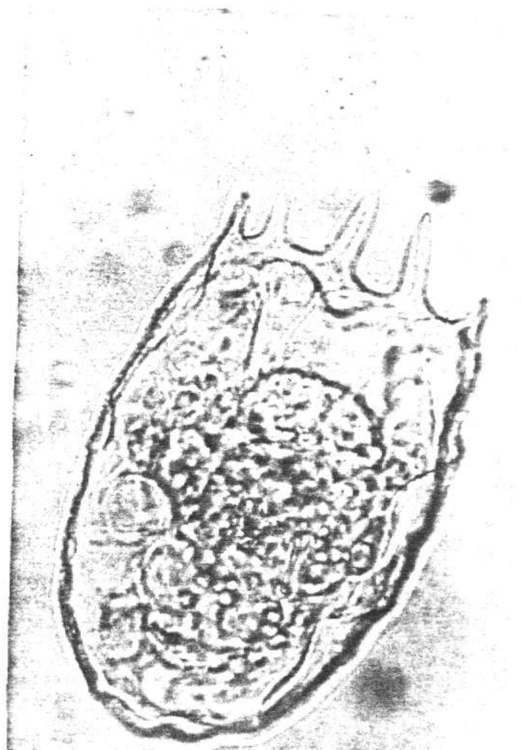

Plate 17 (opposite)

Keratella cochlearis (tailed form and egg)

Plate 18 (opposite)

Cestode cyst within ♂ *Cyclops strenuus abyssorum* body cavity

Plate 19 (opposite)

Cyst dissected from ♂ *C. s. abyssorum* showing hooks inside cyst and 'tape' outside.

Plate 20 (opposite)

Hooks inside cyst

Plate 19

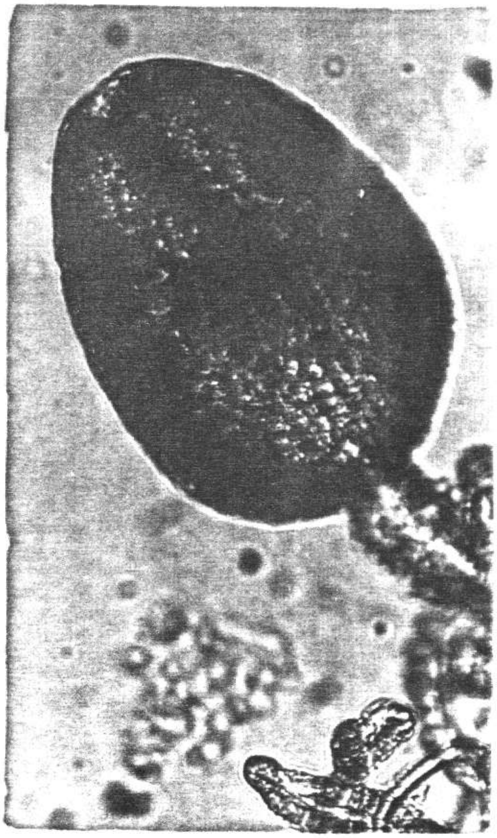

Plate 20

Plate 17

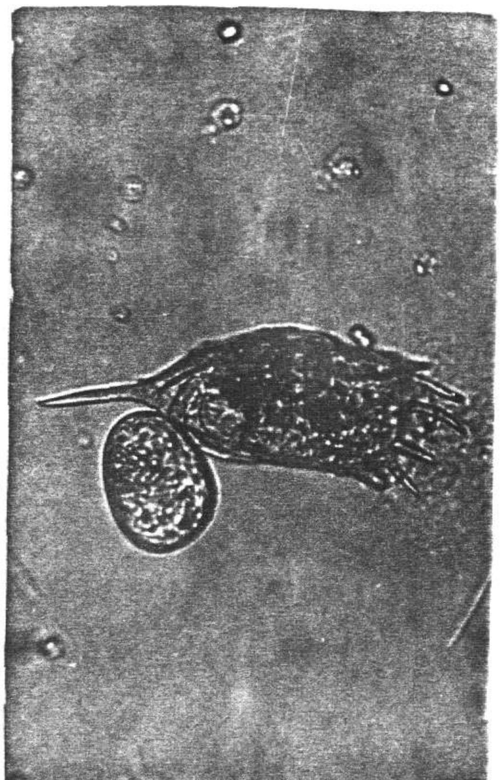

Plate 18

Plate 21 (opposite)

Epizoic infestation upon nauplius larva of C. s. abyssorum

Plate 22 (opposite)

Epizoic infestation on furcal ramus of C. s. abyssorum

Plate 22

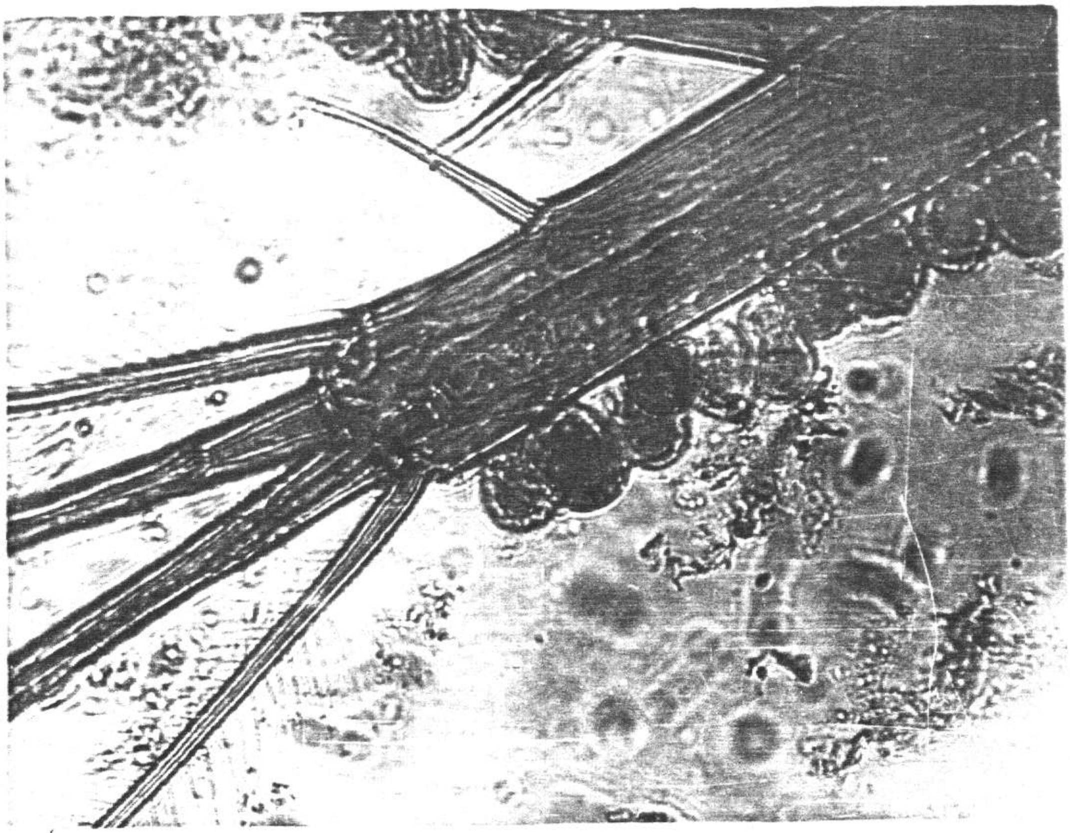

Plate 21

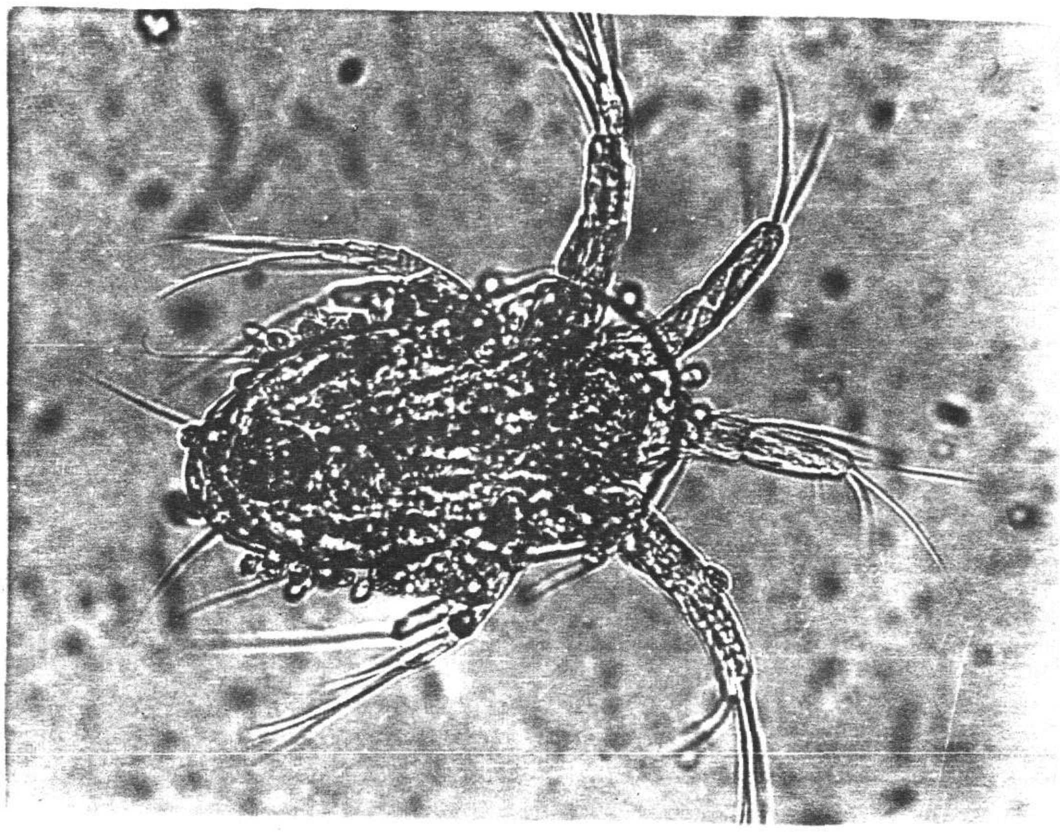

TABLE 17

The Seasonal Standing Crops of C. s. abyssorum in Lech Leven, 1969/70

(mean numbers per 5 litres)

Date 1969/70.	No.of sites/ No.of samples	Nauplii	CI	CII	CIII	CIV	CV♂	♀	♂ + ♀	CVI♂	♀	♀ + egg	♂ + ♀	Total CI-CVI
29.1	4/36	26.6	0.2	0.4	0.5	1.7	0.9	0.6	1.5	4.9	1.8	2.5	9.1	13.6
19.3	3/35	112.6	7.3	0.5	0.3	0.3	0.5	0.9	1.4	4.3	1.7	1.0	7.0	16.6
26.3	8/66	104.2	16.7	1.9	0.2	0.3	0.4	0.7	1.1	3.2	1.6	1.3	6.0	26.2
9.4	1/6	48.2	34.2	36.2	8.5	1.7	0.2	0.5	0.7	6.5	1.7	2.5	10.7	91.8
11.4	2/22	38.9	35.6	41.4	17.1	2.5	0.8	0.6	1.4	3.6	1.9	2.9	8.3	106.2
17.4	8/68	26.0	20.6	30.1	41.1	22.8	2.9	1.5	4.4	3.0	2.0	2.6	7.6	126.9
30.4	2/22	63.6	7.9	12.1	26.8	33.2	21.0	21.7	42.7	18.3	2.6	2.8	23.7	145.2
7.5	8/68	82.0	6.6	7.9	17.2	32.2	11.8	17.8	29.6	24.8	9.5	2.7	37.0	130.5
16.5	2/22	139.0	20.0	6.5	6.3	18.6	4.9	3.9	8.8	21.6	8.9	3.9	34.4	94.4
30.5	2/22	201.1	15.4	20.4	20.0	22.4	5.4	2.7	8.1	23.8	11.5	8.6	43.9	130.3
7.6	8/68	552.4	78.5	26.6	35.4	35.6	6.0	3.9	9.9	19.4	5.8	6.5	31.7	217.7
14.6	2/22	193.8	97.7	112.2	77.0	31.0	9.8	8.8	18.6	13.4	4.2	2.0	19.6	355.1
20.6	1/6	385.3	173.3	310.8	307.0	177.8	28.3	23.0	51.3	34.0	13.5	7.3	54.8	1075.2
24.6	2/22	208.0	81.4	135.2	168.4	181.0	38.5	20.4	58.9	20.3	11.8	3.3	35.4	660.0
4.7	2/12	168.5	10.1	32.6	128.3	278.1	95.4	63.6	159.0	39.5	11.9	3.0	54.4	662.5
8.7	8/68	115.1	6.4	11.0	68.6	200.5	82.1	63.3	145.4	48.5	12.1	3.9	64.5	496.9
15.7	2/22	71.0	4.8	4.7	17.0	85.5	45.6	31.7	77.3	39.3	14.2	4.4	57.8	247.1
28.7	2/22	56.9	9.1	3.7	2.9	129.4	107.0	99.5	206.5	50.7	11.5	2.7	64.9	416.5

Cont'd/.....

Table 17 - Cont'd

8.8	8/68	45.2	9.6	15.4	20.9	40.4	20.8	27.4	48.2	146.2	69.3	9.6	225.1	359.7
13.8	1/6	82.0	3.5	3.8	3.0	16.4	11.5	5.7	17.2	56.7	44.8	43.3	144.8	188.7
29.8	8/68	232.2	28.2	24.5	24.7	35.1	12.5	20.0	32.5	47.9	30.2	6.1	84.2	229.2
12.9	2/22	88.0	26.4	41.1	26.5	38.5	19.3	21.1	40.4	27.5	17.1	1.6	46.2	219.1
1.10	8/68	60.7	6.5	8.0	23.1	73.7	32.2	31.5	63.7	39.8	16.6	1.6	58.0	233.1
16.10	2/12	24.6	5.2	8.2	9.5	31.4	26.6	22.8	49.4	41.7	11.8	0.6	54.1	157.8
22.10	8/68	23.3	2.4	2.9	7.9	22.6	26.9	49.0	75.1	46.0	12.0	2.3	60.3	171.3
5.11	2/22	15.6	2.6	1.4	2.2	11.1	11.4	23.3	34.7	46.6	12.4	0.7	59.7	111.6
12.11	2/22	14.4	1.6	1.6	1.6	8.2	10.1	21.1	31.2	35.4	8.4	0.9	44.4	88.6
5.12	2/22	4.0	0.5	0.5	0.9	3.0	6.0	8.3	14.3	25.1	4.4	2.1	31.6	50.7
20.1	2/22	7.1	0.6	0.5	0.2	0.4	0.4	2.0	2.4	7.2	0.9	1.1	9.2	13.3

TABLE 18

Egg Stock Calculation

Date	No. of samples	No. of egg sacs per sampling date	Mean no. egg sacs/ 5 litres	Mean no. eggs/ egg sac	Egg stock per 5 litres
29.1.69	36	194	5.4	15	80
19.3	35	86	2.5	15	36
26.3	66	208	3.1	16	51
11.4	22	148	6.7	23	151
17.4	68	504	7.4	31	232
30.4	22	144	6.6	37	241
7.5	68	429	6.3	-	-
16.5	22	206	9.4	36	339
30.5	22	448	20.4	29	596
7.6	68	920	13.5	28	378
14.6	22	94	4.3	25	108
24.6	22	154	7.0	21	149
4.7	12	80	6.7	24	159
8.7	68	564	8.3	22	180
15.7	22	200	9.1	17	157
28.7	22	120	5.5	14	75
8.8	68	1302	19.1	15	286
13.8	6	522	87.0	13	1101
20.8	108	5508	51.0	14	711
29.8	68	832	12.2	11	136
12.9	22	72	3.3	12	38
1.10	68	214	3.1	9	27
16.10	12	14	1.2	11	13
22.10	68	338	5.0	14	72
5.11	22	30	1.4	-	-
12.11	22	30	1.4	13	18
5.12	22	94	4.3	14	60
20.1.70	22	50	2.3	17	39

TABLE 19

Overnight Sampling in the North Deeps, Loch Leven on 19/20 August, 1969
(nos./5 litres)

Depth (metres)	A 6-7pm			B 9-10pm			C 12-1am			D 3-4am			E 6-7am			F 9-10am		
	N	C	A	N	C	A	N	C	A	N	C	A	N	C	A	N	C	A
1	49	92	104	79	37	53	75	176	55	68	117	147	173	100	111	133	92	135
1	63	104	101	90	42	47	70	88	84	87	73	70	193	104	118	134	96	114
3	82	42	146	89	43	108	58	61	123	90	122	200	172	93	90	127	131	180
3	63	59	122	85	101	144	66	116	133	68	85	101	197	87	153	153	100	129
5	80	59	128	53	49	84	62	137	166	99	110	149	221	142	125	135	51	91
5	94	37	104	77	88	92	87	109	143	89	81	136	259	121	96	138	91	98
7	89	31	41	76	192	168	97	68	87	80	76	118	172	117	134	134	98	75
7	128	37	46	98	168	203	78	62	90	81	89	127	207	92	122	146	47	75
9	174	34	53	118	261	201	84	45	68	113	52	56	182	51	124	269	65	82
9	319	43	63	126	162	211	68	50	92	75	32	66	221	173	114	246	53	66
11	364	58	38	107	167	158	117	30	62	62	25	101	244	147	77	129	56	68
11	318	79	53	169	172	122	110	36	78	41	29	78	295	179	88	133	66	94
13	125	128	73	272	145	93	362	89	107	86	52	89	354	359	168	76	66	40
13	243	202	77	254	122	116	504	93	119	72	48	123	192	116	129	62	78	57
15	20	117	165	40	175	253	26	173	233	27	138	220	96	171	205	49	100	121
15	17	163	272	33	198	281	29	132	221	43	133	291	42	166	388	31	48	118
17	45	66	50	38	181	227	55	77	128	58	10	15	60	85	118	23	86	201
17	21	128	249	8	186	227	63	81	102	148	30	32	24	23	33	14	112	295
Total	2294	1479	1885	1812	2399	2788	2011	1623	2091	1387	1302	2119	3304	2326	2393	2132	1436	2049
Mean	127.4	82.2	104.8	100.7	133.3	154.9	111.7	90.2	116.2	77.1	72.3	117.7	183.6	129.2	132.9	118.4	79.8	113.9

N = nauplii C = copepodites A = adults